

The influence of pre-recruitment growth on subsequent growth and age at first spawning in Atlantic herring (*Clupea harengus* L.)

Deirdre Brophy and Bret S. Danilowicz

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Calculation of the spawning stock biomass for fisheries management requires information on the numbers or proportions of fish in each age- or length-group that are mature each year. This study was conducted to determine the relationship between growth and age of first reproduction in herring stocks around Ireland. Measurements of otolith size at the onset of the first annulus (O1) were used to compare growth during the first year of life between 1-, 2-, and 3-group spawning herring collected from spawning grounds in the Celtic Sea over a period of 3 years. The 1-group spawning fish had significantly greater mean O1 measurements, and hence showed faster growth on average during the first year of life than 2- or 3-group spawning fish. Fish that exhibited slow growth during the first year were absent from the adult spawning population at age 1, but occurred at similar levels in the samples of 2- and 3-group spawning fish. Regression of O1 radius on fish length at capture showed that growth during the first year of life had a small but significant effect on subsequent growth up to age 3. The relationship between pre-recruitment growth and subsequent growth and age at first spawning has implications for recruitment patterns of juveniles from different nursery areas and for the lifetime fecundity of population components with differential growth.

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D. Brophy, and B. S. Danilowicz: Department of Zoology, University College Dublin, Belfield, Dublin 4, Ireland. Correspondence to D. Brophy; Commercial Fisheries Research Group, Department of Life Sciences, Galway-Mayo Institute of Technology, Dublin Road, Galway, Ireland; tel: +353 91 742484; e-mail: deirdre.brophy@gmit.ie.

Introduction

Variation in age at maturity of fish and other vertebrates can be described in terms of the trade off between growth, survival, and reproduction (Alm, 1959; Beverton and Holt, 1959; Roff, 1984; Charnov, 1993). In general, life history models predict that fast growing fish will mature at an earlier age than slow growers (Charlesworth, 1980; Stearns and Koella, 1986). This relationship between rapid juvenile growth and earlier maturation has been observed in many fish species, between populations and cohorts, and also at the individual level (Hutchings, 1993; Rijnsdorp, 1993; Fox, 1994; Chen and Mello, 1999; Fossen *et al.*, 1999; Morgan and Colbourne, 1999).

Calculation of the spawning stock biomass for fisheries management requires information on the numbers or proportions of fish in each age- or length-group that are mature

each year (Hilborn and Walters, 1992). Within fish populations, temporal or geographic variation in growth during the juvenile phase may help explain variability in the rate at which fish recruit to the adult fishery, and subsequent variation in the spawning stock biomass (Van der Veer *et al.*, 1994; Nash *et al.*, 2000).

In recent years, 2- and 3-group fish (fish with two and three otolith annuli) have dominated both commercial and scientific catches from the Atlantic herring (*Clupea harengus*) fishery in the Celtic Sea. The absence of substantial numbers of older fish in the fishery has raised concerns as to the state of the stock, leading to partial closure of fishing grounds (ICES, 2002). The age structure of the population renders this stock particularly sensitive to fluctuations in the number of fish recruiting to the adult population each year. However, little is known about the factors influencing maturation patterns in Atlantic herring in the Celtic Sea.

In the Celtic Sea, herring spawning occurs from October to January (Molloy, 1980a) and more recently has continued through to February and March (Breslin, 1998). Fish present on the spawning grounds during this period are classified as autumn or winter spawners according to their time of spawning (Molloy, 1968). Results of larval drift studies suggest that movement of Celtic Sea herring into the Irish Sea may occur during the larval phase (Özcan, 1974). Furthermore, vertebral count distributions suggest that juvenile herring of Celtic Sea origin occur at nursery grounds in the Irish Sea (Molloy and Corten, 1975; Molloy, 1980b). Recent evidence from otolith microstructure confirms that there is extensive movement of herring from the Celtic Sea into the Irish Sea during the first year of life. This dispersal of Celtic Sea herring into the Irish Sea produces heterogeneous growth patterns in the surviving 0-group juvenile population, with the highest growth rates observed in the Celtic Sea, intermediate in the East Irish Sea, and lowest in the West Irish Sea (Brophy and Danilowicz, 2002).

Herring recruit to the Celtic Sea fishery at ages 1 and 2. For the purpose of stock assessment, 50% of the population is assumed to mature at age 1 and 100% at age 2 (ICES, 2002). This study examines the consequences of growth during the first year of life (determined from otolith measurements) for subsequent growth and spawning patterns of winter spawning herring in the Celtic Sea. We test the hypothesis that juvenile herring that exhibit slow growth during the juvenile phase delay spawning until age 2.

Results from length back-calculations are discussed in terms of the variation in juvenile length observed across

nursery grounds in the Celtic and Irish Seas and its subsequent implications for the management of the fishery.

Methods

Juvenile herring were collected from midwater trawls in the Celtic and Irish Seas, during herring acoustic surveys conducted by the Marine Institute Ireland and the Department of Agriculture and Rural Development, northern Ireland, on board the RV “Celtic Voyager” and the RV “Lough Foyle”, respectively. Fish were sampled randomly from catches made on the nursery grounds, where juvenile herring were concentrated. These catches were dominated by 0-group (before the onset of the first winter ring in the otolith) and 1-group fish. Samples were collected from the Irish Sea in September 1999 and 2000 and from the Celtic Sea in 2000. Juvenile sampling stations are shown in Figure 1.

