

Differences in otolith microstructure between hatchery-reared and wild chinook salmon (*Oncorhynchus tshawytscha*)

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Abstract: Otolith microstructure exhibited some characteristic differences between hatchery-reared and wild chinook salmon (*Oncorhynchus tshawytscha*) from the Cowichan River. Daily growth increments that formed in the otoliths of the hatchery-reared chinook salmon after exogenous feeding were more regular in width and contrast than those in the otoliths of wild chinook salmon. In addition, otoliths from hatchery-reared individuals frequently produced a check when the fish were released from the hatchery. Eighty-nine percent of a sample of 67 chinook smolts that had been coded-wire tagged in hatcheries and later captured in the Strait of Georgia were correctly identified as originating from hatcheries based on otolith microstructure. These tagged fish originated from at least 17 different hatcheries, indicating that the method could be used to identify chinook salmon originating from other hatcheries.

Résumé : Nous avons observé des différences caractéristiques dans la microstructure des otolithes entre des saumons quinnats (*Oncorhynchus tshawytscha*) d'élevage et des spécimens sauvages capturés dans la rivière Cowichan. Les marques quotidiennes de croissance qui se formaient dans les otolithes des quinnats d'élevage après le début de l'alimentation exogène étaient plus régulières en largeur et en contraste que celles observées dans les otolithes des quinnats sauvages. De plus, les otolithes des poissons d'élevage présentaient souvent une encoche correspondant au moment où les poissons étaient libérés par l'écloserie. Sur un échantillon de 67 smolts de quinnat qui avaient été marqués en écloserie avec des micromarques codées puis recapturés dans le détroit de Géorgie, 89% ont été correctement identifiés quant à l'origine à partir de la microstructure des otolithes. Ces poissons provenaient d'au moins 17 écloseries différentes, ce qui indique que la méthode pourrait être utilisée pour identifier des quinnats provenant d'autres piscicultures.

[Traduit par la Rédaction]

Introduction

Chinook salmon (*Oncorhynchus tshawytscha*) is an important fish in the commercial and recreational fisheries of British Columbia. In the Strait of Georgia, where there is a large recreational fishery for chinook salmon, the catches from 1950 to 1992 were highest during 1976–1978. Catches during this period averaged 750 000 individuals, but by the late 1980s they had declined to about 170 000 individuals. As part of an effort to restore the abundance of adults to the late 1970s level, Canadian hatcheries rear and release large numbers of chinook smolts into the Strait of Georgia.

The hatchery-reared chinook salmon smolts mix with wild smolts, but little is known about the impact of one rearing type on the other. It is known that the survival of

hatchery-reared chinook salmon declined dramatically (Beamish et al. 1995) as releases from hatcheries increased in the 1980s. It is not known if this decline in survival is the result of increased natural marine mortality or mortality specific to the rearing environment and rearing practices in hatcheries. Furthermore, it is not known if a trend similar to the decline in the survival of hatchery-reared chinook is occurring in wild chinook salmon populations. If it were possible to identify all hatchery-reared and all wild chinook salmon, it would be possible to study the marine survival trends. The information from such a study could be used to identify optimal levels of smolt releases and to compare marine survival trends of hatchery-reared and wild chinook salmon smolts.

The method of acquiring survival information of hatchery-reared chinook salmon has been to tag a percentage of the releases (3–15%) and to recapture these marked fish in the commercial and recreational fisheries or when they return to the hatchery. The tag is a piece of wire with a coded message that is inserted into the cartilage in the nasal area. The adipose fin is removed to indicate that the fish has a tag. The head of a recaptured fish is removed and preserved.

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At a later date, the tag is recovered and decoded. Studies have shown that only a small percentage of the tagged and recaptured fish are returned. Thus, the actual returns must be "expanded" to obtain an estimate of the true number of recaptured fish. This expansion introduces a potential error into any estimate of hatchery production. In addition, the tags have been difficult to apply to wild smolts; hence, it has not been possible to compare marine survival trends of hatchery-reared and wild smolts.

In this study, we identify an inexpensive method of identifying hatchery-reared and wild chinook salmon using patterns in otolith microstructure. Our method is not a replacement for the coded-wire tag, but a procedure for directly assessing the percentage of hatchery-reared and wild chinook salmon in any sample.

Materials and methods

Chinook salmon were reared in groundwater at a constant temperature of 10°C in the Cowichan hatchery, located on the east coast of Vancouver Island, British Columbia. After rearing in the hatchery during the yolk sac stage, fry were transferred to rearing ponds outdoors just before onset of exogenous feeding, which occurred at approximately 900 accumulated temperature units.

Five groups of hatchery-reared chinook salmon were studied: incubated eggs, alevins, pond-reared fry, smolts, and hatchery-reared adults (Table 1). The eggs, alevins, and fry, which were sampled from the hatchery, were used to study checks, which were commonly found in otoliths of both hatchery-reared and wild fish. Smolts, which were collected from the hatchery and the Cowichan River, were used to study the pattern of daily growth increments in otoliths. Adults were used to verify that the otolith microstructural pattern formed at the early life stage is unchangeable for the whole life span. Stomachs of fry sampled from the rearing pond were examined to determine if exogenous feeding had started.

