

Abstract—Internal otolith morphometrics, coupled with image analysis procedures and multivariate statistical analyses, were examined to investigate stock structure of haddock (*Melanogrammus aeglefinus*) on Georges Bank in the northwest Atlantic. Samples were collected during spring 1995–97 from the Northeast Peak (eastern Georges Bank) and the Great South Channel (western Georges Bank) spawning components. The structure of transverse sagittal otolith sections were described for individual haddock samples from each spawning component by using a combination of linear morphometrics, shape characteristics, and growth increments. Analyses were structured to account for the effects of size, sex, age, and year class. Significant differences in internal otolith structure were found between eastern and western Georges Bank haddock, providing phenotypic evidence of stock separation between the two spawning components. Eastern Georges Bank haddock tended to have smaller internal otolith dimensions than western Georges Bank haddock; these differences appeared to be related to growth rates. Total classification success for each spawning component varied from 61% to 83% for the different age and year-class combinations. Results from this study may be helpful in forming consistent stock definitions that can be used by both U.S. and Canadian fishery management agencies for rebuilding stocks of haddock on Georges Bank.

The use of internal otolith morphometrics for identification of haddock (*Melanogrammus aeglefinus*) stocks on Georges Bank

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Otoliths are crystalline structures composed of calcium carbonate and are ideal structures for use in fish stock identification, containing a range of measurable characteristics including linear and shape morphometrics, optical density, and microstructural zonation and growth patterns, and elemental constituents (Ihssen et al., 1981; Campana and Neilson, 1985; Pawson and Jennings, 1996). Otoliths grow throughout the life of fish, are metabolically inert, and are typically available as a historical time series because of routine age and growth assessments (Campana and Neilson, 1985; Campana and Casselman, 1993).

Linear and shape morphometrics of otoliths have been widely used for fish stock identification (e.g. Messieh et al., 1989; Dawson, 1991; Smith, 1992; Campana and Casselman, 1993; Friedland and Reddin, 1994), although their use has been questioned because of within-stock differences in sex, age, and year-class variation (Castonguay et al., 1991; Begg and Brown, 2000). Moreover, otolith morphometrics have been found to be strongly correlated with growth, which influences development of otolith crystalline microstructure (Smith, 1992; Campana and Casselman, 1993). Stock definitions based on differences in otolith structure, therefore, depend not only on differential growth rates, but on the consistency of the environment integrated over the life history of fish in each stock (Campana and Cas-

selman, 1993). Although otolith morphometrics cannot be used to differentiate stocks on a genetic basis, they can provide a phenotypic basis for stock separation that is useful for fisheries management (Casselman et al., 1981; Begg and Waldman, 1999).

Fisheries management is moving towards a precautionary approach to ensure sustainable utilization of our marine resources (FAO, 1995; ICES¹). One requirement of the precautionary approach is to consider the full impact of management actions, including explicit consideration of stock complexity (Garcia and Grainger, 1997). For this reason, there is a growing interest in the importance and recognition of individual spawning components within historically established management units (FAO, 1995; Stephenson, 1999).

The importance of individual spawning components has been acknowledged in the management of haddock, *Melanogrammus aeglefinus*, a commercially important groundfish of the northwest Atlantic. The interest in haddock stock complexity is exemplified on Georges Bank (Fig. 1), where this species forms an important transboundary resource among U.S. and Canadian fishermen (Halliday and Pinhorn, 1990; Begg,

¹ ICES (International Council for the Exploration of the Sea). 1997. Report of the study group on the precautionary approach to fisheries management. ICES council meeting (CM) 1997/assess 7, 41 p.

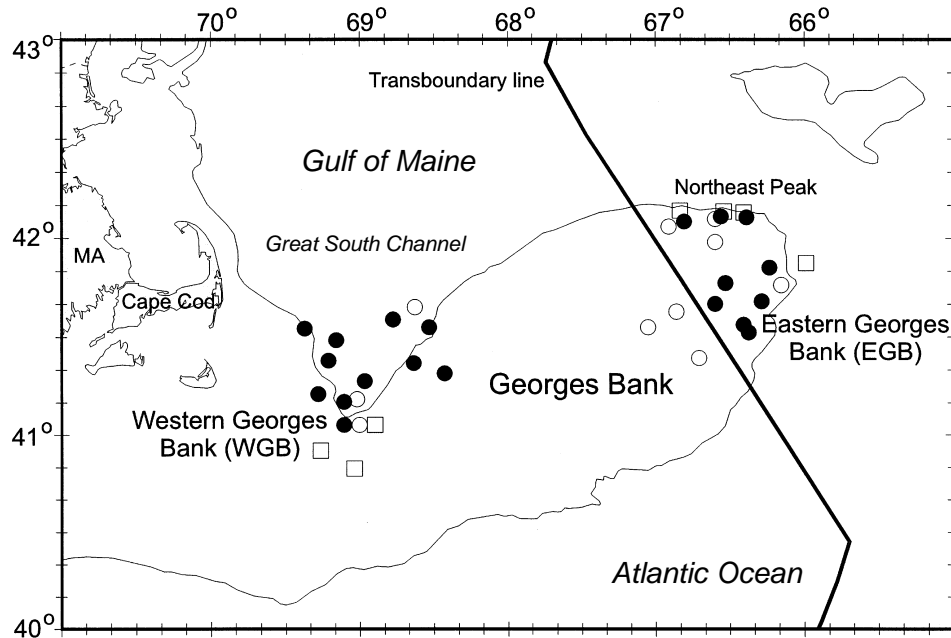


Figure 1

Northeast Fisheries Science Center stratified random survey stations from where eastern and western Georges Bank haddock samples were collected in 1995 (open squares), 1996 (open circles), and 1997 (closed circles) for stock identification based on internal otolith morphometrics.

1998). During 1935 to 1960, annual landings of haddock on Georges Bank averaged 46,000 metric tons (t), before increasing to 150,000 t in 1965 owing to exceptional recruitment from the 1962 and 1963 year classes and intense fishing resulting from the entrance of distant water fleets (Clark et al., 1982). However, following these record landings the resource collapsed, and annual landings declined to less than 5,000 t during the mid-1970s. The resource temporarily increased during the late 1970s and early 1980s when annual landings increased to 27,000 t owing to the large 1975 and 1978 year classes, before declining to a record low level of 2,300 t in 1995 (Brown, 1998).

Currently, the haddock resource on Georges Bank is in a depleted condition and is the focus of rebuilding plans by both the U.S. and Canadian fishery management agencies (Brown, 1998; Gavaris and Van Eeckhaute, 1998). The fact that each nation conducts separate analytical assessments, using different stock definitions for the resource, is problematic. The United States assesses Georges Bank haddock as a single stock, encompassing historical spawning components on the Northeast Peak (eastern Georges Bank) and the Great South Channel (western Georges Bank); whereas Canada assesses only the spawning component on the Northeast Peak (Brown, 1998; Gavaris and Van Eeckhaute, 1998) (Fig. 1). Since the mid-1980s, the majority of the haddock resource has been concentrated over eastern Georges Bank, where the majority of landings have been taken by the Canadian fishery (Brown, 1998). The changing resource status of haddock on Georges Bank has probably been due to greater depletion of the

western Georges Bank spawning component, which may now be contributing at a much lower level to the overall productivity of the resource (Van Eeckhaute et al., 1999). Stock rebuilding plans of both nations need to examine the identity versus the separateness, of spawning components on Georges Bank and develop uniform stock definitions for the resource.