Adult herring were collected from midwater trawls on spawning grounds in the Celtic Sea during herring acoustic surveys on board the RV “Celtic Voyager” in January and February 1999, 2000. The trawl net used during these surveys had a mesh size on the bag end of 18 mm, rising to 1600 mm at the wings.

Adult herring samples were also taken from the commercial fishery in 2002. Scientific and commercial catches were randomly sampled. Sampling locations of adult fish are shown in Figure 2.

Samples were preserved immediately after capture by freezing at -20°C . In the laboratory, fish were thawed, total lengths (TL) were measured, and sagittal otoliths were

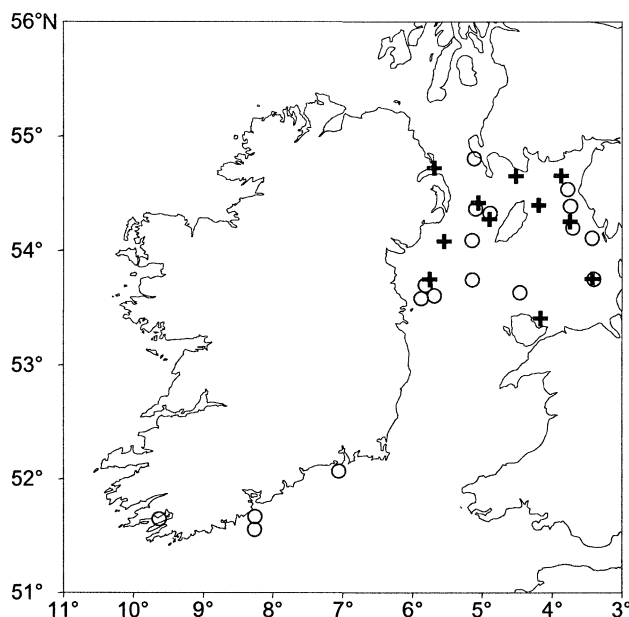


Figure 1. Sampling locations of 0-group herring collected from the Irish Sea in September 1999 (crosses), and from the Celtic Sea in 2000 (circles).

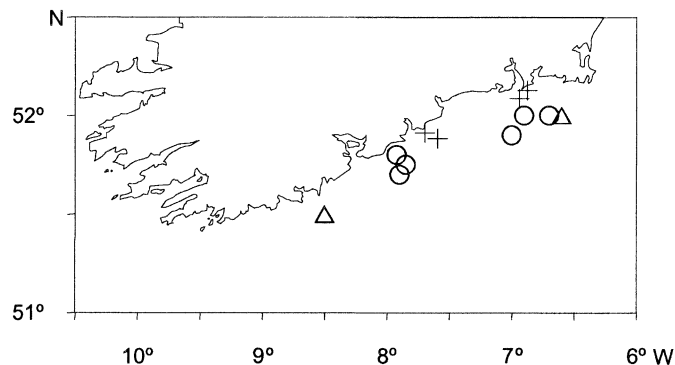


Figure 2. Sampling locations of adult herring collected from spawning grounds in the Celtic Sea in January and February 1999 (triangles), 2000 (crosses), and 2002 (circles).

removed. The TL measurements were taken to the nearest 0.1 cm for the juvenile fish and to the nearest 0.5 cm for the adult fish. The maturity stages of adult fish were determined by visual inspection of the gonads according to the eight-point maturity scale recommended by ICES (ICES, 1962). For juvenile fish, spawning season of origin was determined using otolith microstructure. Fish with a mean otolith increment width of 0.8–2.1 μm , in the region 60–70 increments from the core, were classified as autumn spawned, while fish with mean increment widths of 2.5–5.0 μm in the same otolith region were identified as winter spawned. This method of classification is based on the bimodal distribution of mean increment widths displayed by winter- and autumn-spawned herring in the Irish and Celtic Seas, which allows complete separation of the two groups (Brophy and Danilowicz, 2002). As the adult samples were collected during the winter spawning season, only winter-spawned juveniles were included in subsequent analysis.

Adult fish at stages V (ripe), VI (spawning), and VII (spent) were used to investigate the effect of growth during the first year of life on age at first spawning. Otoliths were stored overnight in water-filled vials. Overnight soaking improved the contrast between the opaque region of summer growth and the translucent winter ring. Otoliths were then placed on a black background and examined through an OlympusTM SX9 binocular microscope using 40 \times magnification. Fish ages were determined by counting growth zones. A complete growth zone was identified as one opaque summer growth region and one translucent winter growth region. As fish were sampled in winter, the marginal winter ring was not completely formed, and so the final growth zone was not included in the count. For example, fish from the 1997/1998 year-class were identified as 1-group (age 1) fish in winter of 1999/2000 and as 3-group (age 3) fish in winter of 2001/2002. This is consistent with the age reading method applied to the annual assessment of the Celtic Sea herring stock (ICES, 2002). Samples were dominated by 1-, 2-, and 3-group fish. Older fish occurred at very low numbers and were excluded from further analysis.

