

Abstract.—This study compared the hatching season and the actual spawning season of spring- and autumn-spawning herring in the northern Gulf of St. Lawrence as determined by otolith characteristics and maturity stages, respectively, to measure the crossover between the two spawning populations. The growth characteristics of two cohorts that showed significant crossover were contrasted with those of a cohort that did not. It was concluded that variable juvenile growth does influence the adoption of the season of first spawning in these populations, and therefore the progeny of a given seasonal-spawning population may recruit to a local population that has a different reproductive season. It was also shown that the twinning of year-class strength can be explained by the crossover of a large number of individuals from one seasonal spawning population to another. The data presented indicate that the spawning season that is established at the time of first maturation is maintained for the remainder of adult life. The present study therefore does not support the concept of discrete sympatric seasonal-spawning populations in Atlantic herring.

Year-class twinning in sympatric seasonal spawning populations of Atlantic herring, *Clupea harengus*

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The current theory on Atlantic herring population structure, as it relates to sympatric spring- and autumn-spawning herring, considers them to be discrete populations with independent life histories (Iles and Sinclair, 1982). This concept has largely been based on evidence of significant homing precision to spawning grounds as revealed by tag returns (Hourston, 1982; Wheeler and Winters 1984, a and b; Stevenson et al.¹; Hart et al.²; Stobo³) and on studies that have noted significant differences in meristic and morphometric measurements, such as fin-ray counts and otolith characteristics (Messieh, 1972; Parsons, 1973; Postuma, 1974), as well as in life history parameters, such as mean fecundities (Baxter, 1959; Messieh, 1976).

However, several observations are difficult to explain within the discrete population concept: 1) typical spring-type otoliths are often found in autumn-spawning herring and vice versa (Messieh, 1972; Aneer, 1985); 2) "twinning" of recruitment strength between spring- and autumn-spawning year classes (see below); and 3) the lack of genetic divergence between seasonal spawning populations as demonstrated from numerous electrophoretic and mtDNA studies (Grant, 1984; Kornfield and Bogdanowicz, 1987; Safford and Booke, 1992). In light of the conflicting evidence for stock discreteness, an alternative

concept has been proposed whereby seasonal spawning populations are seen as subunits of a larger population, within which there exists a "dynamic balance" characterized by extensive gene flow (Smith and Jamieson, 1986).

Otolith characteristics and maturity stages have been used for many decades to determine the spawning affinity of individual herring from sympatric seasonal-spawning populations. Maturity stages are the preferred method for determining the actual spawning season of mature herring because the state of maturation can be used reliably to ascertain the spawning season throughout the year (McQuinn, 1989). On the other hand, otolith characteristics, being related mainly to environmental conditions at birth, are used to determine the hatching sea-

¹ Stevenson, J. C., A. S. Hourston, K. J. Jackson, and D. N. Outram. 1952. Results of the West Coast of Vancouver Island herring investigation, 1951–52. Report of the British Columbia Provincial Fisheries Department, Victoria, British Columbia, Canada, p. 57–87.

² Hart, J. L., A. L. Tester, and J. L. McHugh. 1941. The tagging of herring (*Clupea pallasii*) in British Columbia: insertions and recoveries during 1940–41. Report of the British Columbia Provincial Fisheries Department, Victoria, British Columbia, Canada, p. 47–74.

³ Stobo, W. T. 1982. Tagging studies on Scotian shelf herring. Northwest Atlantic Fisheries Organization (NAFO) Research SCR Document 82/IX/108. Ser. No. N617, 16 p. P.O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

son (Einarsson, 1951; Postuma and Zijlstra, 1958; Messieh, 1972). The comparison of hatching season with spawning season as determined by these two methods, respectively, thus provides us with a rare opportunity to study the reproductive interactions between sympatric seasonal-spawning herring populations.

As with most herring populations, herring from western Newfoundland (Canada) are characterized by the periodic appearance of very large year classes followed by several years of relatively poor recruitment. In addition, the sympatric seasonal-spawning populations in eastern Canadian waters often show year-class twinning (Winters et al., 1986; de Lafontaine et al., 1991). This phenomenon is most evident when a strong autumn-spawning year class of a given year coincides with a strong spring-spawning year class of the following year. Twinning is relatively common with seasonal-spawning populations but does not always occur. It is also true that year-class twinning rarely occurs between successive spring- and autumn-spawning year classes of the same year.

Winters et al. (1986) showed a weak, though significant, relationship between year-class strength (natural log scale) of autumn-spawning herring in eastern Newfoundland and that of spring spawners of the following year. An example where year-class twinning occurred in the western Newfoundland herring populations is with the 1979 autumn-spawning and 1980 spring-spawning year classes, both of which were very large (McQuinn and Lefebvre⁴). However, the 1982 spring-spawning year class was also very large but had no large autumn-spawning twin in 1981. Again we observed twinning with the 1986 and 1987 autumn- and spring-spawning year classes. What then are the characteristics that distinguish these year classes and that might explain why twinning occurred in 1979–80 and 1986–87, but not in 1981–82?

