

# Spawning time variation in Icelandic summer-spawning herring (*Clupea harengus*)

Guðmundur J. Óskarsson and Christopher T. Taggart

**Abstract:** Different fish stocks of the same species are defined by spatial and temporal differences in spawning, though spawning time can vary within and among stocks. Here we address spawning time variation in Icelandic summer-spawning (ISS) Atlantic herring (*Clupea harengus*). We do so by examining influencing factors that include variation in stock size structure, spawning experience (recruit vs. repeat spawners), spawning stock biomass (SSB), sea temperature, and combinations thereof. Our results, based on temporal variation in ovary weight (OW), relative ovary weight (RG), and maturation stage, across a time series of nearly 50 years and eight length classes of ISS herring, show that spawning occurs over a relatively invariant 30-day period defined by day-of-the-year. Logistic regression analyses and temporal development in OW and RG show that maximum spawning invariably occurs on day-of-the-year  $200 \pm 15$  days, and seasonal variation in mesenteric fat content is physiologically consistent with the timing. We show that the smaller recruit spawners tend to spawn ~17 days later, on average, than the larger repeat spawners. Spawning occurs ~7 days later when SSB is greater than the long-term average, and spawning may be delayed by as much as 10 days during periods of colder than average ocean temperature.

**Résumé :** On définit les divers stocks d'une même espèce par les différences spatiales et temporelles dans la fraie, bien que le moment de la fraie puisse varier entre les stocks et à l'intérieur d'un même stock. Nous nous intéressons ici à la variation du moment de la fraie chez les harengs atlantiques (*Clupea harengus*) à fraie estivale d'Islande (ISS). Nous le faisons en examinant les facteurs explicatifs, y compris la variation dans la structure en taille du stock, l'expérience de fraie (recrues par rapport aux reproducteurs multipares), la biomasse du stock reproducteur (SSB), la température de la mer et les combinaisons de ces facteurs. Nos résultats, basés sur la variation temporelle de la masse ovarienne (OW), de la masse ovarienne relative (RG) et du stade de maturation dans une série chronologique de presque 50 ans qui comprend huit classes de longueurs de harengs ISS, montrent que la fraie se produit sur une période relativement invariable de 30 jours définie par le jour de l'année. Des analyses de régression logistique et l'évolution dans le temps de OW et de RG montrent que le maximum de la fraie a lieu au jour  $200 \pm 15$  de l'année et que la variation saisonnière de la graisse mésentérique est physiologiquement compatible avec ce calendrier. Nous démontrons que les recrues plus petites qui se reproduisent ont tendance à le faire en moyenne ~17 jours plus tard que les reproducteurs multipares plus grands. La fraie se produit ~7 jours plus tard lorsque SSB est plus grande que la moyenne à long terme et la fraie peut être retardée de jusqu'à 10 jours durant les périodes où la température de l'océan est inférieure à la moyenne.

[Traduit par la Rédaction]

## Introduction

Different fish stocks of the same species are defined, in part, by their spatial and temporal differences in spawning, which are hypothesized to be a consequence of "adaptation" to ensure a "match" between emergent larvae and their food resources (e.g., Cushing 1969; Bagenal 1971; Ware 1975). However, spawning time varies within, as well as among, stocks. Timing of maximum spawning in many north-temperate stocks varies annually due to variation in ocean temperature

(Lambert 1987 and references therein; Hutchings and Myers 1994), age and size structure (e.g., Hutchings and Myers 1994; Marteinsdottir and Björnsson 1999), or a combination thereof (Carscadden et al. 1997). Spawning time in Baltic herring (*Clupea harengus membras*) can be a function of the feeding conditions experienced prior to spawning (Rajasilta 1992), and the same can be said of captive Pacific herring (*Clupea harengus pallasii*; Hay et al. 1988) and Atlantic cod (*Gadus morhua*; Kjesbu and Holm 1994). Photoperiod (Rijnsdorp and Vingerhoed 1994; Norberg et al. 1995) and tidal phase (e.g., Hay 1990) also appear to influence spawning time. In other cases, the time of maximum spawning is relatively invariant (e.g., Atlantic cod; Pedersen 1984).

There may be two or more spawning waves within a spawning season in some fish species and stocks (McPherson et al. 2003), with the recruit spawners (smaller and younger individuals) tending to spawn earlier (e.g., Hutchings and Myers (1994), protracted spawning for larger individuals; Morgan 2003) or later (Lambert (1987) and references therein for different herring stocks; Ware and Tanasichuk 1989; Slotte et al. 2000) than the larger and older spawners. One consequence of this age- or size-specific

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spawning determination is a contracted or protracted spawning period that depends on stock age or size structure and thus may reflect a mechanism that explains the relation between recruitment and the age (and presumably size) diversity in Icelandic Atlantic cod (Marteinsdottir and Thorarinsson 1998). Similarly, from a multistock herring analysis, it appears that better than average recruitment occurs as the number of age (and presumably size) classes in a stock increases due to protracted and geographically widespread spawning (Lambert 1987). Thus, it can be logically argued that variation in spawning time within and among different stock units will influence subsequent recruitment.

Here we address spawning time variation in Atlantic herring by using Icelandic summer-spawning (ISS) herring data to examine influencing factors that include variations in stock age and size structure, spawning experience (recruit vs. repeat spawners), spawning stock biomass (SSB), sea temperature, and combinations thereof. We do so, in part, because Cushing's (1969) original match–mismatch hypothesis focused on recruitment variation, primarily in herring, resulting from an invariant spawning time and larval emergence and variable timing in the availability of larval food. However, much of the literature has focussed on temporal variation in the production of food and less so on variation in spawning time, originally considered relatively invariant in Cushing's hypothesis.

## Material and methods

### Data sources

Our analyses are restricted to data on female herring drawn from archives at the Marine Research Institute (MRI) in Iceland. The MRI data include measurements of individual females collected over the period 1953 through 2000 from various research surveys (25%) and the commercial fishery (75%) among which sampling intensity differed within and among years in an irregular manner. The data include collection date and location, total length ( $\pm 1.0$  cm), whole-body weight ( $\pm 1$  g), gonad weight ( $\pm 1$  g; 10 181 of 11 370 fish; Table 1), maturity stages (1 to 8; Anonymous 1962), and a qualitative visual index of mesenteric fat content ranging from 0 (no fat) to 3 (organs fully covered with fat). For the latter, estimates are provided when the data are available (1962 through 2000) for female spawners at lengths 28 cm through 35 cm (smaller and larger being excluded due to the paucity of observations). Annual estimates of SSB (Table 1) are derived from sequential population analyses (SPA) conducted in 1992 (G. Stefánsson and J. Jakobsson, Marine Research Institute, Skulagata 4, P.O. Box 1390, 121 Reykjavik, Iceland, unpublished data) that provide stock estimates for 1962 through 1981 and more recently (Marine Research Institute 2002) for 1982 through 2001 (see Óskarsson 2005).

### ISS spawning regions

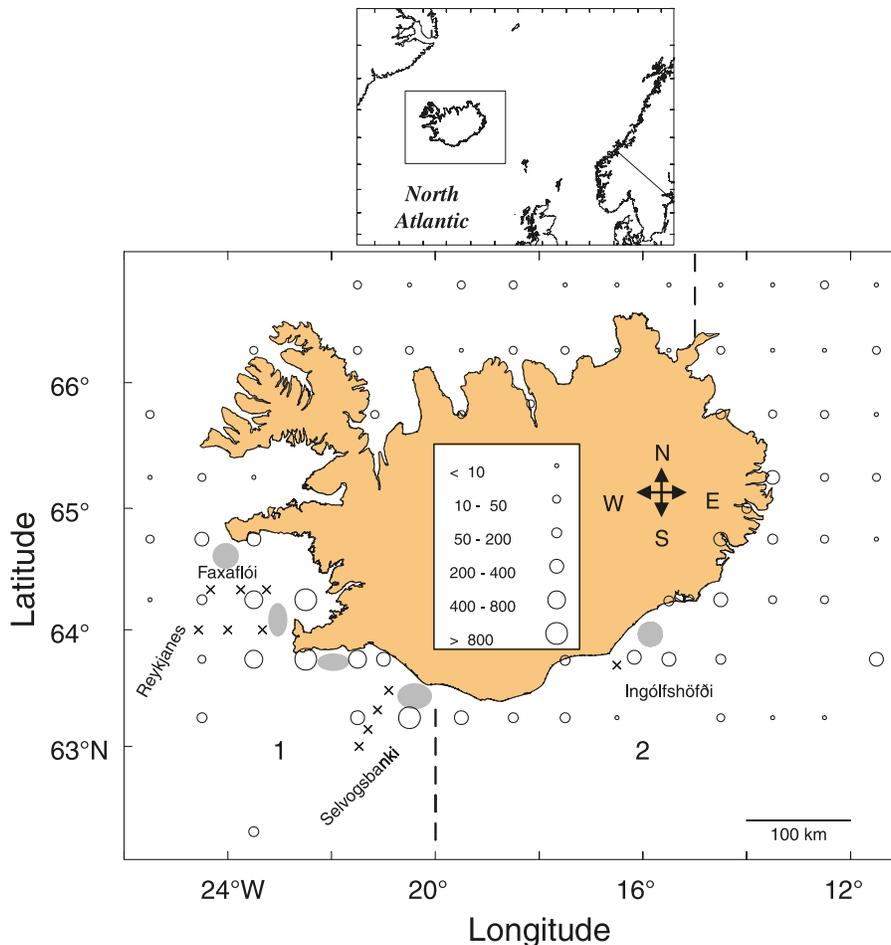
In considering an area effect on the spawning time, we classified the herring samples according to two spawning regions (areas 1 and 2; Fig. 1) that are geographically separated (Fridriksson and Timmermann 1950; Jakobsson and Stefánsson 1999). The Irminger Current, a branch of the North Atlantic Drift (current) brings warm, high salinity water to the

**Table 1.** Summary of the total number of Icelandic summer-spawning female herring (*Clupea harengus*;  $n$ ) collected for morphometric measurements at maturity stages 3 through 7 (Anonymous 1962) in each of areas 1 and 2 (see Fig. 1) over the period 1953 through 2000 and the combined spawning-stock biomass (SSB) estimates. Summary statistics are provided at the bottom of the table.