In each otolith, the distance from the otolith core to the otolith margin (OT radius) was measured along the radius from the core to the rostrum. For the adult fish, measurements were taken from the otolith core to the onset of the first winter ring (O1 radius, Figure 3). Otolith measurements were made with a JVCTM digital CCD camera and OptimasTM 6.1 image-analysis package. The O1 measurements were used as a proxy for growth during the first year of life.

The data set was screened for normality and homogeneity of variance. Results of Bartlett's test showed that the variance in O1 measurements was higher in the 2- and 3-group fish than in the 1-group fish and so violated the homogeneity of variance assumption of ANOVA. Therefore, a non-parametric Kruskal–Wallis one-way ANOVA was used to compare the ranked O1 radii between 1-, 2-, and 3-group fish from all year-classes. When significant differences were detected, the Games and Howell multiple comparison test, which does not assume homogeneity of variances, was used for *a posteriori* comparisons (Games and Howell, 1976; Sokal and Rohlf, 1981).

Ranked O1 radii were also compared between 1- and 3-group fish from the 1997/1998 year-class (sampled in 2000 and 2002, respectively) and between 1- and 2-group fish from the 1996/1997 year-class (sampled in 1999 and 2000, respectively). This removed the potentially confounding effect of variation between year-classes by contrasting growth measurements between age groups of the same cohort. These two group comparisons were carried out using the non-parametric Mann–Whitney U-test. The effect of growth during the first year on subsequent growth was investigated by regressing O1 radius on fish length at capture for 1-, 2-, and 3-group fish.

Fish lengths at the end of the first year were back-calculated using the otolith size–fish length relationship. Mean back-calculated lengths were then compared between age groups. The technique of back-calculating fish size from otolith size at a particular age relies on the assumptions that otolith growth is proportional to fish growth

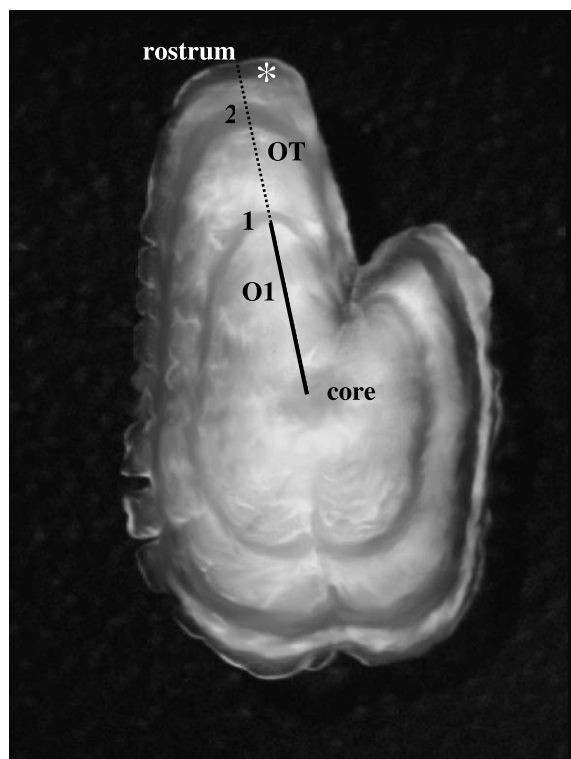


Figure 3. Sagittal otolith from a 2-group herring collected from spawning grounds in the Celtic Sea during the winter spawning season. The otolith core and rostrum are labelled. The OT (total otolith radius) and the O1 measurements (distance to the onset of the first winter ring) are marked with a dashed and a solid line, respectively. Numbers indicate the first and second winter rings. The third growth zone was not completed at the time of capture (January–February), and so the third winter ring (marked with asterisk) is not included in the count for age determination.

(reviewed in Campana, 1990; Francis, 1990). However, the relationship between otolith and somatic growth has been shown to vary with age, growth rate, stock, and ontogeny (Secor and Dean, 1989; Sirois *et al.*, 1998; Vigliola *et al.*, 2000; Morita and Matsuishi, 2001; Otterlei *et al.*, 2002). Various models have been developed to reduce the level of error in back-calculated lengths associated with variation in the otolith size–fish length relationship. In this study, the influence of age and juvenile origin on the relationship between otolith size and fish length was investigated and three back-calculation models were compared.

The relationship between fish length and otolith radius was examined using all adult and winter-spawned juvenile samples. Log transformation of both variables produced an unbiased scatter of the residuals, and so the transformed values were used to derive the regression equations and in subsequent back-calculation of fish lengths.

ANCOVA was used to determine if the slope of the otolith size–fish length regression was influenced by otolith age. Regressions were also compared between juveniles collected

in the Celtic and Irish Seas to determine if juvenile origin influenced the otolith size–fish length relationship.

Fish lengths were back-calculated from O1 radii using the scale proportional hypothesis (SPH), body proportional hypothesis (BPH) (Francis, 1990), and the age-specific back-calculation model developed by Morita and Matsuishi (2001).

The SPH is based on the linear regression of otolith size on fish length and is used to calculate fish length (Francis, 1990)

$$L_i = -\frac{c}{d} + \left(L_c + \frac{c}{d}\right) \frac{O_i}{O_c}$$

where L_i is the TL at annulus i , O_i the measurement to the i th annual ring, L_c the TL at time of capture, O_c the otolith size at capture, and c and d are the intercept and slope, respectively, from the regression of otolith radius on TL.