Haddock stocks on Georges Bank have been examined by using a variety of techniques, although the results in terms of identification have been far from conclusive. Differences in distribution, life history, and otolith shape characteristics have indicated the existence of separate eastern and western Georges Bank spawning components (Smith and Morse, 1985; Gavaris and Van Eeckhaute, 1998; Begg et al., 1999; Begg and Brown, 2000). In contrast, tag-recapture, ichthyoplankton surveys, and genetic analyses have indicated some interchange of haddock across the Bank that may reflect a single spawning component (Needler, 1930; Schroeder, 1942; Morse et al., 1987; Purcell et al., 1996). Hence, there remains considerable uncertainty regarding the stock structure of haddock on Georges Bank.

The limitations associated with traditional stock identification techniques have been a major factor responsible for the remaining uncertainty regarding haddock stock structure on Georges Bank (Begg, 1998). Consequently, we used a new stock identification technique based on internal otolith morphometrics. We considered internal otolith morphometrics as a generic term describing the otolith microstructure of individual growth zones as well as the linear and shape dimensions of transverse otolith sec-

Table 1
Details of haddock samples used in analysis of internal otolith morphometrics for stock identification.

Region	Date captured	Age group (years)	Length range (cm)	<i>n</i>	
Eastern Georges Bank (EGB)	10–11 Apr 1995	1	21–28	7	
		2	31–37	10	
	21–23 Apr 1996	1	21–32	6	
		3	41–53	9	
		4	45–54	9	
		6–8 Apr 1997	2	38–45	18
	6–8 Apr 1997	3	40–47	10	
		4	41–58	16	
		5	49–62	10	
		Western Georges Bank (WGB)	13 Apr 1995	1	24–31
16–20 Apr 1996			2	31–47	9
	3		40–55	9	
	25 Mar–23 Apr 1997		2	36–44	17
25 Mar–23 Apr 1997	3		39–60	44	
	4	47–67	37		
	5	50–73	10		

tions. Although, linear morphometrics and shape analysis of “external” or whole otoliths have been used for fish stock identification, there has been little use of “internal” otolith morphometrics, probably because of the time, expense, and potential difficulties in obtaining consistent otolith sections. However, most fisheries agencies now use a standardized procedure for sectioning otoliths. These standardized procedures enable consistent and comparable otolith sections to be obtained, providing a consistent, rapid, and readily accessible structure that can be examined for stock identification.

We investigated the feasibility of using internal otolith morphometrics for fish stock identification, by considering Georges Bank haddock as a representative case study. For the purposes of our study, we considered a stock, or spawning component, as a semidiscrete, self-reproducing group of fish with definable morphometric characteristics that are assumed to be homogeneous for management purposes (Begg and Waldman, 1999). Variation in these characteristics is assumed to be evidence that distinct geographic regions are partially occupied throughout the life history of the fish, thereby providing a phenotypic basis for stock identification (Ihssen et al., 1981).

Materials and methods

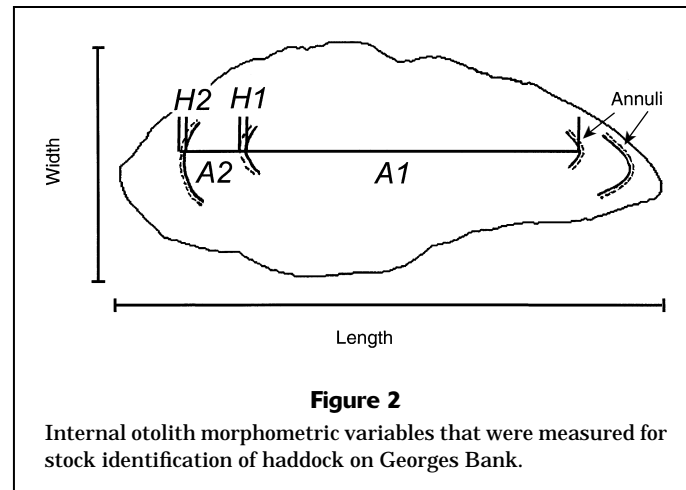
Sample collection

Haddock samples were collected in 1995, 1996, and 1997 during spring Northeast Fisheries Science Center (NEFSC) stratified random bottom trawl surveys, when the fish were assumed to be on or near their spawning

grounds. Most of the adults (ages 2+) sampled were in spawning condition. Samples were collected from survey stations throughout eastern (EGB) and western Georges Bank (WGB) (Fig. 1; Table 1). At sea, haddock samples were measured (fork length [FL], to the nearest cm), sex and maturity were determined by macroscopic examination of the gonads, and sagittal otolith pairs were removed from each sample. In the laboratory, one otolith from each pair was sectioned and assigned an age by following standard methods for northwest Atlantic species (Pentilla and Dery, 1988). Standardized sectioning procedures ensured consistent and comparable otolith sections for morphometric measurements and subsequent statistical analyses.

Internal otolith morphometrics

Internal otolith morphometrics were obtained from each otolith section by using the OPTIMAS™ (version 6.2) image analysis system (Media Cybernetics, 1996). All measurements were taken at a magnification of 15×. The perimeter of each otolith section was traced in a counter-clockwise direction to allow morphometrics to be calculated for each structure (shape). Six linear morphometrics (length, width, $A1$, $H1$, $A2$, and $H2$) were measured for each sample, where $A1$ is the growth increment to the first annulus, $H1$ is the width of the hyaline band of the first annulus, $A2$ is the growth increment to the second annulus, and $H2$ is the width of the hyaline band of the second annulus (Fig. 2). In addition, four shape variables (area, perimeter, circularity, and rectangularity) were measured for each sample. Circularity was defined as the perimeter of the otolith section squared divided by its area, and rectangularity was defined as the otolith section area divided



by the area of its enclosing rectangle oriented along the length of the section (Media Cybernetics, 1996).

Data analysis

Internal otolith morphometrics were compared between eastern and western Georges Bank haddock for stock identification. All variables were first examined for assumptions of normality and homoscedasticity and were subsequently \log_e -transformed prior to statistical analysis if these assumptions were not satisfied. Following transformation, all variables conformed to statistical assumptions. Analysis of covariance (ANCOVA) was then used to determine the effect of fish length on the magnitude of each variable. Those variables found to have significant interactions ($P < 0.05$) between sampling region and fish length (i.e. samples with unequal slopes) were excluded from further statistical analyses. In contrast, those variables found to have samples with equal slopes, but that significantly correlated with fish length, were corrected for fish length by using their respective common within-group slope (b) to standardize the samples.

Potential confounding sources of variation among samples, such as sex, age, and year-class differences, were examined and accounted for in the analyses before interpreting stock differences. Such confounding variables need to be examined to ensure interpretations of stock differences are real and not simply the result of sample variation (Castonguay et al., 1991; Begg and Brown, 2000). Consequently, multivariate analysis of variance (MANOVA) was used to examine differences between the sexes in their internal otolith structure, for samples from the same region and year class, and of the same age, by using the appropriate length-corrected internal otolith morphometric variables. One-way, fixed effects, unbalanced analysis of variance (ANOVA) was then used to examine individual variables to interpret any significant differences detected by the MANOVAs. Significance levels were corrected for multiple testing by using the Bonferroni adjustment factor (Sokal and Rohlf, 1995). The same tests were then used to examine the internal otolith structure of dif-

ferent-age fish (sampled from the same region and year), and fish originating from different year classes (same region and age). Tukey's honestly significant difference (HSD) tests were used for *a posteriori* comparisons for each significant variable. The same multi- and univariate tests were then used to examine the internal otolith structure of haddock sampled from eastern and western Georges Bank. These analyses were used to determine if there was any evidence for stock separation of haddock across the Bank.

Principal component (PC) analysis of the length-corrected internal otolith morphometric variables was conducted for samples of the same age and year class to provide an unbiased indication of separation between eastern and western Georges Bank haddock (i.e. there were no *a priori* assumptions of group membership). ANOVA was used on the significant principal components to examine differences in the PC scores between the proposed groups. Forward stepwise canonical discriminant analysis was then used to detect differences in the internal otolith structure of eastern and western Georges Bank haddock samples. The significant ($P < 0.05$) canonical variate (CV) derived by each analysis represented the optimal combination of morphometric variables that provided the best overall discrimination between the samples. ANOVA was used to examine differences in the CV scores. Jack-knifed cross-validation procedures were used to give unbiased estimates of classification success (SPSS, Inc., 1997).