Year	Area-1 $n$	Area-2 $n$	SSB ( $\times 10^3$ t)
1953	574	21	108
1954	148		147
1955	149	1	169
1956	147		170
1957	18		180
1958	112		200
1959	135		278
1960			
1961	330		287
1962	347	1	310
1963	587		267
1964	194	15	189
1965			
1966	213		84
1967	304	19	89
1968	85		27
1969	703	42	17
1970	662	2	20
1971	466	155	13
1972	6	13	11
1973		60	29
1974	32	13	46
1975	49	28	117
1976	98	89	130
1977	136	187	134
1978	150	60	177
1979	352	257	198
1980	127	102	213
1981	13	10	186
1982	107	66	193
1983	41		220
1984	135	10	233
1985	101		251
1986			
1987	9	6	373
1988	71	54	444
1989	241	4	412
1990	122	94	371
1991	59	199	320
1992	99	79	381
1993	70	36	523
1994	260		532
1995			
1996	58		415
1997	148		417
1998	71	1	494
1999	269	114	496
2000	403	43	520
<b>Summary statistics</b>			
$N$	43	30	44
$n$	8401	1781	—
Mean ( $n \cdot N^{-1}$ )	195.4	59.4	236.2
SE mean	27.4	12.1	23.5

**Note:** Blank fields indicate no data available, therefore excluded in summary statistics.  $N$ , number of years for which there were data.

**Fig. 1.** Chart showing sampling locations in areas 1 and 2 (separation marked by broken lines) around Iceland and number (expanding symbols) of individual Icelandic summer-spawning herring (*Clupea harengus*; maturity stages 3 through 7) collected during 1953 through 2000 ( $n = 10\,182$ ). The locations of the primary spawning grounds (Jakobsson and Stefánsson 1999) are indicated with shading, and the locations (×) of repeated temperature measurements used for calculating the temperature index are noted for the Faxaflói, Reykjanes, Selvogsbanki, and Ingólfshöfði transects.



southern Iceland shelf where part of it is subsequently transported cyclonically around Iceland. Although both spawning regions are influenced by the current (see Stefánsson 1962), the onset of the spring phytoplankton bloom is generally earlier in area 1 than in area 2 (Thórdardóttir 1986), and consequently, higher concentrations of zooplankton are more frequently observed in area 1 (Asthórsdóttir et al. 1983).

### Annual indices

Three different indices are examined to assess interannual variation in ISS herring spawning time: sea temperature anomaly, body condition anomaly, and index of the age composition. The temperature ( $^{\circ}\text{C}$ ) anomaly is calculated using temperature data maintained at MRI (Malmberg 1980; Marine Research Institute 2001) that were collected annually at 50 and 100 m depths ( $z$ ) during the months ( $m$ ) of January through June over the years ( $Y$ ) 1953 through 2000 at a suite of hydrographic stations ( $s$ ) located off southern and southwestern Iceland (Fig. 1: 3 at Faxaflói; 3 at Reykjanes; 4 at Selvogsbanki; and 1 at Ingólfshöfði). Data are restricted to the above depths, months, and stations because they coincide with the depth and seasonal and geographic distribu-

tion of ISS herring during the period of ovarian growth and maturation each year. Average temperature at depth, location, and month ( $\bar{T}_{z,s,m}$ ) was calculated across years. The difference between the average temperature and each datum provides the residual:

$$(1) \quad R_{Y,z,s,m} = T_{Y,z,s,m} - \bar{T}_{z,s,m}$$

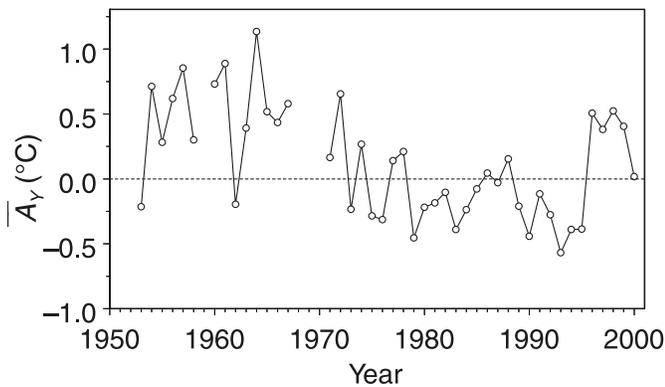
The annual temperature anomaly ( $\bar{A}_Y$ ) is the average residual for each year ( $Y_i$ ):

$$(2) \quad \bar{A}_Y = \left( \sum_{i=1}^{n_Y} R_{Y_i,z,s,m} \right) \cdot (n_Y)^{-1}$$

where  $n_Y$  is the number of measurements in each year (Fig. 2). This formulation ensures that all depths, stations, and months in each region contribute equally to the index despite differences in measurement effort. If more than one datum occurred for each  $T_{Y,z,s,m}$ , the average value is used.

The MRI data were also used to estimate an annual body condition anomaly ( $K_{\text{anomaly},Y}$ ) among individual spawners by year ( $Y$ ) for ISS herring during the prespawning season (February through June). Average condition ( $\bar{K}_{LC,R,I}$ ) among

**Fig. 2.** Time series of sea temperature anomaly ( $\bar{A}_Y$ ) based on average 50 and 100 m depth measurements off southern and south-western Iceland (solid line) for the months of January through June of 1953 through 2000. The dotted horizontal line separates negative and positive anomalies.



individuals within two length classes (LC; 28–31 cm and 32–35 cm inclusive), among five regions ( $R$ ; covering the stock distribution), and at consecutive 15 day-of-the-year intervals ( $I$ ) was calculated across all years. The five regions were chosen because body condition in ISS herring varies spatially within the same season (Óskarsson 2006). The difference between average and individual condition provides the residual

$$(3) \quad KR_{Y,LC,R,I} = K_{Y,LC,R,I} - \bar{K}_{LC,R,I}$$

The residuals averaged over each year ( $Y$ ) provide the annual condition anomaly

$$(4) \quad K_{\text{anomaly},Y} = \sum (KR_{Y,LC,R,I}) \cdot (n_Y)^{-1}$$

where  $n_Y$  is the number of individuals in each year. The standard deviation of the anomaly is calculated as

$$(5) \quad SD(K_{\text{anomaly},Y}) = \left( (n_Y - 1)^{-1} \sum (KR_{Y,LC,R,I} - \bar{K}_{LC,R,I})^2 \right)^{0.5}$$

where  $\bar{K}_{LC,R,I}$  is the mean residual in year  $Y$ .

We use the skew in the frequency distribution of mature herring within each age class ( $X_i$ ; ages 3 through 15) to estimate annual variation in the age composition of the spawning stock. The  $r$ th central moment of a sample ( $m_r$ ) of  $n$  fish is defined as

$$(6) \quad m_r = \frac{1}{n} \sum_{i=1}^n (X_i - \bar{X})^r$$

and for a given sample with 2nd and 3rd central moments ( $m_2$  and  $m_3$ , respectively), the coefficient of skewness,  $b_I$ , becomes

$$(7) \quad b_I = m_3(m_2^{3/2})^{-1}$$

The skew is used to describe the degree of departure from normality in the age distribution, i.e., a positive skew indicates a higher proportion of young spawners, and a negative skew, a lower proportion.

**Table 2.** Number ( $n$ ) and percentage (%) of total of Icelandic summer-spawning herring (*Clupea harengus*) females collected during 1953 through 2000 (44 years, see Table 1) in both areas combined (Fig. 1) at maturity stages 3 through 7 and used in the analyses.

	Maturity stage					Total
	3	4	5	6	7	
$n$	3949	2826	2542	602	1451	11 370
%	35	25	22	5	13	

**Spawning time determination**

**Monitoring of the ovary weight**

A preliminary examination of ISS herring ovary weight (OW, g) demonstrated an exponential increase in OW from the onset of gonad growth through to spawning that was indicated by a marked decrease in OW. As herring are considered capital (sensu contracted spawning period and reproduction supported by energy reserves) or synchronous (eggs are spawned more or less at one time) spawners, a time series of variation in ovary weight can be used to assess development and thus spawning time. As OW is length ( $L$ , cm) dependent, we estimate relative ovary weight ( $RG = 100 \cdot OW \cdot L^{-3}$ ;  $g \cdot cm^{-3}$ ) as in Rijnsdorp (1991). To test the validity of RG as a reliable length-independent measure of OW, the median RG estimates at 5-day intervals for six length classes (28–33 cm, inclusive) are compared among classes. Following the evaluation of RG, we examine overall and length-specific variation in OW and RG over time by first calculating the median ( $\tilde{x}_i$ ;  $i = 1, 2, \dots, 73$ ) OW and RG (statistically defined outliers excluded) in an incremental manner (day-of-the-year order) over sequential 5-day periods (blocks) for all years combined to provide the  $\bar{OW}$  and  $\bar{RG}$  series. We then smooth each series using a three-point running median ( $\tilde{y}_j = \text{median}(\tilde{x}_{i-1}, \tilde{x}_i, \tilde{x}_{i+1})$ ,  $j = 1, 2, \dots, 71$ ) and used Webster’s method (1973; see Legendre and Legendre 1998) to assess the magnitude of discontinuities in each series by first-differencing  $d_k = (\tilde{y}_j - \tilde{y}_{j+1})$  ( $k = 1, \dots, 70$ ). The significance ( $\alpha = 0.05$ ) of a discontinuity (change) in a series ( $\Delta \bar{OW}$  or  $\Delta \bar{RG}$ ) is estimated using a  $t$  statistic:  $t_k = |d_k| S_{\tilde{x}}^{-1}$ , where  $S_{\tilde{x}}$  is the standard deviation of the original series ( $\tilde{x}_i$ ) above. We also determine length-specific discontinuities in  $\bar{OW}$  and median whole-body weight ( $\bar{W}$ ) as above. We use median estimates, as they are less sensitive than the mean to departures from normality.