The BPH is based on the linear regression of fish length on otolith size (Francis, 1990)

$$L_i = \frac{a + bO_i}{a + bO_c} L_c$$

where a and b are the intercept and slope, respectively, from the regression of TL on otolith radius.

Both BPH and SPH assume constant proportionality between otolith size and fish length. The back-calculation model developed by Morita and Matsuishi (2001) incorporates the effect of age on the otolith size–fish length relationship. This model is based on the multiple regression of otolith size and fish age on fish length.

Fish lengths are back-calculated using the equation

$$L_i = -\frac{x}{y} + \left(L_c + \frac{x}{y} + \frac{z}{y}T\right) \frac{O_i}{O_c} - \frac{z}{y}t$$

where t is fish age at time of capture T , and x , y , and z are constants derived from the multiple regression of otolith radius on fish age and length

$$O_c = x + yL_c + zt$$

Each model was fit to the otolith size–fish length data set. Residuals were plotted and their normality was examined using Kolmogorov–Smirnov (K–S) test.

Results

Results of ANCOVA showed that fish age had a significant influence on the slope and intercept of the regression of fish length and otolith radius ($p < 0.001$). There were no significant differences in the fish length–otolith size relationship for 0- and 1-group juveniles from the Celtic and Irish Seas. Linear and multiple regressions showed that fish growth was proportional to otolith growth (Figure 4). Each of the three regression models used gave a good fit to the data. The models had r^2 values of 0.98 and residuals were normally distributed (K–S, $p > 0.05$).

Mean fish length, O1 radius, and back-calculated L1 measurements for each age group and year-class are shown in Table 1. O1 radius differed significantly between 1-, 2-,

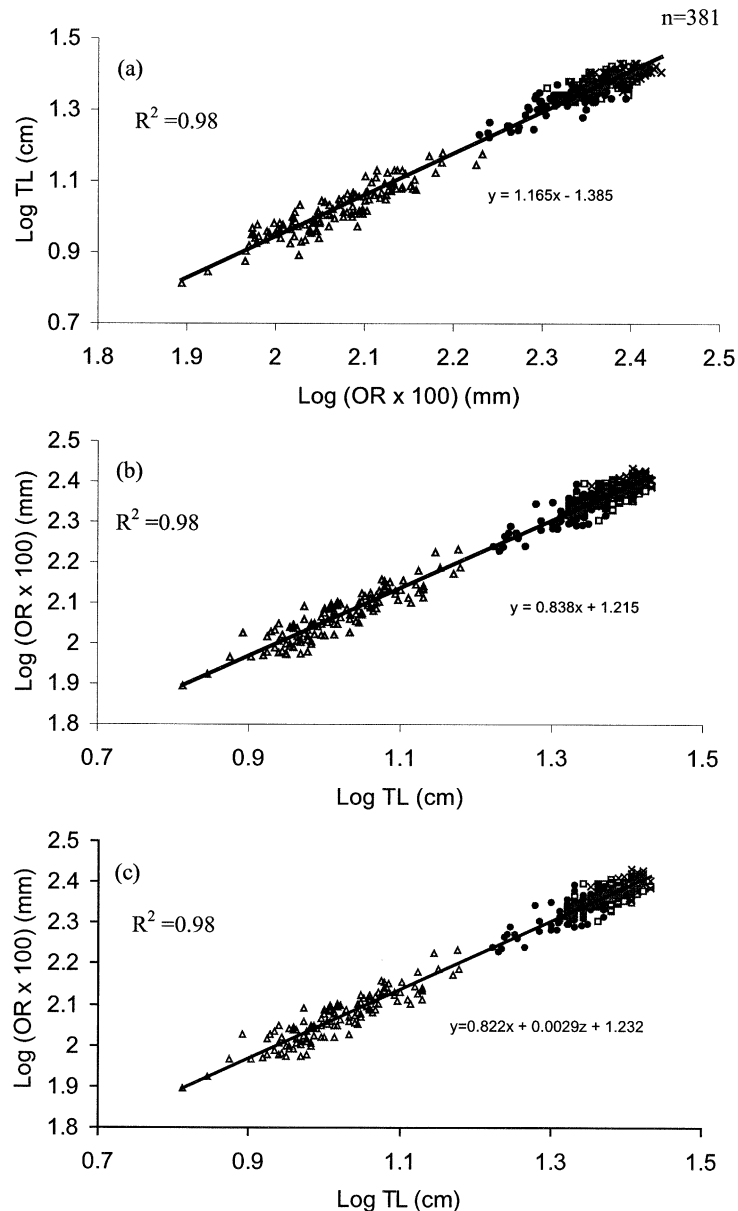


Figure 4. Relationships between fish length, otolith radius, otolith size, and fish length. Regression lines shown are: (a) linear BPH model, (b) linear SPH model, (c) multiple regression of otolith radius and fish age on fish length. Points represent Celtic Sea herring sampled as 0-group (open triangles), 1-group (shaded circles), 2-group (open squares), and 3-group (crosses).

and 3-group fish ($\chi^2 = 80.0$, d.f. = 2, $p < 0.001$; Figure 5). *A posteriori* comparisons found that the mean O1 radius was significantly higher in 1-group than in 2- or 3-group spawning adults ($p = 0.01$) but did not differ significantly between 2- and 3-group fish ($p > 0.05$). Fish with smaller otoliths (and by proxy shorter fish lengths) at the end of the first growing season were absent from the adult spawning population at age 1, but occurred at similar levels in the samples of 2- and 3-group spawning fish.

