Transactions of the American Fisheries Society 124:103–111, 1995

Age Verification of Winter Flounder in Narragansett Bay

R. E. HAAS[1] AND C. W. RECKSIEK

Department of Fisheries, Animal and Veterinary Science, The University of Rhode Island Kingston, Rhode Island 02881, USA

Abstract.—Between October 1987 and December 1988, 732 winter flounder *Pleuronectes americanus*, 91–380 mm total length, were collected during biweekly sampling from Narragansett Bay, Rhode Island. Left sagittal otoliths from these fish were embedded in epoxy resin, and transverse sections through the foci were prepared. With hyaline zones considered as annual increments, ages ranged from 1 to 11 for 608 winter flounder; 97% of the fish were younger than age 5. The dorsoventral otolith diameter was determined by linear regression analyses to be the best (r^2 = 0.90) of six "radial" axes for increment measurements. Marginal increment analyses for ages 1–4 showed that the increments, each composed of one opaque and one hyaline zone, are deposited annually, which clearly verified sectioned otolith ages for age-2 and age-3 fish. Opaque edges were prevalent in May, June, and July. Sectioned otoliths from winter flounder can provide clear increments and measurable increment widths through age 11. Two individuals read 369 sectioned otoliths and 116 whole otoliths; one individual read 155 scales twice. Precision between readers and aging methods was relatively high (average percent error, 1.5–4.5). Comparison of ages from scales and whole and sectioned otoliths from 154 fish showed no significant differences ($P \leq 0.05$).

Winter flounder *Pleuronectes americanus* have been aged by growth of tagged and recaptured fish (Howe and Coates 1975), scale analysis (Arnold 1941; Lux 1973; NUSCO 1987), whole otolith analysis (Landers 1941; Vaillancourt et al. 1985), and sectioned otolith analysis (Beacham 1982). Landers (1941) was the first to use whole otoliths to age winter flounder, but he found whole otoliths from fish older than age 3 to be too thick to read. Berry (1959) attempted age validation of Narragansett Bay winter flounder with scales, edge-type marginal increment analysis of whole otoliths, and length-frequency distribution analysis. He found that scales were unsatisfactory for age determination, that otoliths could only be used to age fish through age 3, and that length-frequency analysis was limited to fish through age 2. Most winter flounder aging studies in the last 25 years have relied on whole otoliths. Reports of difficulties in accurately determining ages of winter flounder have varied widely. Vaillancourt et al. (1985) encountered few problems aging fish through age 9, whereas Poole (1966) found it impossible to validate annuli beyond age 3 because after that age the increments were too small to read accurately. Because of the discrepancies in accuracy of whole otolith aging techniques, most recent studies have relied on the sectioned otolith method. Beacham (1982) sectioned winter flounder otoliths by breaking them through the focus and grinding the posterior piece down to a smooth, flat section. Variations of otolith sectioning methods were described by Chilton and Beamish (1982) and Bedford (1983).

This study documents relationships between fish length and otolith section dimensions, verifies the ages of Narragansett Bay winter flounder by marginal increment analysis of sectioned otoliths (Johnson 1983), and compares the ages determined from sectioned otoliths to those from whole otoliths and scales.

Methods

Collection and storage.—Weekly bottom trawl sampling has been conducted in Narragansett Bay and Rhode Island Sound since 1966 (Jeffries and Terceiro 1985). From those sampling episodes, winter flounder were collected biweekly, October 1987–December 1988, from the center of Narragansett Bay (41°25'N, 71°25'W) and the mouth of the bay, where it meets Rhode Island Sound (41°33'N, 71°25'W). Total length (TL, cm), wet weight (g), sex, and stage of maturity (immature, mature, ripe, or spent), of each fish were recorded. Sagittal otoliths were extracted and stored dry in vials. Scales were collected from a subsample of the fish from May to December 1988 for comparison. The scales were removed from the lateral line area a few centimeters anterior to the caudal peduncle and stored dry in envelopes (Fields 1988).

Preparation and examination of age struc-

[1] Present address: National Marine Fisheries Service, Northeast Fisheries Science Center, 166 Water Street, Woods Hole, Massachusetts 02543, USA.