Year-class twinning was first reported in herring by Einarsson (1952), who termed it “year-class strength parallelism.” He speculated that favorable oceanographic and feeding conditions occurring from the fall of one year until the following summer resulted in a parallelism in larval survival between the two spawning populations. However, an alternative explanation is that year-class twinning is simply a consequence of straying between sympatric spring- and autumn-spawning populations, i.e. significant numbers of individuals from a large cohort of one

seasonal-spawning population subsequently spawn in the other season, creating a strong year class in both populations. Jean⁵ and Graham (1962) suggested that the determination of spawning season of sympatric herring populations may be influenced by juvenile growth rates. Winters et al. (1986) presented data in support of their hypothesis that faster-growing spring-spawned juveniles may become autumn-spawners and conversely that slow-growing autumn-spawned juveniles may spawn in the spring. The objective of the present study is to use the otolith characteristics and maturity stage methods to establish whether indeed juvenile growth rates (as represented by size at age) have an effect on the determination of the onset of first maturation and thus the establishment of spawning season in Atlantic herring.

Materials and methods

Data for this study were collected from the west coast of Newfoundland herring fishery from 1982 to 1990 (after 1990 otolith characteristics of mature herring were no longer determined by our agers). Samples were frozen and shipped to the Fisheries and Oceans laboratories for detailed analyses. Basic biological data (total length, total weight, gonad weight, and otolith characteristics, as well as the number of winter rings from which age was determined) were recorded for all specimens.

The hatching season was ascertained for each fish from otolith characteristics by applying the standard criteria (the size and type—opaque or hyaline—of the nucleus) developed by the Canadian Atlantic Fisheries Scientific Advisory Committee as described by Cleary et al.⁶ These criteria were developed from the rationale that rapid growth in the first summer of spring-spawned herring results in a small opaque otolith nucleus. Conversely, the slow first-winter growth of autumn-spawned herring results in a large hyaline otolith center and the first-winter ring is formed only in their second year (Jakobsson et al., 1969; Postuma, 1974). Although the assignment of hatching season is determined subjectively from these criteria, consistency between agers has been shown to be relatively high. A comparative study was

⁴ McQuinn, I. H., and L. Lefebvre. 1994. An assessment of the west coast of Newfoundland (NAFO division 4R) herring resource up to 1993. Department of Fisheries and Oceans (DFO) Res. Doc. 94/43, 48 p. Atlantic Stock Assessment Secretariat, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

⁵ Jean, Y. 1956. A study of the spring and fall spawning herring *Clupea harengus* L. at Grande-Rivière, Bay of Chaleur, Québec. Contribution 49 of the Department of Fisheries, Québec, Québec, Canada, 76 p.

⁶ Cleary, L., J. J. Hunt, J. Moores, and D. Tremblay. 1982. Herring aging workshop; St. John's, Newfoundland, March 1982. Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) Res. Doc. 82/41, 10 p. CAFSAC, Department of Fisheries and Oceans, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

conducted involving our ager and several other experienced otolith readers who used otoliths collected from throughout the Gulf of St. Lawrence (Savard and Simoneau⁷). This study showed a high agreement between two agers from our laboratory in Quebec (87%) and agers from the southern Gulf of St. Lawrence and eastern Newfoundland (75 and 76%, respectively) in the assignment of seasonal-spawning type from otoliths.

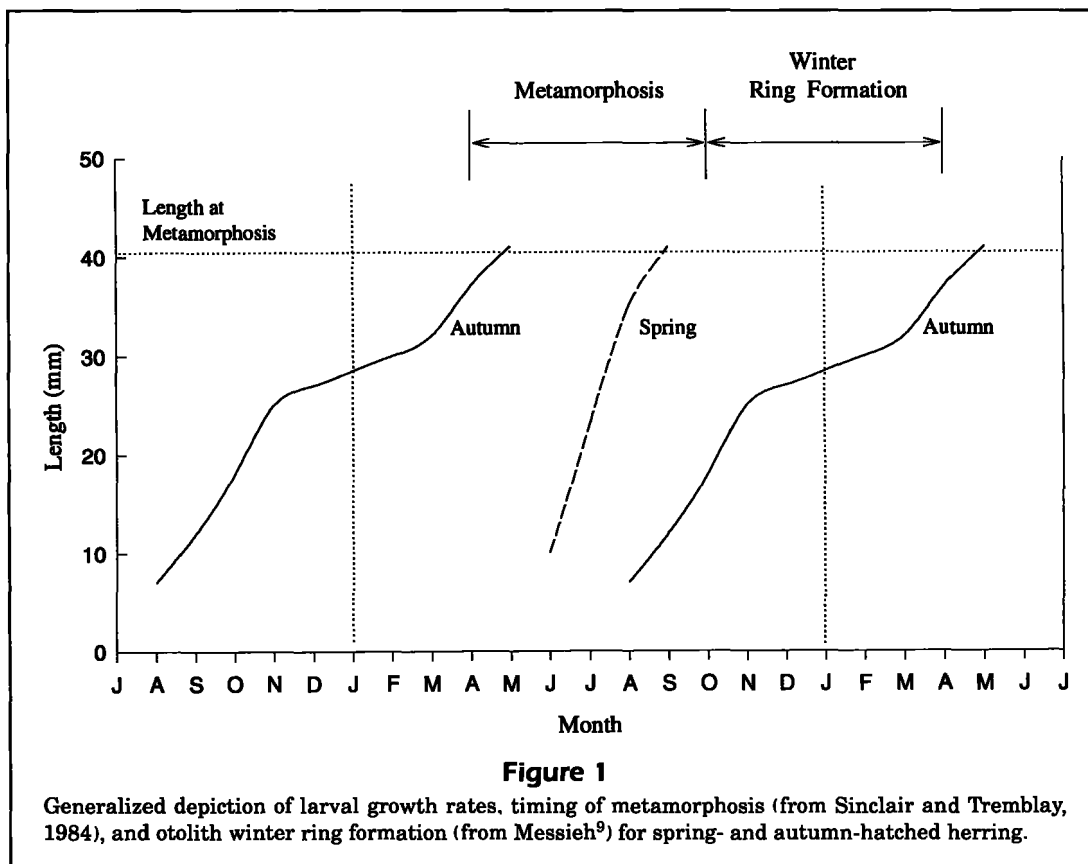
The actual spawning season of the mature individuals was determined from the stage of sexual maturity of each individual by using a temporal gonadosomatic index model (McQuinn, 1989). This model identifies the spawning season by first determining the maturity stage from the ratio of the gonad weight to a power function of the total length and by relating this state of maturation to the month of capture. Although spawning can occur from April