A 5-day-interval average mesenteric fat index ( $\bar{MF}$ ) is determined using data aggregated over the period 1962 through 2000 among the 28 through 35 cm spawners at maturity stages 3 (mature) through 8 (recovering). This determines the nature of seasonal variation in comparison with ovary development and spawning time estimates.

**Logistic regression on spawning stage**

Female herring are divided into two classes based on maturation stage for the logistic regression. The dependent variable is binary: 0 (prespawning; maturity stages 3 to 5 inclusive) or 1 (spawning and postspawning; maturity stages 6 and 7, respectively). Stage 6 represents 5% of the observations and stage 7 represents 13% (see Table 2). Stage 7 is

**Table 3.** Summary of the independent variables used in logistic regression analyses to explain spawning time variation in Icelandic summer-spawning herring (*Clupea harengus*).

Variable	Symbol	Values or units
Day-of-the-year	$D$	1 through 365
Total length	$x_1$	$\pm 1$ cm
Age	$x_2$	Number of years (scale annuli)
Spawning experience	$x_3$	0; recruit spawner (<30 cm) 1; repeat spawner ( $\geq 30$ cm)
Prespawning female mean annual body condition (Fulton's $K$ )	$x_4$	$\text{g}\cdot\text{cm}^{-3}$
Spawning location	$x_5$	1; area 1 0; area 2
Spawning-stock biomass (SSB)	$x_6$	Tonnes (t)
Spawning-stock biomass (SSB class)	$x_7$	0; <250 000 t 1; >250 000 t
Skew in spawning-stock age distribution	$x_8$	Dimensionless coefficient*
Temperature index <sup>†</sup>	$x_9$	Anomaly, °C
Temperature index class	$x_{10}$	0: <average 1: >average

\*See Materials and methods, annual indices.

<sup>†</sup>Calculated using measurements at several stations off southern Iceland (Fig. 1) during January through June each year (see Materials and methods).

considered identifiable at ~15 days after spawning (Jakobsson et al. 1969), and we assume that the duration does not unduly compromise the analyses.

The independent variables that we examine include sample collection day-of-the-year ( $D$ ), 10 presumed-relevant variables ( $x_1$  to  $x_{10}$ ; see Table 3), and various interaction terms. As there is variation in sampling intensity within and among locations and years (Table 1), it is necessary to combine some years and areas, though this is achieved in a systematic manner. For example, annual ISS data are aggregated according to low (<250  $\times 10^3$  tonnes (t)) and high ( $\geq 250 \times 10^3$  t) estimates of SSB (Table 1; SSB class), where the divisional criterion approximates the average SSB for ISS (240  $\times 10^3$  t) herring over the data series. Similarly, years are classified according to above- and below-average sea temperature (temperature-index class).

The logistic regression model is

$$(8) \quad \text{logit } y_i = \log_2(y_i(1 - y_i)^{-1}) = \beta_0 + \beta_D D + \beta_1 x_1 + \dots + \beta_n x_n$$

where  $i$  denotes individual fish,  $\beta$  represents the model constants and those associated with each variable ( $x_1, \dots, x_n$ , etc.), and the reference model is the spawning characteristic ( $y_i$ ) as a function of day-of-the-year ( $D$ ). Models that include  $n$  other variables ( $x_n$ ) are compared with the reference model using a decrease in deviance  $X^2$  test (Ramsey and Schafer 1997) to determine the best model. Thus, the probability that a fish is spawning or has spawned ( $y = 1$ ) is estimated as

$$(9) \quad P(y = 1) = \exp(\beta_0 + \beta_D D + \beta_1 x_1 + \dots + \beta_n x_n) \times (1 + \exp(\beta_0 + \beta_D D + \beta_1 x_1 + \dots + \beta_n x_n))^{-1}$$

A diagnostic procedure is applied to the best model using a deviance goodness-of-fit test (Neter et al. 1996). Inappropri-

ate (poorly fitting) models are omitted here. To estimate the day-of-the-year when 50% spawning is achieved,  $P(y = 0.5)$ , the model becomes

$$(10) \quad D = -(\beta_0 + \beta_1 x_1 + \dots + \beta_n x_n) \beta_D^{-1}$$

where the confidence interval (CI) for  $D$  is defined using the standard error of the mean (SE) and the  $Z$  statistic with a standard normal distribution and confidence coefficient  $\alpha$ , as

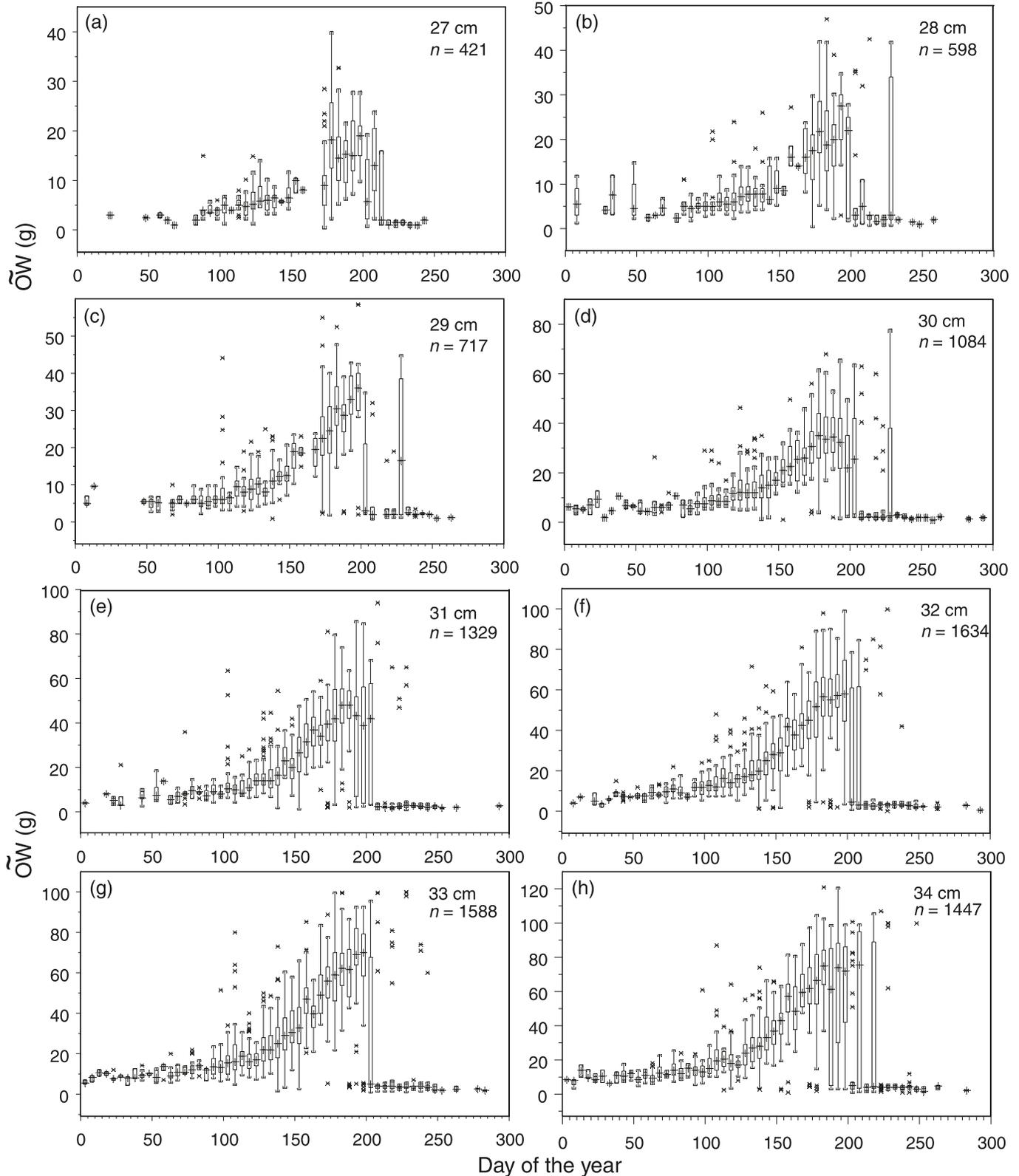
$$(11) \quad \text{CI}(y_i) = y_i \pm Z_{\alpha/2} (\text{SE}(\beta_0)^2 + \text{SE}(\beta_D)^2 D^2 + \text{SE}(\beta_1)^2 x_1 + \dots + \text{SE}(\beta_n)^2 x_n)$$