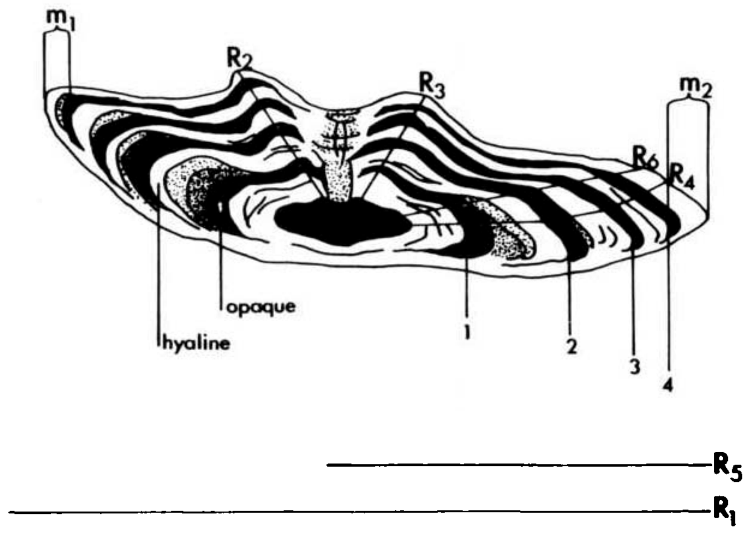

FIGURE 1.—Illustration of a sectioned otolith of an age-5 winter flounder showing the six otolith dimensions, R_1–R_6, along which measurements were made to the beginning of each opaque zone. Otolith dimension R_1 is defined as the dorsoventral distance, R_2 as the distance from the focus to the dorsal edge of the sulcus, R_3 as the distance from the focus to the ventral edge of the sulcus, R_4 as the segmented distance from the focus to the ventral edge, R_5 as the linear distance from the focus to the ventral edge, and R_6 as the linear distance from the focus to the ventral edge at the plateau. The sum of the marginal increments, m_1 and m_2, is used in marginal increment analysis. The proximal surface is at the top of the diagram; the sulcus acousticus is between R_2 and R_3.

tures.—The otolith sectioning technique in this study was similar to that used by Penttila and Dery (1988). The left sagittal otolith, which is more symmetrical than the right otolith, was embedded, sulcus side up, in West® epoxy resin in a Fisher® 30 × 24 × 5-mm base mold. Otoliths were sectioned transversely through the focus with a Buehler® Isomet low-speed jewelers saw and double Norton® F0565977 diamond blades (see also Haas 1992). Sections were then mounted on glass slides with Permount® and ordinary glass cover slips for viewing and storage. Sectioned otoliths were viewed by transmitted light with a compound microscope at 32× magnification.

Whole otoliths were examined in water on a black background through a dissecting microscope at 2.5× magnification by reflected light. The number of hyaline zones observed, the type of growth

TABLE 1.—Otolith-section age distribution and total lengths (mm) at age for male and female winter flounder collected October 1987–December 1988 from Narragansett Bay, Rhode Island.

	Females			Males		
		Length (mm)			Length (mm)	
Age	*N*	Range	Mean ± SD	*N*	Range	Mean ± SD
1	115	91–307	181 ± 30	124	104–266	183 ± 37
2	178	140–380	274 ± 34	88	161–315	245 ± 20
3	50	237–373	315 ± 20	11	250–320	263 ± 20
4	19	275–405	340 ± 30	1	292	
5	7	354–402	370 ± 17	2	332–348	340 ± 11
6	2	365–380	373 ± 11	2	295–360	323 ± 30
8				1	336	
9	1	405				
10	1	417		1	348	
11	1	380				
Total[a]	374			230		

[a] In all, 692 fish were aged; table includes only those age-1 and older individuals whose sectioned otoliths were found suitable for increment measurement (see Haas 1992).

TABLE 2.—Results of linear regression analyses of total fish length (mm) on otolith dimensions (mm) for winter flounder from Narragansett Bay, Rhode Island, October 1987–December 1988.

Otolith dimension[a]	N	r^2	MSE[b]	Slope	Intercept (mm)	Rank[c]
R_1	632	0.90	457	126	−76	1
R_2	630	0.81	845	416	−3	5
R_3	630	0.79	921	427	−2	6
R_4	626	0.89	498	256	−65	2
R_5	633	0.88	545	237	−68	3
R_6	629	0.87	569	289	−39	4

[a] See Figure 1.
[b] Mean square error.
[c] Rank 1 (highest r^2, lowest MSE) is best; rank 6 (lowest r^2, highest MSE) is worst.

