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## Walleye pollock *Theragra chalcogramma* during transformation from the larval to juvenile stage: otolith and osteological development

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**Abstract** Walleye pollock [*Theragra chalcogramma* (Pallas, 1814)] were collected from the Gulf of Alaska from 1991 to 1998 to examine the relationship between otolith and osteological development during transformation from the larval to juvenile life stage. Five stages of otolith development were determined for walleye pollock in conjunction with landmarks in osteological development during juvenile transformation. The first stage of otolith development (12–19 mm SL) is identified by the first accessory growth center (AGC) forming on sagittal otoliths. At this stage, the notochord is undergoing flexion as the teeth, jaws, branchiostegal rays, neural spines, and abdominal vertebral centra are ossifying. The second and third stages of otolith development (19–21 and 21–24 mm SL) are defined by the formation of the anterior, posterior, and dorsal AGCs on the otolith. This occurs during postflexion in conjunction with ossification of the principal caudal-fin rays, haemal spines, and caudal vertebral centra. The fourth stage of otolith development (24–37 mm SL) is defined by the AGCs on the ventral edge of the otolith. By this stage of development, the pelvic-, pectoral-, dorsal-, and anal-fin ray elements have started ossification and the fish has entered the transformation stage. The fifth stage of otolith development (36–48 mm SL) is identified by a completely formed sagittal otolith, which has AGCs that have grown together so that the otolith shape resembles an adult otolith, the ossification of all vertebrae and fin rays is complete, and the fish is a juvenile. By estimating what length a fish was, based solely

on otolith development, would prove helpful for those who wish to reconstruct length frequencies of walleye pollock from otoliths of fish that have been damaged due to gear and/or poor handling during the preservation process.

### Introduction

Despite the many studies on larval and juvenile growth and development of walleye pollock (*Theragra chalcogramma*, family Gadidae), little is known about the transitions between these life history stages. These transitions may result in fish becoming more vulnerable to predation or other sources of mortality due to physical transformations as well as changes in behavior and habitat.

Walleye pollock larval and juvenile growth rates are best represented by linear equations, but combining growth data for these life stages results in a non-linear relationship, well depicted by a Schnute model (Brown and Bailey 1992; Bailey et al. 1996). This model shows that there are several lengths at which transitions in growth occur throughout development. Furthermore, age-at-length may vary considerably at these transition points, indicating that development of the fish may be delayed or prolonged at certain ages. The transition points visually identified from the Schnute model appear to fit into length ranges (defined by osteological studies) for the flexion, postflexion, and juvenile stages (Dunn and Matarese 1984).

At the time of transformation from larva to juvenile, otoliths from several species of fish have been reported to undergo changes in shape as accessory growth centers (AGCs) form or as the otoliths exhibit changes in increment definition. For example, AGCs have been documented for flatfish (Sogard 1991; Lagardère and Troadec 1997), pink salmon, *Oncorhynchus gorbuscha* (Volk et al. 1995), Japanese eel, *Anguilla japonica* (Arai et al. 1997), and tropical reef fish (Wilson and McCormick 1997). Several studies on flatfish also suggest a link

