

An individual-based analysis of the variability of eggs and their newly hatched larvae of Atlantic cod (*Gadus morhua*) on the Scotian Shelf

Thomas J. Miller, Tomasz Herra, and William C. Leggett

Abstract: We assessed the seasonal pattern of size variation in cod eggs on the Scotian Shelf region of the Northwest Atlantic during the period March 1991 – May 1993. Cod eggs were present from October to May during the surveys. Spawning was not strongly bimodal. There was a dominant autumn peak, in contrast to the historically dominant spring spawning. Egg diameter varied seasonally. Seasonal temperature patterns explained 52% of the variation in egg diameter. By incubating the eggs on-board ship, we also assessed the seasonality of the standard length (SL) of larvae that hatched from these eggs. Larval SL also varied seasonally. Egg diameter and SL were significantly correlated, but the correlation was weak ($r^2 = 0.3$). However, the strength of correlation was consistent with laboratory estimates based on individual data. The results suggest that previous estimates of the egg size – larval size correlations are inflated. Temperature exerted a significant effect on both egg diameter and larval size, and is hypothesized to be the agent responsible for the observed seasonal variation.

Résumé : Nous avons évalué l'évolution saisonnière de la taille des oeufs de la morue dans la région de la plate-forme de la Nouvelle-Écosse, dans le nord-ouest de l'Atlantique, de mars 1991 à mai 1993. Les oeufs de morues étaient présents dans le milieu d'octobre à mai. La ponte n'était pas fortement bimodale. On observait un pic automnal dominant, contrairement aux observations historiques faisant état d'une ponte printanière plus importante. Le diamètre des oeufs variait selon la saison. Les variations saisonnières de la température expliquaient 52% de la variation observée dans le diamètre des oeufs. L'incubation des oeufs à bord du bateau nous a en outre permis de déterminer que la longueur standard (SL) des larves issues de ces oeufs varie elle aussi selon la saison. On a observé une corrélation significative, mais faible ($r^2 = 0,3$) entre le diamètre des oeufs et leur longueur standard. Toutefois, ce degré de corrélation concordait avec les estimations établies en laboratoire à partir de données individuelles. Les résultats portent à croire que les estimations antérieures de la corrélation entre la taille des oeufs et la taille des larves sont exagérées. La température a exercé un effet significatif tant sur le diamètre des oeufs que sur la taille des larves, ce qui donne à penser qu'elle pourrait être l'agent responsable de la variation saisonnière observée.

[Traduit par la Rédaction]

Introduction

Owing to the highly variable nature of recruitment in fishes, a mechanistic understanding of its regulation has been elusive (Taggart and Frank 1990). Yet, this understanding is critical to our ability to effectively regulate and exploit fisheries (Fritz et al. 1990). Recruitment variability is thought to result from variable survival during early life stages (for reviews see Sissenwine 1984; Crowder et al.

1992). Consequently, much effort has been directed at investigating changes in abundance and mortality during this phase. However, this traditional approach has shortcomings. Bradford (1992) has pointed out that estimates of abundance and mortality rates with the precision necessary for accurate prediction of recruitment are unlikely to be achieved. Furthermore, even if the estimates are perfect, the processes controlling recruitment may not be well described by average values (Pepin and Miller 1993; Rice et al. 1993). As the

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dynamics of the average individual may not be equivalent to the average dynamics of all individuals, the use of single aggregate values may produce misleading results and predictions (Lomnicki and Symonides 1990; Chambers 1993; Pepin and Miller 1993). For example, Rice et al. (1993) demonstrated that knowledge of average growth rate is insufficient to predict survival rates in a cohort of larvae exposed to size-dependent predation. Therefore, to understand the underlying mechanisms, we must include variability among individuals. These problems with the traditional approach have led to a shift in focus toward investigating the characteristics of those few animals that do survive to recruit to the population (see reviews in DeAngelis and Gross 1992).