Results

All the internal otolith morphometric variables, except for $A1$ and rectangularity, were \log_e -transformed prior to statistical analysis to correct for nonnormality and inequality of variances. ANCOVA indicated a significant correlation between fish length and region for otolith width (homogeneity of slopes test, $P < 0.0222$) (Table 2). Significant region-specific differences in the correlation between fish length and otolith width (i.e. regional differences in growth rate) made it necessary to remove otolith width as an analysis

Table 2

Internal otolith morphometric variables significantly correlated with fish length, and the corresponding regression coefficients (*b*) required to standardize the variables for fish length.

Otolith morphometric variable	Length × region			Length			<i>b</i>
	<i>F</i>	df	<i>P</i>	<i>F</i>	df	<i>P</i>	
<i>A1</i>	0.85	15,200	0.6195	1.70	1,215	0.1936	—
<i>H1</i>	1.27	13,183	0.2333	1.22	1,196	0.2713	—
<i>A2</i>	0.92	12,181	0.5274	2.36	1,193	0.1261	—
<i>H2</i>	1.19	12,155	0.2918	11.62	1,167	0.0008	0.01810
Length	1.16	15,200	0.3082	103.65	1,215	0.0001	0.00922
Width	1.93	15,200	0.0222	—	—	—	—
Area	1.53	15,200	0.0971	91.91	1,215	0.0001	0.01514
Perimeter	1.48	15,200	0.1165	88.05	1,215	0.0001	0.00837
Circularity	1.06	15,200	0.4007	2.92	1,215	0.0889	—
Rectangularity	1.63	15,200	0.0695	8.50	1,215	0.0039	-0.00092

Table 3

Results of MANOVA and ANOVA showing significant differences in the length-corrected internal otolith morphometric variables between age groups for eastern (EGB) and western Georges Bank (WGB) haddock.

Region	Year	Age group comparison (years)	MANOVA			Significant variable	ANOVA		
			<i>F</i>	df	<i>P</i>		<i>F</i>	df	<i>P</i>
EGB	1995	1 vs. 2	15.51	6,10	0.0002	length	19.16	1,15	0.0005
						area	28.70	1,15	0.0001
						perimeter	12.39	1,15	0.0031
	1996	1,3 vs. 4	3.98	12,34	0.0007	length	32.79	2,21	0.0001
						area	127.78	2,21	0.0001
						perimeter	23.13	2,21	0.0001
						circularity	6.93	2,21	0.0049
	1997	2,3,4 vs. 5	4.05	24,135	0.0001	<i>A1</i>	6.87	3,50	0.0006
						<i>H1</i>	4.75	3,50	0.0054
WGB	1996	2 vs. 3	4.71	8,9	0.0163	length	11.99	1,16	0.0032
						perimeter	9.19	1,16	0.0079
						area	7.71	3,50	0.0002
	1997	2,3,4 vs. 5	5.46	24,297	0.0001	length	10.81	3,104	0.0001
						circularity	7.46	3,104	0.0001
						rectangularity	4.96	3,104	0.0029

variable. The same ANCOVAs also indicated that *H2* and otolith length, area, perimeter, and rectangularity were correlated with fish length ($P < 0.004$), resulting in those variables being corrected for fish length by using their respective within-group regression coefficient (Table 2).

Internal otolith morphometrics were not significantly different between the sexes (MANOVA, $P > 0.05$), resulting in the sexes being pooled within each region, year and age strata to increase the statistical power used in

subsequent analyses. In contrast, significant differences were found between the different age groups of haddock (Table 3). Not unexpectedly, haddock that were 1 and 2 years of age tended to have significantly smaller otoliths than haddock that were 3, 4, and 5 years of age (HSD, $P < 0.05$). Likewise, there were significant differences indicative of annual growth differences found in the internal otolith morphometrics of haddock sampled from different year classes (Table 4). Hence, the remaining

Table 4

Results of MANOVA and ANOVA showing significant differences in the length-corrected internal otolith morphometric variables between year classes for eastern (EGB) and western Georges Bank (WGB) haddock.

Region	Age (yr)	Year-class comparison (yr)	MANOVA			Significant variable	ANOVA		
			<i>F</i>	df	<i>P</i>		<i>F</i>	df	<i>P</i>
EGB	1	1994 vs. 1995	1.23	6, 6	0.4034	—	—	—	—
	2	1993 vs. 1995	7.82	8, 18	0.0002	—	—	—	—
	3	1993 vs. 1994	2.22	9, 9	0.1255	<i>H2</i>	11.83	1, 17	0.0031
	4	1992 vs. 1993	1.90	9, 15	0.1309	perimeter circularity	11.57 9.14	1, 23 1, 23	0.0025 0.0060
WGB	2	1994 vs. 1995	1.76	8, 17	0.1549	—	—	—	—
	3	1993 vs. 1994	3.55	9, 43	0.0023	<i>H1</i>	15.59	1, 51	0.0002

Table 5

Results of MANOVA and ANOVA showing significant differences in the length-corrected internal otolith morphometric variables between haddock from eastern and western Georges Bank.

Year	Age (yr)	MANOVA			Significant variable	ANOVA		
		<i>F</i>	df	<i>P</i>		<i>F</i>	df	<i>P</i>
1995	1	1.60	6, 11	0.2357	rectangularity	5.76	1, 16	0.0289
1996	3	1.18	9, 8	0.4109	—	—	—	—
1997	2	2.10	8, 26	0.0726	circularity	10.37	1, 33	0.0029
	3	4.30	9, 44	0.0005	<i>A1</i>	22.76	1, 52	0.0001
					<i>A2</i>	7.84	1, 52	0.0072
					<i>H2</i>	7.41	1, 52	0.0088
	4	3.22	9, 43	0.0045	<i>A2</i>	3.97	1, 51	0.0518
	5	5.53	9, 10	0.0067	<i>A1</i> <i>H2</i>	9.70 9.90	1, 18 1, 18	0.0060 0.0056