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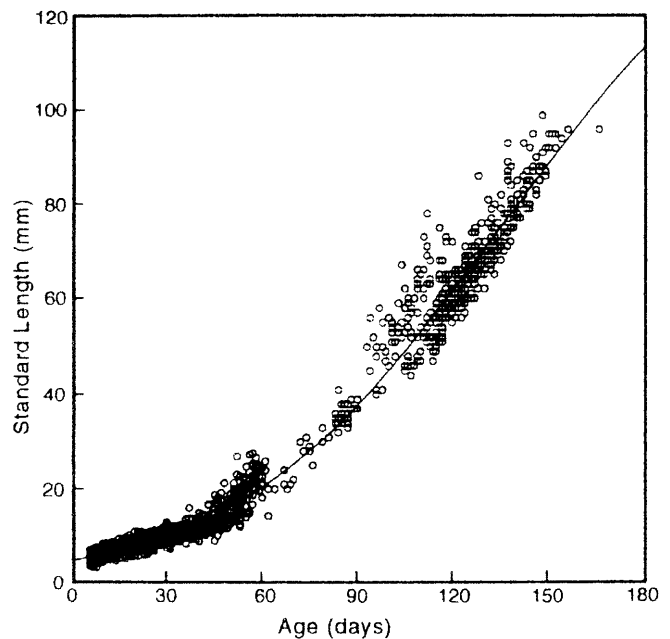
between otolith and body morphology, the most pronounced change coincided with eye migration, settlement, and change in habitat (Jearld et al. 1993; Modin et al. 1996). Walleye pollock from the Gulf of Alaska have sagittal otoliths that undergo several morphological changes as fish transform from larvae to juveniles. One of the changes in otolith morphology was first described by Nishimura and Yamada (1984) as a fan-shaped area probably resulting from a change in crystal orientation.

The transformation from the larval to juvenile stage, reported as length ranges, is traditionally defined by ossification of an adult complement of fin elements and vertebrae, squamation, and resemblance to a small adult (Kendall et al. 1984). In the present study, we examined the relationship between otolith and osteological development through the early life stages of walleye pollock to better define the transition from the larval to juvenile stage. Stages of otolith development from mid-larval to juvenile stages were determined from field-collected specimens by examination of otolith shape and development of accessory growth centers (AGCs). Cleared and stained fishes in the larval to juvenile stages were examined to determine the progression of osteological development. A better definition of transformation from the larval to juvenile stage will help determine whether the transformation from larvae to juvenile fish is length or age dependent, and if the variation of size-at-age at growth transition points is a sign of potential aging error or a natural occurrence. To examine this problem, we fit the data to a Schnute model to determine if the transition points observed on the curve coincide with the transition stages observed in osteological and/or otolith development.

## Materials and methods

Sagittal otoliths were removed from 95% ethanol-preserved larval and juvenile walleye pollock [*Theragra chalcogramma* (Pallas, 1814)] collected from the Shumagin Island region of the Gulf of Alaska. Samples from several years (1991–1998) were used to obtain a large sample size ( $n=228$ ) with a broad range in standard length (SL, measured in mm). The size range of fish examined was chosen such that the development periods before, during, and after transformation [as defined by the osteological criteria reported by Dunn and Matarese (1984) and Dunn and Vinter (unpublished data, AFSC)] would be analyzed. Whole otoliths were examined for AGCs with the number and placement of the growth centers noted.

Larval, transforming, and juvenile walleye pollock were collected from the Gulf of Alaska (1991–1998) to examine osteological development. Fish used in this study ranged from 12 to 53 mm SL ( $n=103$ ) and were originally preserved in 5% formalin and then transferred to 70% ethanol for storage. The method of Taylor (1967) was used to clear and stain the specimens. Skeletal structures were considered ossified upon uptake of Alizarin red-s stain. Since squamation is often used as an important developmental criterion of transition to the juvenile stage, 41 fish ranging from 31 to 93 mm SL were selected from the ethanol-preserved fish used for otoliths, and examined for scales under a stereomicroscope at 50× magnification. To ensure that newly developed scales would not go undetected, skin and tissue samples were removed from each fish



**Fig. 1** *Theragra chalcogramma*. Schnute growth model fit to larval and juvenile walleye pollock data from the Gulf of Alaska (data from Bailey et al. 1996)

behind the head and above the lateral line area and examined at the same magnification.