The variation present in egg and larval sizes, together with variability in other early life-history traits, represent the material on which sources of differential mortality can act, and from which survivors will be drawn (Chambers et al. 1988, 1989). Thus, quantifying this variation is an essential first step to determining the degree of phenotypic selection (Chambers 1993) and, ultimately, of recruitment variability. Variation in early life-history traits occurs at different levels of organization. For example, egg size varies among populations and stocks within species (Blaxter and Hempel 1963; Bagenal 1969; de Ciechowski 1973; Marsh 1984; Hinckley 1990; Buckley et al. 1991a; Bradford and Stephenson 1992 and others), among individuals within a population (Bagenal 1969; Rana 1985; Springate and Bromage 1985; Chambers et al. 1989; Kjesbu 1989; Hinckley 1990 and others), and within individuals, both over a female's lifetime and seasonally (Marsh 1984; Kjesbu 1989; Buckley et al. 1991b; McEvoy and McEvoy 1991 and others). As egg size and larval hatching size are correlated (Miller et al. 1988), there is similar variation in larval hatching size at all three levels. Moreover, variation in egg and larval size at all three levels appears to have important implications for larval survival (Bagenal 1969; Knutsen and Tilseth 1985; Rana 1985; Marsh 1986; Chambers et al. 1988, 1989; Buckley et al. 1991b; Hutchings 1991).

Atlantic cod (*Gadus morhua*) exhibit variation in egg and larval sizes at all three levels of organization outlined above. Cod are widely distributed in the North Atlantic, inhabiting coastal waters from 37°N to the sub-Arctic (Scott and Scott 1988). They are determinate spawners with high fecundity and a prolonged spawning season. Over their entire range, spawning occurs almost year round, with peak spawning activity varying among locations (Hardy 1978). In Northeast Atlantic waters, spawning typically occurs between February and April (Serebryakov and Aldanov 1984; Ellertsen et al. 1989; Hessen and Rijnsdorp 1989), whereas in Northwest Atlantic waters, spawning can peak from November to May (McKenzie 1940; Fahay 1983; Markle and Frost 1985; Brander and Hurley 1992). Cod eggs are pelagic, spherical, and vary in diameter from approximately 1.1 to 1.7 mm (Knutsen and Tilseth 1985; Markle and Frost 1985). Individual females may spawn many times in a season (Kjesbu 1989; Kjesbu et al. 1991). The mean size of eggs in the first batch of eggs produced in a season increases with the size

and age of the female (Kjesbu 1989). However, the size of eggs in subsequent batches declines (Kjesbu 1989). Egg and larval sizes are positively correlated (Knutsen and Tilseth 1985). Larval standard lengths at hatching vary between 3 and 5 mm (Hardy 1978). Larvae remain in the pelagic zone for several months, feeding principally on copepods (Skreslet 1989) and then gradually shift to the benthic habitat characteristic of the juveniles.

The Ocean Production Enhancement Network (OPEN) research programme was designed, in part, to provide detailed information on all life-history stages of Atlantic cod. One of OPEN's objectives was to quantify the variability in cod eggs and larvae in time and space. As many traits related to early survival are size dependent (Miller et al. 1988) we focus on initial size variability. Here we report the seasonal pattern in egg size and subsequent larval size of cod on the Scotian Shelf. The data we present are unique for field specimens, because they relate directly, and at the individual level, the patterns of covariance in egg size and larval hatching size.