to October, the vast majority of spring herring spawn in May and June, whereas the autumn herring spawn mainly from mid-August to September (Haegele and Schweigert, 1985). The date separating the two spawning seasons was arbitrarily chosen to be 1 July, as relatively little spawning occurs in late June and early July (McQuinn, 1989; Cleary et al.⁶).

Throughout this paper, a distinction is made between the number of rings read from the otoliths and the actual age of the fish because age determination depends upon whether an individual is assigned as a spring spawner or an autumn spawner. Most autumn-spawning herring (August–November) do not produce a winter ring on the otolith in their first year of life (Einarsson, 1951; Jakobsson et al., 1969; Rosenberg and Palmen, 1982; Hunt et al.⁸). The formation of the winter ring takes place between October and April–May in metamorphosed juveniles

⁷ Savard, L., and M. Simoneau. 1983. Lecture comparative d'otolithes de hareng et utilisation des stades de maturité sexuelle pour l'attribution du groupe reproducteur. Canadian Atlantic Fisheries Scientific Advisory Committee (CAFSAC) Res. Doc. 83/86, 28 p. Department of Fisheries and Oceans, P.O. Box 1006, Dartmouth, Nova Scotia, Canada B2Y 4A2.

⁸ Hunt, J. J., L. S. Parsons, J. E. Watson, and G. H. Winters. 1973. Report of the herring ageing workshop; St. Andrews, New Brunswick, 11–13 December 1972. International Commission for the Northwest Atlantic Fisheries (ICNAF) Res. Doc. 73/2, Ser. 2901, 2 p. ICNAF, P.O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.



(Postuma, 1974; Messieh⁹), whereas newly hatched autumn spawners are still larvae (Fig. 1). Thus to assign correctly the age of a herring hatched in the autumn, one must add one year to the number of winter rings read from the otolith. Because spring-hatched herring metamorphose before their first winter and thus produce a winter ring in their first year, their proper age is equal to the number of winter rings. However, for any spring-hatched herring that subsequently reproduces in the autumn, its spawning season would be considered autumn with the maturity-stage method, and one year would be added to the number of rings read from the otolith. Following the same logic in reverse, if an autumn-hatched individual subsequently spawned in the spring, a year would not be added to the number of rings read from the otoliths and it would be assigned an age that was one year younger than its actual age. Therefore, the number of rings will be used when compar-

ing the biological characteristics for a given age between an autumn-spawning year class with the spring-spawning year class of the following year.

Results

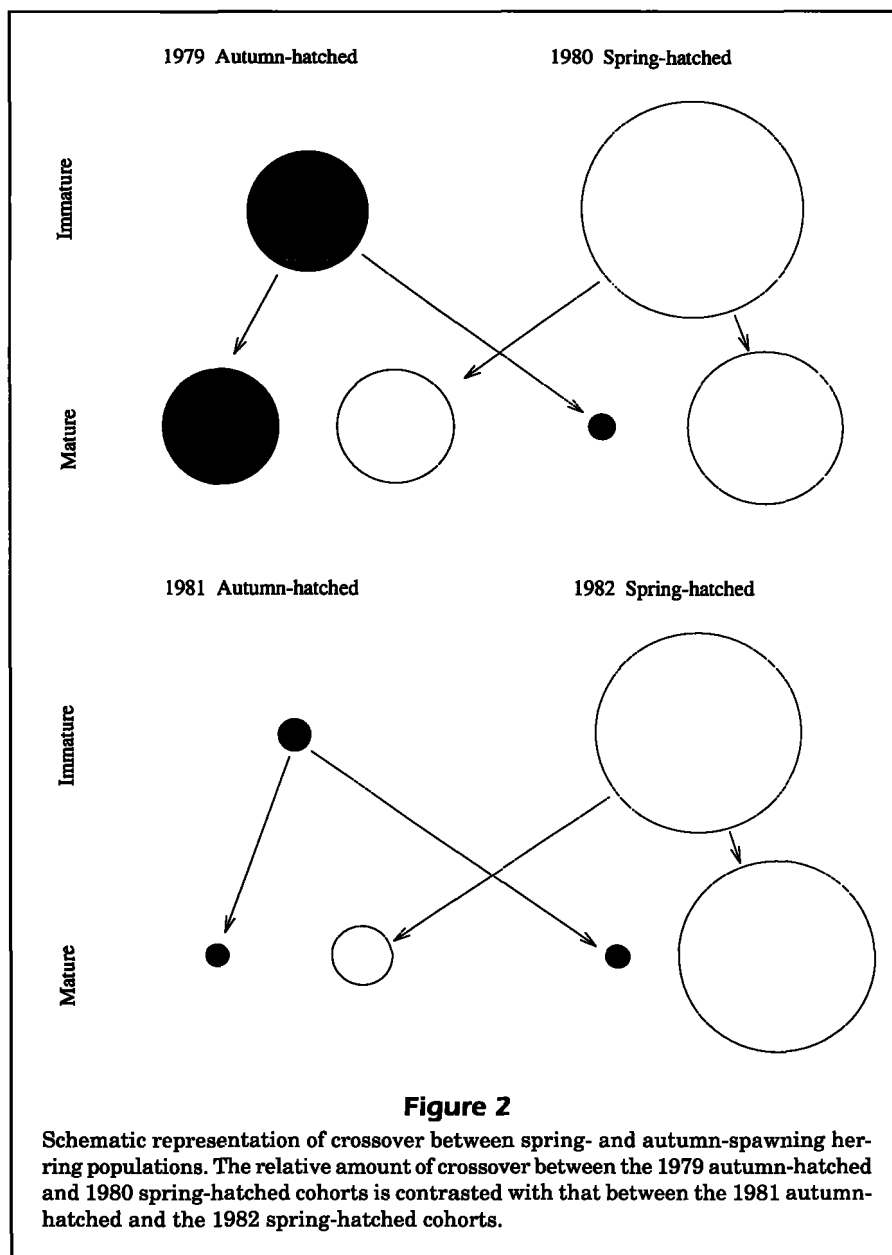
The proportion of spring- and autumn-hatched herring was estimated from the mature members of the 1979–80, 1981–82 and 1986–87 autumn- and spring-spawning year classes, respectively (Table 1). According to their otolith characteristics, the vast majority (>90%) of the 1980 and 1982 spring-spawning herring were also spring hatched. This pattern is consistent from age 3 through age 5 (age=no. of rings). However, a large percentage of the 1979 (40%) and 1981 (77%) autumn-spawning herring were also spring hatched, as judged from their otolith characteristics. Therefore, in both situations, there was a significant crossover from the strong spring-hatched cohort to the autumn-spawning population, in comparison with the number of autumn-hatched individuals. However, because the resulting 1979 autumn-spawning year class was also large, whereas the 1981 autumn-spawning year-class was not, this