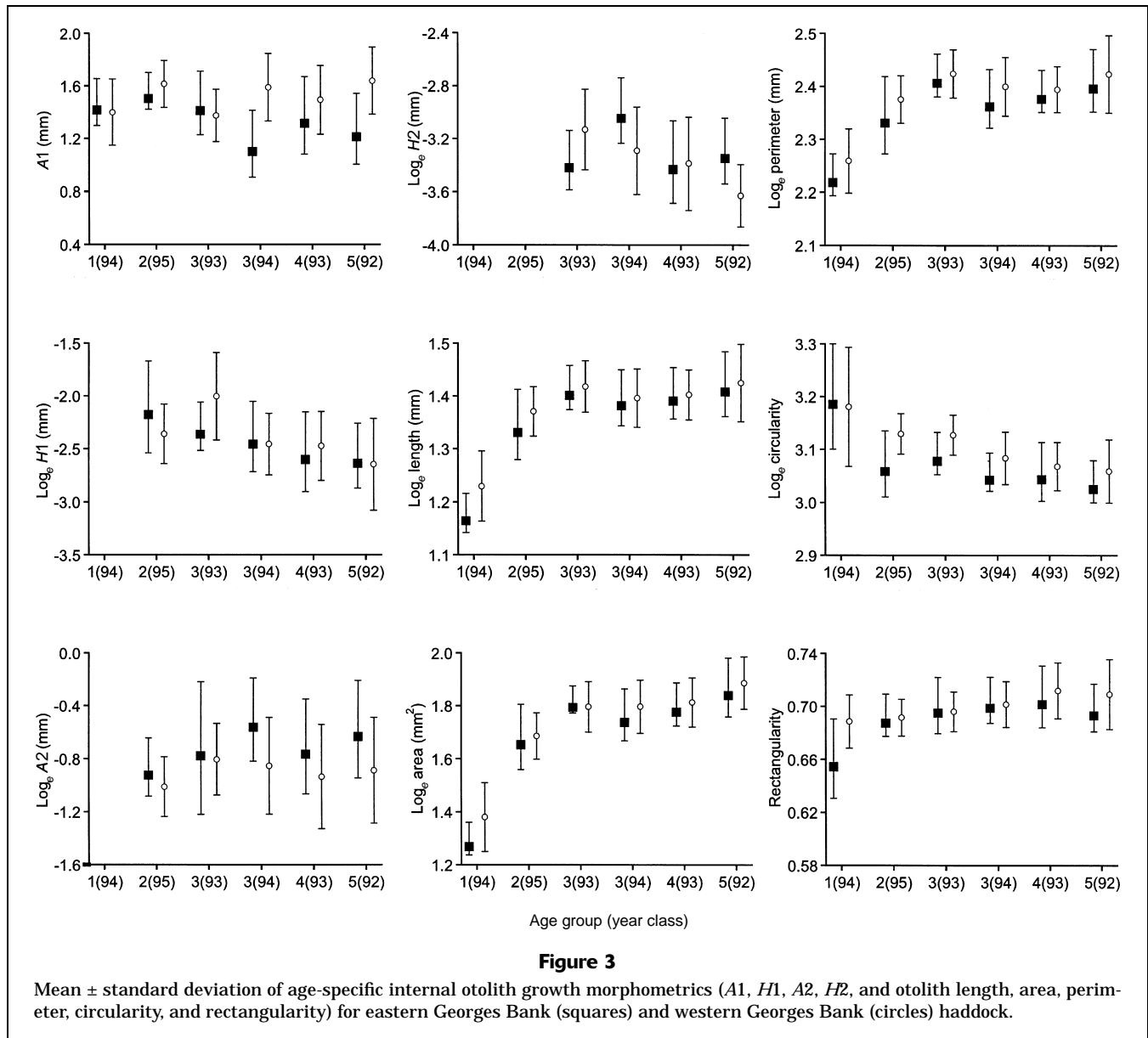
analyses were conducted for samples of individual ages and year classes in order to minimize the effects of these confounding variables.

Significant differences in the internal otolith morphometrics between haddock sampled on eastern and western Georges Bank were found in three out of six comparisons (Table 5). Eastern Georges Bank haddock tended to have smaller otoliths (i.e. length, area, perimeter, circularity and rectangularity) than western Georges Bank haddock; this finding was derived mainly from the first growth increment (*A1*) which also tended to be smaller (Fig. 3). For the three significant comparisons, scatter plots of the most significant individual internal otolith morphometrics for samples from each age group typically showed separation patterns between eastern and western Georges Bank haddock, albeit with some overlap (Figs. 4–6).

Principal component analysis provided further support that haddock from eastern and western Georges Bank separated into two groups (Fig. 7). Eastern and western

Georges Bank haddock samples, 1 and 3 (1994 year class) years of age were mainly separated on the first principal component (PC I) (ANOVA, $P < 0.06$), whereas samples that were 2, 3 (1993 year class), and 5 years of age were mainly separated on the second and third principal components (PC II and PC III) (ANOVA, $P < 0.05$). Principal components I, II, and III accounted on average for $38.7 \pm 5.3\%$ SD, $22.6 \pm 5.9\%$, and $15.6 \pm 0.7\%$ of the total variation in the data. Differences in length, area, and perimeter were mainly responsible for the observed separations along the first principal component, whereas *A1*, *H1* and *A2* were the main variables responsible for separation along the second and third principal components.

Discriminant analysis also indicated that haddock comprise two groups on Georges Bank (Fig. 8). Significant differences in the discriminant (CV I) scores between eastern and western Georges Bank haddock were found for all age groups (ANOVA, $P < 0.05$), except age group 4. Total classification success varied from 61% to 83% for the different age and year-class combinations (Table 6).



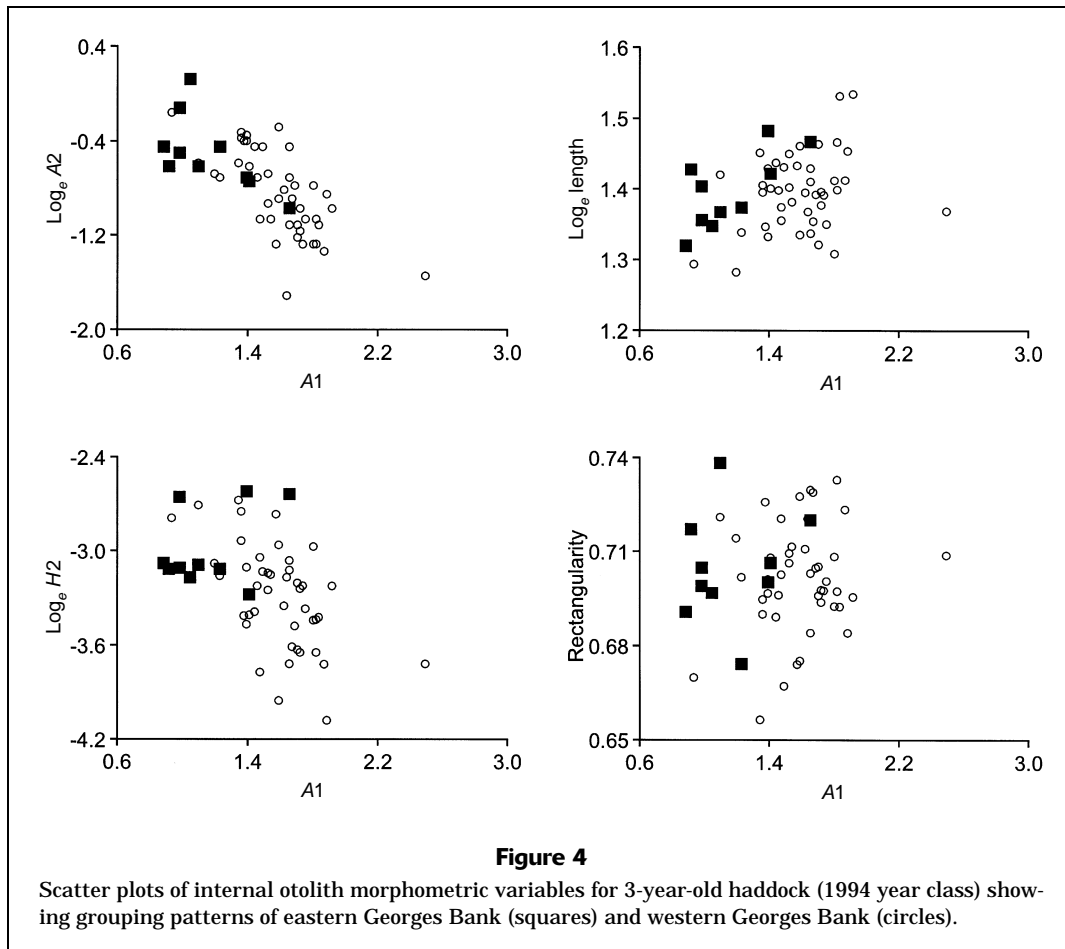
Discussion

We found significant differences in the internal otolith structure between eastern and western Georges Bank haddock in three out of six comparisons; providing a phenotypic basis for stock separation across the Bank. Of the three nonsignificant comparisons, two were influenced by low sample sizes ($n=18$), whereas the third was marginally nonsignificant ($P>0.07$) (Table 6). Eastern Georges Bank haddock tended to have smaller internal otolith morphometrics than western Georges Bank haddock, particularly during the first year of life when growth differences between progeny from the two spawning components may be most apparent.