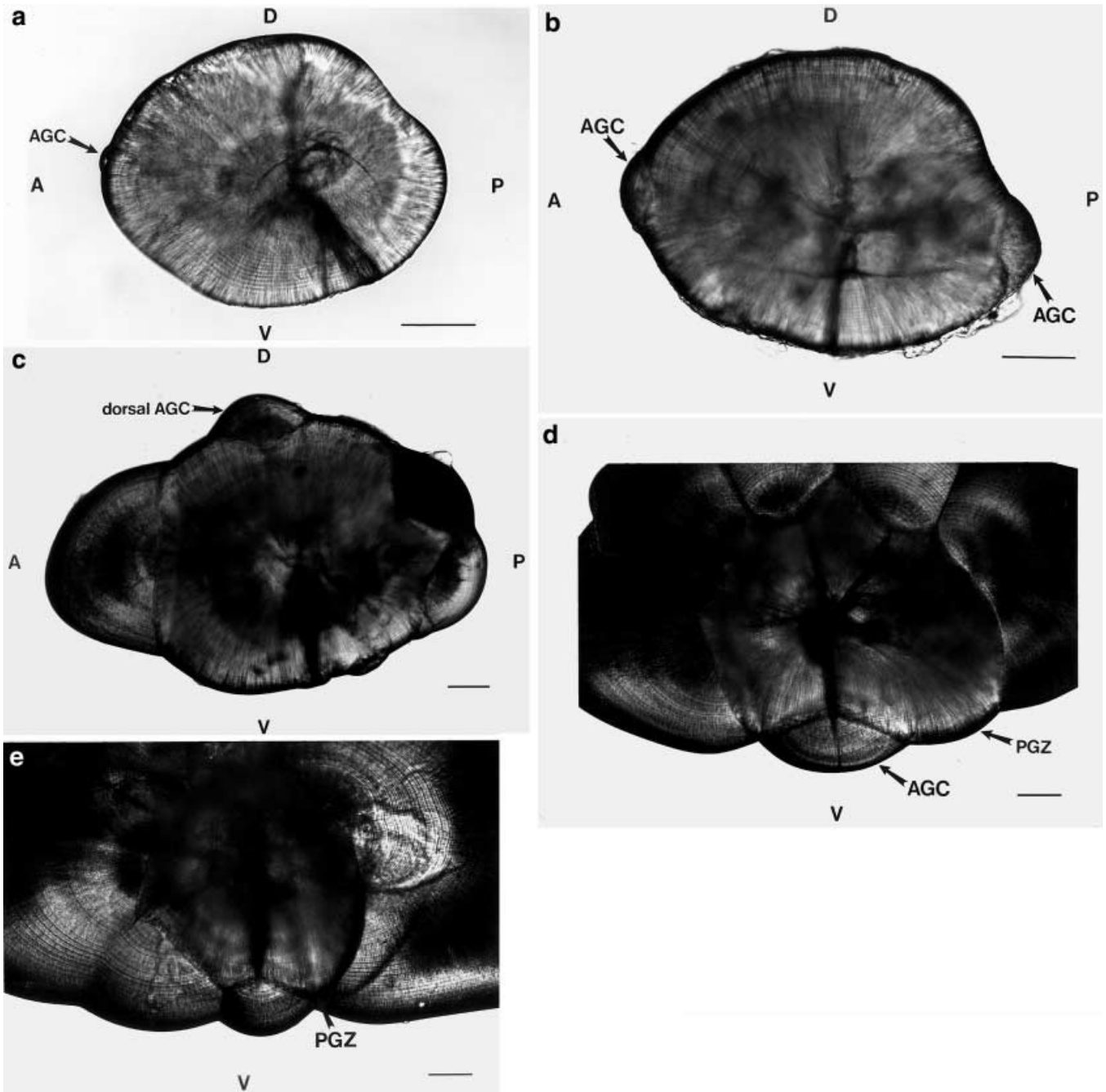
A Schnute growth model was fit to larval and juvenile data (see Bailey et al. 1996) to illustrate overall growth of young walleye pollock (Fig. 1). In order to determine the length ranges (all given as SL in mm) for the growth changes seen on the curve, a piecewise linear regression was fit to the data with no continuity restrictions (Montgomery and Peck 1982). An iterative method was used to find the optimal knots, or natural breakpoints in the regression, using the Schnute model as a guide. Models with 1, 2, and 3 knots were tried with knots for three age groups: 40, 45, or 50 days; 55, 60, or 65 days; and 95, 100, or 105 days – in all possible combinations. These ages were chosen for testing based on visual inspection of the breaks in the growth curve. Only two models had breakpoints falling near definite breaks in the regression. Of these, the one with the smallest mean square error (MSE) and the greatest  $R^2$  was chosen as the best model. The general model of order  $j$  used to fit the data is described as:

$$E(y) = \sum_{j=0}^1 \beta_{0j}x^j + \sum_{i=1}^h \sum_{j=0}^1 \beta_{ij}(x - t_i)^j,$$

where  $h$  is the total number of knots,  $t_i$  is the  $x$ -coordinate (age) of the  $i$ th knot, and  $(x - t_i)^j = 1$  if  $x > t_i$  and 0 if  $x \leq t_i$ . The first term in the model expands to a simple linear regression, while the last term forces a discontinuity at  $t_i$ .

## Results

Sagitta development for walleye pollock (*Theragra chalcogramma*) may be divided into five stages from late larval to early juvenile. Stage 1 (Fig. 2a) occurred from 12 to 19 mm SL. At this stage, the otolith shape changed from the spherical form of larval otoliths to an oblong shape with the first accessory growth center (AGC) formed on the anterior end of the otolith. Stage 2



**Fig. 2** *Theragra chalcogramma*. Sagittal view of whole otoliths viewed with transmitted light demonstrating the five stages of walleye pollock sagitta otolith development (for all photographs: *A* anterior; *P* posterior; *D* dorsal; *V* ventral). **a** Stage 1 otolith at SL = 15.5 mm, scale bar = 50  $\mu$ m. Note the small protrusion on the left side of the otolith which is the first accessory growth center (*AGC*) to form. **b** Stage 2 otolith at SL = 20.5 mm, scale bar = 50  $\mu$ m. The size of the *AGCs* forming on the anterior and posterior ends may vary drastically at this stage. **c** Stage 3 otolith at SL = 21.0 mm, scale bar = 100  $\mu$ m. Note the *AGC* forming on the dorsal edge of the otolith as the anterior and posterior growth centers continue development. **d** Stage 4 otolith at SL = 34 mm, scale bar = 100  $\mu$ m. Note that although an *AGC* has formed on the ventral edge of the otolith, a section of the primary growth zone (*PGZ*) is still part of the otolith edge. **e** Stage 5 otolith at SL = 40 mm, scale bar = 100  $\mu$ m. The *AGCs* have fused to create an adult-like otolith shape. The *PGZ* is no longer part of the overall otolith shape

(Fig. 2b), observed at 19–21 mm SL, was characterized by the formation of both the anterior and posterior *AGCs*. The number and size of growth centers varied. Stage 3 (Fig. 2c) occurred at 21–24 mm SL and was identified by the development of one or two dorsal *AGCs*. The fan-shaped area (Nishimura and Yamada 1984) was easily observed at this stage of otolith development. Stage 4 (Fig. 2d), when the last of the *AGCs* formed on the ventral edge, occurred at 24–37 mm SL (note that the ventral edge of the fan-shaped area is still part of the otolith shape and will continue to be so until stage 5). Stage 5 (Fig. 2e) was characterized by the completion of otolith development occurring at 36–48 mm SL. By this stage, all of the *AGCs* had fused

**Table 1** *Theragra chalcogramma*. Developmental stages, standard length (SL) ranges, and osteological landmarks for walleye pollock