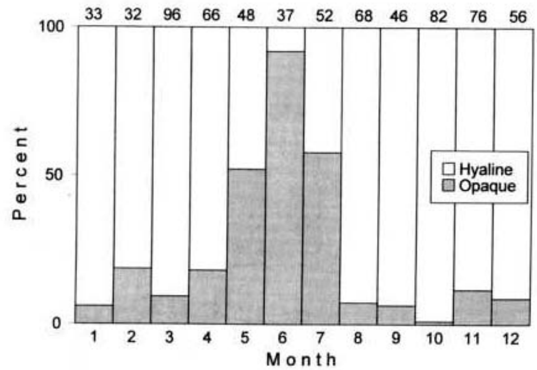

FIGURE 2.—Monthly percent occurrences of opaque and hyaline edges of otoliths, hyaline zone groups 1–4 combined, for winter flounder collected from Narragansett Bay, Rhode Island, October 1987–December 1988. Month 1 is January. Numbers above each bar are numbers of fish.

zone (hyaline or opaque) seen at the edge, and the readability of the otolith were recorded according to Jensen (1965).

Scale impressions were made in laminated plastic with a roller press. Five or six scales from each fish were placed, sculptured side up, on a heavy base slide of 1-mm-thick cellulose acetate plastic. The laminated slide was placed over the scales and the stack of slides was passed through the roller press. The impressions were then examined on a microprojector at a magnification of 40×.

Otolith section radial measurements.—To determine the closest proportionality between otolith section dimension and total length of winter flounder, six otolith dimensions (R_1–R_6) were used to make measurements to the beginning of each opaque zone (Figure 1). Measurements of R_1 were made along the diameter of the otolith, from the dorsal edge, through the focus, to the ventral edge. Otolith dimensions R_2 and R_3 ran from the center of the focus along the respective dorsal and ventral sides of the sulcus to the edge. Radius R_4 followed the curve of the otolith from the focus to the ventral edge. Radius R_5 ran from the focus to the ventral edge in a straight line. Radius R_6 was also a straight line from the focus to the plateau on the proximal surface of the ventral edge. The measurements were made with a microcomputer-based system. A black-and-white video camera attached to a compound microscope transferred the image to a color monitor that was interfaced to a personal computer. The Optimas® program (BioScan 1990) was used to digitize the sectioned otolith measurements and convert them to millimeters.

Fish total length was regressed on the six otolith dimensions. The dimension with the best linear relationship to fish total length (i.e., the highest r^2 and the lowest mean square error [MSE]) was used for subsequent analyses (Haas 1992).

Marginal increment analysis.—Edge-type (Solomon et al. 1987) and marginal-width analyses (Manooch and Drennon 1987) were performed on sectioned otolith data. For the edge-type analysis, the percent occurrence of hyaline and opaque conditions of otolith margins was determined for each hyaline-zone group (grouped by the number of hyaline zones present in the otolith, complete or incomplete) for each month of capture. The percent occurrence was graphed to allow us to search for patterns in the formation of the otolith (Beckman et al. 1990).

The marginal-width analysis used measurements along the R_1 otolith dimension, which had the best linear relationship to the total length of the fish (see Results and Discussion). The increment was the distance from the otolith margin to the outer edge of the outermost complete hyaline zone (Figure 1). Mean marginal increment widths were calculated for each hyaline-zone group and plotted against the month of capture to allow us to search for patterns in the otolith growth.

Whole and sectioned otolith comparisons.—To compare hyaline-zone counts, whole and sectioned otoliths were read independently by two readers. A linear regression was fit to the data, and Beamish and Fournier's (1981) index of average percent error (APE) was calculated to indicate the level of precision in independent readings. The index of APE was used because it is not independent of age and provides a better estimate of precision than merely calculating the overall percent agreement;