Differences in the internal otolith structure of eastern and western Georges Bank haddock corresponded with ap-

parent differences in their growth rates. Commercial landings data indicated smaller mean lengths and weights at age for eastern than for western Georges Bank haddock, indicative of slower growth rates (and resultant smaller otoliths) for eastern Georges Bank haddock (Brown²). Likewise, other studies have found significant relationships between linear and shape otolith morphometrics and fish growth (e.g., Mosegaard et al., 1988; Reznick et al., 1989; Secor and Dean, 1989; Smith and Kostlan, 1991; Fowler and Short, 1996). Consequently, regional differences in growth rate may be a principal determinant in

² Brown, R. W. 2000. Annual assessment data (unpubl. data). Food Web Dynamics Program, Population Dynamics Branch, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.

**Table 6**

Age- and year-class-specific jack-knifed cross-validation classification matrices of the frequency of assigned haddock samples from eastern (EGB) and western Georges Bank (WGB).

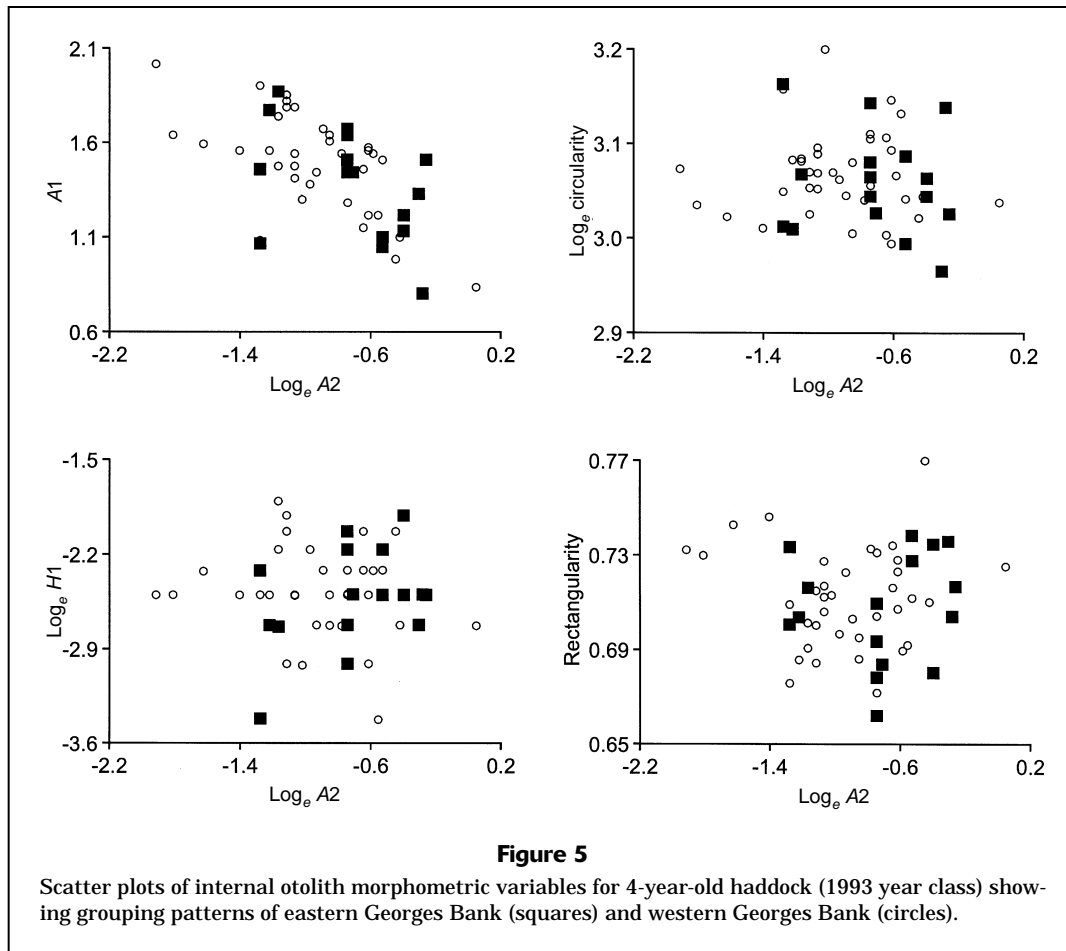
	Correct classification (%) of haddock samples by age group (year class)					
	Age 1 (1994)	Age 2 (1995)	Age 3 (1993)	Age 3 (1994)	Age 4 (1993)	Age 5 (1992)
<i>n</i>	18	35	18	54	53	20
EGB	71	72	67	80	75	80
WGB	64	88	56	84	59	70
Total	67	80	61	83	64	75

the development of regional differences in otolith morphometrics (Smith, 1992; Campana and Casselman, 1993). Growth (i.e. metabolic activity) alters the rate of otolith crystalline growth, which determines the size and shape of individual crystals, and ultimately the size and shape of individual otoliths (Gauldie, 1990). Differences in oto-

lith shape may be mediated through differences in orientation and packing of otolith crystals that are influenced by rate of crystalline growth (Smith, 1992). Fast growth tends to form long thin crystals, in contrast to slow growth which forms short compacted crystals (Gauldie and Nelson, 1990).

Differences in growth rates (and hence, otolith structure) of eastern and western Georges Bank haddock appear to derive mainly from differences in water temperature and diet. Eastern Georges Bank haddock are affected more by colder Scotian Shelf waters than western Georges Bank haddock, which are affected more by warmer Gulf of Maine waters (Drinkwater and Mountain, 1997). Furthermore, eastern Georges Bank haddock appear to have less available food and have a diet that is less rich in protein (Garrison³). Hence, the colder waters and poorer diets experienced by eastern Georges Bank haddock correspond to slower growth rates. Moreover, this correspondence suggests that environmental factors are major determinants of otolith growth as has been inferred in other

³ Garrison, L. P. 2000. Unpubl. data. Food Web Dynamics Program, Population Biology Branch, Northeast Fisheries Science Center, 166 Water St., Woods Hole, MA 02543.



studies (Campana and Neilson, 1985; Mosegaard et al., 1988; Campana and Casselman, 1993), although there may also be a genetic contribution (Gauldie and Nelson, 1990; Friedland and Reddin, 1994).