Wild fry ($N = 118$) were collected in the Cowichan River in 1991 before the release of hatchery-reared fish into the river. The microstructural pattern of the otoliths of these fish was compared with the pattern in the otoliths from hatchery-reared fish.

Fish were frozen before the removal of the otoliths (we used sagittae in this study). Otoliths were washed in 0.1% sodium hydroxide and distilled water to remove soft tissue. Left otoliths from the eggs and alevins were mounted on glass slides using clear fingernail polish and examined without further processing. The left otoliths of fry and smolts were mounted using thermosetting plastic resin. Each otolith was then ground on lapping film of 60 or 30 μm , depending on otolith size, until the primordia were revealed. At this stage, the resin was melted on a hotplate and the otolith was turned over. The other side of the otolith was ground in a similar manner until the microstructure was clearly visible. The otolith was then polished on a lapping film of 0.3 μm to remove scratches caused by the grinding. If the otolith was damaged or the microstructure was not clearly revealed, the right otolith of the pair was used. Otolith microstructure was studied with a compound light microscope using transmitted light.

Table 1. Number and life stages of Cowichan hatchery-reared chinook salmon used in this study.

Year	Eggs	Alevins	Fry	Smolts	Adults
1991	15 ^a	39 ^b	68 ^c	108 ^d	59 ^e
1992	—	—	—	142 ^f	—

^aApproximately 3 days before hatching.

^bComposed of 20 and 19 alevins sampled 4 days after hatching and 1 day before transferring to the rearing pond, respectively.

^cComposed of 25, 20, and 23 fry sampled 3, 6, and 12 days, respectively, after being transferred to the rearing pond.

^dComposed of 39 fish from the rearing pond and 69 tagged fish captured in the Cowichan River after release of Cowichan hatchery-reared fish.

^eCoded-wire tagged adults collected in the Cowichan River after they had spawned.

^fCoded-wire tagged smolts captured in the Cowichan River after release of Cowichan hatchery-reared fish.

All otoliths exhibited a hatching check and most otoliths exhibited a first-feeding check (see Results section for definition of the two checks). In some otoliths, these checks were visible in all areas of the otolith, while in others they were discernible only in some portions of the otolith. The former otoliths were selected from the Cowichan hatchery (reared fry and smolts) and from the Cowichan River (wild fry). The length of the hatching check and first-feeding check in these selected otoliths was measured from the anterior to the posterior end under a compound light microscope.

The widths of daily growth increments in 54 randomly selected otoliths from Cowichan hatchery-reared smolts and 49 randomly selected otoliths from wild fry from the Cowichan River were measured using a Bio-Scan digitizing system. For each otolith, 25–60 daily growth increments that formed after the first-feeding check were measured along the axis intercepting the daily growth increments at their widest portion in the dorso-posterior quadrant.

Otoliths from adults were thinned through decalcification. All decalcification in this study was carried out in 40- or 25-mL beakers with a 1.5-cm-high, close-fitting polyethylene ring at the bottom supporting a close-fitting metal mesh. Resting on the mesh, the otoliths were completely immersed in 8% EDTA ((ethylenedinitrilo)tetraacetic acid, disodium salt) solution, which was stirred with a magnetic stirrer.

The otolith primordia in these fish otoliths are located towards the dorsal edge, which is thinner than the ventral edge. To control the amount of decalcification from the dorsal side, clear fingernail polish was spread carefully along the dorsal edge so that the polish did not extend to the area over the central region. After the polish had set, the otoliths were put into the EDTA solution and decalcified until the hatching check or first-feeding check could be observed under a dissecting microscope using reflected light. These checks are always first revealed from the exterior side, as the otolith primordia are closer to the exterior

Fig. 1. Otolith section from a wild chinook salmon fry presenting an overall view of the internal otolith structure. Note that numerous increments are present within the hatching check (curved arrow), surrounding the fused primordia (white arrow). The rostral primordium (arrowhead) is formed after hatching. The first-feeding check (straight arrow) marks the end of the alevin stage and the beginning of the fry stage. A, anterior end; P, posterior end; D, dorsal side; V, ventral side. Scale bar = 135 μm .

