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Crystalline otoliths in teleosts: Comparisons between hatchery and wild coho salmon (*Oncorhynchus kisutch*) in the Strait of Georgia

R.M. Sweeting, R.J. Beamish & C.M. Neville
Pacific Biological Station, Nanaimo, BC, Canada V9T 6N7
(Phone: (250) 729-8359; Fax: (250) 756-7141; E-mail: sweetingr@pac.dfo-mpo.gc.ca)

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Contents

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Abstract

Otoliths, or 'ear stones', are calcium carbonate structures found in all vertebrates. In teleosts, they have a number of sensory functions, including hearing. Daily growth increments of these structures have permitted advanced age and population studies of teleosts. Whereas 'normal' otoliths are composed of crystals imbedded within a protein matrix as aragonite, a 'crystalline' form of calcium carbonate termed vaterite is also found. A review of the otolith literature demonstrates a significant level of understanding of the structure and function of otoliths, but the cause for crystalline otolith structure remains speculative. Pairs of otoliths from hatchery and wild juvenile and adult coho salmon (*Oncorhynchus kisutch*) were examined visually for determination of otolith microstructure type. The vateritic or crystalline otoliths were found in much higher percentages in juvenile hatchery-reared coho salmon than in juvenile wild coho salmon, supporting previous studies. There did not seem to be any negative impact on size or survival. There was also no correlation between crystalline otoliths and premature maturation in coho males. A preliminary study of adult coho salmon returning to Big Qualicum and Chilliwack hatcheries showed even higher ratios of vateritic otoliths than observed in juveniles.

Introduction

Bony structures in vertebrates, such as antlers, teeth, or bone, provide permanent or semi-permanent records of growth. In the bony fishes, scales and spines have often been used for descriptions of growth rates. However, within the auditory canals of all fishes are small calcium carbonate ($CaCO_3$) deposits called statoliths, or otoliths, or 'ear stones'. They are believed to be implicated in hearing, balance and depth resolution (Degens et al., 1969), but are probably also critical for sensitivities to gravity and linear acceleration (Carlstom, 1963). In fact, all vertebrates have been shown to have homologous structures and studies of ancient vertebrates have also shown homologous structures. Most otoliths also have characteristic species-specific shapes which can be useful for taxonomy (eg., Casteel, 1974; Gaemers, 1984). At the turn of the 19th century, it was discovered that patterns of the $CaCO_3$ deposition could be used as annual growth

markers (Reibisch, 1899), which ultimately led to a significant use of otoliths for fish ageing and population studies, and have proved especially useful for management programs. Panella (1971) took otolith microstructure even further when he noted that the deposition of $CaCO_3$ into otoliths occurred concentrically on a daily basis. Otolith ring pattern is now used to study daily, monthly, seasonal and annual growth in a wide array of fish species from both freshwater and saltwater, from polar regions to the tropics and from nearshore to bathypelagic depths (Panella, 1971; Rannou and Thiriot-Quievreaux, 1975; Townsend, 1980; Neilson and Geen, 1982; Campana, 1983a, b; Radtke and Targett, 1984; Campana and Neilson, 1985; Zhang and Beamish, 1994; Gauldie et al., 1995; Zhang et al., 1995). Otoliths have also been reported to be the first calcified structures to appear in embryonic or larval stages (Brothers, 1981; Radtke, 1984). Of critical importance in these studies is the fact that otoliths are metabolically inert; i.e., there is no resorption once the $CaCO_3$ mineral is deposited within the otolith, and thus these structures are particularly suitable as long-term records of growth.