⁹ Messieh, S. N. 1974. Problems of ageing Atlantic herring (*Clupea harengus harengus* L.) in the ICNAF area. International Commission for the Northwest Atlantic Fisheries (ICNAF) Res. Doc. 74/59, Ser. 3274, 6 p. ICNAF, P.O. Box 638, Dartmouth, Nova Scotia, Canada B2Y 3Y9.

Table 1

Percentage of autumn- and spring-hatched herring that became mature autumn and spring spawners within the 1979, 1981, and 1986 autumn-spawning and within the 1980, 1982, and 1987 spring-spawning year classes off western Newfoundland (age is expressed as the number of otolith rings—see text).

Year	No. of rings	1979 autumn-spawning year class			1980 spring-spawning year class		
		Autumn-hatched (%)	Spring-hatched (%)	<i>n</i>	Spring-hatched (%)	Autumn-hatched (%)	<i>n</i>
1983	3	34.5	65.5	712	90.6	9.4	402
1984	4	55.6	44.4	1923	92.3	7.7	1438
1985	5	60.4	39.6	1760	92.4	7.6	2590
Year	No. of rings	1981 autumn-spawning year class			1982 spring-spawning year class		
		Autumn-hatched (%)	Spring-hatched (%)	<i>n</i>	Spring-hatched (%)	Autumn-hatched (%)	<i>n</i>
1985	3	54.4	45.6	68	92.2	7.8	192
1986	4	30.7	69.3	140	95.2	4.8	481
1987	5	22.6	77.4	186	97.2	2.8	966
Year	No. of rings	1986 autumn-spawning year class			1987 spring-spawning year class		
		Autumn-hatched (%)	Spring-hatched (%)	<i>n</i>	Spring-hatched (%)	Autumn-hatched (%)	<i>n</i>
1990	3	86.0	14.0	57	68.8	31.2	32



crossover was much less important in absolute terms in the latter (Fig. 2). This pattern is different for the 1986 and 1987 autumn- and spring-hatched cohorts (Table 1). There appears to have been a larger net migration (31%) from the autumn-hatched cohort towards the spring-spawners at age 4 (age=no. of rings + 1). Furthermore, the 1979 autumn-spawning year class showed a trend of a decreasing proportion of spring-hatched individuals from age 4 to 6 as more autumn-hatched individuals matured and recruited to the year class (Table 1). Conversely, the 1981 autumn-spawning year class showed an increasing percentage of spring-hatched individuals with age owing to the overwhelming dominance of the large 1982

spring-hatched cohort compared with the small 1981 autumn-hatched cohort (Fig. 2).

I have also summarized the mean lengths and standard deviations of the immature 1980 and 1982 spring-hatched cohorts to compare their average growth characteristics prior to their first spawning (Table 2). Although the means are similar at similar ages, the standard deviations are quite different, those for the 1980 cohort being 44% to 79% greater than the 1982 cohort from age 2 to age 3. The difference between the two cohorts is even more obvious when their length-frequency distributions at age 3 are compared (Fig. 3, A and B). The length distribution of the 1980 cohort is wider and bimodal. The