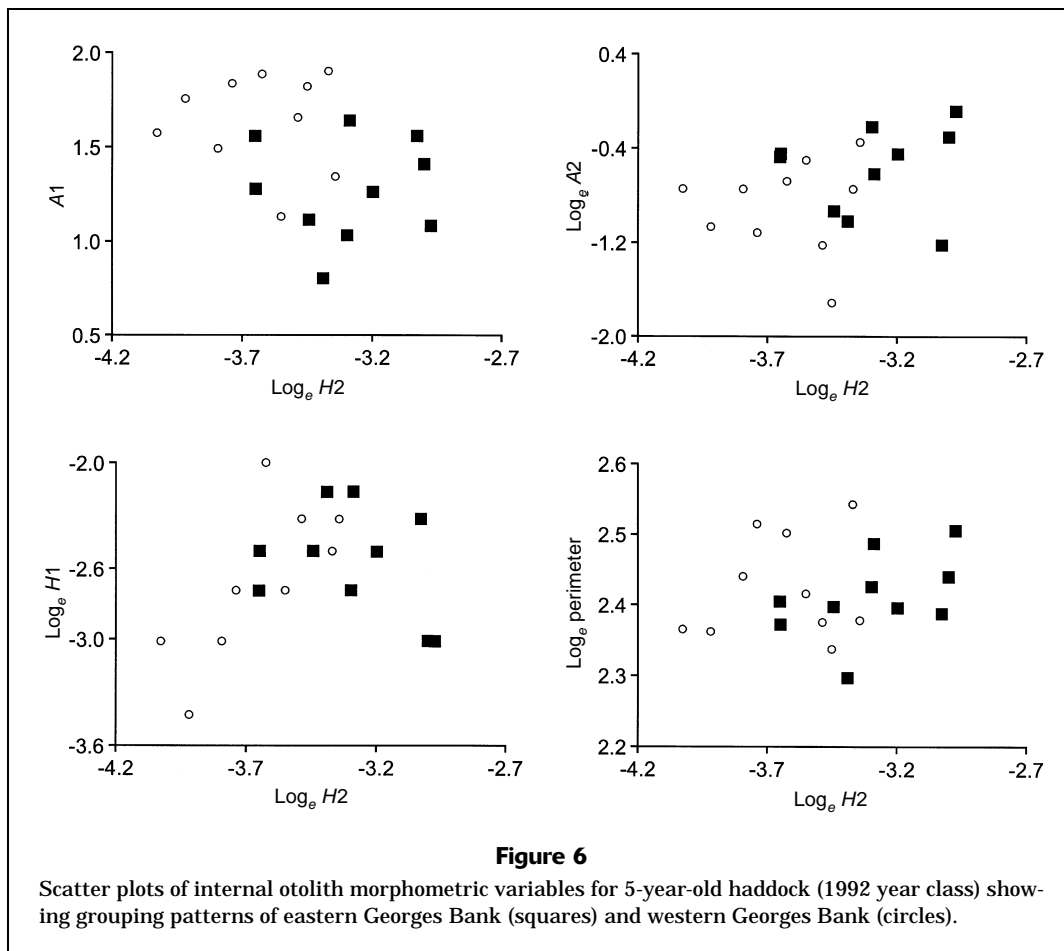
The eastern and western Georges Bank spawning components, therefore, probably comprise phenotypically separate individuals that reflect differences in otolith structure due to environmental variation. These types of morphological differences indicate growth rate differences linked to the environment, rather than any genetic differences. Our results concur with previous studies that indicate separate spawning components on Georges Bank (Smith and Morse, 1985; Begg et al., 1999; Begg and Brown, 2000), although the degree of connectivity between the two components is not known. Larvae spawned on the Northeast Peak recruit to the central part of the Bank as they develop and are advected from there along its southern flank (Lough and Bolz 1989), whereas some larvae spawned throughout the Great South Channel are advected along the northern flank, with the result that there is some mixing between progeny. Further studies need to examine mixing rates and spawning-site fidelity of individual fish originating from the eastern and western Georges Bank spawning components in order to determine if there is an underlying genetic basis for stock separation.

Analysis of internal otolith morphometrics may provide a more detailed description of individual fish stocks than morphometric analysis of whole otoliths because the use of internal otolith morphometrics specifically incorporates individual growth zones, as well as characteristic shape qualifiers. Measurement of the first growth zone in whole otoliths has commonly been used in stock identification studies, although the results have been far from conclusive (e.g. Dawson, 1991; Hopkins⁴; Marecos⁵). Likewise, mixed results have been found for microstructure analysis of otolith nuclear dimensions and growth incremental widths (e.g. Rybock et al., 1975; Neilson et al., 1985; Mosegaard and Madsen⁶). Certainly, the use of more than one growth or shape dimension improved our ability to identify groups, but the utility or cost-effectiveness of internal otolith morphometrics may be questioned when compared to shape analysis of whole otoliths.

⁴ Hopkins, P. J. 1986. Mackerel stock discrimination using otolith morphometrics. ICES CM 1986/H 7, 16 p.

⁵ Marecos, M. L. 1986. Preliminary analysis of horse mackerel (*Trachurus trachurus* L.) otolith (L1) measurements. ICES CM 1986/H 72, 8 p.

⁶ Mosegaard, H., and K. P. Madsen. 1996. Discrimination of mixed herring stocks in the North Sea using vertebral counts and otolith microstructure. ICES CM 1996/H 17, 8 p.

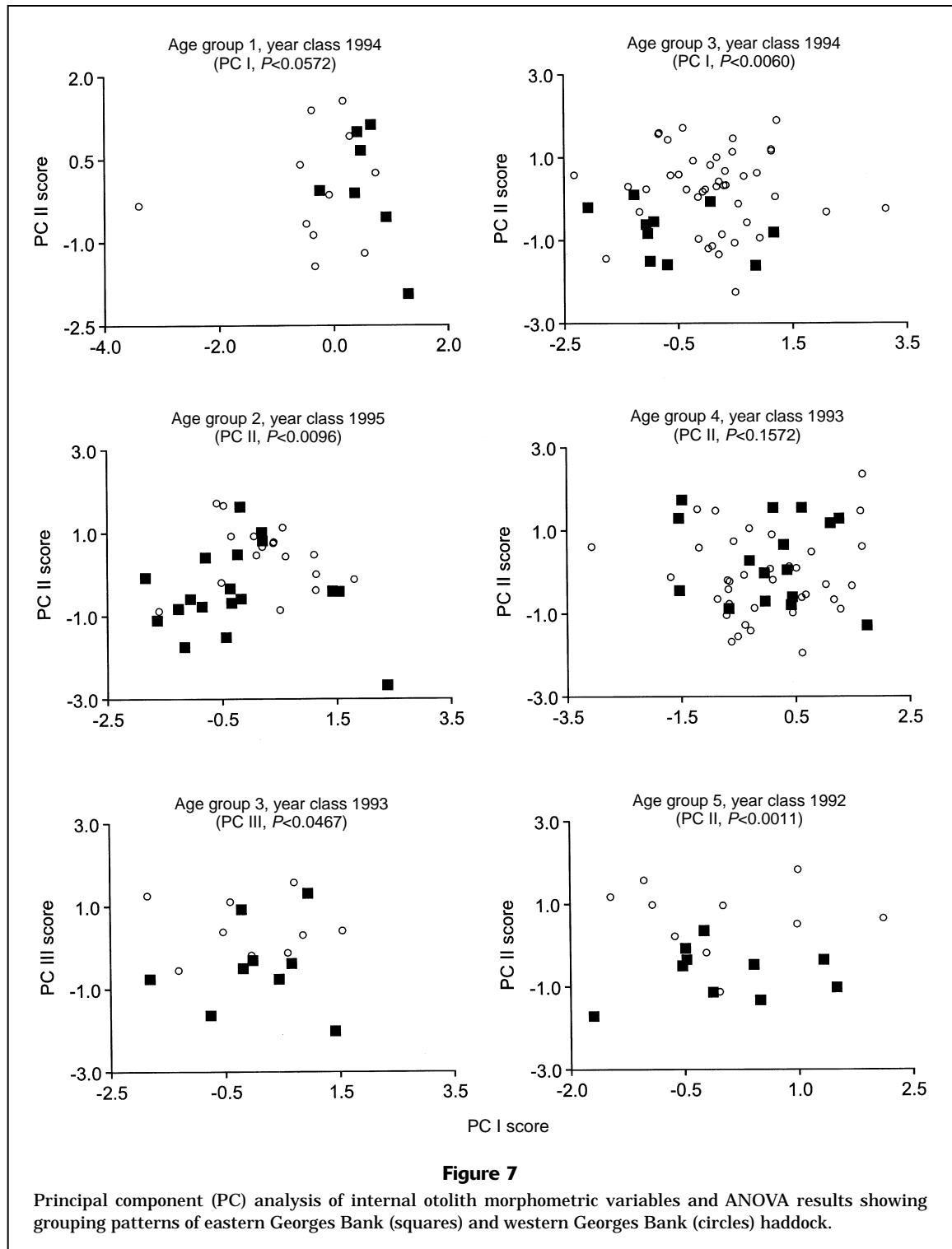


Classification success similar to our present study was found between eastern and western Georges Bank haddock in a comparable study where whole-otolith shape analysis was used (Begg and Brown, 2000). However, the use of internal otolith morphometrics entailed a few more caveats than that of whole-otolith shape analysis; therefore internal otolith morphometrics was questioned as a preferred tool for stock identification. Although our approach was semi-automated, with an aim to increasing objectivity and decreasing processing time, the use of internal otolith morphometrics still required some interpretation by the person taking the measurements. This was particularly true for growth zones, where interpretation partly compromised our goals of increasing objectivity and speed. Difficulties in interpreting measurements when growth zones are poorly defined can also be a source of uncertainty (Hopkins⁴). These sources of uncertainty should be minimized, provided the person taking the measurements is also an experienced reader of otolith growth increments.