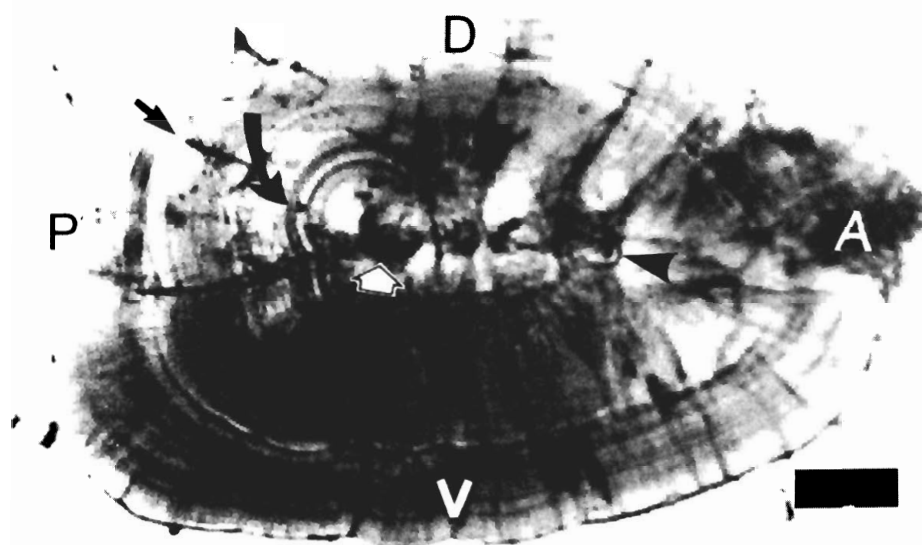


Table 2. Origin of coded-wire-tagged chinook salmon smolts sampled in the Strait of Georgia and Fraser River plume in 1992 and 1993.

Hatchery	Number of hatchery-reared fish	
	1992	1993
Big Qualicum	1	20
Bonoparte	—	1
Bridge River	—	1
Capilano	2	2
Chehalis	1	1
Chilliwack	3	5
Clearwater	13	—
Eagle	3	2
Harrison	—	2
Nicola	—	2
Little Qualicum	—	16
Penny	1	—
Quesnel	1	1
Spus	5	—
Shuswap	—	3
Stuart River	—	1
Tenderfoot	—	1
U.S. hatcheries	—	4
Unknown hatcheries ^a	—	5

^aDue to loss of tags.

surface. It took 4–14 h to remove sufficient calcareous material, depending on the size of the otolith.

Once the hatching check or first-feeding check was visible from the exterior side, the otolith was dried and carefully placed, exterior side down, on a drop of fingernail polish on a small piece of a broken slide coverslip so that the polish did not overflow onto the interior surface. After the polish had set, the otolith was again put into 8% EDTA solution. The presence of polish prevented any further decalcification from the exterior side. The decalcification was terminated after 6–20 h, when the hatching check or first-feeding check could be observed from the interior side. The processed otolith, which was thin and small, was dried and put into acetone to remove the polish. It was then mounted on a glass slide using thermosetting plastic resin and polished on a lapping film of 30 or 0.3 μm until the primordia were clearly revealed under a light microscope. The otolith was turned over and the other side was also polished until the increments formed after the first-feeding check were clearly revealed.

Samples of a mixture of hatchery-reared and wild chinook salmon smolts were collected using surface beam trawls (R.J. Beamish, unpublished data) from the Strait of Georgia and the Fraser River plume in May, June, and July of 1992 and 1993. Some of these fish had been tagged at the hatchery using coded-wire tags and an adipose fin clip and thus were known to be hatchery-reared fish. Thirty and 67 chinook salmon smolts with coded-wire tags were obtained in 1992 and 1993, respectively. From the coded-wire-tag information, these fish were known to have originated

Fig. 2. Higher magnification of Fig. 1 showing that the appearance of daily growth increments deposited after the first-feeding check (arrow) is more prominent than the appearance of those formed before the first-feeding check. Scale bar = 100 μm .

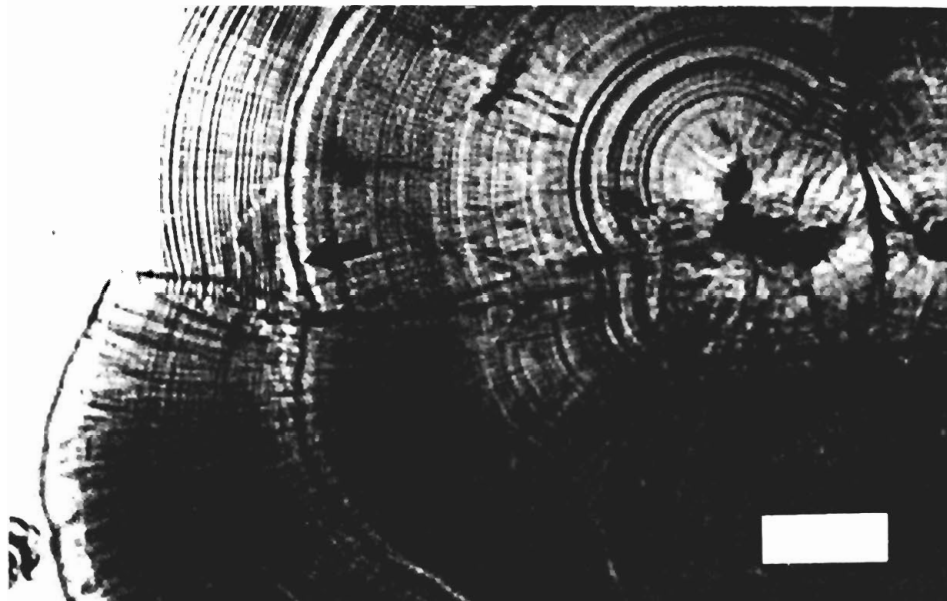


Table 3. Size of hatching check and first-feeding check in the otoliths of Cowichan hatchery-reared chinook salmon and wild chinook salmon from the Cowichan River.