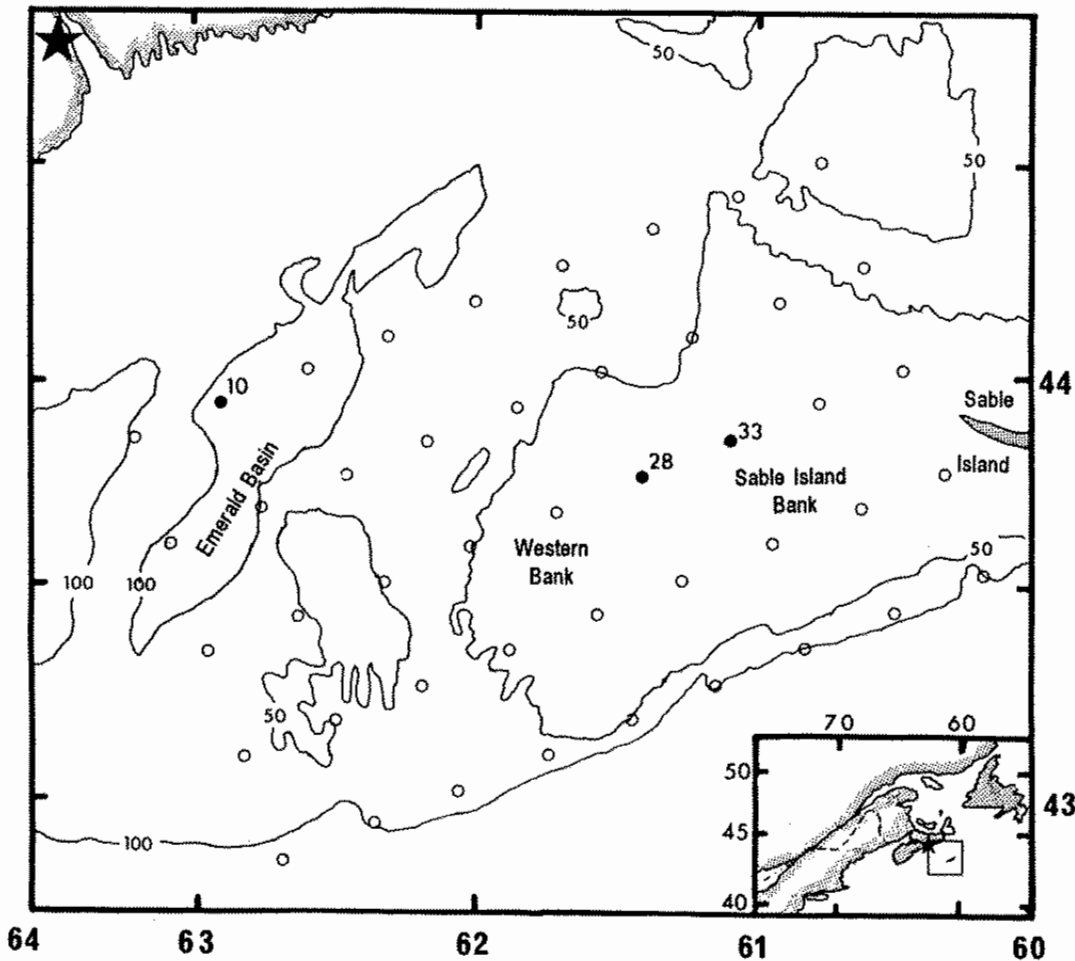
Methods

We conducted 29 cruises on the Scotian Shelf from March 1991 to May 1993 (Fig. 1). The Scotian Shelf is a coastal system characterized by a series of shallow banks and deep basins that were formed during the last glaciation. Banks are characterized by water depths of less than 50 m, and basins by depths of greater than 100 m. Maximum water depth in the area we sampled was 148 m. The shelf is affected by two currents. The Nova Scotian current brings cold, freshwater southwestward along the coast from the Gulf of St Lawrence. The Gulf Stream brings warm, salty water northeastward along the shelf break from midlatitudes. O'Boyle et al. (1984) give a general description of the Scotian Shelf system.

On twenty-six cruises we sampled a rectangular grid of 45 stations separated by a distance of approximately 30 km at monthly intervals (Fig. 1). These broad-scale survey cruises were designed to provide information on the temporal and spatial distribution and abundance of cod eggs, larvae, and juveniles. Three of the 29 cruises were designed to track a single patch of eggs and larvae over smaller spatial scales for up to 20 days to investigate the biology of the cohort over time. On these tracking cruises, stations were distributed irregularly in space.

We deployed a variety of sampling gear over the course of the study. The majority of grid stations on the broad-scale survey cruises were sampled with a fully instrumented 8 + 2 m rectangular midwater trawl (RMT) that provided continuous information on the depth, temperature, salinity, pressure and volume of water filtered during deployment (Clark 1969). The upper net dimensions (height × width × length) were 2.0 × 1.415 × 11.88 m with a 333-µm mesh. The dimensions of the main net were 2.83 × 4.0 × 9.8 m with a 1600-µm mesh. At a few stations (<10% of total), inclement weather or technical difficulties with the RMT forced us to use a paired 1.4-m² rectangular frame net, fitted with 250- and 500-µm mesh nets. On the first three broad-scale survey cruises the RMT was not available, and consequently, we deployed a 0.61-m diameter bongo

Fig. 1. Map of the Scotian Shelf. Principal banks and basins are marked. Plotted circles indicate the stations of the broad scale sampling grid. Filled circles indicate the three stations chosen for analysis of water column stability. On-bank stations were defined as those within the 50-m isopleth. ★ indicates the location of Halifax, N.S.