Internal otolith morphometrics are useful for stock *identification*, but significant overlap among variables may preclude their use for stock *discrimination*, that is to say for classifying unknown fish according to origin of spawning component. Although mean values may differ

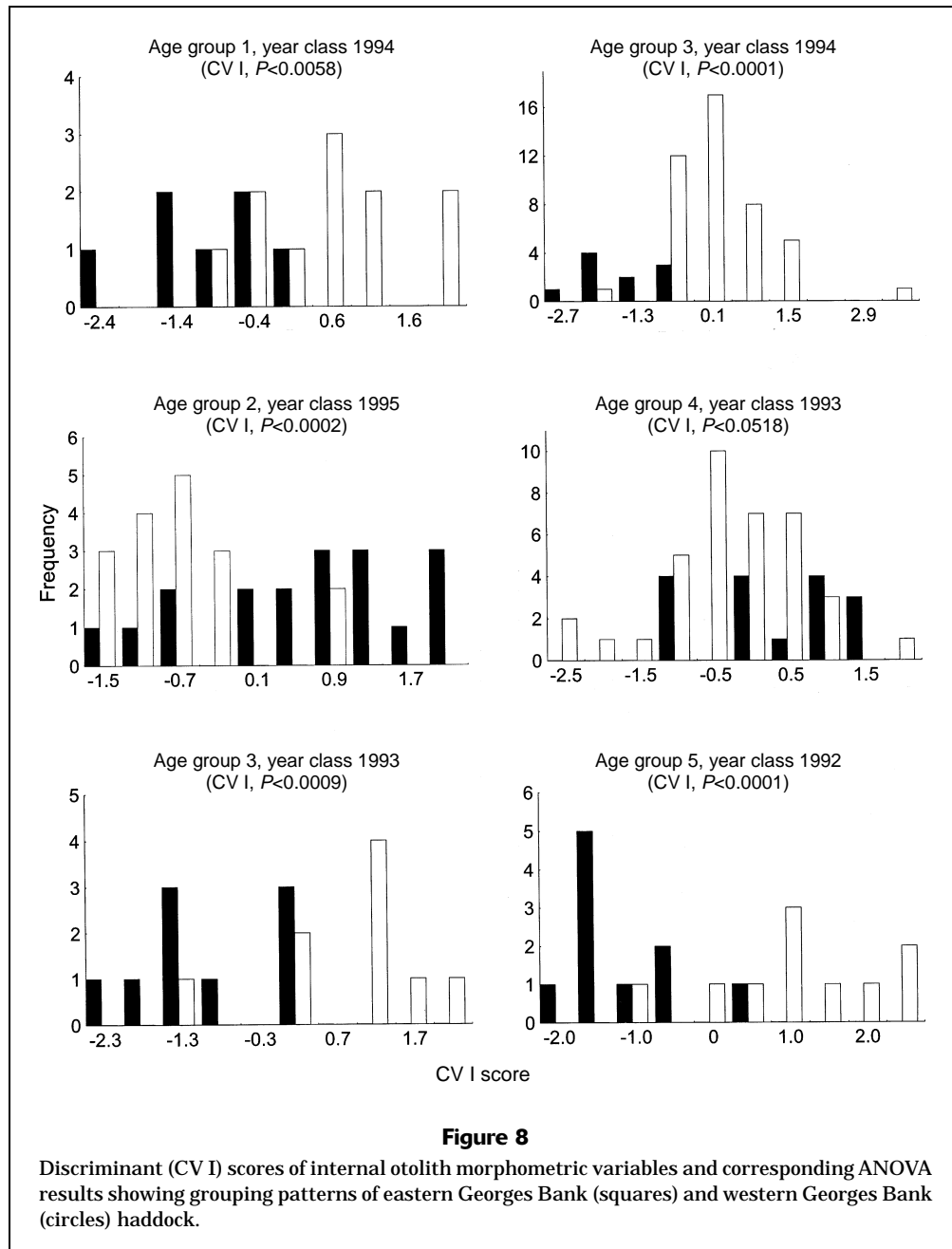
between stocks, measurements from individual fish may not allow them to be classified to a particular stock because of individual within-stock growth differences (Pawson and Jennings, 1996). For example, slow-growing fish from a fast-growing stock may be incorrectly classified with a slow-growing stock (Campana and Casselman, 1993). However, provided growth differences exist and analyses are conducted to account for samples of mixed ages and year classes to minimize the effects of these confounding variables, internal otolith morphometrics can be a useful phenotype-based stock identification tool.

Results from this analysis on internal otolith morphometric differences have added to the evidence indicating separation between the eastern and western Georges Bank haddock spawning components. Although these differences do not provide a genetic basis for separation between the two spawning components, they do reflect the phenotypic characteristics of each spawning component, indicative of stock separation during life history. Studies such as this one, are needed to provide evidence of stock structure if historically established management units are to be changed in response to changing exploitation and resource patterns. Evidence of stock separation within the Georges Bank haddock resource may be useful in forming stock definitions that can be used by both the U.S. and Canada in defining



management units that are consistent and account for the underlying stock structure of the resource. An incorrect decision could lead to significant shifts in resource distribution, changes in stock productivity, or declines in recruitment across stock unit boundaries. Although the precautionary approach would imply that we accept the two

stock hypothesis as the default scenario until proven otherwise, this has not been the case. It would be desirable to ensure the conservation and stock rebuilding potential of both spawning components, particularly because we do not know at present the relative contribution of each to the overall status of haddock on Georges Bank.



Acknowledgments

We would like to thank Russell Brown, Steve Murawski, Kevin Friedland, and two anonymous reviewers for their comments; Ruth Haas-Castro for assistance with OPTIMAS; and Frank Almeida, George Bolz, Jay Burnett, and Christine Esteves for their suggestions and assistance with ageing and collection of samples. This work was performed while G.A.B. held a National Research Council (NOAA/NMFS/NEFSC) Research Associateship.

Literature cited

- Begg, G. A.
1998. A review of stock identification of haddock, *Melanogrammus aeglefinus*, in the northwest Atlantic Ocean. *Mar. Fish. Rev.* 60(4):1-15.
- Begg, G. A., and R. W. Brown.
2000. Stock identification of haddock *Melanogrammus aeglefinus* on Georges Bank based on otolith shape analysis. *Trans. Am. Fish. Soc.* 129:935-945.