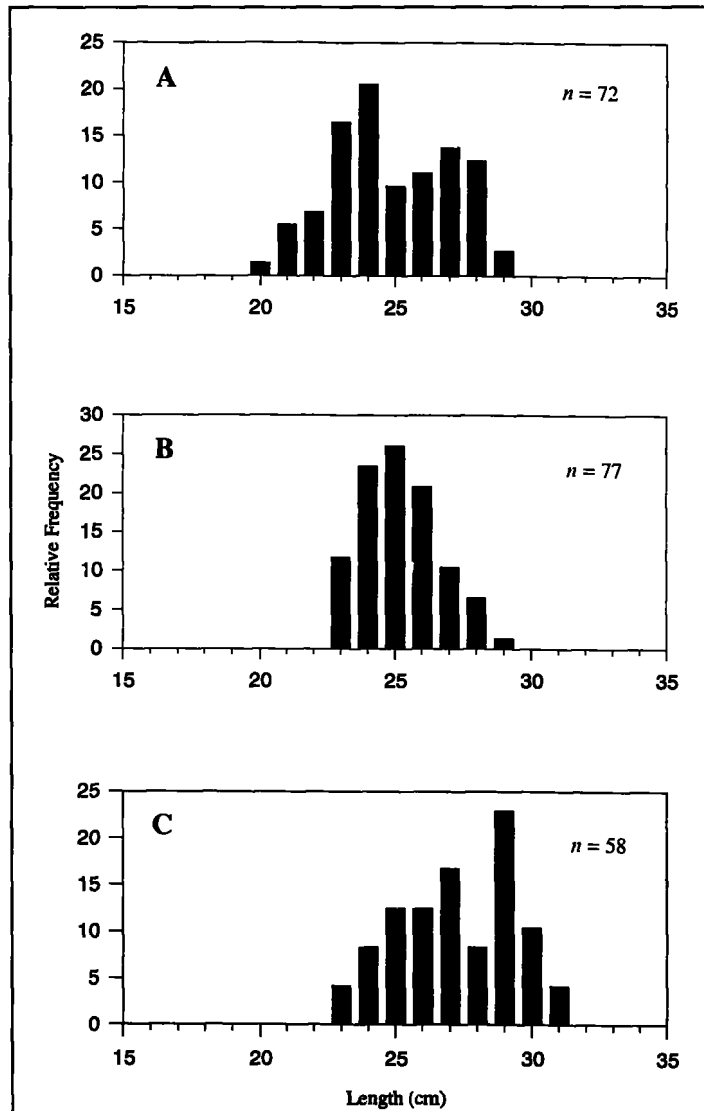


Figure 3
 Length-frequency distributions of the (A) 1980 spring-hatched, (B) 1982 spring-hatched, and (C) 1986 autumn-hatched cohorts as immature 3-year-olds in 1983, 1985, and 1989, respectively.

Table 2

Mean lengths and standard deviations of immature western Newfoundland herring from the 1980 and 1982 spring-hatched cohorts as 2- and 3-year-olds in the spring (April–June) and the fall (October–December) fisheries.

1980 spring-hatched cohort						1982 spring-hatched cohort					
Year	Age	Fishery	Mean length (cm)	SD	n	Year	Age	Fishery	Mean length (mm)	SD	n
1982	2	Spring	—	—	—	1984	2	Spring	187.96	12.87	11
		Fall	248.91	27.23	35			Fall	248.47	15.17	75
1983	3	Spring	247.86	20.87	72	1985	3	Spring	252.11	14.50	77
		Fall	278.80	17.43	585			Fall	283.27	10.56	310