The location and morphological features of otoliths and the associated auditory canal are shown in Figure 1a and b. Located near the base of the brain, the auditory canals (on either side) are composed of three loops roughly orientated on *X,Y,Z* axes. These loops are situated on top of the sacculus, within which are the otoliths. Each teleost has, in fact, three pairs of otoliths, the names of which are derived from their general shape in the carp: the sagitta ("arrow"), the lapillus ("small stone") and the asteriscus ("star") (Carlstrom, 1963). These otoliths are located, respectively, in the sacculus, the utriculus, and the lagena (Figure 1b). Increase in otolith size occurs when $CaCO_3$ is mineralized out of the endolymphatic fluid of the auditory canal and laid down on a keratin-like protein (otolin) matrix (Degens et al., 1969; Mugiya et al., 1981; Murayama et al., 2002). This protein is water-insoluble, has high abundance of acidic amino acids, and generally comprises approximately 50% of the total otolith protein. A second water-soluble, calcium-binding protein has recently been isolated from tilapia otoliths (Asano and Mugiya, 1993) which may also be involved in regulation of calcification rates. While otoliths are primarily composed of $CaCO_3$

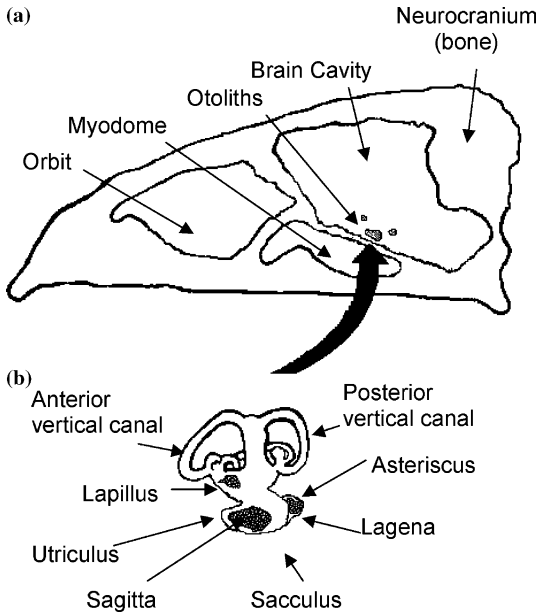

Figure 1. a. Diagrammatic representation of the skull of a bony fish. b. The location of the otoliths (sagittae) within the inner ear. Redrawn from Degens et al., 1969.

(92–96%) and the organic protein matrix (1–8%), minor (>100 ppm) and trace (<100 ppm) impurities of a number of elements are present (eg., Na, Sr, K, S, N, Cl, P and Mg, Zn, Si, Fe, Cu Al, Pb, Co, Cd) (Carlstom, 1963; Campana and Neilson, 1985).

The endolymphatic fluid surrounding otoliths has been shown to have very high concentrations of both calcium and sodium bicarbonate (Na_2CO_3), the latter contributing to a very alkaline pH. Mugiya (1974) showed that the macular cells of the auditory canals secreted Ca^{++} into the endolymphatic fluid. It was subsequently shown (Mugiya et al., 1981) that the rate of accretion of Ca^{++} on various parts of the individual otoliths was in fact proportional to the concentration of Ca^{++} in the adjacent macular cells and independent of environmental calcium levels. Campana and Neilson (1985) suggested that it is probable that an otolith begins as one or more partially calcified primordia in the inner ear. Once incremental growth has begun, the organic matrix likely acts as a template for the crystallization of $CaCO_3$. The alternating mineral-poor (dark) and mineral-rich (light) bands within the otolith possess differing optical properties under transmitted light, and are often referred to as L-zones and D-zones

(light and dark). As well, acid etching of otoliths for scanning electron microscopy also provides alternating bands.

The inorganic salts composing boney structures in terrestrial vertebrates are composed of calcium phosphates ($CaPO_3$), rather than the $CaCO_3$ observed in teleosts. In many species of teleosts, the microstructure of the otoliths may be altered somewhat by the deposition of an alternate form of $CaCo_3$. In biological systems, $CaCO_3$ can be deposited in three iso-morphs, having identical chemical formulas but different crystalline structure, densities and hardness (Carlstrom, 1963). In non-living systems, calcite is the most common and stable chemical form of $CaCO_3$, and possesses rhombohedral crystalline structure. In biological systems, calcite is found in mollusc shells and coral skeletons (Carlstrom, 1963). In teleosts, however, the $CaCO_3$ crystals within the otoliths are generally arranged in the aragonite form, an orthorhombic crystal. However, the normal aragonitic-type of $CaCO_3$ can be partially or completely replaced by vaterite, which is also orthorhombic but pseudo-hexagonal, and has slightly differing optical properties (Carlstrom, 1963). Calcite is extremely stable, whereas aragonite is meta-stable and vaterite is quite unstable, especially when in contact with water (Irie, 1960). This instability infers that there must be some stabilizing factor in either the endolymph or within the structure of the otolith.