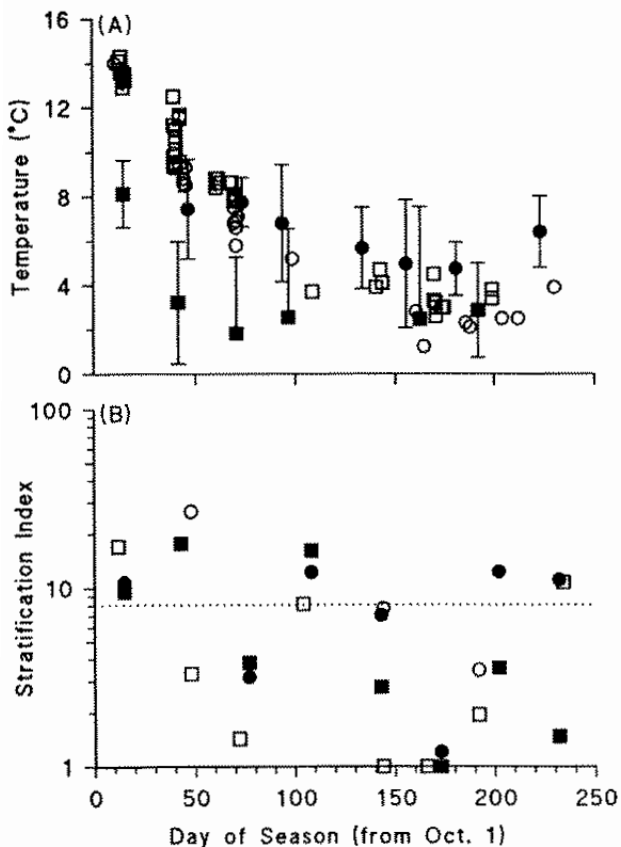
fitted with one 150- and one 250- μm mesh net. All of these gears were deployed to within 10 m of the bottom or to 75 m depth. Deployment rates were the same for all gear. If the tow duration for a single oblique tow was less than 10 min, a double oblique sample was collected. Net speeds were maintained at approximately $1 \text{ m}\cdot\text{s}^{-1}$ by regulating the ship speed. Depth information for both the bongo and frame net was estimated from cable angles and length deployed. At stations where the RMT could not be deployed, a conductivity-temperature-depth (CTD) cast was made to obtain physical data.

During broad-scale survey cruises a BIONESS was deployed at the grid station with the highest larval abundance (Sameoto et al. 1980). The BIONESS was equipped with ten, 1-m^2 333- μm mesh nets. A CTD, fluorometer, and optical particle counting system provided continuous, real-time data during deployments. The BIONESS sampled discrete 5-m depth strata in the upper 25 m of the water column and 10-m depth strata at deeper depths to within 10 m of the bottom. Each net was open for 5 min. Tow speeds were maintained at $1 \text{ m}\cdot\text{s}^{-1}$. When conditions permitted, deployments were made at 4-h intervals for 48 h.

On the three tacking cruises we deployed only BIONESS and bongos. The bongo was used to conduct a survey of the area to be tracked using the same deployment criteria as in the broad-scale survey cruises. The deployment of the BIONESS was determined by the predictions of a physical oceanographic model and occurred at irregular intervals in time and space (S.E. Lochmann Dalhousie University, Halifax, NS, personal communication, detailed sampling methodology).