## Results

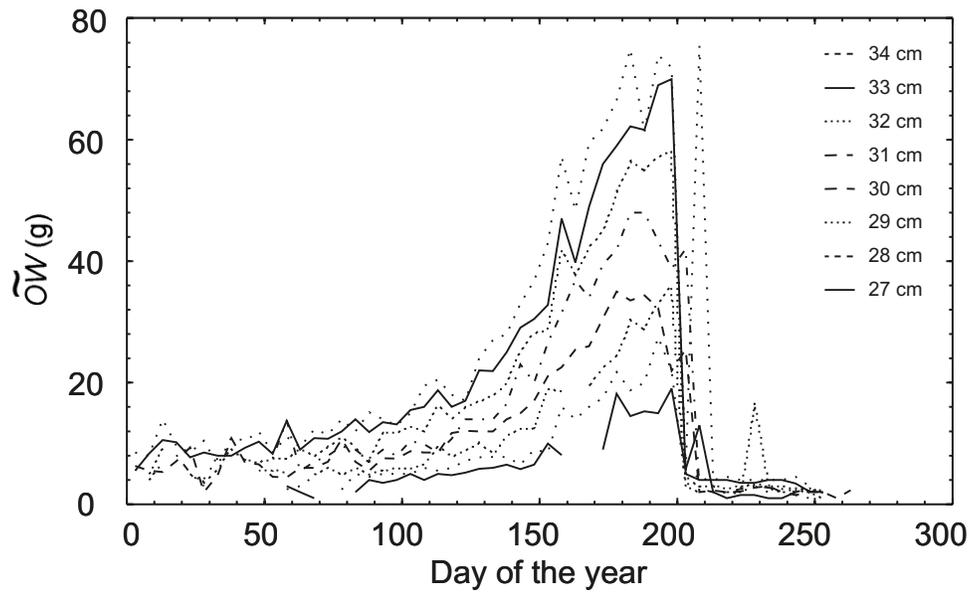
### Ovary weight

Median length-specific OW ordered across 5-day sequential intervals aggregated over all years shows a similar pattern for all length classes between 27 and 34 cm (Fig. 3). It is apparent that a marked decrease in  $\overline{\text{OW}}$  occurs around day 200, a change that we interpret as indicating spawning time. A comparison of the  $\overline{\text{OW}}$  estimates among length classes (Fig. 4) is consistent with the above interpretation for spawning time, although the largest herring (34 cm) display a secondary and sharp increase and decrease in  $\overline{\text{OW}}$  near day 210. This latter observation may be anomalous due to the influence of 12 prespawning herring in a total of 22 fish collected on the same day in 1967 in area 1. The discontinuity analyses (Fig. 5) of the  $\overline{\text{OW}}$  series indicate differences of approximately  $\pm 5$  to  $\pm 10$  days in spawning time, and there is no indication that spawning time varies with length class ( $p \approx 1$ ). Around day 200 and among the eight length classes, there was one major discontinuity ( $p \leq 0.05$ ) in the 29, 32, 33, and 34 cm length classes, one marginal discontinuity ( $0.05 < p <$

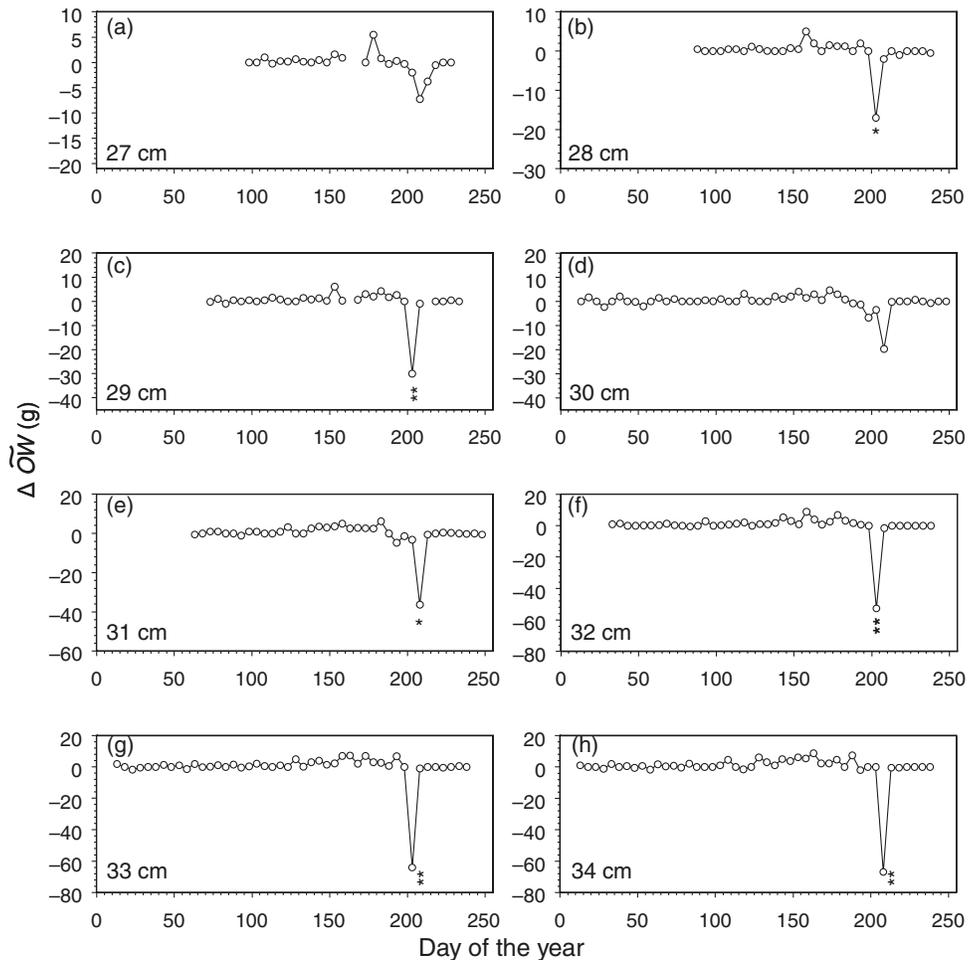
**Fig. 3.** Box-and-whisker plots (median, +; 1st and 3rd quartile, box; non-outlier minimum and maximum, whiskers; extreme outliers beyond 1.5 interquartile range, ×) of Icelandic summer-spawning herring median ovary weight ( $\bar{O}W$ ; g) at 5 day-of-the-year intervals aggregated over the period 1953 through 2000 among eight different length classes (27–34 cm) at maturity stages 3 (mature) through 7 (recently spawned).



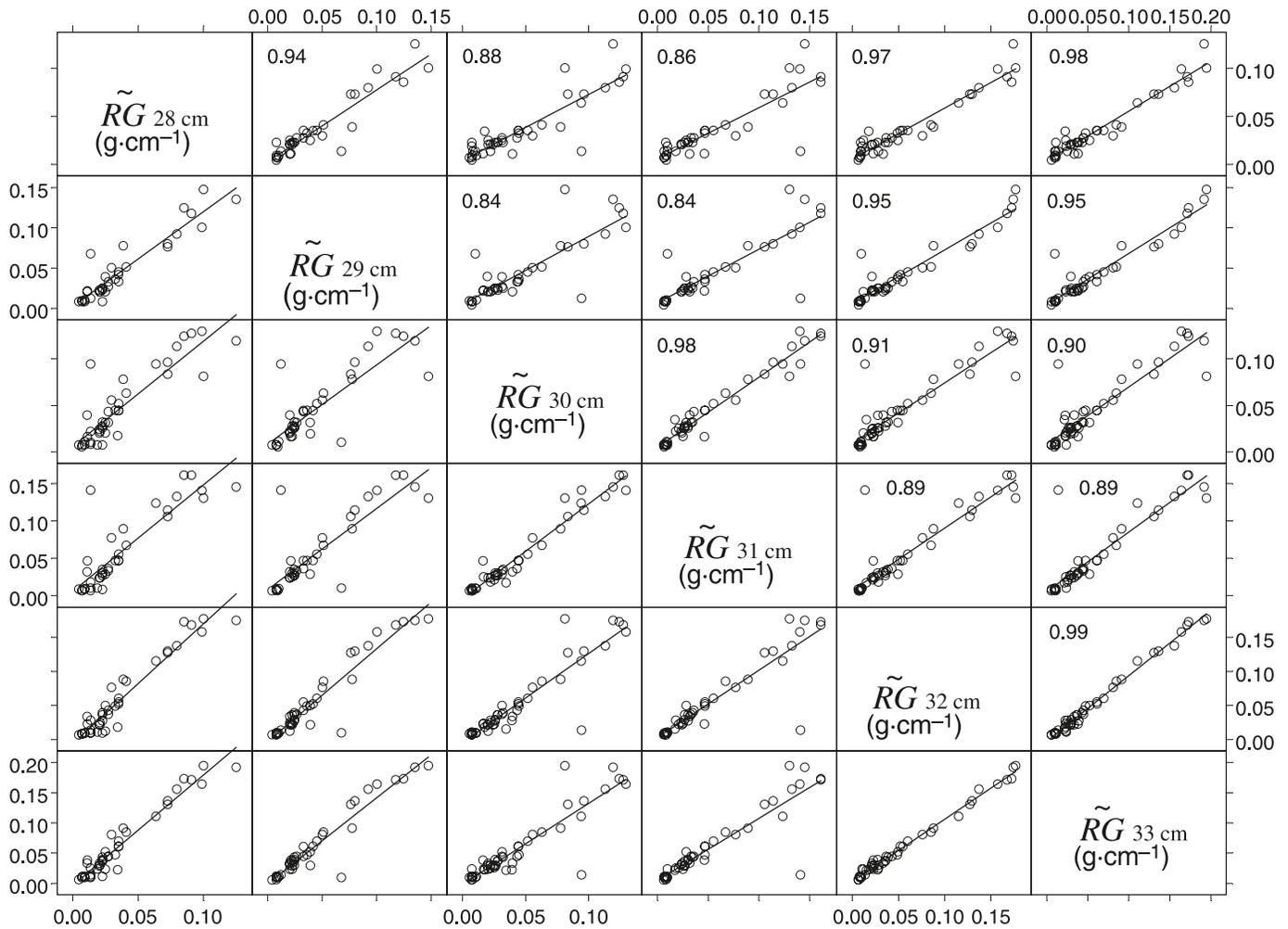
**Fig. 4.** Time series illustrating variation in Icelandic summer-spawning herring median ovary weight ( $\bar{O}W$ , g) at 5 day-of-the-year intervals aggregated over the period 1953 through 2000 among eight different length classes (27–34 cm) at maturity stages 3 (mature) through 7 (recently spawned).



**Fig. 5.** Time series of discontinuities in median ovary weight ( $\Delta\bar{O}W$  (g),  $\circ$ ) for Icelandic summer-spawning herring at 5 day-of-the-year intervals aggregated over the period 1953 through 2000 among eight different length classes (27–34 cm) at maturity stages 3 (mature) through 7 (recently spawned). Significant discontinuities: \*\*,  $p \leq 0.05$ ; \*,  $0.05 < p < 0.1$ .