Fish origin	Mean length of hatching check (μm) \pm SD	Mean length of first-feeding check (μm) \pm SD
Cowichan hatchery	336.07 \pm 23.39 ($N = 42$)	764.34 \pm 46.74 ($N = 62$)
Wild from Cowichan River	347.50 \pm 32.05 ($N = 67$)	814.06 \pm 55.65 ($N = 81$)

from at least 17 different hatcheries (Table 2). Otolith microstructure was examined and compared with the otolith microstructure from the Cowichan hatchery-reared and wild chinook salmon. The accuracy of classification of wild and hatchery-reared chinook salmon was assessed using the 1993 sample of young chinook salmon. The rearing type of the total sample ($N = 1264$) was classified using the otolith microstructure, without prior knowledge of which fish had coded-wire tags, and the percentage of the known hatchery-reared fish that were correctly identified was determined. The 1992 sample was not used to test the accuracy because the otoliths were known to be from hatchery-reared fish.

Results

Otolith microstructure before exogenous feeding

All otoliths from hatchery-reared and wild chinook salmon contained a prominent hatching check. Within the check, numerous increments surrounded the multiple primordia (Fig. 1). The hatching check was found to be present near the margin of otoliths of fish sampled 4 days after hatching, while the check was not visible in the otoliths of unhatched fish. The mean length of the hatching check in

Cowichan hatchery-reared fish was smaller than in Cowichan wild ones, although the difference was not significant (ANOVA, $0.05 < P < 0.1$) (Table 3). A second prominent check was present in most of the otoliths (92.7%). Increments formed before this second check in general appeared less prominent than those deposited after the second check (Figs. 1 and 2). This second check was found in the otolith margin of fish that had just started exogenous feeding and was not present in fish that had not started exogenous feeding. This check is presumably associated with the transition from yolk absorption to exogenous feeding and we referred to it as the “first-feeding check.” The average length of this check in the Cowichan hatchery-reared chinook was significantly smaller than in wild chinook from the Cowichan River (ANOVA, $P < 0.005$) (Table 3).

Otolith microstructure in Cowichan hatchery-reared chinook salmon after exogenous feeding

Daily growth increments formed in the hatchery-reared chinook immediately after the first-feeding check were uniform in width and contrast. The average width of increments was 3.97 μm (SE = 0.016, $N = 2013$) in the dorso-posterior quadrant (Fig. 3). This uniform pattern changed

Fig. 3. Otolith section from a Cowichan hatchery-reared chinook salmon fry showing the regular postfeeding daily growth increments in the dorsoposterior quadrant. Scale bar = 12 μm .