The physical data from each deployment were averaged into 1-m depth intervals. Temperature data resulting from RMT and CTD casts were treated differently from those obtained from BIONESS deployments. In the former, case temperature data for that station were averaged to produce a mean temperature for the 0- to 30-m strata, the depth range typical for cod eggs on the Scotian Shelf. For BIONESS deployments, we calculated the average temperature for the period during which each net was open. The average station temperature was calculated as the average temperature of those nets that sampled the 0- to 30-m depth strata. To investigate the stability of the water column, we selected three broad-scale grid stations to represent conditions

Fig. 2. (A) Time series of seasonal variation in sea and incubation temperatures. Field temperature data are averages for the 0- to 30-m depth strata for all stations occupied during a cruise. \circ , 1991–1992; \square , 1992–1993. Cruise mean nursery incubation temperatures (solid symbols, years as above) estimated from daily recordings (mean \pm SD). (B) Stratification Index calculated from equation 1 (see text). Data station 10 for 1991–1992 is shown as \circ , and for 1992–1993 as \square . Average data for stations 28 and 33 for the period are shown as solid symbols. The horizontal line separates samples characterized by stratified conditions (index >8 , above line) from those characterized by nonstratified conditions (index <8 , below line).



on and off the bank. Station 10 ($45^{\circ}55.8'N$, $62^{\circ}56.0'W$) was chosen to represent off-bank conditions, and stations 28 ($43^{\circ}45.0'N$, $61^{\circ}26.0'W$) and 33 ($43^{\circ}50.0'N$, $61^{\circ}7.5'W$) to represent on-bank conditions. For these stations we calculated a stratification index given by

$$[1] \quad H = \left(\frac{\sigma_{t_{z=\max}} - \sigma_{t_{z=5}}}{Z_{\max} - Z_5} \right) \cdot 1000$$

where σ_t is density ($\text{kg}\cdot\text{m}^{-3}$), and z is water depth (m). Following Frank and McRuer (1989), we defined stratified waters as those for which $H > 8$. The median day was calculated for each cruise. As cod spawning begins late in the year, we chose October 1 as a reference day. Days from October 1 are used in subsequent analyses.

All net samples were sorted on-board ship and the eggs and larvae of cod and selected target species were removed. In this paper, we focus solely on the data derived from cod eggs. Late-stage eggs, that appeared healthy and undamaged by the collection process, were videotaped under a dissecting microscope at 6–50 \times magnification. Samples were sorted with a constant level of effort. A maximum of 20 eggs was videotaped from a single station. Thus, the number of eggs incubated at each station is an underestimate of the abundance of eggs at that station. However, on a cruise-by-cruise basis the number of eggs incubated on board will represent an index of egg abundance for that cruise. Individual eggs were incubated separately in 35-mL glass vials on a 12 h light – 12 h dark cycle in a refrigerator. Light from blue incandescent bulbs mimicked the light environment at depth. Nursery temperatures were recorded daily and maintained at near ambient temperature. Incubation temperatures were adjusted to the average water temperature at 0–30 m depth. BIONESS samples indicated that over 70% of the eggs we collected came from this depth layer. All eggs from the same cruise were incubated at the same temperature. However, because sea temperatures varied across the sampling grid, and with depth, there were unavoidable differences between incubation and ambient temperatures for individual eggs. Vials were checked every 12 h for hatching. When a larva hatched, it was immediately videotaped.

Videotape recordings were analyzed in the laboratory using an image analysis system (Optimas v3.11, Bioscan Corporation, Seattle, Wash.). We measured egg diameter and staged the egg according to Thompson and Riley's (1981) system. Egg diameters were calculated from three digitized points on their circumferences using the geometric formula for the diameter of an inscribed circle. Standard lengths of larvae that hatched from these eggs were measured.

All statistical analyses were conducted using SAS (SAS Institute Inc. 1985). Most analyses were conducted only on those cod eggs that hatched successfully. We restricted our analyses to these eggs because early stage cod, haddock (*Melanogrammus aeglefinus*), and witch flounder (*Glyptocephalus cynoglossus*) eggs are indistinguishable. To ensure that this procedure did not bias our results, we compared the size of all eggs that we could identify as cod, but did not hatch, to all those that successfully hatched using analysis of variance. Owing to the timing of the cruises, only the 1991–1992 and the 1992–1993 spawning seasons were fully sampled. Therefore, we restricted our analysis of the seasonal pattern in egg and larval traits to these two seasons. We asked two simple questions. (i) Is there a seasonal pattern in egg size? (ii) What is the correlation between egg and larval size? To analyze the seasonal pattern in egg diameter, and in particular, to test for bimodalities in the pattern, we used a simple sinusoidal model. We used least-squares techniques to provide parameter estimates of the equation:

$$[2] \quad \Phi_{ijt} = \beta_0 + \mu_j + \sum_{k=1}^{k=2} (\beta_{1k} \sin(k\omega) + \beta_{2k} \cos(k\omega)) + \epsilon_{ijt}$$

where Φ_{ijt} is the mean diameter of eggs (mm) from the i th station on the t th day of the j th season, μ_j is a year

effect (year was coded as a dummy variable with 1991–1992 = 0 and 1992–1993 = 1), β s are estimated parameters for $k = 1$ and 2, and ω is given by $(2\pi t_i/365)$. Significant first-order terms, i.e., $k = 1$, indicate a simple seasonal temperature effect. Significant second-order terms, i.e., $k = 2$, indicate a bimodal pattern in egg diameter. We investigated the direct effects of mean ambient station temperature on mean station egg diameter using ANCOVA with year as a class variable and ambient temperature as the covariate. We tested for homogeneity of slopes, and conditional on this finding we tested for equality of intercept.

We used standard length at hatch (SL) as our principal measure of larval size. We analyzed the seasonality and temperature dependence of SL in a similar fashion to egg diameter. To analyze the correlation between egg diameter and SL we used individual egg and larval measurements, not station means. Assuming environmental variability within a cruise to be negligible, we calculated correlations between egg diameter and SL for each cruise. As we cannot make this assumption for the full data set, we calculated partial correlation coefficients between egg diameter and SL with the seasonal (given by Eq. 2), and temperature effects removed.

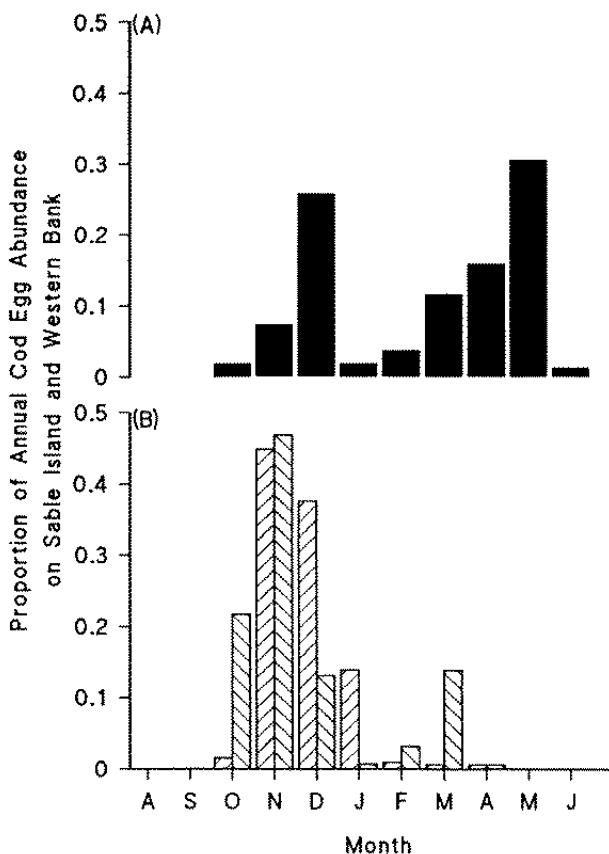
Results

The average temperature on the grid in the 0- to 30-m depth strata varied seasonally. This temperature peaked at approximately 15°C in late summer (August–September), and was at a minimum of approximately 1–2°C in March and April of both years (Fig. 2A). The maximum and minimum average temperatures observed at these depths were 19.3 and –1.2°C, respectively. Incubation temperature followed a similar seasonal cycle, but showed less variation (Fig. 2A). The water column, both on and off the bank, was generally well mixed from November to May of both years (Fig. 2B). We conclude that the 0- to 30-m temperature is a reliable index of the ambient temperature experienced by cod eggs.

On the Scotian Shelf, cod spawning was prolonged, occurring from October until May. The earliest viable egg sorted and videotaped on-board ship was collected on October 11, and the latest was collected on May 19. Eggs were not equally abundant throughout the season (Fig. 3, Table 1). Eggs were most abundant in November–December in both years in which the full spawning season was sampled.