**Fig. 6.** Correlation matrix and the correlation coefficients ( $p < 0.05$  in all cases) of median relative ovary weight ( $\tilde{RG}$ ,  $\text{g}\cdot\text{cm}^{-3}$ ) among the 28–33 cm length classes of summer-spawning Icelandic herring at 5 day-of-the-year intervals aggregated over the period 1953 through 2000 at maturity stages 3 (mature) through 7 (recently spawned).



**Table 4.** Day-of-the-year (5-day interval combined over 1953 through 2000) serial cross-correlation estimates between median relative ovary weight ( $\tilde{RG}$ ,  $\text{g}\cdot\text{cm}^{-3}$ ) and median ovary weight ( $\tilde{OW}$ , g) among the 27 through 34 cm length classes of female Icelandic summer-spawning herring at maturity stages 3 through 7, with number of observations ( $n$ , at all lags) in each length class and the lag-specific correlation coefficients.

$\tilde{RG}$	$\tilde{OW}_{27\text{cm}}$	$\tilde{OW}_{28\text{cm}}$	$\tilde{OW}_{29\text{cm}}$	$\tilde{OW}_{30\text{cm}}$	$\tilde{OW}_{31\text{cm}}$	$\tilde{OW}_{32\text{cm}}$	$\tilde{OW}_{33\text{cm}}$	$\tilde{OW}_{34\text{cm}}$
$n$	16	41	42	53	43	50	51	51
lag -2	0.426	0.602	0.596	0.769	0.686	0.737	0.713	0.661
lag -1	<b>0.838</b>	0.813	0.769	0.886	0.815	0.869	0.854	0.783
lag 0	<b>0.837</b>	<b>0.963</b>	<b>0.946</b>	0.928	0.911	<b>0.994</b>	<b>0.990</b>	<b>0.897</b>
lag +1	0.547	0.825	0.842	<b>0.949</b>	<b>0.968</b>	0.886	0.883	0.793
lag +2	0.409	0.772	0.711	0.832	0.841	0.764	0.766	0.856

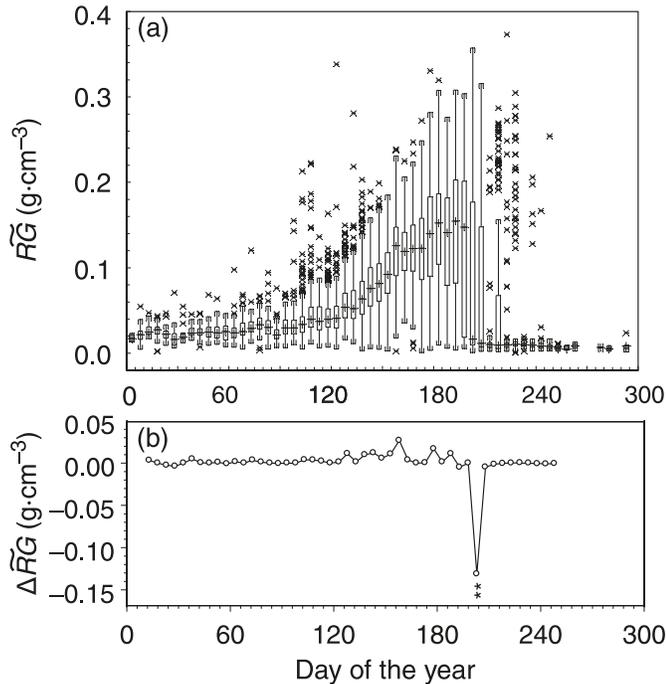
**Note:** Positive lag indicates that  $\tilde{RG}$  is leading  $\tilde{OW}$ , and vice versa for negative lags. The largest coefficient is in bold type.

0.1) in the 28 and 31 cm length classes, and one questionable discontinuity in the 27 and 30 cm length classes.

All length-specific estimates of the median  $\tilde{RG}$  estimates at 5-day intervals for the six length classes (28–33 cm, inclusive) were strongly correlated: coefficients ranging between  $r = 0.88$  and  $r = 0.99$  (Fig. 6). From this, we infer that the  $\tilde{RG}$  series among length classes is similar to that observed for  $\tilde{OW}$  among length classes (see Figs. 3 and 4) and

together they indicate synchronous increases beginning at around day 90, the apparent onset of maturation. The 5-day median estimates of  $\tilde{RG}$  indicate that spawning is most prevalent around day 200 (Fig. 7a), and this is consistent with the discontinuity analyses; i.e.,  $\Delta\tilde{RG}$  (Fig. 7b). The serial cross-correlation between  $\tilde{OW}$  and  $\tilde{RG}$  for the different length classes also indicates that spawning time is consistent among length classes (Table 4) with the highest correlation

**Fig. 7.** (a) Box-and-whisker plot (median, +; 1st and 3rd quartiles, box; non-outlier minimum and maximum, whiskers; extreme outliers beyond 1.5 interquartile range, ×) of median relative ovary weight ( $\widetilde{RG}$ ,  $\text{g}\cdot\text{cm}^{-3}$ ). (b) Time series of discontinuities in relative median ovary weight ( $\Delta\widetilde{RG}$ , ○) of Icelandic summer-spawning herring at 5 day-of-the-year intervals aggregated over the period 1953 through 2000 among all length classes (24–40 cm) at maturity stages 3 (mature) through 7 (recently spawned), where  $n = 10\,182$ . Significant discontinuities: \*\*,  $p \leq 0.05$ ; \*,  $0.05 < p < 0.1$ .

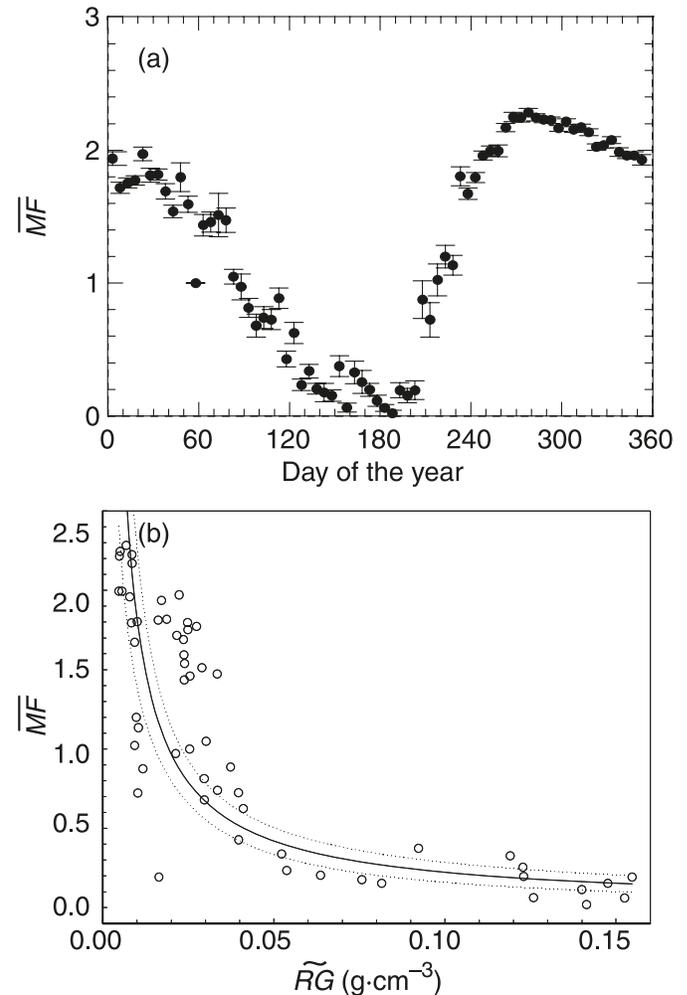


at lag 0 in all cases except for the 30 and 31 cm length classes (lag +1; i.e.,  $\widetilde{OW}$  5 days later relative to  $\widetilde{RG}$ ).

The 5-day-interval average mesenteric fat index ( $\overline{MF}$ ) shows a clear seasonal cycle (Fig. 8a). The index reaches a minimum near day 190 ( $\pm 10$  days), consistent with the spawning time estimates described above. The  $\overline{MF}$  index subsequently increases rapidly over a 3-month period to reach a maximum near day 280, presumably as a result of postspawning feeding. The index then decreases slowly over ~4 months through early winter, and subsequently, the decay accelerates over ~5 months during late winter and through to the early spring prespawning season. The  $\widetilde{RG}$  and  $\overline{MF}$  series are coupled as shown through a cross-correlation analysis with a maximum  $r = 0.76$  ( $n = 53$ ) at lag 0 and  $\overline{MF}$  decays exponentially with increasing  $\widetilde{RG}$  (Fig. 8b).