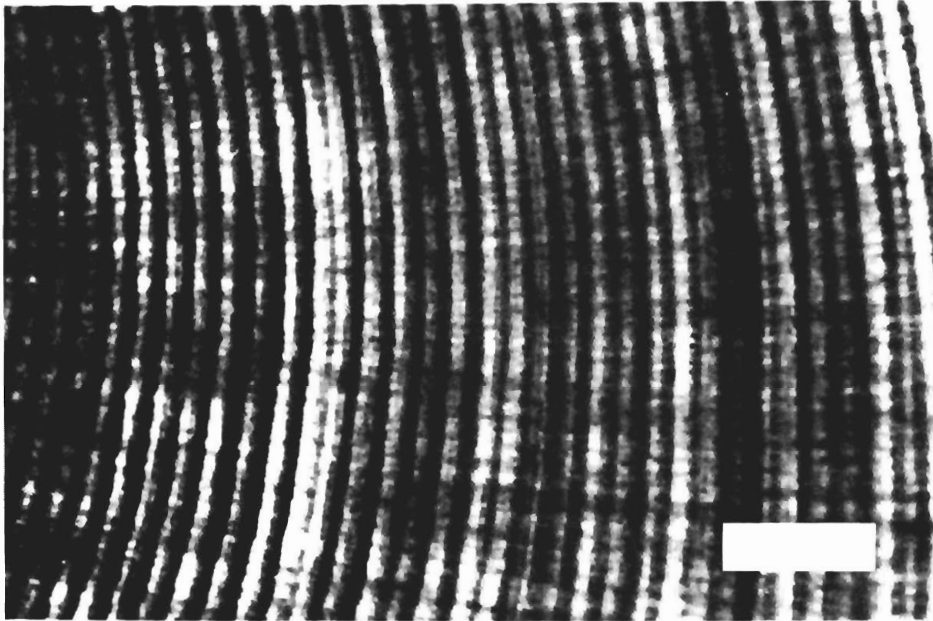
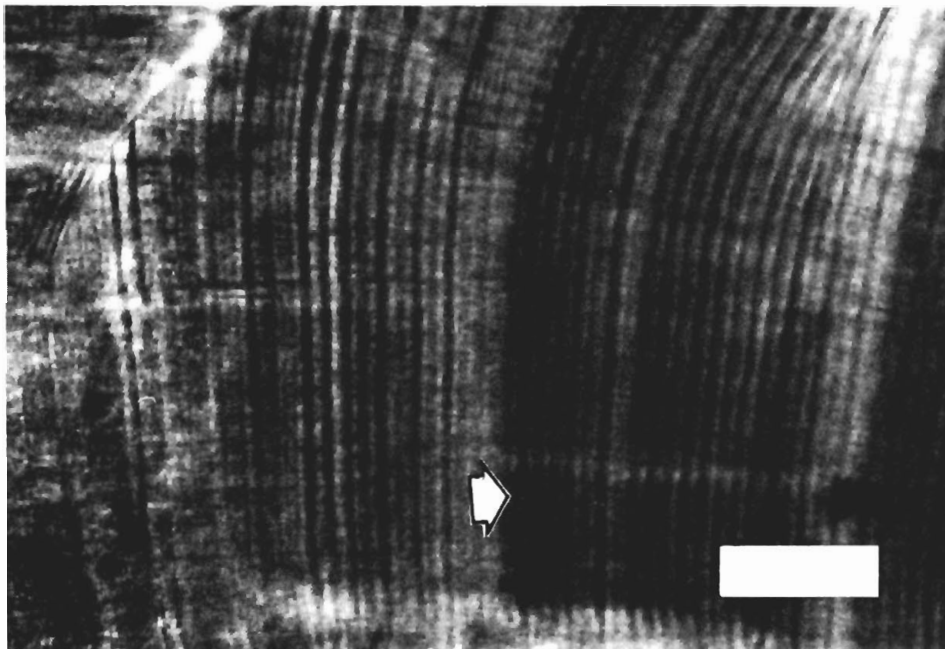


Fig. 4. Otolith section from a Cowichan hatchery-reared chinook salmon smolt caught in the Cowichan estuary showing the transition (arrow) in the dorsoposterior quadrant between regular postfeeding daily growth increments and irregular daily growth increments formed in the wild after release from the hatchery. Scale bar = 30 μm .

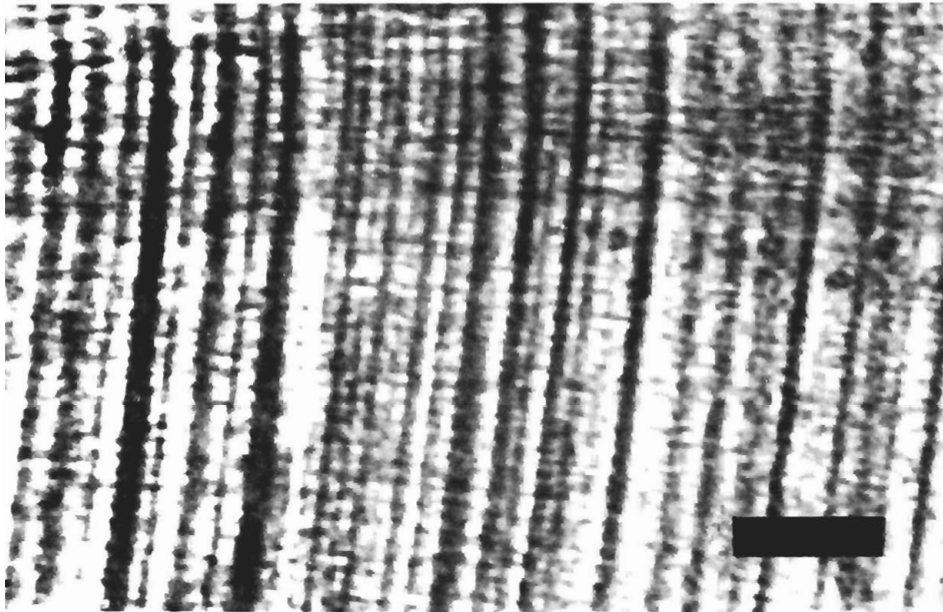


following the release of the fish from the hatchery into the river. Daily growth increments that formed immediately after the release from the hatchery often appeared relatively irregular and narrow. The transition between these two different patterns of daily growth increments frequently (88%) corresponded to the formation of a check

that we called a "releasing check". The different appearance in the pattern of daily growth increments before and after release aids in identifying the hatchery-reared fish (Fig. 4).