Vateritic otoliths are often visually clearer than the normal aragonitic otolith type (Figure 2), and are referred to as crystalline otoliths. However, in some species, a granular otolith may result. Both calcite (inorganic salts for invertebrate skeletons) and aragonite (otoliths) are common biogenic compounds, even existing together (alternating layers in mollusc shells and pearls). Vaterite, on the other hand, is quite rare in natural systems, although it is the principle otolith crystal formation on hagfish, lamprey and sturgeons (Carlstrom, 1963). Interestingly, while aragonite is the normal crystalline structure found in teleost otoliths and lapilli, most asteriscii are composed of vaterite (Lowenstein and Weiner, 1989; Oliviera et al., 1996). Within the Gnathostome supergroup, aragonite and vaterite are found exclusively in the cold-blooded animals, whereas all warm-blooded vertebrates have otoliths composed of calcite. Reptiles, forming the bridge between warm- and cold-blooded vertebrates, generally have a mixture of aragonite and calcite. In the class Actinopterygii, all species investigated belonging to the super-orders Chondrostei and Holostei had stataconia composed of vaterite. The coelacanth has teleost-type statoliths (Carlstrom, 1963).

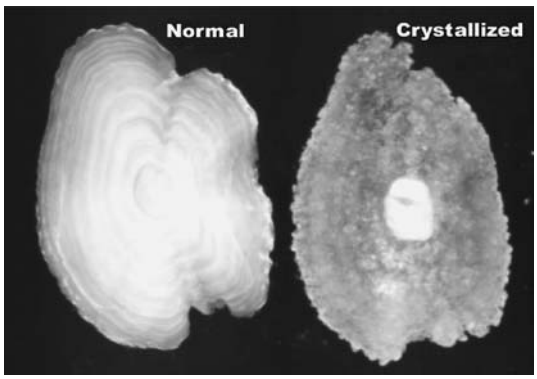

Figure 2. Photo of normal and crystalline type otolith, courtesy or International Pacific Halibut Commission.

Brothers (1984) noted that the calcium dominant zones (C-zones) appeared to be deposited during daylight hours or during elevated water temperatures. In contrast, the matrix dominant zone (M-zone) appeared to be deposited during the night or during times of decreased water temperatures. This circadian rhythm was also proposed by Mugiya et al. (1981) and Mugiya (1984), who noted that macular secretion of Ca^{++} into the endolymph slowed at sunrise, thus inhibiting C-zone formation. However, as noted by Campana and Neilson (1985), structures similar to daily increments have also been observed in Arctic (Townsend and Shaw, 1982), Antarctic (Townsend, 1980; Radtke and Targett, 1984), and deep sea fishes (Rannou and Thiriot-Quievreux, 1975), where diel light cycles are absent for all or a major portion of the year. Current theory on otolith growth suggests that the crystalline microstructure is laid down continually, but that deposition of the protein matrix is under some internal control independent of metabolic rate. However, there does exist in most teleosts a linear relationship between otolith size and body size (but see Taubert and Cole, 1977). Vaterite replacement in otoliths generally does not change the morphology or the overall size grossly, although large irregular projections, holes, and other deformities are sometimes found (Palmork and Taylor, 1963;

Mugiya, 1972; Gauldie, 1986; Zhang et al., 1995). However, Gauldie (1996) noted that there were indications of substitution of strontium by magnesium in vateritic or crystalline otoliths, indicative of some subtle metabolic differences.

To date, a cause for the deposition of this alternative form has not been determined. Previous studies (Peck, 1970; Campana, 1983a; Zhang et al., 1995; Sweeting et al., 2003) noted that the presence of crystalline otoliths appear to occur more often in hatchery-reared salmon than in their wild counterparts. This paper examined otoliths from juvenile salmon surveys conducted in the Strait of Georgia, British Columbia, Canada (Figure 3) from 1997 to 2000 to examine this question in more detail.