Osteological:				Otolith:		
Devl. stage	SL (mm)	<i>n</i>	Landmarks	Devl. stage	SL (mm)	<i>n</i>
Flexion	12–16	9	Teeth, upper and lower jaws, branchiostegal rays, neural spines, abdominal vertebral centra	1	12–19	28
Postflexion	16–24	18	Principal caudal-fin rays	2	19–21	28
	19–24		Haemal spines, caudal vertebral centra	3	21–24	48
Transformation	24–31	19	Pelvic fins	4	24–37	103
	28–35	21	Pectoral fins, hypurals, epurals			
	34–46	17	Dorsal and anal-fin rays			
Transformation complete, juvenile stage begins	36–46	14	Procurrent (supplementary) caudal rays	5	36–48	21
	42–46	5				

together to form the new otolith shape, and the sagittal otolith resembled a smaller version of an adult walleye pollock otolith. The fan-shaped area, now referred to as the primary growth zone (PGZ), was isolated from the otolith edges and no longer influenced the shape of the otolith.

Most of the major landmarks in osteological development corresponded with the stages and length categories described in otolith development. The beginning of the flexion stage was not only the start of ossification of several important structures, but also the stage when the AGCs began to form on the sagittal otoliths (Table 1). The mandible, maxilla, premaxilla, first teeth, branchiostegal rays, neural spines, and abdominal vertebral centra were ossified during the flexion stage, which began at 12 mm SL and ended at 16 mm SL. Ossification of the principal caudal-fin rays occurred early in the postflexion stage, which began at 16 mm SL and was complete at 24 mm SL. Haemal spines and caudal vertebral centra ossified during mid-postflexion beginning at approximately 19 mm SL. Ossification of neural spines, vertebral centra, and haemal spines progressed from anterior to posterior.

The pelvic-fin rays and supporting basipterygium ossified immediately after postflexion at 24 mm SL. Pectoral-fin rays completed ossification at lengths from 28 to 35 mm SL, while the supporting scapula, coracoid, and radials ossified at 30–40 mm SL. The hypural and epural bones of the isocercal caudal-fin complex ossified at lengths from 28 to 35 mm SL. Hypurals 2–3 are fused to the first ural centrum and hypurals 4–6 support four principal caudal-fin rays. Walleye pollock have three dorsal and two anal fins, which ossified completely during transformation at 34–46 mm SL. Proximal and distal radials supported the fin rays and ossified shortly after them. The first anal fin completed ossification first, followed by the third dorsal fin. Dorsal and anal fins subsequently ossified simultaneously. Procurrent (supplementary) caudal-fin rays were the last median-fin elements to ossify at 36–46 mm SL. The transformation stage ended and the juvenile stage began when all paired

and median-fin elements and vertebrae were ossified at 42–46 mm SL. In addition to the bony structures previously mentioned, all other bones of the skeleton were ossified by the beginning of the juvenile stage. Counts of completely ossified meristic structures in cleared and stained walleye pollock were variable and are summarized in Table 2.

By observing whole fish as well as skin and tissue samples, it was determined that scale development began at 60 mm SL under the skin behind the head. By 70 mm SL, scales became obvious but were still beneath the skin. It was not until 80 mm SL that scales were easily observed behind the head and on the sides of the body emerging through the skin. From 80 to 90 mm SL, scales were still partially under the skin but were fully developed.

By determining where breaks in the model occurred, we defined length ranges for the suspected changes in growth rate seen in the Schnute model used by Bailey et al. (1996). The piecewise linear regression yielding the best fit had breakpoints at 40, 60, and 100 with an ad-

**Table 2** *Theragra chalcogramma*. Ranges of counts for ossified meristic features observed in cleared and stained walleye pollock