Otoliths from adults originating from the Cowichan hatchery also exhibited the hatching check and first-feeding check, and daily growth increments following the first-feeding

Fig. 5. Otolith section from a wild chinook salmon fry from the Cowichan River showing the irregular postfeeding daily growth increments in the dorsoposterior quadrant. Scale bar = 12 μm .



check were regular and wide. These regular and wide daily growth increments were often followed by a releasing check and then relatively narrow and irregular daily growth increments. This microstructural pattern was similar to the pattern found in the otoliths of Cowichan hatchery-reared juvenile chinook salmon.

Otolith microstructure in wild chinook salmon after exogenous feeding

Increments deposited in otoliths from wild fish following the first-feeding check varied a great deal in width and contrast. The average width of the increments was 2.37 μm in the dorsoposterior quadrant, smaller than in the hatchery-reared fish (Fig. 5). The coefficient of variation (standard deviation/mean) of daily growth increments of individual otoliths from the wild and Cowichan hatchery-reared chinook ranged between 0.2504 and 0.4112 and between 0.0614 and 0.1723, respectively. The coefficients of variation for the two rearing types were completely separated (Fig. 6). The coefficient of variation for the wild fish was significantly higher than for the Cowichan hatchery-reared fish (*t*-test, $P < 0.005$). The wild fish otoliths also did not contain a check equivalent to the releasing check found in the otoliths of most hatchery-reared fish.

Otolith microstructure in chinook salmon from at least 17 different hatcheries

Daily growth increments deposited following the first-feeding check in the otoliths of most of the coded-wire-tagged chinook (92%) were regular in width and contrast (Fig. 7) and considerably different from the daily growth increment pattern found in the otoliths of wild fish from the Cowichan River. Although the daily growth increments in the coded-wire tagged chinook were not as wide as those in the otoliths of Cowichan hatchery-reared fish (an average

width of 2.89 μm in the dorsoposterior quadrant), they were wider on average and more regular in their formation than those of wild fish otoliths. Seventy-six percent of the otoliths from these hatchery-reared fish contained a releasing check, immediately after which daily growth increments often appeared relatively irregular (Fig. 7).

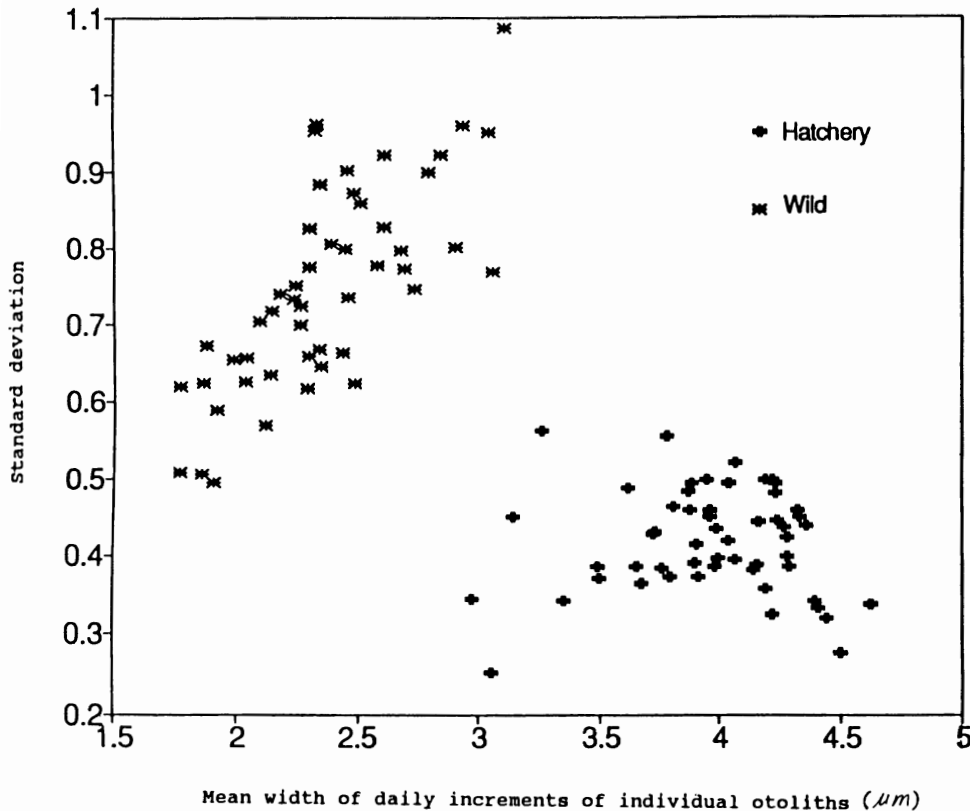
Classification accuracy

Among the sample of 1264 chinook salmon smolts collected from the Strait of Georgia in 1993, 633 were identified as wild fish, 620 were identified as hatchery-reared fish, and 11 were unidentified because of crystalline otolith structure or poor otolith preparation. The sample contained 67 fish from various hatcheries identified by the coded-wire tags (Table 2). Approximately 10% of hatchery-reared chinook have coded-wire tags. Thus, in the sample of 1264 fish, the 67 tags would indicate that approximately 670 were of hatchery origin and 594 were wild. Our estimates of hatchery and wild chinook were similar to the expected number. Of the 67 coded-wire tagged fish, 59 were correctly identified, seven were misidentified as wild, and one was not identified because of crystalline otolith structure. Thus, the accuracy of identifying chinook salmon smolts known to have been released from various hatcheries was approximately 89%.