Material and methods

Systematic surveys were conducted in the Strait of Georgia in September of 1997, 1998 and 1999 and July of 2000 (for survey details, see Beamish et al., 2000). Approximately 800–1000 pairs of otoliths from juvenile coho salmon were collected on each of these surveys. The fork length for each fish was measured, and sex of each fish was determined. All males were also examined for evidence of precocious maturation (ie., jacking). We randomly selected 100 pairs of otoliths from the September surveys for visual examination. Following this initial examination, 884 pairs of otoliths were randomly selected from the July 2000 survey. We used data from this survey because the crystalline structure is initiated in the freshwater phase, and July is our earliest marine survey conducted. Virtually all coho are reared in freshwater in hatcheries for over one year. Lastly, adult coho returning to Big Qualicum and Chilliwack River hatcheries in the fall of 2000 were also sampled for otoliths, fork length, and sex. Again, 100 pairs of these otoliths were randomly selected. In every case, each otolith was examined visually for determination of 'normal' (aragonite) or 'crystalline' (vaterite) type, using a 0–3 scale (Figure 2). Fork length and sex of each fish were considered to determine whether crystalline otoliths had impacted on growth, sex or sexual maturation (in males).

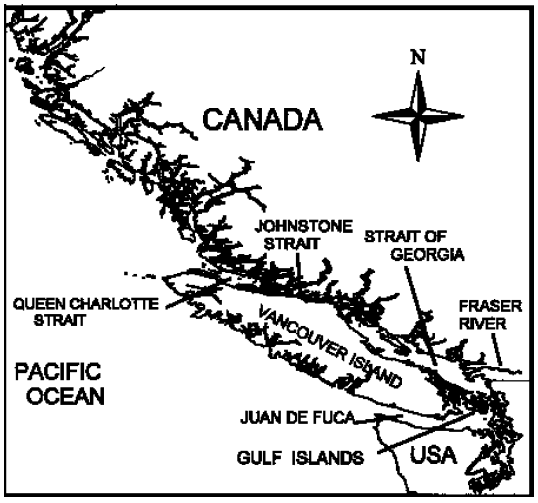

Figure 3. Map of the Pacific coast of Canada, showing the location of the Strait of Georgia and the Fraser River.

Coho were recognized as originating from a hatchery if they had the adipose fin removed, a management program initiated in the late 1990s to conserve wild stocks. Approximately 50% of all coho in the Strait of Georgia from 1997 to 2000 were fin clipped (Sweeting et al., 2003). Small percentages of both hatchery and wild fish also have coded wire tags (CWTs) implanted in the nasal region, and data from these tags were additionally used to determine whether the coho were hatchery-reared or wild. Hatchery-reared coho may have a CWT with or without an associated adipose fin clip, but wild coho never have the adipose fin removed (i.e., CWT only). The remaining fish (i.e., no fin clip and no CWT) are thus a mixture of wild and unclipped hatchery-reared coho.

Transverse otolith sections from 30 adult coho salmon from Big Qualicum and Chilliwack hatcheries were also mounted and examined under a microscope to determine whether seawater entry and the intervening months of marine existence may have altered the type of $CaCO_3$ deposited. Each otolith was mounted in epoxy and a section approximately 1 mm thick was taken dorso-ventrally from the centre of the otolith. Each section of each otolith was examined using a reflected light and a dissecting microscope.

Results

The incidence of crystalline-type otolith structure in the 100 pairs of otoliths from each of the September surveys was observed to consistently be 2–4

Table 1. General classification of otolith types, from normal to completely crystalline