The potential influence of temperature on  $\widetilde{RG}$ , and thus spawning time, independent of length, is illustrated through a comparison of the relatively warm (1954 to 1967) and relatively cold (1979 to 1995) periods off southern and southwestern Iceland (Fig. 9). It appears that spawning is advanced by approximately 10 days during the warmer period, though close examination indicates that relatively few years were largely responsible for the observed difference. For example, during the warm period, the low  $\widetilde{RG}$  values at days 173, 178, and 193 and the high  $\widetilde{RG}$  values at day 198 resulted from a dominance of the 1967 samples, whereas the

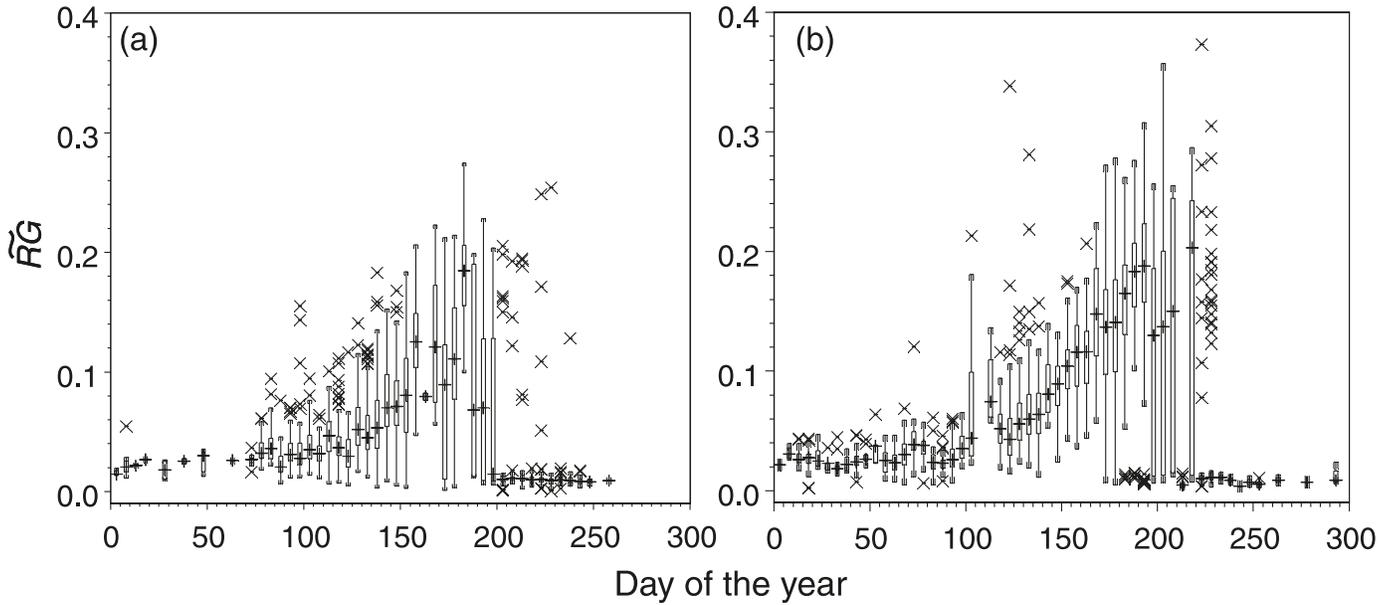
**Fig. 8.** (a) Illustration of time series of average ( $\pm 2$  standard error, SE) mesenteric fat index ( $\overline{MF}$ , 0 to 3; qualitative visual estimate) for Icelandic summer-spawning female herring at 5 day-of-the-year intervals aggregated over the period 1962 through 2000 among spawners (28–35 cm length) at maturity stages 3 (mature) through 8 (recovering), where  $n = 54\,690$  ( $n > 100$  for each interval except between days-of-the-year 58 and 113). (b) Scattergram of observations (○) and least square regression (solid line) with 95% confidence interval around the regression (dotted lines) illustrating the decrease in the  $\overline{MF}$  as a function of median relative ovary weight ( $\widetilde{RG}$ ,  $\text{g}\cdot\text{cm}^{-3}$ ) at 5 day-of-the-year intervals aggregated over the period 1953 through 2000 among all length classes (24–40 cm) at maturity stages 3 (mature) through 7 (recently spawned), where  $\overline{MF} = 1.76 \times 10^{-1} \widetilde{RG}^{-0.485}$ ;  $r^2 = 0.608$ ,  $n = 57$ ,  $p < 0.0001$ .



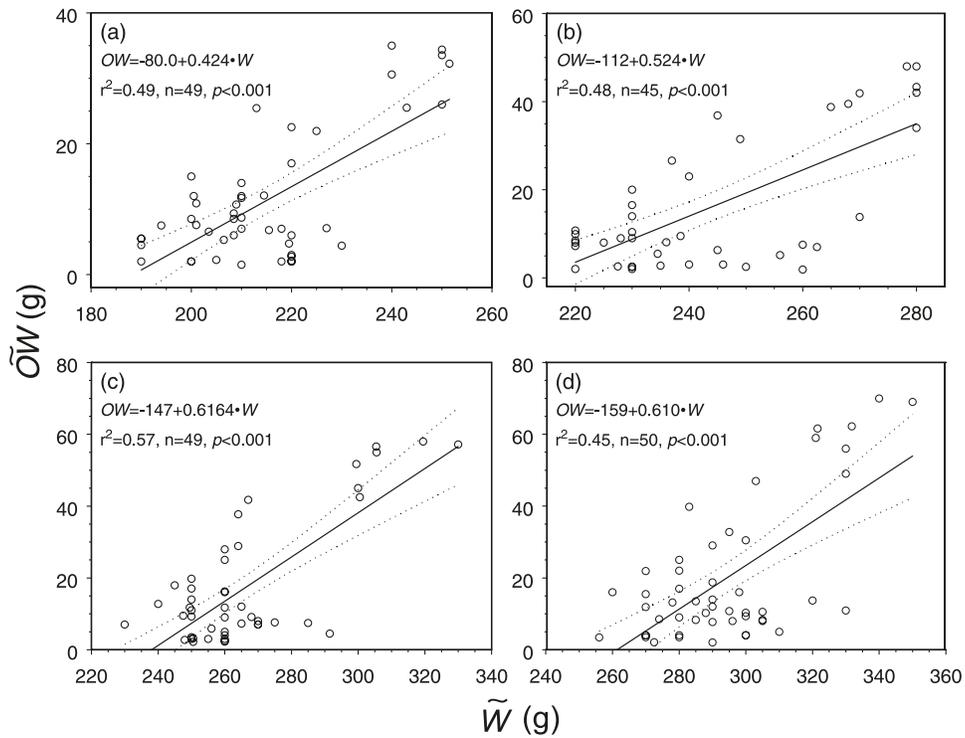
low  $\widetilde{RG}$  at day 188 can be explained by few individuals ( $n = 5$ ). During the cold period, the retardation in spawning was largely an effect of high median  $\widetilde{RG}$  values in 1991, 1993, and 1994 and low  $\widetilde{RG}$  values in 1980 and 1984 (i.e., earlier spawning near day 198). A serial (day-of-the-year) cross-correlation analysis of median  $\widetilde{RG}$  in cold years with warm years showed the highest correlation coefficient at lag -2 ( $r = 0.78$ ,  $n = 49$ ), indicating that spawning was delayed by approximately 10 days during the cold period, as illustrated above.

Changes in median length-specific whole-body weight

**Fig. 9.** Box-and-whisker plots (median, +; 1st and 3rd quartiles, box; non-outlier minimum and maximum, whiskers; extreme outliers beyond 1.5 interquartile range, ×) of Icelandic summer-spawning herring median relative ovary weight ( $\bar{R}G$ ,  $g \cdot cm^{-3}$ ) variation at 5 day-of-the-year intervals aggregated among all length classes (24–40 cm) at maturity stages 3 (mature) through 7 (recently spawned) over (a) a period of warm years off southern and southwestern Iceland (1954 through 1967;  $n = 3032$ ) and (b) a period of cold years (1979 through 1995;  $n = 2954$ ).



**Fig. 10.** Relations between median ovary weight ( $\bar{O}W$ , g) and median whole-body weight ( $\bar{W}$ , g) for Icelandic summer-spawning herring at 5 day-of-the-year intervals aggregated over the period 1953 through 2000 for four different length classes: (a) 29 cm, (b) 30 cm, (c) 31 cm, and (d) 32 cm at maturity stages 3 (mature) through 7 (recently spawned).



( $\bar{W}$ ) with day-of-the-year are related to the changes in length-specific  $\bar{O}W$  during the prespawning and spawning periods (Fig. 10) and all length classes reach a maximum near day 200, although all relations are insignificant ( $p > 0.05$ ) when the data near spawning time (days-of-the-year

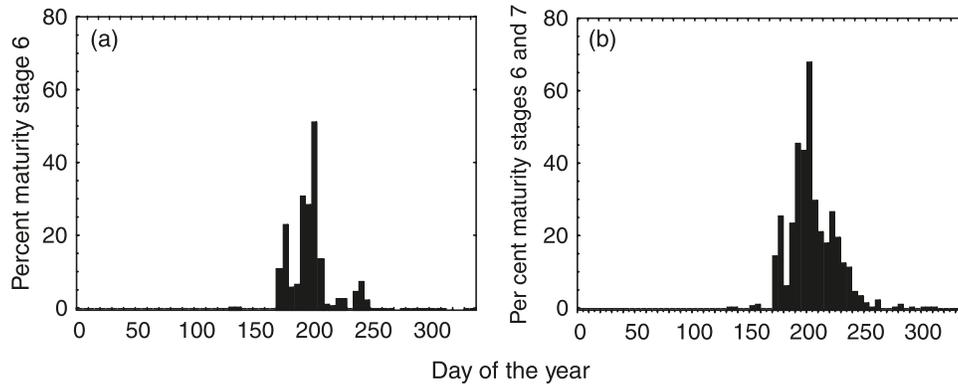
165 through 210) are excluded. The serial cross-correlation between  $\bar{R}G$  and  $\bar{W}$  among different length classes indicates that  $\bar{W}$  generally leads  $\bar{R}G$  by 5–10 days (Table 5), a lag likely reflecting the duration of physiological processes involved in gonad growth. Overall, it appears that spawning

**Table 5.** Day-of-the-year (5-day interval combined over 1953 through 2000) serial cross-correlation estimates between relative median ovary weight ( $\tilde{RG}$ , g-cm<sup>-3</sup>) and median whole-body weight ( $\tilde{W}$ , g) among the 27 to 34 cm length classes of female Icelandic summer-spawning herring at maturity stages 3 through 7.