When analysed separately, fish from the 1997/1998 and the 1996/1997 year-classes also showed significant differences in O1 radius between age groups. The mean O1 radius of 1-group spawning fish from the 1997/1998 year-class collected in 2000 exceeded the mean O1 radius of 3-group fish from the same year-class collected in 2002 (Mann–Whitney $U = 2992$; $p < 0.001$). Similarly, 1-group fish from the 1996/1997 year-class, collected in 1999, had a higher mean O1 radius than 2-group fish from the same

Table 1. Mean values for fish length, otolith radius at the end of the first growing season (O1), and back-calculated fish length at the end of the first growing season (L1) for adult fish from each year-class collected from the Celtic Sea in January and February 1999, 2000, and 2002. Mean L1 estimates are shown for each back-calculation model used. The range of the estimates are shown in brackets.

Sampling year	Winter rings	Year-class	N	Mean length (cm)	Mean O1 radius (mm)	Back-calculated L1 (cm)		
						BPH	SPH	Morita–Matsuishi model
1999	1	1996/1997	9	22.5	1.47	13.9 (11.9–15.8)	13.7 (11.6–15.7)	13.6 (11.5–15.6)
	2	1995/1996	20	23.5	1.18	10.9 (8.2–14.0)	10.7 (8.0–13.9)	10.5 (7.7–13.7)
	3	1994/1995	8	25	1.26	11.8 (9.6–15.1)	11.6 (9.4–14.9)	11.3 (9.1–14.9)
2000	1	1997/1998	57	21.5	1.44	13.5 (9.9–17.1)	13.3 (9.7–17.1)	13.2 (9.5–17.0)
	2	1996/1997	34	23	1.23	11.3 (7.8–15.3)	11.1 (7.6–15.3)	10.9 (7.4–15.0)
	3	1995/1996	14	25	1.13	10.1 (7.1–12.9)	9.9 (6.9–12.7)	9.5 (6.6–12.4)
2002	1	1999/1990	3	21.5	1.41	13.5 (11.9–14.5)	13.4 (11.8–14.4)	13.3 (11.7–14.2)
	2	1998/1999	104	23.5	1.27	11.7 (7.5–16.0)	11.5 (7.3–15.9)	11.3 (7.1–15.6)
	3	1997/1998	51	25.5	1.28	11.7 (8.8–14.9)	11.5 (8.6–14.7)	11.2 (8.3–14.3)
All years pooled	1	Pooled	69	21.5	1.44	13.5 (9.9–17.1)	13.4 (9.7–17.1)	13.2 (9.5–17.0)
	2	Pooled	158	23.5	1.25	11.5 (7.5–16.0)	11.4 (7.3–15.9)	11.1 (7.1–15.6)
	3	Pooled	73	25.0	1.25	11.4 (7.1–15.1)	11.2 (6.9–14.9)	10.9 (6.6–14.5)

year-class collected in 2000 (Mann–Whitney $U = 284$; $p < 0.001$). There was no significant difference in O1 radii between 2- and 3-group fish from the 1995/1996 year-class, collected in 1999 and 2000, respectively (Mann–Whitney $U = 152$; $p = 0.4$). This confirmed that the pattern observed in the collective year-classes also occurred in individual cohort, and so the interpretation of these results is not confounded by variation between year-classes.

The mean and range of back-calculated lengths derived using BPH, SPH, and the model of Morita and Matsuishi (2001) are shown in Table 1. There were small but significant differences in the L1 estimates derived from each model ($p < 0.001$). The discrepancy between estimates tended to increase with age (Table 2). Comparison of mean back-calculated lengths among age groups yielded the same result, regardless of the back-calculation method used. L1 values estimated using the BPH, SPH, and the Morita and Matsuishi (2001) models differed significantly between age groups ($\chi^2 = 68.1$, 68.1, and 75.1, respectively, d.f. = 2, $p < 0.001$). *A posteriori* comparisons found that all mean L1 estimates were significantly higher in 1-group than in 2- or 3-group spawning adults ($p = 0.01$), but did not differ significantly between 2- and 3-group fish ($p > 0.05$).

L1 estimates from the three models were averaged to provide an indication of length at the end of the first growing season for each age group. The frequency distribution of mean back-calculated L1 estimates are shown in Figure 6.

Averaged L1 estimates for 1-group spawning adults ranged from 9.7 to 17.0 cm with a mean value of 13.4 cm. For the 2- and 3-group spawning adults, the L1 estimates ranged between 7.3–15.8 and 7.8–14.8 cm, respectively. The 2-group fish had a mean L1 value of 11.3 cm, while the 3-group fish had a mean L1 of 11.2 cm. It appears that fish with a TL less than 9.7 cm at the end of the first

growing season only occurred in samples of 2- and 3-group fish.

Regression of fish length at capture on O1 radius showed that growth during the first year of life had a small but significant effect on subsequent growth. Length at capture was proportional to O1 radius for 1-group ($r^2 = 0.18$, $p < 0.001$), 2-group ($r^2 = 0.21$, $p < 0.001$), and 3-group ($r^2 = 0.12$, $p = 0.003$) fish (Figure 7).