Otolith type	Description
 0	Normal opaque otolith, no crystalline structure evident
 1	Center of the otolith is opaque but surrounded by crystalline type structure
 2	Most of otolith is normal opaque structure, but edge is crystalline type structure
 3	Entire otolith is clear, crystalline type structure

times higher in hatchery fish (ranged from 20 to 36%) than in the non-hatchery group (ranging from 2 to 10%). The percentage of hatchery-reared coho salmon with crystalline otoliths was again 4–5 fold higher than for either wild coho salmon (as identified by CWT data) or the mixture (unmarked, unclipped coho salmon for the otoliths obtained from the July 2000 survey (Table 1). The percentages of coho salmon with crystalline otoliths ranged from 46.3 to 56.3% among the three groups (adipose fin clipped, clipped with CWT, and CWT only) comprising hatchery fish. The level of crystalline otoliths found in wild fish was 11.8%, similar to the ranges observed in the September 1997–1999 surveys. In addition, 21.1% of otoliths in the mixed group (consisting of unknown percentages of unclipped hatchery and wild coho), were crystalline. In the hatchery-reared fish, there was no significant difference in fork length between coho with crystalline or normal otoliths (Table 2; T-test, $P > 0.05$). There was, however, a significant difference in fork lengths in wild coho (''true'' wild combined with ''potential'' wild) coho, with the wild fish possessing crystalline-type otoliths being slightly larger than those with normal otolith microstructure (*T*-test, $P = 0.023$). Note that this group will contain hatchery-reared fish which did not have the adipose clip removed, or any other identifying marks.

From this larger study from July 2000, we also examined whether there was any correlation between crystalline otoliths and precocity, or 'jacking', in males. Hatchery-reared coho jacks had approximately a 3.5-fold higher incidence of

Table 2. Percentages of crystalline otoliths observed in juvenile coho salmon captured in July of 2000 in the Strait of Georgia

		Total	Crystalline otoliths	Normal otoliths	Percentage with Crystalline otoliths
Hatchery	AD only	295	166	129	56.3
	AD/CWT	95	44	51	46.3
	CWT only	69	33	36	47.8
	Totals	**459**	**243**	**216**	**52.9**
Wild	CWT only	51	6	45	11.8
Mixture		375	79	296	21.1
Total		**884**	**328**	**556**	**37.1**

Hatchery fish were identified as either AD only (adipose fin clipped, but no coded wire tag), AD/CWT (adipose fin clip with a coded wire tag), or CWT only (coded wire tag present, but no adipose fin clip). Wild fish were determined as being of wild origin from the CWT database. Those coho in the 'mixed' group had no adipose fin clip or CWT.

Table 3. Forklengths (mm)(mean ± standard deviation) of hatchery and non-hatchery juvenile coho salmon captured in the Strait of Georgia during July 2000

	Crystalline otoliths	Normal otoliths
Hatchery coho	205.7 ± 17.80 (N = 209)	204.1 ± 20.39 (N = 390)
Non-hatchery coho	204.8 ± 23.01[a] (N = 118)	198.9 ± 28.79[b] (N = 376)

Groups with different letters are significantly different than its counterpart.

Table 4. Percentage of crystalline otolith structure in precocious male juvenile coho salmon captured in the Strait of Georgia in July of 2000

Group	Total	Crystalline otoliths	Normal otoliths	Percentage with Crystalline otoliths
Hatchery	11	6	5	54.5
Wild	6	1	5	16.7
Mixed	18	3	15	16.7
Totals	35	10	25	28.6

Fish were identified as a particular group as noted in Figure 1.

crystalline otoliths than wild jacks (54.5 versus 16.7%), with jacks in the mixed group having the same percentage as wild coho (Table 3).

The final group examined were adult coho salmon which returned one of two major coho release facilities in British Columbia, either Big Qualicum Hatchery or Chilliwack Hatchery. The levels of crystalline otoliths observed in the returning adult fish were even higher than observed in the juveniles (Table 4), ranging from 70 to 80%. The microscopic examination of 30 randomly selected pairs of otoliths from each hatchery did not show any evidence that crystalline otoliths had reverted to non-crystalline type in the marine environment.

Discussion

Earlier studies (Peck, 1970; Zhang and Beamish, 1994; Zhang et al., 1995) had suggested that crystalline otoliths, while overall in small proportion, were more prevalent in fish reared under hatchery conditions than wild. The results from this study confirm these reports. Crystalline otoliths were consistently found to be more prevalent in juvenile coho salmon raised under hatchery conditions than wild coho salmon. This result was observed across four years of systematic surveys in this study, as well as for adult coho which had returned to the hatchery (Table 5).