Discussion

It has been verified that increment deposition is daily in otoliths of juvenile chinook salmon (Neilson and Geen 1982; Neilson et al. 1985; Gauldie 1991), although this deposition rate could be affected by fish activity patterns (Neilson and Geen 1982). Hatchery-reared and wild chinook salmon in general have patterns in the otolith microstructure that reflect the rearing environment. The identification

Fig. 6. Standard deviation versus mean of daily growth increment width of individual otoliths from the Cowichan hatchery-reared and wild chinook salmon showing that the daily growth increment width is greater and the variation is smaller for hatchery-reared fish.



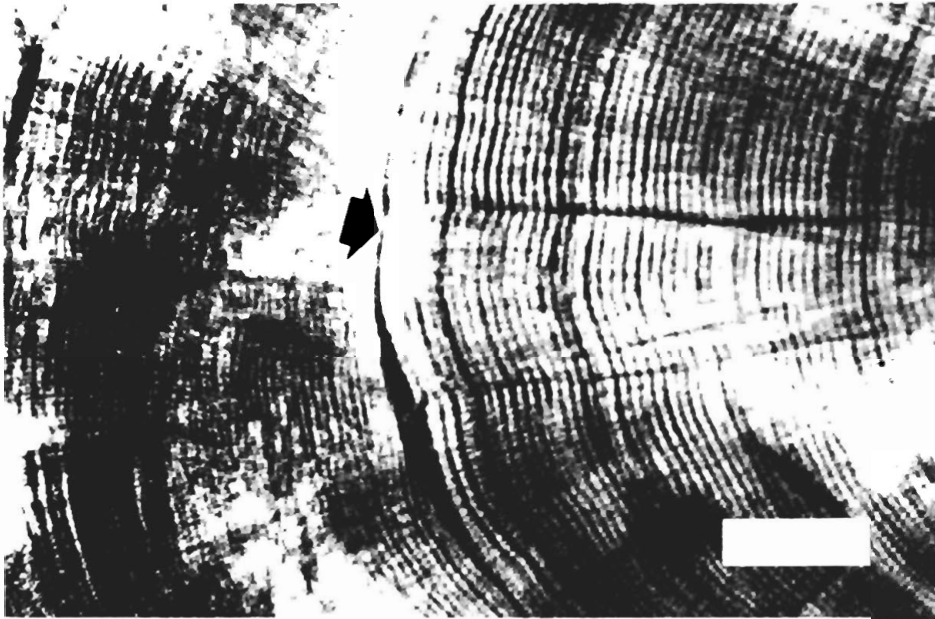
of the two rearing types relies primarily on the difference in the daily growth increment pattern formed immediately after exogenous feeding. The otoliths of hatchery-reared chinook salmon have wider daily growth increments and a more regular pattern of postfeeding daily growth increments than the otoliths of wild fish. The existence of the releasing check and irregular daily growth increments deposited following release from the hatchery provide additional criteria to identify hatchery-reared fish from wild fish. The first-feeding check, which is also present in the otoliths of sockeye salmon (*Oncorhynchus nerka*) (Marshall and Parker 1982), serves as a good bench mark, allowing daily growth increments deposited immediately after the beginning of exogenous feeding to be readily and correctly defined and examined.

Examination of adult chinook salmon of Cowichan hatchery origin indicates that the pattern of early otolith microstructure formation remains constant over the whole life span. While scale resorption is common, resorption of completely formed otolith increments is unlikely to occur except under severe stress (Campana 1983; Mugiya and Takahashi 1985; Mugiya and Uchimura 1989). Although a recent study demonstrates that calcium deposited onto a mineralizing increment may be dissolved at night, the net accumulation of calcium onto the otoliths is significantly greater than net losses each day (Wright et al. 1992). The conservative nature of otolith microstructure enables us, therefore, to identify the origin of adult chinook salmon

based on the otolith microstructural pattern formed at the early stage.

Our assumption that the technique can be used to separate chinook salmon of other hatcheries from wild chinook salmon is based on the observations from the hatchery-tagged fish caught in the Strait of Georgia in 1992 and 1993. In the sample of 67 coded-wire tagged smolts, only seven were inaccurately identified. Six fish were incorrectly identified because their otoliths did not contain a regular pattern of daily growth increments following the first-feeding check, as expected in the otoliths of hatchery-reared chinook. The other fish was initially erroneously identified as wild because the otolith was not well prepared and the otolith microstructure was not adequately revealed. A regular pattern of daily growth increments after the first-feeding check was observed in the other otolith of the pair, which was more carefully prepared. The accuracy level for identifying other hatchery-reared chinook is probably not as high as that for identifying Cowichan hatchery-reared chinook among a mixture of Cowichan hatchery-reared and wild chinook salmon, as suggested by Fig. 6. Nonetheless, the high level of accuracy (89%) of identifying tagged fish among the sample collected in 1993 indicates that the determinations were reliable and that the method applies to other hatchery-reared chinook salmon. The ability to identify the rearing type from a large sample of chinook smolts indicates that the method applies for both wild and hatchery-reared chinook.