Discussion

The results confirm that growth during the first year of life influences subsequent growth and age at first spawning for winter-spawned herring from the Celtic Sea. The comparison of O1 measurements shows that 1-group spawning fish exhibited faster juvenile growth than 2- and 3-group spawning fish. The majority (99%) of 1-group spawning fish had O1 measurements above 1.25 mm and corresponding back-calculated L1 values greater than 11.0 cm. In contrast, 44% of the 2-group and 51% of 3-group spawning adults had O1 measurements below 1.25 mm, and L1 values less than 11.0 cm. Evidently, for the year-classes studied, juveniles exhibiting fast growth during the first year of life began spawning at age 1, while slow growing juveniles did not recruit to the adult spawning population until age 2. The distribution of L1 estimates suggests that for winter-spawned herring from the Celtic Sea, fish with a TL below 11.0 cm at the end of the first growing season are unlikely to begin spawning at age 1.

The absence of slow growing fish from catches of spawning 1-group herring cannot be attributed to size selective sampling methodology. Samples of 1-group fish from the 1996/1997 and 1997/1998 year-classes were collected during herring acoustic surveys in the Celtic Sea.

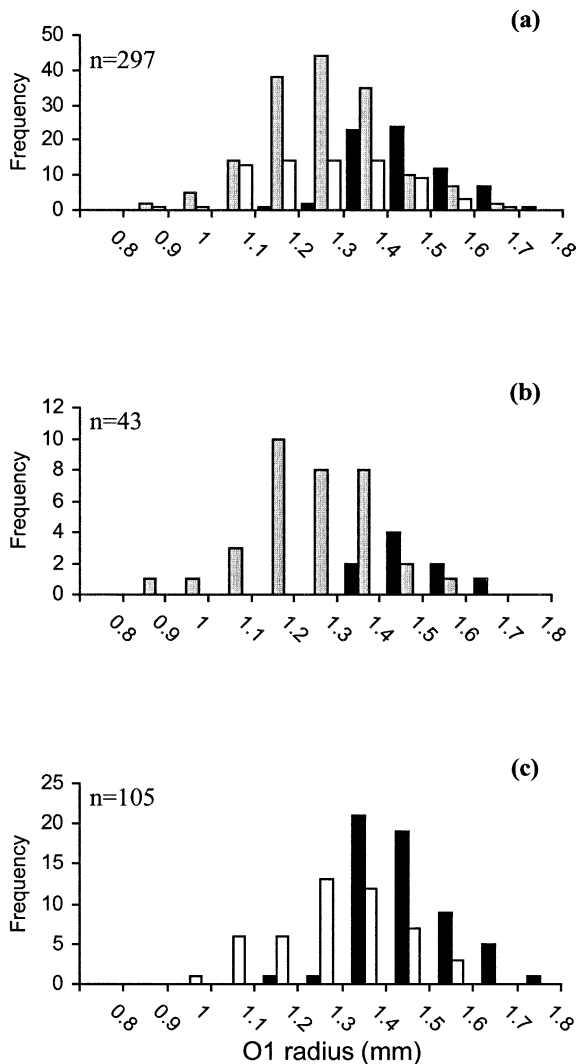


Figure 5. Frequency distribution of otolith radius at the onset of the first winter ring (O1 radius) for 1-group (black bars), 2-group (grey bars), and 3-group (clear bars) adult herring, collected from Celtic Sea spawning grounds. Fish from all sampling years pooled are shown in (a), fish from the 1996/1997 year-class, sampled as 1-group fish in 1999 and as 2-group fish in 2000 are shown in (b), and fish from the 1997/1998 year-class, sampled as 1-group fish in 2000 and as 3-group fish in 2002 are shown in (c).

The design of the net used during these surveys facilitates the capture of juvenile fish down to 2 cm in diameter (Ciarán Kelly, pers. comm.). Herring catches taken during the surveys included non-spawning 0-group and 1-group juvenile fish, ranging in size from 13 to 18 cm. Therefore, smaller herring were not excluded from the catches. The use of samples from the commercial fishery did not introduce bias into the analysis. These samples comprised mainly 2- and 3-group fish, which had similar first year growth rates (as indicated by O1 radii) compared with 2- and 3-group fish

Table 2. Pairwise mean differences in L1 estimates (in cm) between the three back-calculation models used: BPH, SPH, and Morita and Matsuishi (2001) model (M&M).

		BPH	SPH	M&M
BPH	1-Group		0.16	0.28
	2-Group	—	0.18	0.42
	3-Group		0.20	0.55
SPH	1-Group	−0.16		0.12
	2-Group	−0.18	—	0.24
	3-Group	−0.20		0.34
M&M	1-Group	−0.28	−0.12	
	2-Group	−0.42	−0.24	—
	3-Group	−0.55	−0.34	

from the acoustic survey samples. The small number of 1-group fish taken from the fishery also displayed similar growth rates during the first year when compared with 1-group fish from the acoustic survey samples.