- Begg, G. A., J. A. Hare, and D. D. Sheehan.
1999. The role of life history parameters as indicators of stock structure. *Fish. Res.* 43:141–163.
- Begg, G. A., and J. R. Waldman.
1999. An holistic approach to fish stock identification. *Fish. Res.* 43:35–44.
- Brown, R. W.
1998. Haddock. *In* Status of the fishery resources off the northeastern United States for 1998, p. 53–56. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-NE-115.
- Campana, S. E., and J. M. Casselman.
1993. Stock discrimination using otolith shape analysis. *Can. J. Fish. Aquat. Sci.* 50: 1062–1083.
- Campana, S. E., and J. D. Neilson.
1985. Microstructure of fish otoliths. *Can. J. Fish. Aquat. Sci.* 42:1014–1032.
- Casselman, J. M., J. J. Collins, E. J. Crossman, P. E. Ihssen, and G. R. Spangler.
1981. Lake whitefish (*Coregonus clupeaformis*) in the Great Lakes region. *Can. J. Fish. Aquat. Sci.* 38:1772–1789.
- Castonguay, M., P. Simard, and P. Gagnon.
1991. Usefulness of fourier analysis of otolith shape for Atlantic mackerel (*Scomber scombrus*) stock discrimination. *Can. J. Fish. Aquat. Sci.* 48:296–302.
- Clark, S. H., W. J. Overholtz, and R. C. Hennemuth.
1982. Review and assessment of the Georges Bank and Gulf of Maine haddock fishery. *J. Northwest Atl. Fish. Sci.* 3:1–27.
- Dawson, W. A.
1991. Otolith measurement as a method of identifying factors affecting first-year growth and stock separation of mackerel (*Scomber scombrus* L.). *J. Cons. Int. Explor. Mer* 47:303–317.
- Drinkwater, K. F., and D. G. Mountain.
1997. Climate and oceanography. *In* Northwest Atlantic groundfish: perspectives on a fishery collapse (J. Boreman, B. S. Nakashima, J. A. Wilson and R. L. Kendall, eds.), p. 3–25. Am. Fish. Soc., Bethesda, MD.
- FAO (Food and Agriculture Organization of the United Nations).
1995. Code of conduct for responsible fisheries. FAO, Rome, 41 p.
- Fowler, A. J., and D. A. Short.
1996. Temporal variation in the early life-history characteristics of the king george whiting (*Sillaginodes punctata*) from analysis of otolith microstructure. *Mar. Freshwater Res.* 47:809–18.
- Friedland, K. D., and D. G. Reddin.
1994. Use of otolith morphology in stock discriminations of Atlantic salmon (*Salmo salar*). *Can. J. Fish. Aquat. Sci.* 51:91–98.
- Garcia, S. M., and R. Grainger.
1997. Fisheries management and sustainability: a new perspective of an old problem? *In* Developing and sustaining world fisheries resources: the state of science and management: second world fisheries congress proceedings (D. A. Hancock, D. C. Smith, A. Grant, and J. P. Beumer, eds.), p. 631–654. CSIRO Publishing, Collingwood, Australia.
- Gauldie, R. W.
1990. A measure of metabolism in fish otoliths. *Comp. Biochem. Physiol.* 97A:475–480.
- Gauldie, R. W., and D. G. A. Nelson.
1990. Otolith growth in fishes. *Comp. Biochem. Physiol.* 97A:119–135.
- Gavaris, S., and L. Van Eeckhaute.
1998. Assessment of haddock on eastern Georges Bank. *Can. Dep. Fish. Oceans, DFO Atl. Fish. Res. Doc.* 98/66, 75 p.
- Halliday, R. G., and A. T. Pinhorn.
1990. The delimitation of fishing areas in the northwest Atlantic. *J. Northwest Atl. Fish. Sci.* 10:1–51.
- Ihssen, P. E., H. E. Booke, J. M. Casselman, J. M., McGlade, N. R. Payne, and F. M. Utter.
1981. Stock identification: materials and methods. *Can. J. Fish. Aquat. Sci.* 38:1838–1855.
- Lough, R. G., and G. R. Bolz.
1989. The movement of cod and haddock larvae onto the shoals of Georges Bank. *J. Fish Biol.* 35 (suppl. A):71–79.
- Media Cybernetics
1996. OPTIMAS, version 6.2, eighth ed. Media Cybernetics, Silver Spring, Maryland, vol. I: xiii + 474 p., vol. II: viii + 630 p.
- Messieh, S. N., C. MacDougall, and R. Claytor.
1989. Separation of Atlantic herring (*Clupea harengus*) stocks in the Gulf of St. Lawrence using digitized otolith morphometrics and discriminant function analysis. *Can. Tech. Rep. Fish. Aquat. Sci.* 1647, 22 p.
- Morse, W. W., M. P. Fahay, and W. G. Smith.
1987. MARMAP surveys of the continental shelf from Cape Hatteras, North Carolina, to Cape Sable, Nova Scotia (1977–1984). Atlas 2: annual distribution patterns of fish larvae. U.S. Dep. Commer., NOAA Tech. Memo. NMFS-S/NEC 47, 215 p.
- Mosegaard, H., H. Svedang, and K. Taberman.
1988. Uncoupling of somatic and otolith growth rates in Arctic char (*Salvelinus alpinus*) as an effect of differences in temperature response. *Can. J. Fish. Aquat. Sci.* 45:1514–1524.
- Needler, A. W. H.
1930. The migrations of haddock and the interrelationships of haddock populations in North American waters. *Contrib. Can. Biol.* 6:241–313.
- Neilson, J. D., G. H. Green, and B. Chan.
1985. Variability in dimensions of salmonid otolith nuclei: implications for stock identification and microstructure interpretation. *Fish. Bull.* 83:81–89.
- Pawson, M. G., and S. Jennings.
1996. A critique of methods for stock identification in marine capture fisheries. *Fish. Res.* 25:203–217.
- Pentilla, J., and L. M. Dery.
1988. Age determination methods for Northwest Atlantic species. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 72:37–40.
- Purcell, M. K., I. Kornfield, M. Fogarty, and A. Parker.
1996. Interdecadal heterogeneity in mitochondrial DNA of Atlantic haddock (*Melanogrammus aeglefinus*) from Georges Bank. *Molecular Mar. Biol. Biotech.* 5:185–192.
- Reznick, D., E. Lindbeck, and H. Bryga.
1989. Slower growth results in larger otoliths: an experimental test with guppies (*Poecilia reticulata*). *Can. J. Fish. Aquat. Sci.* 46:108–12.
- Rybock, J. T., H. F. Horton, and J. L. Fessler.
1975. Use of otoliths to separate juvenile steelhead trout from juvenile rainbow trout. *Fish. Bull.* 73:654–659.
- Schroeder, W. C.
1942. Results of haddock tagging in the Gulf of Maine from 1923 to 1932. *J. Mar. Res.* 5:1–19.
- Secor, D. H., and J. M. Dean.
1989. Somatic growth effects on the otolith-fish size relationship in young pond-reared striped bass, *Morone saxatilis*. *Can. J. Fish. Aquat. Sci.* 46:113–121.
- Smith, M. K.
1992. Regional differences in otolith morphology of the deep

- slope red snapper *Etelis carbunculus*. *Can. J. Fish. Aquat. Sci.* 49:795–804.
- Smith, M. K., and E. Kostlan.
1991. Estimates of age and growth of ehu *Etelis carbunculus* in four regions of the Pacific from density of daily increments in otoliths. *Fish. Bull.* 89:461–472.
- Smith, W. G., and W. W. Morse.
1985. Retention of larval haddock *Melanogrammus aeglefinus* in the Georges Bank region, a gyre-influenced spawning area. *Mar. Ecol. Prog. Ser.* 24:1–13.
- Sokal, R. R., and F. J. Rohlf.
1995. *Biometry*, third ed. Freeman and Company, New York, NY, 887 p.
- SPSS, Inc.
1997. *SYSTAT 7.0 statistics*. SPSS Incorporated, Chicago, IL, 751 p.
- Stephenson, R. L.
1999. Stock complexity in fisheries management: a perspective of emerging issues related to population sub-units. *Fish. Res.* 43:247–249.
- Van Eeckhaute, L. A. M., S. Gavaris, and E. A. Trippel.
1999. Movements of haddock, *Melanogrammus aeglefinus*, on eastern Georges Bank determined from a population model incorporating temporal and spatial detail. *Fish. Bull.* 97:661–679.