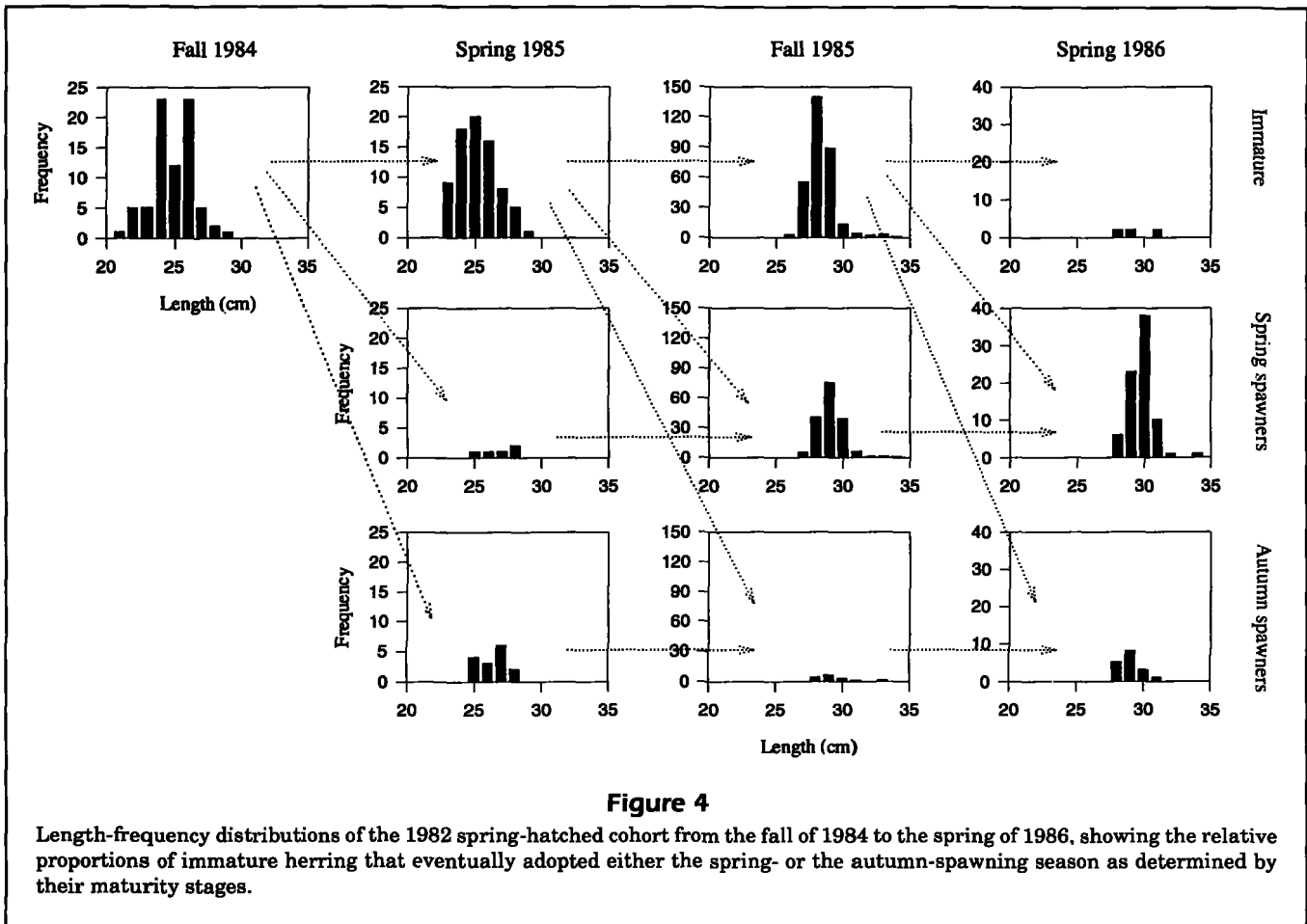


Figure 4

Length-frequency distributions of the 1982 spring-hatched cohort from the fall of 1984 to the spring of 1986, showing the relative proportions of immature herring that eventually adopted either the spring- or the autumn-spawning season as determined by their maturity stages.

same pattern is evident for the 1986 autumn-hatched cohort, which also showed a large bimodal length-frequency distribution at age 3 (Fig. 3C).

The significance of these differences in length composition is shown by following these cohorts as they became mature and began to spawn. We observed that when the length-frequency distribution of the juvenile spring-hatched herring was unimodal and had a relatively small variance (1982 cohort), the majority of them spawned in the spring of 1986 at age 4 (Fig. 4). Conversely, when the juvenile length-frequency distribution was bimodal and had a relatively large variance (1980 cohort), there was an almost even split between those that became spring spawners and those that eventually became autumn spawners (Fig. 5). In addition, if one follows the 1980 spring-hatched cohort after maturity, those that became spring spawners were significantly smaller (t -test: $P < 0.0001$, SAS Institute Inc., 1985) than those that became autumn spawners (Fig. 6A). This length difference was sustained throughout their early adult life, i.e. from age 3 through age 6. A similar pattern

was also seen with the 1979 autumn-hatched cohort. Those that became spring-spawners were smaller at age (Fig. 6B), although the differences are not significant for certain ages owing to small sample sizes.

Discussion

Einarsson (1952) hypothesized that year-class parallelism (twinning) in sympatric seasonal-spawning herring populations came about through a correlation between larval survival conditions in the fall of one year with conditions in the spring of the following year, assuming the larval stage to be the critical phase that determines year-class strength. However, given the ontogeny of the larvae of sympatric seasonal-spawning populations, it is difficult to conceive of a single mechanism by which both cohorts would experience similar survival conditions over a 10-month period, especially since twinning does not normally occur with two successive year classes within the same year. If one follows the development