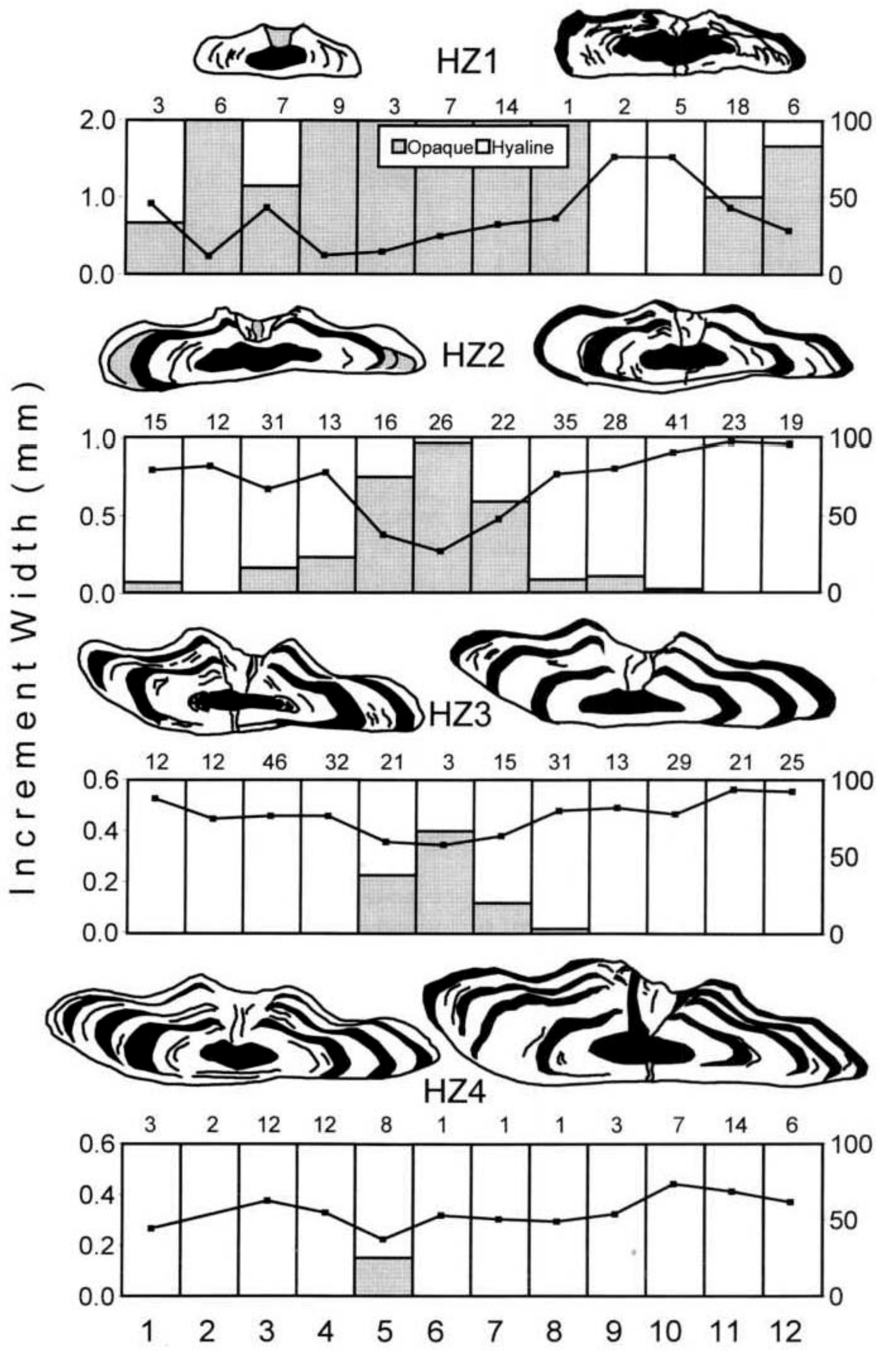

FIGURE 3.—Yearly cycles of mean marginal increment widths on otoliths since the last hyaline band was completed and monthly percent occurrences of opaque and hyaline edges, by hyaline zone group (HZ1–HZ4), for winter flounder collected from Narragansett Bay, Rhode Island, October 1987–December 1988. Month 1 is January. Numbers above each bar are numbers of fish. Otolith section diagrams represent appearances of edge types from each hyaline zone group: hyaline edge, left; opaque edge, right.

TABLE 3.—Comparisons of readings and aging techniques for winter flounder from Narragansett Bay, Rhode Island, October 1987–December 1988.

Method or comparison	Number of Readers	Number of Occasions	N	APE[a]	t-value[b]
Reading comparisons					
Otolith section	2	1	369	1.6	
Whole otolith	2	1	116	4.5	
Scale	1	2	155[c]	1.5	
Technique comparisons					
Whole versus sectioned otolith			154[c]	1.6	0.083 (NS)
Scale versus sectioned otolith			154[c]	2.9	−0.050 (NS)

[a] Index of average percent error (Beamish and Fournier 1981).
[b] Critical t-value in Student's t-test; NS, no significant difference at $P \leq 0.05$.
[c] Same group of fish.

also, it can be used to compare determinations or readers. A smaller index indicates greater precision.

Precision in scale annulus counts.—All scales were examined twice, at different dates, by the senior author. Annular zones were zones on the scale where the circuli were crowded and seemed to cross over or cut off each other (Cailliet et al. 1986). The age of each scale, determined by the number of completed annual zones present, was recorded. Estimated scale ages were compared to whole and sectioned otolith ages by matched-pair t-tests, indices of APE (Beamish and Fournier 1981), and linear-regression analyses.