Meristic features	Element count ranges (mode)
Fin rays	
First dorsal	11–13 (11)
Second dorsal	12–17 (17)
Third dorsal	18–22 (20)
First anal	19–24 (21)
Second anal	20–23 (21)
Pectoral	17–20 (19)
Pelvic	6 (6)
Dorsal procurrent caudal	22–25 (23)
Principal caudal	4 (4)
Ventral procurrent caudal	23–26 (24)
Branchiostegal rays	7–8 (7)
Vertebral centra	
Abdominal	18–20 (19)
Caudal	32–34 (32)
Total	50–53 (51)

justed  $R^2=0.986$  and  $MSE=15,741.199$ . The lengths associated with these statistically determined break-points were used to define the length intervals coinciding with defined early life history stages. These intervals were  $SL < 12.28$  mm,  $12.28 \leq SL < 23.01$  mm, and  $23.01 \leq SL < 51.41$  mm (Fig. 3). The bend that sometimes occurred just to the right of the breakpoint was a change in the intercept for that particular interval due to the lack of continuity restrictions. A piecewise regression without continuity restrictions was used to define sections of the curve that were different.

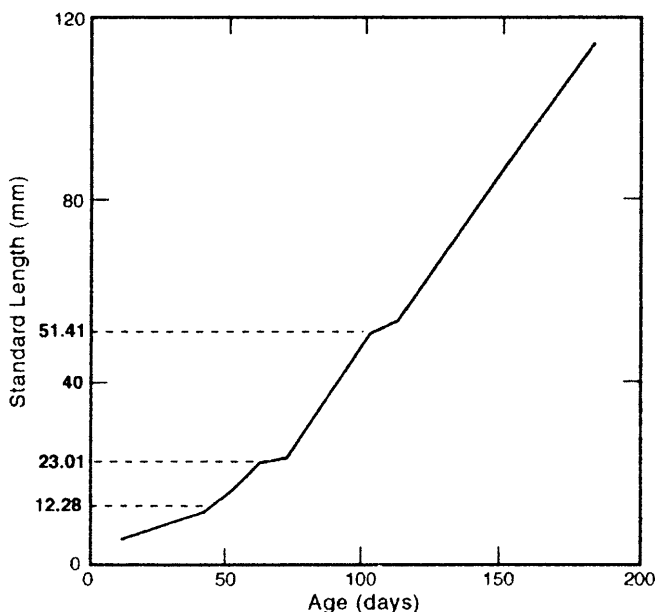
## Discussion and conclusions

Transition points in the growth of walleye pollock (*Theragra chalcogramma*) are associated with major changes in sagitta morphology and osteological development. A fish that is 12–26 mm SL not only experiences notochord flexion and ossification of the jaws and teeth, but also develops the first of many AGCs in the sagittal otoliths, which results in the shape of adult-like otoliths. During the postflexion stage (16–24 mm SL), ossification of vertebrae and principal caudal-fin rays occurs and the otoliths develop AGCs on the anterior, posterior, and dorsal edges. Transformation to the juvenile stage occurs at 24–37 mm SL, when most bones ossify and sagittal otoliths develop AGCs on the ventral edge. When a walleye pollock has completed ossification and resembles a small adult at approximately 42 mm SL,

the sagittal otoliths have completed their development and resemble the shape of adult otoliths. From these results, it is apparent that certain landmarks in osteological and otolith development are closely related to each other by length. By breaking the Schnute model (Bailey et al. 1996) down into length intervals using piecewise linear regression, it was determined that some of the length intervals identified by otolith and osteological methods can also be observed as transition points (beginning and ending points of linear length intervals) on the curve. For example, the first transition point (12.28 mm) coincides with the flexion stage. The next transition point, 23.01 mm, identifies the ending of the postflexion stage. The last transition point, 51.41 mm, coincides with the completion of the transformation to the juvenile stage. From these results, it appears that this method of determining life stage transitions is not as sensitive as examining the otolith or osteological structures, but it is useful in that it does identify where there are potential difficulties in either fish growth or aging errors.