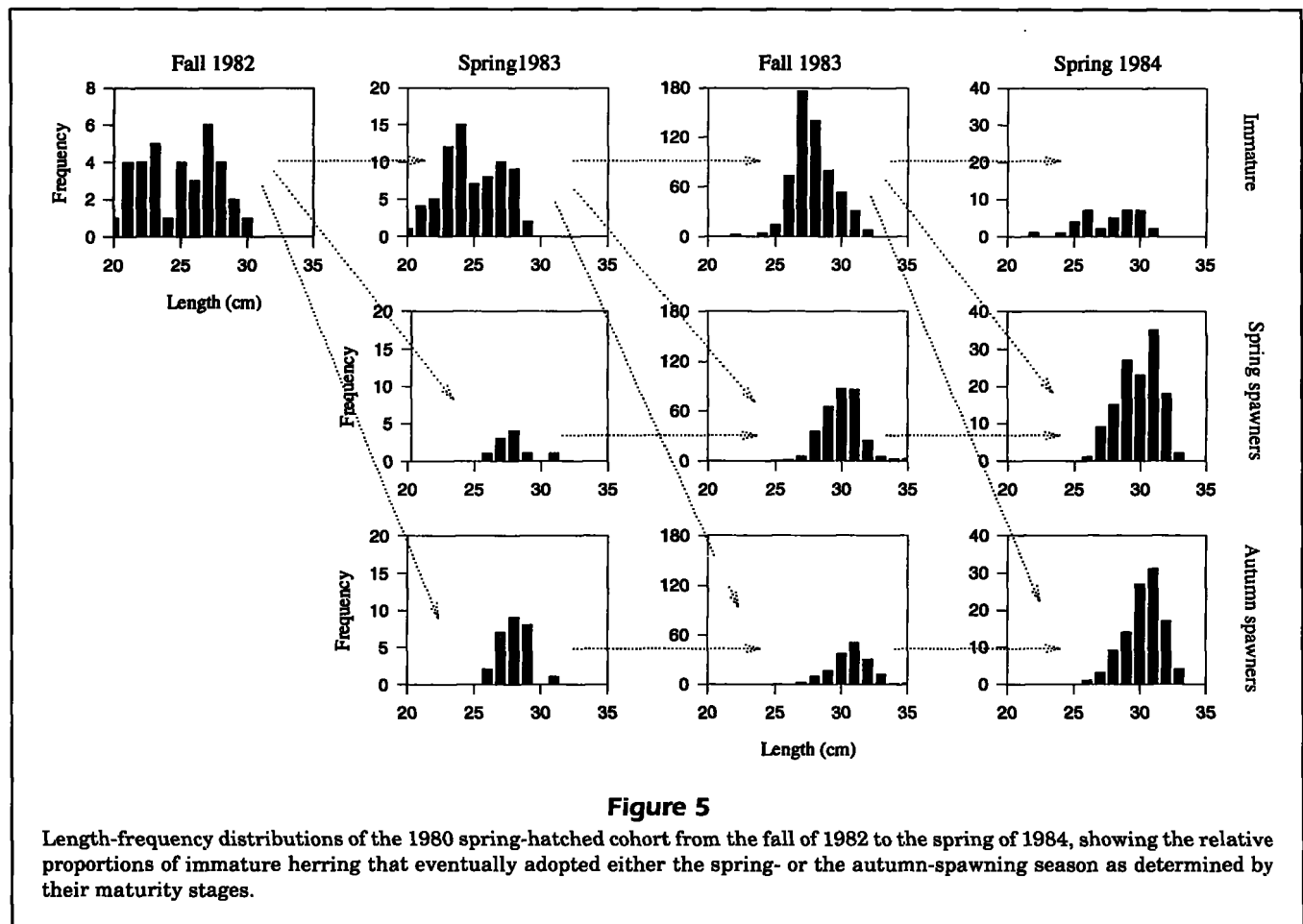


Figure 5

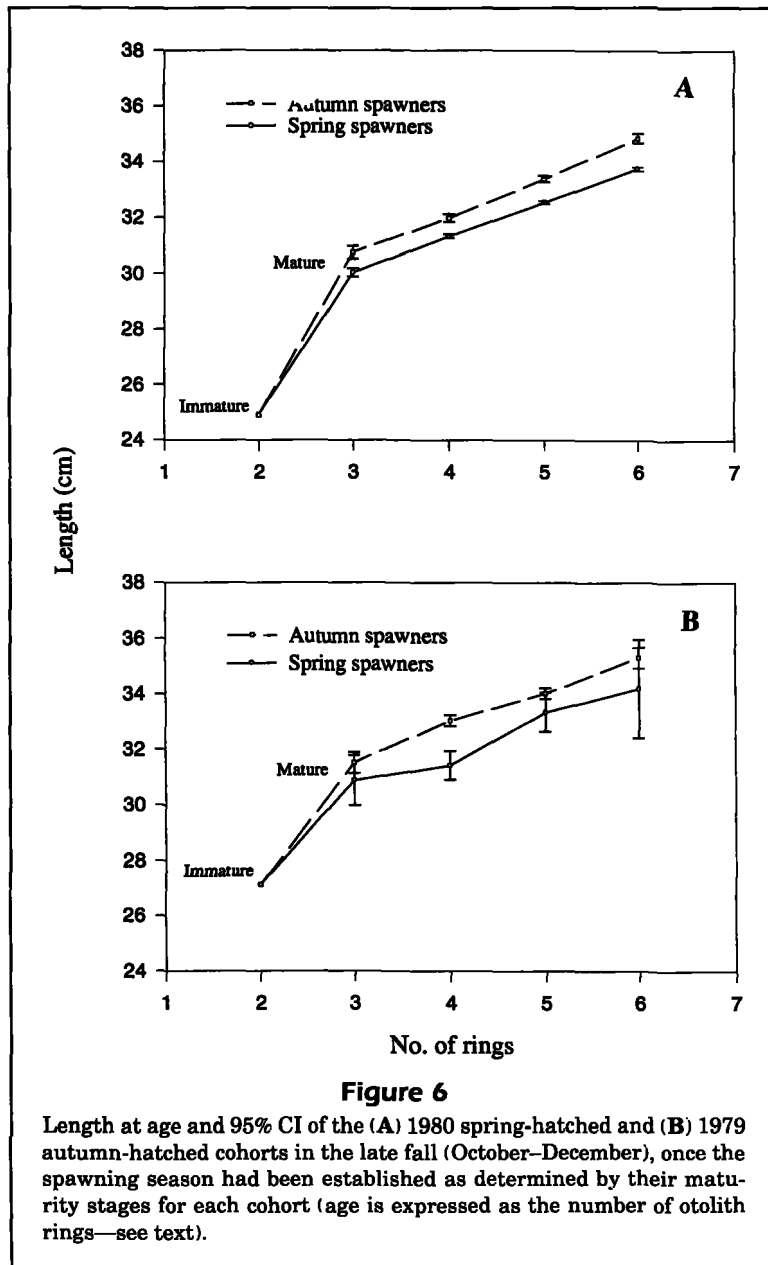
Length-frequency distributions of the 1980 spring-hatched cohort from the fall of 1982 to the spring of 1984, showing the relative proportions of immature herring that eventually adopted either the spring- or the autumn-spawning season as determined by their maturity stages.

of an autumn-hatched cohort and that of the spring-hatched cohort of the following year, from hatching through metamorphosis (Fig. 1), it is apparent that at no time are these two cohorts in the larval stage at the same time, i.e. the autumn spawners have metamorphosed before the spring spawners of the following year have hatched. Autumn-spawned herring in the northwest Atlantic hatch from August to November (Iles and Sinclair, 1982), and metamorphose within a "window" between March and May (Sinclair and Tremblay, 1984). Larvae hatched in June or July from the spring-spawning event reach the required size for metamorphosis during September or October of their first year. Conditions affecting larval survival would therefore have to be favorable from September of one year to June of the next, but unfavorable between July and August for Einarsson's explanation to be credible.