Results and Discussion

We collected 732 winter flounders, 91–380 mm TL, from Narragansett Bay during biweekly sampling, October 1987–December 1988 (Table 1). Sagittal otoliths examined from 692 of these fish showed they were age 1–11 and that most (97%) were age 1–4 (Table 1).

Otolith Radial Measurements

We found 633 otoliths suitable for increment measurements along radial dimensions R_1–R_6 (Figure 1). Regression analyses of otolith length on fish total length, performed for each otolith axis, revealed that R_1 was the best predictor of fish length (Table 2). Consequently, marginal increment width measurements were made along the R_1 radius.

Marginal Increment Analysis

Edge-type analysis was performed for all hyaline-zone (HZ) groups combined (Figure 2), whereas both edge-type and marginal increment width analyses were performed for individual groups, HZ1–HZ4; beyond HZ4, sample sizes were too small for analysis (Figure 3). For all HZ groups combined and HZ groups 1–4, monthly percent occurrence of hyaline and opaque edges in otolith sections indicated that each edge type formed once during the sampling year (Figures 2, 3). Opaque edges were prevalent in May, June, and July. The hypothesis of annual cycles of hyaline and opaque zone deposition is also supported by the yearly cycle of increasing mean marginal increment widths, which showed minimal margins in the early summer for HZ groups 1–4 (Figure 3).

Age Verification

The direct methods of age validation suggested by Beamish and McFarlane (1983), with known-age or marked fish, were not attempted in this study. However, the combined results of the several indirect methods that we used suggest that ages determined from sectioned otoliths are accurate for age-2 and age-3 fish, and probably accurate for age-1 and age-4 fish.

Although the edge-type analysis indicated that opaque zone formation occurred in May, June, and July, it may begin sooner because deposition must occur for some time before it is thick enough to be discernible in the section. Our finding that opaque zone formation in winter flounder otoliths occurs in May–July is supported by the findings of Berry (1959) and Poole (1966). Opaque zone formation may follow spawning, which Narragansett Bay winter flounder do in February–April (Klein-MacPhee 1978), but other factors, including water temperature and diet, may also be important. Opaque deposition is visible as early as November in otoliths of age-0 and age-1 winter flounder, which tend to remain inshore throughout the winter (Jeffries and Johnson 1974). In these fish, opaque material is deposited until August, when a hyaline zone forms (Figure 3; Berry 1959). The coincidence of spawning and opaque material deposition makes the beginning of the opaque zone a reasonable birthday mark for winter flounder.

Precision of Age Estimates

Two readers independently aged 369 sectioned otoliths and 116 whole otoliths, and one reader aged 155 scales twice (Table 3). Scales and whole

TABLE 4.—Deviations in age readings of otoliths and scales of winter flounder from Narragansett Bay, Rhode Island, October 1987–December 1988. Sectioned and whole otolith readings were the numbers of otolith hyaline zones as read by two readers; those of scales were numbers of scale annuli as read twice by one reader.

Hyaline zone or annulus group[a]	N	Number of second counts deviating from first counts by:							Percent of second counts within deviations of:			
		−2	−1	0	1	2	3	4	0	0 ± 1	0 ± 2	0 ± 3
Otolith sections												
1	39			32	7				82	100		
2	139			125	14				90	100		
3	132		2	127	3				96	100		
4	35			34	1				97	100		
5	14			14					100			
6	2			2					100			
7	3			3					100			
9	2			2					100			
10	1			1					100			
11	2			2					100			
Total	369		2	342	25				93	100		
Whole otoliths												
1	32		1	26	5				81	100		
2	65		1	59	4			1	91	98	98	98
3	15		1	13	1				87	100		
4	3	1		1		1			33	33	100	
5	1		1						0			
Total	116	1	4	99	10	1		1	85	97	99	99
Scales												
0	1			1					100			
1	47			45	2				96	100		
2	87		3	82	2				94	100		
3	12			11	1				92	100		
4	4		1	3					75	100		
5	1			1					100			
6	2			2					100			
8	1			1					100			
Total	155		4	146	5				94	100		

[a] Group identity was established by the first reading. Not all groups were represented in these counts.

and sectioned otoliths from 154 fish were used to compare aging techniques (Table 3). The relatively high precision between readers for whole and sectioned otoliths and the precision for scales, measured by percent agreement, regression analysis, and APE, indicated positive bias by the second reader; it also showed that the readability of scales and otoliths was relatively good. Readers were in complete agreement about the number of hyaline zones present in sectioned otoliths in 93% of cases, and readings were within 0 ± 1 count in 100% of cases (Table 4). For whole otoliths, readers agreed fully in 85% of cases and were within one count in 97% of cases (Table 4). Scale readings were in complete agreement in 94% of cases and within one annulus in 100% of cases (Table 4).