The observed differences in back-calculated growth are not an artefact of Lee's phenomenon. Lee's phenomenon (Ricker, 1969) describes the apparent change in back-calculated growth rates with increasing age, which can occur as a result of length-dependent mortality, non-representative sampling, use of the wrong back-calculation equation, or ageing errors. The occurrence of Lee's phenomenon is manifested as a progressive increase or decrease in back-calculated growth measurements with increasing age (Duncan, 1980). The absence of any significant difference between the O1 measurements (or the back-calculated lengths) of 2- and 3-group fish in this study confirms that Lee's phenomenon did not occur to any measurable extent in the age-classes studied. Therefore, the growth rate differences observed between 1-group fish and the older age-classes reflect a real difference in juvenile growth between herring that mature as 1-group fish and those that delay spawning until age 2.

The low level of variation between the three back-calculation techniques suggests that the back-calculated lengths were not greatly influenced by bias in the back-calculation models. While the goodness-of-fit and the distribution of residuals give an indication of the appropriateness of a back-calculation model, the accuracy of the back-calculated length estimates can only be verified by comparison of actual lengths through mark-recapture experiments. In this study, the otolith size–fish length relationship was shown to vary with age. Therefore, the use of an age-specific back-calculation procedure may be the most appropriate. Back-calculation methods that incorporate age as a regression variable can reduce overestimation in back-calculated lengths of older, slow growing fish (Bartlett *et al.*, 1984; Miller and Storck, 1984; Morita and Matsuishi, 2001). However, variation in growth rate between age groups may also produce a bias in age-specific regression parameters (Campana, 1990).

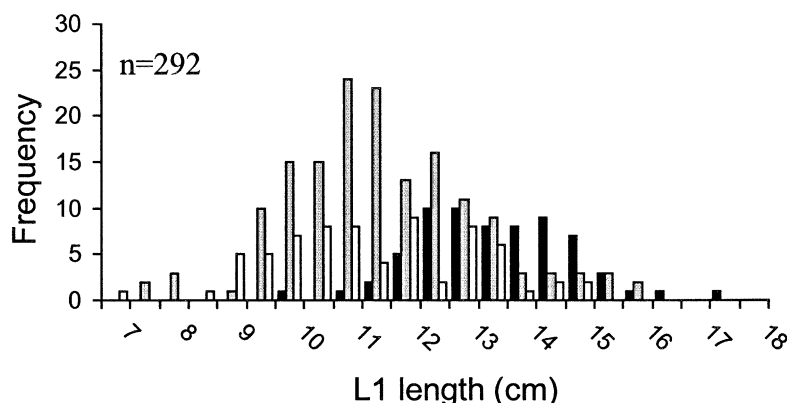


Figure 6. Frequency distribution of length at the end of the first growing season (L1) for 1-group (black bars), 2-group (grey bars), and 3-group (clear bars) adult herring collected from spawning grounds in the Celtic Sea in January–February 1999, 2000, and 2002. The L1 values are back-calculated from the relationship between fish length and otolith radius. The sample size is reduced slightly, as TL were not available for all fish.

Back-calculation of individual fish length is more sensitive to bias in the back-calculation technique than estimation of mean lengths (Campana, 1990). Mean back-calculated lengths in each age group were of interest in this analysis. The three regression models used produced similar estimates of length at the end of the first growing season and there was a consistent difference in L1 estimates between 1-group and older fish in all back-calculation results. Therefore, the findings of this study are not dependent on the choice of back-calculation technique. The average of the L1 estimates from the three models used provides a good indication of mean length at the end of the first growing season for each age group.

During the juvenile phase, herring from a single spawning stock can be widely dispersed and exposed to a range of different environments. This can produce variations within the same population, each with their own characteristic growth maturation and recruitment patterns (De Barros and Holst, 1995). For Norwegian spring spawning herring, fish from nursery areas with more favourable conditions for growth recruit to the spawning population sooner than slower growing components of the population (Holst and Slotte, 1998). A recent study has shown that there is considerable variation in larval and juvenile growth rates between nursery grounds in the Celtic Sea, West Irish Sea, and East Irish Sea (Brophy and Danilowicz, 2002). For winter-spawned herring of Celtic Sea origin, the largest 0-group juveniles occurred in the Celtic Sea (mean TL, 13.4 cm), juveniles of intermediate size were found in the East Irish Sea (mean TL, 10.8 cm), and the smallest juveniles occurred in the West Irish Sea (mean TL, 9.7 cm). Earlier studies also report greater mean lengths for juvenile herring from the Celtic Sea than from the Irish Sea (Bracken, 1961), and provide evidence of faster juvenile growth in the East Irish Sea compared with the West Irish Sea (Molloy and Corten, 1975). This implies that there are consistent differences in the biotic or abiotic environment,

which produce variation in growth rates between the three nursery areas. Results from tagging studies have shown that recruits to the Celtic Sea herring stock originate from nursery grounds in the Celtic and Irish Seas (Molloy *et al.*, 1993). Given the influence of length at the end of the first year of life on age at first spawning, it is likely that fish from each nursery area will recruit to the adult spawning population in the Celtic Sea at different rates. Larger juveniles from the Celtic Sea are more likely to begin spawning at age-1 than juveniles from the Irish Sea, and similarly, the majority of the slow growing juveniles from the West Irish Sea will probably delay spawning until age-2. Consequently, interannual variability in the dispersal of Celtic Sea herring into the Irish Sea during the first year of life would influence the relative proportions of mature fish in each age-class.