Einarsson (1952) speculated that a strong standing stock of copepods in the autumn of one year may be correlated with enhanced copepod egg production

the following spring, thus favoring larval herring survival over this extended period, although the data available to him did not show this correlation. In addition, these enhanced survival conditions would not only have to exist over a long, but nonetheless precise period of time (September–June), but would also have to be extremely widespread. Twinning occurs in most if not all sympatric herring populations in the northwest Atlantic (de Lafontaine et al., 1991) and sympatric spring- and autumn-spawners do not necessarily use the same breeding locations nor the same larval retention mechanisms, i.e. spring and autumn spawners along the west coast of Newfoundland (McQuinn and Lefebvre⁴).

The present study supports the alternative hypothesis that the twinning of year classes can be explained by the crossover or straying of a significant number of individuals from one seasonal-spawning population to the other. Our results also support the hypothesis of Jean⁵, Graham (1962) and Winters et al. (1986) that variable growth rates in the juvenile phase lead to this crossover. Results from several



studies have concluded that either density-dependent (Anthony, 1971; Lett and Kohler, 1976) or density-independent factors (Moores and Winter, 1982), or both (Anthony and Fogarty, 1985; Haist and Stocker, 1985), contribute to the significant inter- and intra-annual variations in the growth rates of juvenile herring. There has developed a general consensus among these authors that differences observed in length at age between year classes of adult herring originated in the juvenile phase, before maturation. Further, Toresen (1990) compared the growth of juvenile Norwegian herring from the 1950's with that from the 1970's and concluded that variable growth

rates depended mainly on where the juveniles spent their early years. Large cohorts showed both density-dependent growth when these cohorts were distributed in the fjords, as well as environmentally induced growth variations when components of the cohort were distributed in less productive areas of the Barents Sea. This study demonstrated that different components of a single cohort can encounter different growth conditions before maturation and thus can experience different growth rates.

Density-dependent and environmentally induced variability in growth and condition in the juvenile phase is believed to affect the onset of first maturation.

tion in several teleost species (Lett and Doubleday, 1976; Holdway and Beamish, 1985; Rowe and Thorpe, 1990), including Atlantic herring (Marti, 1959; Raitt, 1961; Anthony and Fogarty, 1985; Haist and Stocker, 1985). Several studies have concluded that length, rather than age, is the "critical" factor determining the onset of first maturation in herring (Burd, 1962; Beverton, 1963; Toreson, 1990). Variations in growth rates within a cohort, whether they are density-dependent or not, will therefore influence the age at which different components of a cohort will reach the critical length.

We have seen in the present study that variable juvenile growth rates do influence the onset of first maturation in herring (the age of maturity) and thus affect which season is adopted for spawning. When the growth characteristics of a cohort were relatively uniform in early life, as represented by the unimodal length distribution of the immature 1982 cohort as 3-year-olds, most of the cohort subsequently matured in synchrony and spawned in the spring of 1986 as 4-year-olds. However, when the immature 3-year-old length-frequency distribution showed signs of differential growth rates, as with the 1980 spring-hatched and 1986 autumn-hatched cohorts, maturation was asynchronous. Those individuals from the 1980 cohort with an advanced length at age matured as autumn spawners in the fall of 1983 at age 3 years and 4 months. A large proportion of this cohort subsequently spawned the following spring at age 4, and the remainder took advantage of an additional growth season before spawning in the fall of 1984 as autumn spawners. The autumn-spawning individuals of this cohort were therefore significantly longer at age than those of the same cohort that remained spring-spawning (Fig. 6A). Winter et al. (1986) also concluded that the faster-growing spring-hatched individuals matured as autumn-spawners. Conversely, the 1979 autumn-hatched individuals that became spring spawners did so the previous spring at age 3 years and 8 months and thus showed a shorter length at age than those that remained autumn spawners and matured at age 4 (Fig. 6B). We also observed that the adopted season was maintained after the initial spawning because this length difference persisted until at least age 6.

This crossover also explains the observed pattern of twinning—that is to say a strong spring-spawning year class matched with a strong autumn-spawning year class from the previous year. The fact that twinning is seldom seen between spring- and autumn-spawning year classes of the same year is due to the ageing convention for herring (Hunt et al.⁸), which does not consider the possibility of crossover between these populations. The present study has demon-

strated that this crossover can occur in both directions, i.e. spring-hatched herring can contribute to an autumn-spawning year class (1980) and vice versa (1986). It should also be mentioned that although the effects of crossover between sympatric herring populations is more striking when large year classes are involved, resulting in year-class twinning, the significant correlation found between subsequent autumn- and spring-spawning year classes in eastern Newfoundland (Winters et al., 1986) indicates that crossover undoubtedly occurs to some extent with all year classes.

The present study therefore does not support the concept of discrete sympatric seasonal-spawning populations in Atlantic herring. The data presented here suggest that the progeny of a given seasonal population do not necessarily recruit to the parental population but may indeed contribute to a local population of another reproductive season. Furthermore, the spawning season that is established at the time of first maturation is maintained for the remainder of adult life.

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