The APE indicated relatively high reading precision, with 1.6% for sectioned otolith readings, 4.5% for whole otolith readings, and 1.5% for scale readings (Table 3). Regression analyses affirmed the precision indicated by the percent agreement between readings and indices of APE. However, the coefficient of determination of whole otolith readings (reader versus reader) was lower than expected ($r^2 = 0.89$ for sectioned otolith readings, 0.60 for whole otolith readings, and 0.94 for scale readings).

Matched-pair t-tests showed no significant differences among aging techniques (Table 3). Disagreements between whole and sectioned otolith readings were greater, yet fewer, than those between scales and sectioned otoliths, especially for older fish (Table 5). Complete agreement between whole and sectioned otolith ages was 94%; agreement within ± 1 count was 97%. Complete agreement between scale and sectioned otolith ages was 89%; agreement within ± 1 count was 99% (Table 5).

The high precision between aging methods indicated by percent agreement was supported by

TABLE 5.—Deviations of whole otolith and scale readings from readings of sectioned otoliths for individual winter flounder from Narragansett Bay, Rhode Island, October 1987–December 1988. Whole otoliths are not necessarily from the same individuals as the scales.

Hyaline zone or annulus group[a]	*N*	Number of counts deviating from sectioned otolith counts by:							Percent of counts within deviations of:		
		−4	−3	−2	−1	0	1	2	0	0 ± 1	0 ± 2
						Whole otolith					
0	1					1			100		
1	50					49	1		98	100	
2	80				1	77	1	1	96	99	100
3	17				1	16			94	100	
4	3				1	1	1		33	100	
6	2	1		1					0	0	50
10	1			1					0	0	100
Total	154	1		2	3	144	3	1	94	97	99
						Scales					
0	1					1			100		
1	51					44	7		86	100	
2	80				3	77			96	100	
3	16				2	11	2	1	69	94	100
4	3				1	2			67	100	
6	2								100		
10	1			1		2			0	0	100
Total	154			1	6	137	9	1	89	99	100

[a] Group identity was established by the sectioned otolith reading. Not all groups were represented in these counts.

indices of APE which were 1.6% for whole and sectioned otoliths and 2.9% for scales and sectioned otoliths (Table 3). The results of regression analyses of aging methods were less favorable than the use of APE indices but still they produced relatively high coefficients of determination for whole and sectioned otoliths (r^2 = 0.81) and for scales and sectioned otoliths (r^2 = 0.87).

Aging Technique

The precision of all three aging methods was relatively high. The APE values we report (1.5–4.5) were similar to those (0–11.2) reported for various other species and aging methods (see Haas 1992 for a summary of APE values from eight studies). Values below 10% are considered to be within the accepted level of precision for the use

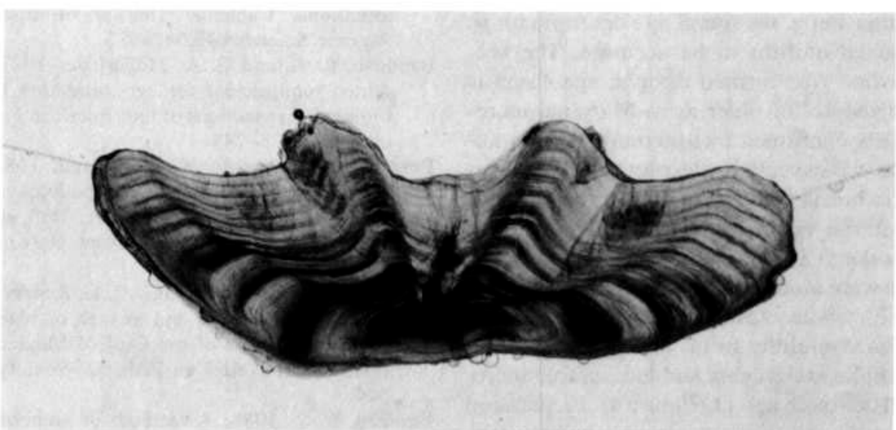

FIGURE 4.—Sectioned otolith of an age-11, 405-mm female winter flounder collected from Narragansett Bay, Rhode Island, 8 March 1988. The section's maximum dimension (R_1, the dorsoventral distance; see Figure 1) is 3.9 mm.

of an aging technique in stock assessment (Powers 1983). Other investigators have found that age determinations from whole otoliths are comparable to those from sectioned otoliths for relatively young fish, but that as fish become older, sectioned otoliths give older age estimates than whole otoliths (Beamish 1979; Campana 1984). Variability in age determination increases for older fish because of decreasing sample size, a problem caused by mortality at the upper end of the size range (Smale and Taylor 1987).