The diameter of eggs that hatched successfully, and those that failed to hatch did not differ overall ($F_{1,637} = 1.99$, ns). The majority (>90%) of eggs incubated were stage IV, and there was no significant difference between the stages of eggs that hatched and those that did not ($\chi^2_1 = 1.6$, ns). The modal incubation time was 1 day (mean \pm SD = 1.51 ± 1.65 , maximum = 10 d). There was no effect of incubation temperature on incubation time. Overall, 57% of all eggs we incubated hatched successfully, but on individual cruises, hatching success varied from 27 to 100% (Table 1). In the 1991–1992 season there was no trend in the seasonal pattern of hatching success. However, in 1992–1993 there was a distinctly bimodal pattern in hatching success, with peaks in January and April and a trough in February. We conclude that there is no evidence that analyzing only those eggs that successfully hatched

Fig. 3. Monthly seasonal distribution of egg abundance on the Scotian Shelf expressed as a proportion of the annual production. (A) Relative abundance of stage IV eggs on Sable Island bank from SSIP data for the years 1979–1981, (after Brander and Hurley 1992; Table 2). (B) Relative abundance of stage IV eggs that successfully hatched in the ship-board nursery. Data for 1991–1992 are shown as ▨, and for 1992–1993 as ▩.



on-board ship, which we have done in all subsequent analyses, biases our results.

Cod eggs were not evenly distributed spatially across the sampling grid. The majority (87%) of all cod eggs were collected in the central region of Sable and Western banks. Autumn-spawned eggs were almost exclusively restricted to this region (97% of all eggs videotaped). The highly aggregated nature of the egg distribution meant that comparisons of egg stages and sizes between on- and off-bank stations within each cruise were impossible. However, there were no overall differences in egg stage or size between on- and off-bank samples. The small spring peak in abundance in 1993, apparent in Fig. 3, represents eggs collected on one cruise from a localized area in the southwest corner of the grid. These eggs were not different in size from those collected on the bank.

Overall, egg diameters varied from 1.19 to 1.88 mm (1.47 ± 0.11 mm). The distribution was not significantly different from normal (Shapiro–Wilks $W = 0.984$, $n = 384$, ns). Egg diameter varied seasonally (Fig. 4A). Harmonic analysis indicated a dome-shaped seasonal pattern (Table 2A). However, there was also a significant second-order term,

Table 1. Summary of eggs sorted and incubated during cruises on the Scotian Shelf from March 1991 – May 1993.

Season	Cruise dates	Median day of cruise from Oct. 1	Cod eggs incubated	% hatched	Number hatched by gear type			Size (mm) ^a		Correlation between egg and larval size, r
					RMT	BIONESS	Tucker	Bongo	Egg	
1990–1991	27/4/91–11/5/91 ^b	213	11	82	9			1.67 (0.072)	4.41 (0.86)	0.51*
1991–1992	8/10/91–17/10/91	11	3	100	3			1.29 (0.085)	4.47 (0.58)	0.98ns
	11/11/91–21/11/91	46	42	93	39			1.35 (0.11)	4.29 (0.21)	0.51***
	6/12/91–15/12/91	71	37	100	21		16	1.45 (0.079)	4.43 (0.27)	0.26ns
	6/1/92–18/1/92	99	11	100	11			1.36 (0.052)	5.04 (0.25)	0.35ns
	15/2/92–26/2/92	138	3	0				— ^c	—	—
	9/3/92–20/3/92	163	2	100	1		1	1.51 (0.11)	5.34 (0.31)	—
	4/4/92–14/4/92	187	2	100	2			1.54 (0.004)	0.52 (0.30)	—
	17/4/92–8/5/92 ^b	207	3	100			3	1.53 (0.13)	4.77 (0.31)	0.33ns
	16/5/92–26/5/92	230	1	100	1			1.41	4.87	—
1992–1993	11/10/92–19/10/92	15	184	49	9		81	1.39 (0.063)	4.04 (0.26)	0.03ns
	8/11/92–16/11/92	41	208	53	91		24	1.53 (0.064)	4.31 (0.42)	0.28**
	22/11/92–16/12/92 ^b	65	62	65			37	1.51 (0.061)	4.52 (0.30)	0.63***
	11/1/93–22/1/93	109	3	100			3	1.60 (0.051)	5.00 (0.13)	0.65ns
	16/2/93–25/2/93	143	15	27	4			1.68 (0.14)	5.11 (0.64)	0.96*
	19/3/93–25/3/93	173	61	57			36	1.60 (0.087)	5.04 (0.31)	0.69***
	16/4/93–24/4/93	199	2	100	2			1.56 (0.093)	4.65 (0.22)	—
	16/5/93–24/5/93	229	0					—	—	—