Matarese et al. (1989) reported the sequence of fin development for walleye pollock as caudal, first anal, second anal, third dorsal, second dorsal, first dorsal, pelvics, and pectorals. This is somewhat different from our observations: principal caudal, pelvics, pectorals, first dorsal, and procurrent caudal rays. Of the median fins that appeared to ossify nearly simultaneously, the third dorsal was more darkly stained, suggesting that its ossification occurred slightly before the others. It is not clear when the procurrent caudal-fin rays were completed in the study by Matarese et al. (1989), as their reference to “caudal” was probably to principal rays. The discrepancy noted between these accounts of fin developmental sequence are likely attributable to differences in preservation and/or staining techniques. Perhaps the most important difference is that we omitted the procedure for staining cartilage with Alcian blue in our study to eliminate the possibility of acetic acid etching away calcium formed in early stages of ossification during transformation (as suggested by Cubbage and Mabee 1996; Mabee and Trendler 1996). To ensure that the lengths reported in the present study for initial ossification in the smallest fish were not affected by this problem, all fish were processed using the method of Taylor (1967). In contrast to many other species of fish, scale development in walleye pollock should not be used as a defining criterion for the juvenile stage because scales are not a prominent feature until much later in development (60–70 mm SL). Because scale development varies among species (Copp and Kovac 1996), each species should be studied for this attribute to determine if it can be used as an important indicator of change in a fish's life history.

Although the two species are unrelated, flatfish and walleye pollock do have the formation of AGCs in common. It has been well documented that the AGCs reported in flatfish otoliths define a change in habitat and behavior (settlement period) and that length and not



**Fig. 3** *Theragra chalcogramma*. Growth model constructed by piecewise linear regression based on data from Bailey et al. (1996). Note that the transition points found by this method coincide with flexion, postflexion, and the juvenile life stage

age was the determining factor. This type of well-defined action/behavior to explain why AGCs are formed is not documented for walleye pollock, making flatfish a key species for understanding AGC development. Chambers and Legget (1987) reported length as a less variable indicator of metamorphosis to the juvenile stage for flatfish. Jearld et al. (1993) reported that the otoliths from older winter flounder (*Pleuronectes americanus*) that had not undergone metamorphosis did not develop AGCs. Sogard (1991) suggested that, for winter flounder, the variation observed in timing for the formation of AGCs may be partially due to the variation in fish size. Since the duration of larval life stages may vary due to environmental conditions such as temperature and food availability, it is possible for the otoliths to be affected as well. This may explain why we see variation of size-at-age at the transition points in the growth model. Natural variation in size-at-age that occurs in wild fish may be the major contributor to the variation observed rather than aging errors.

Walleye pollock do not have a definite settlement period or habitat change as do flatfishes (Toole et al. 1993) during their transformation from the larval to juvenile stage. Presently, AGCs on walleye pollock otoliths may be used to determine the developmental stage of the fish and hence obtain an estimated length. With future research, the AGCs may also be discovered to be indicators of environmental and behavioral changes. Such behaviors already reported for juvenile walleye pollock include schooling, vertical migration for food, and predator avoidance through barriers such as thermoclines (Merati and Brodeur 1996; Sogard and Olla 1996), but these behaviors have not been studied for transforming walleye pollock as of yet. A properly ossified caudal fin and vertebral column will increase swimming ability and enhance locating and catching prey. A transforming otolith, which will result in an adult-like form, may also be necessary to navigate through different environments to pursue prey and detect approaching predators. As a fish grows and progresses through developmental stages, it will experience different levels of vulnerability to predation due to its changing body size and swimming ability (Paradis et al. 1996).

In the present study we have determined that otolith and osteological development can be used separately to estimate the life stage and SL of a transforming walleye pollock if the body has been damaged either due to the type of gear/mesh used or from handling and preservation (e.g. tail broken off when fish are frozen and transported). Although it was not an objective of this study to define why we see variance of age at certain lengths, it is most likely a natural occurrence that cannot be corrected for.

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