The precision between readings of scales was better than that of sectioned or whole otoliths. The scales were read twice by the same person, which ought to have produced lower variability than if they had been read once by two different readers. The relatively high precision of the scale readings may also be due to the lack of older fish in the samples. The collection of scales from winter flounder began halfway through the sampling period, in May 1988, the time of year when older winter flounder begin to move out of Narragansett Bay into deeper, cooler waters (Klein-MacPhee 1978). This would compound the effects of sample truncation and lessen the variability in scale readings. The use of the scale method is often desirable because the fish can remain alive, but it has not been validated for winter flounder and has been found to underestimate age in several other species (Beamish and McFarlane 1987).

The lower level of precision between readers of whole otoliths suggests that they are more difficult to read, particularly for older fish. Table 5 shows that the few whole otoliths from fish in HZ groups 6 and 10 that were compared to sections were assigned at least two hyaline zones fewer.

During this study, we found age determinations from sectioned otoliths to be accurate. The sectioning method was verified through age 4 and is probably accurate for older ages. Marginal increment analysis confirmed that increments form annually. This was especially clear for age-2 and age-3 fish. It was not as evident in younger fish because opaque material occurred in the otoliths almost throughout the year. Edge type and the number of increments were more discernible in sectioned otoliths than in whole otoliths, especially for older fish. Sectioned otoliths from winter flounder can provide definite increments and measurable increment widths through age 11 (Figure 4). Preparation of otolith sections is time consuming and perhaps necessary only for older fish, whose otolith increments are crowded together at the otolith margin. In cases where older winter flounder are being aged and accuracy is important (i.e., for back-calculation of length at age), the sectioning technique described here would provide the most accurate results.

Acknowledgments

Perry Jeffries, Graduate School of Oceanography, University of Rhode Island, provided winter flounder specimens. Independent age readings were performed by Mark Johnson, Connecticut Department of Environmental Protection. Jay Burnett and Frank Almeida, National Marine Fisheries Service, Northeast Fisheries Science Center, helped process scales, otoliths, and image analysis data. Linda Birely, John Castleman, Chris Gauthier, and Ernesto Lorda, Northeast Utilities Environmental Laboratory, Waterford, Connecticut, assisted with data analysis and graphics. Sheila Polofsky and Richard Wolke, University of Rhode Island, helped with otolith illustrations and photographs. This is contribution 2835 of the Rhode Island Experiment Station.

References

Arnold, E. L. 1941. Validity of scale analysis as a means of age determination of the winter flounder. Master's thesis. University of Rhode Island, Narragansett.

Beacham, T. D. 1982. Biology and exploitation of winter flounder in the Canadian Maritimes area of the northwest Atlantic Ocean. Canadian Technical Report of Fisheries and Aquatic Sciences 1113.

Beamish, R. J. 1979. Differences in the age of Pacific hake (*Merluccius productus*) using whole otoliths and sections of otoliths. Journal of the Fisheries Research Board of Canada 36:141–151.

Beamish, R. J., and D. A. Fournier. 1981. A method for comparing the precision of a set of age determinations. Canadian Journal of Fisheries and Aquatic Sciences 38:982–983.

Beamish, R. J., and G. A. McFarlane. 1983. The forgotten requirement for age validation in fisheries biology. Transactions of the American Fisheries Society 112:735–743.

Beamish, R. J., and G. A. McFarlane. 1987. Current trends in age determination methodology. Pages 15–42 *in* R. C. Summerfelt and G. E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.

Beckman, D. W., A. L. Stanley, J. H. Render, and C. A. Wilson. 1990. Age and growth of black drum in Louisiana waters of the Gulf of Mexico. Transactions of the American Fisheries Society 119:537–544.

Bedford, B. C. 1983. A method for preparing sections of large numbers of otoliths embedded in black polyester resin. Journal du Conseil, Conseil International pour l'Exploration de la Mer 41:4–12.

Berry, R. J. 1959. Critical growth studies of winter flounder, *Pseudopleuronectes americanus*, in Rhode Island waters. Master's thesis. University of Rhode Island, Narragansett.