Fig. 7. Otolith section from a hatchery-reared chinook salmon smolt caught in the Strait of Georgia in 1992 showing the regular postfeeding daily growth increments in the dorsoposterior quadrant and a check (arrow) associated with release from the hatchery into the wild. Daily increments formed after the release are relatively irregular. Scale bar = 60 μm .



More detailed studies from a selection of these other hatcheries and from more wild stocks must, however, be carried out to verify that the method can be applied to fish reared in other hatcheries and from one year to the next.

Among the whole sample of chinook fry and smolts collected from the hatchery and wild from 1991 to 1993, there was a small percentage (3%) of fish with both otoliths of crystalline structure. When both otoliths were crystalline and the crystalline structure started to develop immediately after exogenous feeding, we could not determine the rearing type, as the microstructure was not clear in the crystalline structure. When crystalline structure of one or both otoliths of a pair developed some time (approximately 40 days or more) after the exogenous feeding, the origin of the fish could still be determined.

Otolith microstructure pattern is known to be closely related to environmental factors, such as temperature and amount of food (Volk et al. 1984; Campan and Neilson 1985; Moksness and Fossum 1991; Wright et al. 1991; Tzeng and Yu 1992; Zhang and Runham 1992). Hatchery-reared chinook salmon in general, and Cowichan hatchery-reared chinook in particular, are well fed and reared in a stable environment, while the wild fish must endure variation in food supply and in the physical environment. Indeed, the postfeeding daily growth increments formed in the hatchery are not only more regular than those in the wild-fish otoliths, but also more regular than daily growth increments formed after the fish are released from the hatchery. The highly uniform and wide daily growth increments in the Cowichan hatchery-reared fish, as compared with other hatchery-reared fish, are possibly due to the constant and high temperature of the rearing water and the abundant food supply.

The formation of the releasing check described in our study was also reported in the otoliths of hatchery-reared kokanee salmon (*O. nerka*) (Paragamian et al. 1992). The physiological mechanism for otolith check formation is unclear, although the check is known to contain a very high concentration of protein (Zhang 1992), and check production has been found to be related to stress (Campana and Neilson 1985). A check was produced when sablefish (*Anoplopoma fimbria*) were transferred from the field to the laboratory (Boehlert and Yoklavich 1985) and when there was an abrupt change in salinity after the transfer (Umezawa and Tsukamoto 1990). Transfer of tilapia (*Oreochromis niloticus*) either from an optimal to a suboptimal condition or from a suboptimal to an optimal condition without evident physical stress also results in check formation (Zhang and Runham 1992), suggesting that adaptation to a new environment itself may be a stressful event to the fish, inducing check production. The releasing check, demarcating the regular increments formed in the hatchery and irregular ones formed after release from the hatchery, was probably due to adaptation to a new environment rather than physical stress during the release, as in most hatcheries, fish were released simply by opening the barriers. Otoliths of some hatchery-released chinook salmon did not contain such a releasing mark, possibly because they adapted to the new environment more quickly.

The average length of the hatching check in the otoliths of Cowichan hatchery-reared chinook was less than that of wild chinook from the Cowichan River, although the difference was not significant. The average length of the first-feeding check from the former fish was significantly less than from the wild fish. This indicates that otoliths of the Cowichan hatchery-reared fish, possible upon hatching

and probably upon yolk absorption, were, on average, smaller than those of wild ones. This difference in otolith size perhaps resulted from the different water temperature, as exogenous feeding was not involved. Heming (1982) demonstrated that chinook salmon reared at high temperature were smaller and lighter upon hatching and yolk absorption than those at lower temperature because less energy in the yolk was converted overall for tissue growth. Peterson et al. (1977) also showed that alevins of Atlantic salmon (*Salmo salar*) that hatched at higher temperature were progressively smaller. For a given amount of energy supplied by the yolk, the Cowichan hatchery-reared chinook possibly convert less energy overall for otolith growth, resulting in relatively small otoliths. The difference in size of hatching check and first-feeding check could be used as a supplementary check for identification of Cowichan hatchery-reared and Cowichan wild chinook salmon.

This study identifies a practical and direct method for identifying hatchery-reared and wild chinook salmon, which may be used to study differences in abundance, recruitment, survival, movement, and growth without the need for a large-scale tagging and recovery program. In addition, growth history of individual fish, which is otherwise difficult to obtain, could be studied by using the width of the daily growth increments.

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