Size at the end of the first growing season reflects both larval and juvenile growths. Studies of juvenile herring distribution report that recently metamorphosed herring (4–5 cm TL) occur at nursery grounds in the Irish and Celtic Seas from May to July (Bracken, 1961; Bowers, 1964), indicating that the larval to juvenile transition takes place during this time. Thus Celtic Sea winter-spawned herring hatching in February experience a larval phase of 4–6 months duration, which represents a considerable proportion of the first year of growth. Analysis of otolith microstructure has shown that the growth differences observed across nursery grounds in the Irish and Celtic Seas are also evident during the larval phase (Brophy and Danilowicz, 2002). Therefore, length at the end of the first growing season is determined by both larval and juvenile growth rates. Consequently, conditions experienced during the larval as well as the juvenile phases are likely to influence maturation of Celtic Sea herring.

The effect of larval and juvenile growth rates on age at first spawning has further consequences for adult fecundity. Fast growing juveniles may increase their lifetime

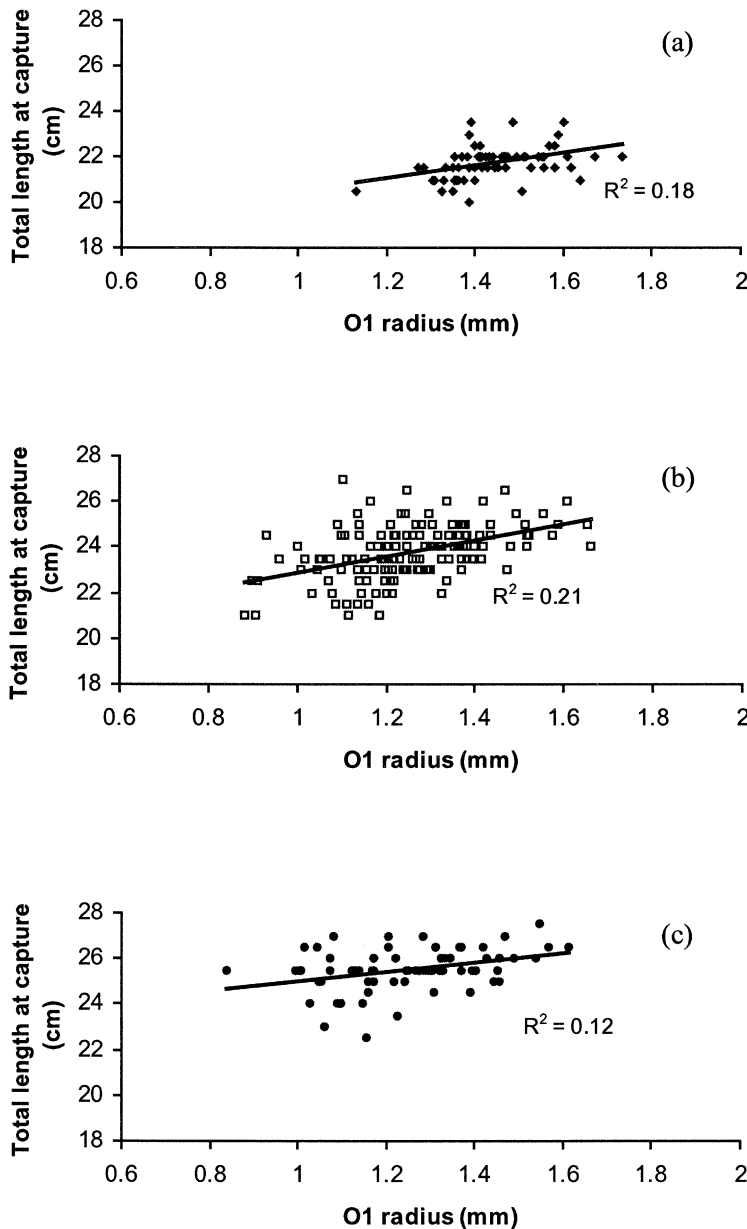


Figure 7. Regression of fish length on O1 radius for (a) 1-group, (b) 2-group, and (c) 3-group adult herring collected from spawning grounds in the Celtic Sea in January–February 1999, 2000, and 2002.

reproductive output by recruiting to the adult spawning population a year earlier than slow growing juveniles. In addition, the small but significant correlation between O1 radius and fish length of adult herring shows that adult growth up to age 3 is to some extent determined by the growth achieved during the pre-recruit phase. As fecundity in teleost fish is related to body length (Wootton, 1979), fast growth during the first year of life could increase fecundity in later years through its influence on adult length. Therefore, initial growth rates can have a long-term impact on fecundity, and the variation in larval and juvenile growth

associated with the dispersal of Celtic Sea herring may influence egg production in the adult population.

The observed differences in otolith size at the end of the first year of life between 1- and 2-group spawning adults from the Celtic Sea herring stock highlight the importance of growth during the pre-recruit phase for subsequent growth and maturation to the adult stock. The authors suggest that for a given year-class, the relative proportions of fish maturing at age 1 and age 2 may, in part, depend on the distribution of that year-class across nursery grounds in the Irish and Celtic Seas and the resultant variation in larval and juvenile

growth rates. Information on the annual variation in distribution and growth of 0-group juvenile herring in the Irish and Celtic Seas may help explain fluctuations in the number of fish recruiting to the adult population each year.

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