Table 5. Percentage of crystalline otoliths in 100 adult coho salmon that returned to either Big Qualicum or Chilliwack River hatchery in fall of 2000

	N	%Crystalline	%Normal
Big qualicum	100	68	32
Chilliwack R.	100	72	28

A mass marking program was instituted in British Columbia in the late 1990s as a management strategy to conserve wild coho salmon stocks. This study benefited greatly from this decision, as it provided a simple and effective method for identifying hatchery-reared coho salmon. The remaining fish within any sample are thus a mixture of wild coho and non-clipped hatchery-reared coho. There is no simple way to determine the difference between these two groups, although microscopic analysis of the circuli patterns has been shown to be useful in this regard (Zhang and Beamish, 1994; Zhang et al., 1995). In this case, it is possible to assign an estimated hatchery:wild ratio to these fish, without being able to necessarily assign a particular fish to either category.

Data from the literature (Table 6) appear to support the statement that salmonids in general have high rates of crystalline otolith formation, with levels ranging from 7–70% compared to 1–5% for non-salmonids (with the notable exception of the sand dab, 20%). It has been also suggested that stress, induced by the high intensity hatchery environment, may play a significant role in the transition to the vateritic isoform. This also seems to be supported in Table 6, where hatchery fish consistently have higher rates of vaterite replacement than corresponding wild fish, regardless of the species. It has further been proposed that otolith growth rate is governed by metabolic activity and not somatic growth rate (Mosegaard et al., 1988). Thus, the hatchery environment may lead stress-induced enhancement of metabolic activity (both catabolic and anabolic). As a proxy for environmental stress, we examined rates of vateritic otolith formation in precocious males

Table 6. Range (in percent) of vateritic otoliths found in selected teleosts. Unless denoted, data are for wild fish

Authors	Species	Vateritic Otoliths
Blacker, 1974	Atlantic cod (*Gadus morhua*)	1%
	Haddock (*Melanogrammus aeglefinus*)	5%
Bowen et al., 1999	Lake Trout (*Salvelinus namaycush*)	7–15% - wild 53–84% - hatchery 14–21% - stocked
Campana, 1983b	Steelhead Trout (*Oncorynchus mykiss*)	27%
Casselman, 1990	Lake trout (*Salvelinus namaycush*)	70%
David et al., 1994	Red drum (*Sciaenops ocellatus*)	0% -wild 0.8–4.8% - hatchery
Gauldie, 1986	Chinook salmon (*O. tshawytscha*)	~21–24%
Johansson,1966	Sand dab (*Limanda limanda* L.)	20%
Munk and Smikrud, 2002	Yelloweye rockfish (*Sebastes ruberrimus*)	1–2%
	Quillback rockfish (*S. malliger*)	2.24%
Tobin et al., 2005	Pacific Halibut (*Hippoglossus stenolepis*)	3.2%
Strong et al., 1986	Scotia Pollock (*Pollachius virens*)	2.7–3.1%
Sweeting et al., (this study)	Coho salmon (*O. kisutch*)	12% - wild 46–56% - hatchery

captured in our studies, as these fish would also experience enhanced metabolic activity (increased growth, development of reproductive tissues). However, in this study, the occurrence of crystalline otoliths did not appear to be influenced by precocious maturation of male coho salmon. While not included in this manuscript, we also found no correlation between crystalline otoliths and sex of the individual salmon. This supports the study by Gauldie (1996), who also noted no trends in handedness (i.e., left versus right otoliths).

The lack of a difference in fork lengths between hatchery-reared coho salmon with aragonitic or vateritic otoliths suggests that there is no compromise in growth from the different calcium carbonate structure, at least following the freshwater phase and early marine existence. As the presence of crystalline otoliths was 4–5 times higher in hatchery-reared coho than in wild coho, and hatchery coho are generally released at a larger size than wild coho, it is possible that the significantly larger fork lengths observed in the non-clipped coho with crystalline otoliths was evidence of the estimated 20% hatchery-reared coho that would be included within this group. Note, however, that even within the hatchery-reared fish (adipose clipped), there was a trend towards larger average size in those coho with crystalline otoliths. In the adults returning to the hatchery, there was no trend in the fork lengths between fish possessing crystalline or non-crystalline type otoliths (data not shown).