BioScan. 1990. OPTIMAS (tm) version 2.0 Beta 44 (9/6/90). BioScan, Edmonds, Washington.

Cailliet, B. M., M. S. Love, and A. W. Ebeling. 1986. Fishes: a field laboratory manual on their structure, identification and natural history. Wadsworth, Belmont, California.

Campana, S. E. 1984. Comparison of age determination methods for the starry flounder. Transactions of the American Fisheries Society 113:365–369.

Chilton, D. E., and R. J. Beamish. 1982. Age determination methods for fishes studied by the groundfish program at the Pacific Biological Station. Canadian Special Publication of Fisheries and Aquatic Sciences 60.

Fields, B. 1988. Winter flounder *Pseudopleuronectes americanus*. NOAA (National Oceanic and Atmospheric Administration) Technical Report NMFS (National Marine Fisheries Service) 72:103–107.

Haas, R. E. 1992. Age validation of Narragansett Bay winter flounder using marginal increment analysis of sectioned otoliths. Master's thesis. University of Rhode Island, Kingston.

Howe, A. B., and P. G. Coates. 1975. Winter flounder movements, growth, and mortality off Massachusetts. Transactions of the American Fisheries Society 104:13–29.

Jeffries, H. P., and W. C. Johnson. 1974. Seasonal distribution of bottom fishes in the Narragansett Bay area: seven-year variations in the abundance of winter flounder, *Pseudopleuronectes americanus*. Journal of the Fisheries Research Board of Canada 31: 1057–1066.

Jeffries, H. P., and M. Terceiro. 1985. Cycle of changing abundances in the fishes of the Narragansett Bay area. Marine Ecology Progress Series 25:239–244.

Jensen, A. C. 1965. A standard terminology and notation for otolith readers. International Commission for the Northwest Atlantic Fisheries Research Bulletin 2:5–7.

Johnson, A. G. 1983. Age and growth of yellowtail snapper from south Florida. Transactions of the American Fisheries Society 112:173–177.

Klein-MacPhee, G. 1978. Synopsis of biological data for the winter flounder, *Pseudopleuronectes americanus* (Walbaum). FAO (Food and Agriculture Organization of the United Nations) Fisheries Synopsis 117.

Landers, W. S. 1941. Age determination of the winter flounder of Narragansett Bay by otolith analysis. Master's thesis. Rhode Island State College, Narragansett.

Lux, F. E. 1973. Age and growth of winter flounder, *Pseudopleuronectes americanus*, on Georges Bank. U.S. National Marine Fisheries Service Fishery Bulletin 71:505–512.

Manooch, C. S., III, and C. L. Drennon. 1987. Age and growth of yellowtail snapper and queen triggerfish collected from the U.S. Virgin Islands and Puerto Rico. Fisheries Research (Amsterdam) 6:53–68.

NUSCO (Northeast Utilities Service Company). 1987. Winter flounder studies. Pages 1–151 *in* Monitoring the marine environment of Long Island Sound at Millstone Nuclear Power Station. Summary of studies prior to unit 3 operation. NUSCO, Waterford, Connecticut.

Penttila, J., and L. M. Dery, editors. 1988. Age determination methods for northwest Atlantic species. NOAA (National Oceanic and Atmospheric Administration) Technical Report NMFS (National Marine Fisheries Service) 72.

Poole, J. C. 1966. Growth and age of winter flounder in four bays of Long Island. New York Fish and Game Journal 13:206–220.

Powers, J. E. 1983. Some statistical characteristics of ageing data and their ramifications in population analysis of ocean pelagic fish. NOAA (National Oceanic and Atmospheric Administration) Technical Report NMFS (National Marine Fisheries Service) 8:19–24.

Smale, M. A., and W. W. Taylor. 1987. Sources of back-calculation error in estimating growth of lake whitefish. Pages 189–202 *in* R. C. Summerfelt and G. E. Hall, editors. Age and growth of fish. Iowa State University Press, Ames.

Solomon, G., M. Sano, M. Shimizu, and Y. Nose. 1987. Age and growth of the pleuronectid flounder *Limanda yokohamae* in Tokyo Bay, Japan. Bulletin of the Japanese Society of Scientific Fisheries 53:711–716.

Vaillancourt, R., J-C. F. Brêthes, and G. Desrosiers. 1985. Croissance de la plie rouge (*Pseudopleuronectes americanus*) de l'estuaire maritime du Saint-Laurent. Canadian Journal of Zoology 63:1610–1616.

Received April 28, 1993
Accepted July 15, 1994