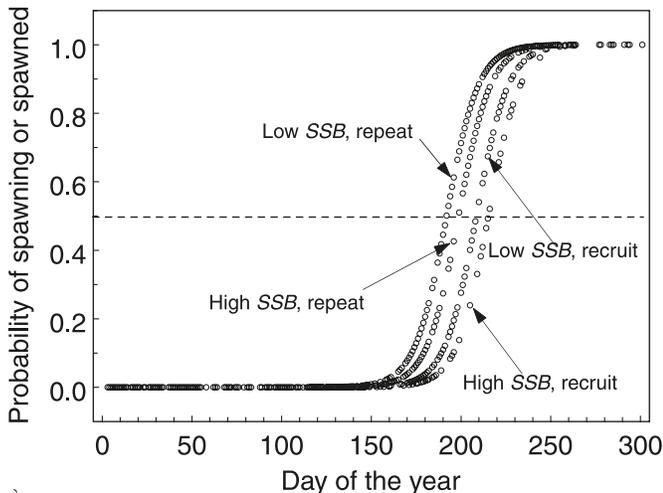
$\tilde{RG}$	$\tilde{W}_{27\text{cm}}$	$\tilde{W}_{28\text{cm}}$	$\tilde{W}_{29\text{cm}}$	$\tilde{W}_{30\text{cm}}$	$\tilde{W}_{31\text{cm}}$	$\tilde{W}_{32\text{cm}}$	$\tilde{W}_{33\text{cm}}$	$\tilde{W}_{34\text{cm}}$
<i>n</i>	16	32	19	51	49	51	51	51
lag -2	0.104	0.289	0.230	0.426	0.340	0.359	0.325	0.357
lag -1	<b>0.630</b>	0.428	0.331	0.578	0.478	0.560	0.491	0.451
lag 0	0.524	0.555	<b>0.438</b>	0.633	0.550	0.730	0.625	0.512
lag +1	0.432	0.577	0.406	<b>0.686</b>	0.636	<b>0.775</b>	0.643	0.490
lag +2	0.314	<b>0.583</b>	0.352	0.575	<b>0.650</b>	0.748	<b>0.658</b>	<b>0.579</b>

**Note:** The table shows the number of observations (*n*, at all lags) in each length class and the lag-specific correlation coefficients, with the highest coefficient in bold type. Positive lag indicates  $\tilde{RG}$  is leading  $\tilde{W}$ , and vice versa for negative lags.

**Fig. 11.** Time series of percent Icelandic summer-spawning herring females (a) at maturity stage 6 (spawning, *n* = 602) among all females at maturity stages 3 through 7 (*n* = 9919); and (b) at stage 6 or stage 7 (spawning and recently spawned, *n* = 2053) among all females at maturity stages 3 through 8 (*n* = 68 472) at 5 day-of-the-year intervals aggregated over the period 1953 through 2000.



**Fig. 12.** Logistic regression estimates of the probability in time (day-of-the-year) that an Icelandic summer-spawning herring will be spawning or will have spawned under high (>250 × 10<sup>3</sup> tonnes) or low (<250 × 10<sup>3</sup> tonnes) spawning stock biomass (SSB) conditions and whether a recruit (<30 cm) or repeat (≥30 cm) spawner. Fifty percent of females are most likely to be spawning or to have spawned at the date at which the dotted horizontal line (0.5) intersects the probability curves.



time can also be inferred from temporal changes in  $\tilde{W}$  that correspond to changes in  $\tilde{OW}$  (cf. Fig. 3).

**Logistic regression on spawning stage**

The proportional (percentage) distribution of the qualitative maturity indices for ISS females at stages 6 (spawning) and 7 (recently spawned), and aggregated over all length classes for the period 1953 to 2000, indicate that the majority of spawning occurs around day 200, though there is evidence that spawning can begin as early as day 170 and may not be entirely complete until as late as day 250 (Fig. 11). The logistic regression analyses show that depending on conditions (see below), 50% of the herring will be spawning or will have spawned near day-of-the-year 200 (Fig. 12). According to deviance goodness of fit ( $X^2_{0.95, 11\ 334} > 11\ 583$ ), the best-fitting logistic regression model describing ISS spawning probability includes day-of-the-year, SSB class (high or low), and spawning experience (Table 6). Using a 50% spawning or spawned criterion ( $y_i = 0.5$ ), the estimated spawning day for recruit spawners is retarded by 17 days relative to repeat spawners and the 95% confidence intervals for the estimates do not overlap (Table 6; Fig. 12). Spawning is retarded when SSB is large relative to small, and though the uncertainties (95% CI) in the estimates do overlap (Table 6), the diagnostic deviance goodness-of-fit test (see Materials and methods) does not indicate an inap-

**Table 6.** (a) Parameters derived from logistic regression analyses (intercept, day-of-the-year, SSB class, and spawning experience) used to estimate spawning day ( $\pm 95\%$  confidence interval, CI) where  $y = 0$  indicates maturity stages 3 to 5 inclusive and  $y = 1$  indicates maturity stages 6 and 7 (see eq. 8) for Icelandic summer-spawning females aggregated over the years 1953 through 2000 where the null deviance of the model equals 10 714 on 11 337 df, giving pseudo- $r^2 = 0.643$  and (b) estimated spawning day ( $\pm 95\%$  CI) based on  $y = 0.5$  (50% spawning or spawned; see eq. 10).

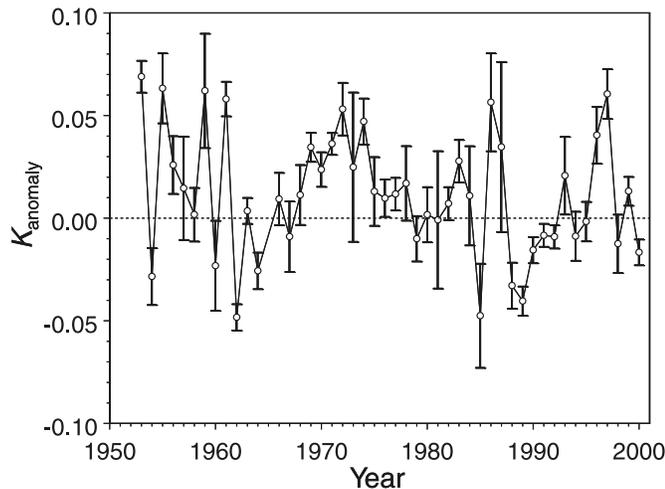
(a) Parameters derived from logistic regression analyses.					
Variable	$\beta$	SE	95% CI( $\pm$ )	Deviance	Total deviance (%)
Intercept	$-2.278 \times 10^1$	$6.081 \times 10^{-1}$	1.192		
Day-of-year	$1.123 \times 10^{-1}$	$2.969 \times 10^{-3}$	$5.938 \times 10^{-3}$	6264	58.4
SSB class	$-7.553 \times 10^{-1}$	$8.682 \times 10^{-2}$	$1.702 \times 10^{-1}$	388	3.6
Spawning experience	1.874	$1.285 \times 10^{-1}$	$2.518 \times 10^{-1}$	241	2.3
Total				6893	64.3

(b) Estimated spawning day.				
SSB class	Spawning experience	Spawning day	Lower 95% CI	Upper 95% CI
1	1	192	185	199
1	0	209	202	215
0	0	202	195	208
0	1	185	179	192

**Note:** Variables are defined in Table 3.

**Fig. 13.** Time series of average Fulton’s body condition anomaly ( $K_{\text{anomaly}} \pm 2$  standard error, SE) for the period 1953 through 2000 for prespawning (February through June only) Icelandic summer-spawning female herring at lengths of 28 to 35 cm and maturity stages 3 (mature) through 5 (fully mature). No data were available in 1960, 1965, 1986, or 1995. The dotted horizontal line separates negative and positive anomalies.



appropriate model. None of total length, prespawning condition (Fulton’s  $K$ ; Fig. 13), spawning location, SSB, skew in the spawning-stock age distribution, or temperature (index or index class) provided significant contribution to an appropriate model.

**Discussion**

Spawning time in Icelandic summer-spawning herring appears relatively “fixed” near day-of-the-year 200 and con-

tracted ( $\pm 15$  days). All of the above results related to measures and indices of spawning time are consistent with the interpretation that the majority of spawning in the ISS herring across nearly 50 years, eight length classes, and spawning grounds occurs over a relatively invariant 30-day period defined by day-of-the-year. The logistic regression results and the temporal variation in  $\overline{OW}$  and  $\overline{RG}$  are each consistent in showing that maximum spawning occurs around day-of-the-year 200 ( $\pm 15$  days). Seasonal variation in mesenteric fat content provides clear evidence that this interpretation is physiologically consistent. These results are surprisingly consistent with much earlier and very different observations made by Einarsson (1956), who used the occurrence of newly hatched larvae to estimate spawning time from early July (day 185) to mid-August (day 230).

Although spawning time appears relatively fixed in ISS herring overall, we provide new evidence of size dependency wherein recruit spawners (females  $< 30$  cm) appear to delay spawning by  $\sim 17$  days relative to the repeat spawners ( $\geq 30$  cm). We also provide new evidence of stock biomass dependency wherein subtle shifts in spawning time appear to be a function of SSB. Thus, there is some small but sufficient evidence to reject the null hypothesis that spawning time in the ISS stock is constant, though it is demonstrably limited to small temporally contracted shifts that are dependent on stock size structure and (or) SSB.

The logistic regression analyses that rely on the well-distinguished maturity stages 6 and 7 (at least relative to stages 3 through 5) appears sufficient in explaining spawning time variation that results from variation in spawning experience (recruit or repeat spawner) and SSB, despite the assertion that qualitative maturity indices are too subjective for such purpose (Ware and Tanasichuk 1989).