To our knowledge, a cause for the shift between aragonitic and vateritic otolith microstructure has yet to be elucidated, although several theories have been proposed: induced movement of sagittae within the sacculus (Morales-Nin, 1995), mechanical stress (Strong et al., 1986), temperature stress (Johansson, 1966), and stocking (density) stress (Casselman, 1990). While these theories remain speculative, Panella reported that mechanical trauma to developing bivalve larvae induced vaterite formation (cited from Bowen et al., 1999). It is also possible that the actual mechanism of vaterite formation is linked to alterations of the protein matrix, through genetic or metabolic irregularites. Kitano and Hood (1965) showed that replacement of glycine by glutamic acid in a $CaCO_3$ solution will favour the formation of vaterite over aragonite. Similarly, Degens (1976) demonstrated that the presence of basic and neutral amino acids accelerated the aragonite to calcite transition, but that glutamic and aspartic acids strongly inhibited this pathway. These studies would suggest that the pH and/or chemical properties of the endolymph fluid may be critical factors in this matter. This is supported by Campana (1999), who noted that otolith calcification differs from that of bone, shell or teeth in that the otolith epithelium is not in direct contact with the region of calcification, and that the concentration of bicarbonate ions (i.e., pH) in the endolymph is controlled via the saccular epithelium. Shinobu and Mugiya (1995) found that the incorporation of calcium into goldfish (*Carassius auratus*) otoliths was dramatically depressed by hypophysectomy and that bovine growth hormone was effective in restoring deposition rates whereas

neither triiodo-L-thyronine or ovine prolactin were effective. It thus appears that the regulation of otolith formation is under the control of a number of genetic and neuroendocrine factors, and that perturbation of one or more of these components along multiple pathways may induce the shift to vateritic otolith formation. It is, however, important to recall that it is very common that only one of the pair of otoliths is vateritic, and that many otoliths have only partial replacement. Finally, to our knowledge, there have been no reports in the literature of the opposite crystallization pattern occurring, i.e., the change to the vaterite crystalline structure appears to be irreversible.

Bowen et al. (1999) found that vateritic otoliths in stocked juvenile lake trout (*Salvelinus namaycush*) were composed of a central region of aragonite, suggesting that the majority of transitions occur early in life (65–75% in first year). Further, all vateritic otoliths found in wild lake trout transitioned during first summer, roughly at 3–4 months. Bowen et al. (1999) also reported that an earlier study by Bronte et al. (1995) examining 3-month old wild fingerling lake trout found no vateritic saggitta in 288 fish examined. However, it is clear from the literature that the switch to the vaterite isoform can occur later in the life history, in that otoliths can have significant portions of aragonite in the central regions of the otoliths surrounded by relatively thin borders of vaterite (i.e., partial crystallization).

The large number of crystalline otoliths observed in the adult coho salmon returning to the two hatcheries, although preliminary, was somewhat surprising. Whether the presence of crystalline otoliths infers any survival advantage, as possibly suggested by the high levels observed in adults that successfully returned to the hatchery, remains to be examined. Future studies will examine the levels of aragonitic and vateritic otoliths in juvenile and adult coho captured in the overwintering areas outside the Strait of Georgia.

In summary, hatchery-reared coho were consistently found to have a 3–5 fold higher incidence of crystalline otoliths than wild coho. Precocious maturation of either wild or hatchery male coho did not have any impact on the incidence of crystalline otoliths. Adult coho salmon returning to two different hatcheries maintained the high level of crystalline otoliths, indicating that the presence of either the normal aragonitic or the crystalline vateritic type of otolith did not appear to have a negative impact on marine survival. Neither juveniles, precocious males nor adults returning to the hatchery exhibited any clear impacts of otolith type on fork length. The results from this study confirm the high natural rates of crystalline otoliths in salmon in general, as well as significant increases in incidence of crystalline otoliths in teleosts of hatchery or stocked origin.

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