The analyses of ovary weight variation and the regression models showed some differences regarding size-specific

spawning time in ISS herring. In the former, spawning time appears more or less fixed around days-of-the-year 200 through 210, where the range in timing appears to be retarded spawning due to smaller recruit spawners and advanced spawning due larger repeat spawners. Generally, it can be concluded that ISS recruit spawners spawn later than repeat spawners. It is typical for the smaller recruit spawners to spawn later in herring (e.g., Lambert (1987) and references therein; Slotte et al. 2000; Óskarsson et al. 2002) and in cod (e.g., Marteinsdottir and Petursdottir 1995; Bleil and Oeberst 1997), although the opposite is also observed in cod (Hutchings and Myers 1994) and American plaice (*Hippoglossoides platessoides*; Morgan 2003). Moreover, our results reflect the Slotte et al. (2000) results for Norwegian spring-spawning herring, using very different methods in which spawning time of repeat spawners is not a function of size or age, which had been postulated earlier by Lambert (1987) for the same stock. Delayed spawning among recruit spawners may be due to a delayed onset of maturation rather than protracted ovary development (Slotte et al. 2000), although the inverse has been observed (Ware and Tanasichuk 1989). Regardless of explanation, what is important in the context of this study is the question of what might be the effect of the observed spawning time variation on eventual recruitment? The positive influences of protracted spawning on recruitment that result from a large diversity in the size and age composition of a stock (e.g., Marteinsdottir and Thorarinsson 1998) were summarized above. Thus, a similar influence may be expected among ISS herring as some of our results indicate spawning time is, in part, size dependent. Absolute size composition in the stock may therefore influence recruitment of ISS herring through variation in spawning time over and above the variation attributable to relative fecundity (Óskarsson and Taggart 2006) and egg size (Óskarsson 2005).

The literature implies that the life history among different herring stocks in the North Atlantic varies considerably in terms of spawning time and migration pattern. Spawning occurs over a 30-day period or less among ISS herring (above), nearer 50 days among Norwegian spring spawners (Lambert 1987), and 90 days or more among Scotia–Fundy summer–autumn spawners (Óskarsson 2005). For the former two stocks, there is an indication of at least two spawning waves, whereas many disorganized waves are typically observed for the latter (Óskarsson 2005) when analysed in a manner similar to that described here. In all the three cases, the temporal distribution of spawning within the “fixed” spawning period can influence the recruitment success if linked to variation in the larval food production cycle (Cushing 1969), the basis of the match–mismatch hypothesis (Cushing 1975). However, spatial distribution can additionally influence recruitment indirectly. Spawning among ISS herring (Óskarsson 2005) and Norwegian spring-spawning herring (Slotte 1999) occurs upstream relative to the nursery grounds. In contrast, it is suggested that Scotia–Fundy herring larvae are retained near the spawning grounds (e.g., Iles and Sinclair 1982). Thus, the spatial and temporal distribution of spawning works to distribute the larvae spatially and temporally in relation to productive (larval food) regions. Accordingly, the “adaptation” to ensure a “match” between emergent larvae and their food resources can be ei-

ther primarily dependent on spatial variation (e.g., ISS herring and Norwegian spring-spawning herring) as originally inferred by Hjort (1914), or temporal variation (e.g., Scotia–Fundy summer–autumn spawning herring) in spawning as inferred by Cushing (1969).

Spawning stock biomass had a small and marginally significant effect on spawning time in ISS herring. Similar findings of stock-dependent (SSB) effects on maturation have been observed for Baltic cod in which spawning time was found to be influenced by temperature, SSB, and food availability (Wieland et al. 2000). We postulate that the SSB effect on ISS herring spawning may be related to feeding conditions during the maturation process, when in high SSB years, more individuals would feed on the same (average) amount of food. This is reasonable as there is little difference in average zooplankton (dry weight) biomass ( $\text{g}\cdot\text{m}^{-2}$ , 0–50 m depth) off southern Iceland (Selvogsbanki) during years of low SSB and during years of high SSB over the period 1971 to 2000 (Marine Research Institute 2001). This implies that feeding success under high SSB may be reduced and lead to reduce ovary growth and thereby delayed spawning. It is well documented that feeding conditions and food availability during the prespawning season can affect the spawning time in herring (e.g., Hay et al. 1988; Rajasilta 1992). However, body condition ( $K_{\text{anomaly}}$ ) did not contribute to explained variation in spawning time, as noted above, and has little influence on fecundity variation (Óskarsson and Taggart 2006). The appropriateness of using the  $K_{\text{anomaly}}$  among prespawning herring to represent energy status has been questioned by Óskarsson (2008) due to hydration of both somatic and reproductive tissues during this period and due to the variability in stomach content.

The relatively low variation in the temperature anomaly off southern and southwestern Iceland, at least in comparison with other areas in Icelandic waters (Marine Research Institute 2001), appears to affect the spawning time of ISS herring as illustrated by temporal variation in  $\bar{R}G$  and serial cross-correlation (warm years advancing spawning by about 10 days). However, the difference between warm years (1954 to 1967) and cold years (1979 to 1994) may be equally attributable to differences in SSB, as indicated by the logistic regression models. During the warm period, the average SSB was  $198 \times 10^3$  t relative to  $323 \times 10^3$  t during the cold period when spawning time was delayed. Furthermore, SSB consistently increased during the cold period. Given these facts, in addition to the results of the logistic regression in which SSB was found to contribute to the annual variation in spawning time but sea temperature did not, it is reasonable to conclude that SSB is more influential on spawning time of ISS herring than is temperature.

Warmer ocean temperatures have been documented to influence the spawning time of herring (Lambert (1987) and references therein; Ware and Tanasichuk 1989) and other species (e.g., haddock (*Melanogrammus aeglefinus*; Page and Frank 1989) and capelin (*Mallotus villosus*; Carscadden et al. 1997)) where it serves to advance spawning. In others cases, warmer temperature appears to retard spawning (e.g., English sole (*Parophrys vetulus*; Kruse and Tyler 1983); Atlantic cod (Hutchings and Myers 1994)). For ISS herring, there is no substantive evidence that the sea temperature influences the annual variation in spawning time when based

on a typical temperature index such as we developed. Although a preferable measure such as the integral of the thermal environment experienced by the fish (e.g., degree-day; Neuheimer and Taggart 2007) is not easily accessible, it does raise the issue of how appropriate are such temperature indices. The existing, but limited information on the distribution of the ISS herring during the period of ovary growth (e.g., Jakobsson et al. 1993) suggest that it occurs within the spatial domain that we used to calculate the index; it is also the area of early phytoplankton blooms (e.g., Thórdardóttir 1986) and high productivity (e.g., Astþórsson et al. 1983). However, the seasonal distributions and migration patterns of ISS herring exhibit periodic variation among years (e.g., Jakobsson 1980; Jakobsson and Stefánsson 1999), leading to the concern that such temperature indices might not adequately describe the thermal conditions experienced by a stock among years.

The relatively new insights provided by monitoring the variation in mesenteric fat of ISS herring are not only consistent with the analyses of the spawning time where the average MF was at minimum around day 190, they are generally consistent with Norwegian spring-spawning herring (Slotte 1999), and together they provide general implications for herring biology. The exponential rate of decay in mesenteric fat content ( $\overline{MF}$ ), as a function of  $\widetilde{RG}$ , and the seasonal cycle in  $\overline{MF}$  suggest that the fat accumulated over and above the metabolic demand during the spring feeding period and prior to spawning is used for reproduction, consistent with no accumulation of fat during the spring feeding period in March and April. However, as the fat content of gonads is generally low (Kaitaranta and Ackman 1981; Tocher and Sargent 1984) and gonad growth is mainly supplied by the translocation of proteins (Iles 1984; Bradford 1993), the fat must be responsible primarily for sustaining metabolic requirements during the prespawning season. Postspawning feeding likely provides the energy requirements needed for the overwintering period and somatic growth (Óskarsson 2008), whereas the fat remaining in the spring will presumably contribute to the pending spawning.

The herring data analysed here are derived from the commercial fleet (75%) and from research vessel surveys (25%). During the years 1953 to around 1970, most data were derived from the commercial fleet that was targeting herring during the prespawning period (Jakobsson 1980), whereas in the later years, the data were derived mainly from commercial bycatch and from research vessels. Could the results of the spawning time variation for the ISS herring be influenced by such sampling protocols that may bias the observations? The pattern of ISS herring  $\overline{OW}$  variation is very well behaved (systematic and progressive) in all circumstances, even when aggregated over years with data mainly derived from a targeted fishery (1954 through 1967) and over years derived from bycatch and research surveys (1979 through 1995). Although the occurrence of maturity stage 6 relative to stages 3 through 7 illustrates the possibility of spawning waves, closer examination of the various maxima in the distribution can be traced to particular years. For example, the maximum around days 238 to 243 is a result of four repeat spawners in 1976 and five in 1977. It does indicate that some spawning was delayed in 1976 and 1977 but only to a

small degree because postspawning fish were numerous around these days (33 fishes at stage 7 and 1600 fishes at stage 8). Further, examination of the data for the two years cited above showed that fish at maturity stage 5 (fully mature) around day 180 were as numerous as in other years. The explanation for this apparent delay in spawning in these two years is unknown, though there is no clear indication that sampling protocol is involved.

Several different methods can be used to estimate spawning time, and each is related to the purpose of the investigation. Spawning time can be estimated using abundance estimates and (or) developmental stages of eggs and (or) larvae (e.g., Einarsson 1956; Page and Frank 1989; Warlen 1994), but this excludes the ability to easily address phenotypic variation among the spawners. In some studies, oocyte size and growth and (or) development are used to estimate the spawning time (e.g., Juo and Musick 1991; Fargo and Tyler 1994; Óskarsson et al. 2002). Others focus on maturation stage (e.g., Hutchings and Myers 1994; Bleil and Oeberst 1997). Ovary growth rate or the ratio of ovary weight to body weight (the gonado-somatic index, GSI) can also be used (e.g., Ware and Tanasichuk 1989; Rijnsdorp 1991; Slotte et al. 2000). Generally, such studies rely on any one of the above methods, but typically only one. Here, we have used several methods and argue that two or more methods have the advantage of (i) overcoming data limitations, (ii) using different data sources, (iii) allowing for comparisons, (iv) validating assumptions and (or) inferences, and (v) determining consistency, including consistency with metabolic expectations. For ISS herring, the various series derived from monitoring maturity stage, ovary weight, and relative ovary weight not only illustrated spawning time variation, but also inferred consistency among years and size classes and one relatively invariant and contracted spawning time. The use of the logistic regression provided additional and consistent evidence, as well as new insights related to stock size structure and biomass.

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