Note: Empty cells indicate that no eggs hatched for that gear type. Reported correlations between egg and larval sizes are from analyses of individual eggs and resulting larvae. Significance levels are reported as ns, not significant; * $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$.

^aValues are means with standard deviations given in parentheses.

^bCruises on which the BIONESS was the principal sampling gear.

^cValues could not be calculated.

Table 2. Regression parameter estimates of the seasonality of (A) egg diameter for the model, given by Eq. 2 (in text) for 1991–1992 and 1992–1993 and (B) SL for 1991–1992 and 1992–1993. Higher order terms were not significant.

(A) Egg diameter (overall $R^2 = 0.58$, $n = 86$, $p < 0.001$).

Parameter	Estimate	SE	$t_{(\text{coefficient}=0)}$	p
Intercept, β_0	1.36	0.034	40.30	<0.001
1st order sine, β_{11}	0.11	0.046	2.44	0.017
1st order cosine, β_{21}	-0.13	0.018	-6.86	<0.001
2nd order sine, β_{12}	0.058	0.024	2.4	0.019
2nd order cosine, β_{22}	0.018	0.026	0.69	0.49
Year, μ_j	0.10	0.018	5.77	<0.001

(B) SL (overall $R^2 = 0.74$, $n = 86$, $p < 0.001$).

Parameter	Estimate	SE	$t_{(\text{coefficient}=0)}$	p
Intercept, β_0	4.55	0.059	76.6	<0.001
1st order sine, β_{11}	0.23	0.072	3.25	<0.01
1st order cosine, β_{21}	-0.50	0.035	-14.41	<0.001
Year, μ_j	-0.066	0.055	-1.19	0.24

suggesting a bimodal pattern in egg size (Fig. 4A, Table 2A). Eggs were larger in 1992–1993 than in 1991–1992 ($\mu_j = 0.10$, $t_{\mu=0} = 5.77$, $p < 0.001$; Table 2A). Egg diameter was well correlated with ambient temperature (Fig. 4B). ANCOVA results indicated that the temperature-dependent slopes for the 2 years were equal, but that their intercepts were significantly different (Table 3A). Overall temperature and year effects explained 52% of the variation in egg diameter (Fig. 4B).

The SL of larvae that hatched from the eggs varied from 2.4 to 6.1 mm (4.39 ± 0.47 mm). The lower limit of this range may reflect prehatched individuals. SL was also normally distributed overall (Shapiro–Wilks $W = 0.98$, $n = 384$, ns). SL varied seasonally (Fig. 5A). However, year effects and second-order terms were not significant (Table 2B). There was a significant but weak correlation between SL and incubation temperature ($r = 0.1$, $n = 384$, $p < 0.001$). ANCOVA for ambient temperature indicated equality of slopes and intercepts for the 2 years (Fig. 5B, Table 3B). This infers that there is a common relationship between temperature and hatching size. Temperature accounted for 70% of the variability in SL. Correlations between egg diameter and SL for individual cruises were highly variable (Table 1). For 6 of the 12 cruises the correlation was not significant (Table 1). The lack of significance does not simply reflect small sample sizes; one of the nonsignificant correlations comes from the second largest sample. Partial correlation analysis of all of the individual egg and larval data indicated a significant correlation between egg and larval sizes (partial $r = 0.29$, $n = 373$, $p < 0.001$; Fig. 6).

Discussion

On Sable and Western banks, cod spawning was prolonged. Viable cod eggs were present from October to May in all

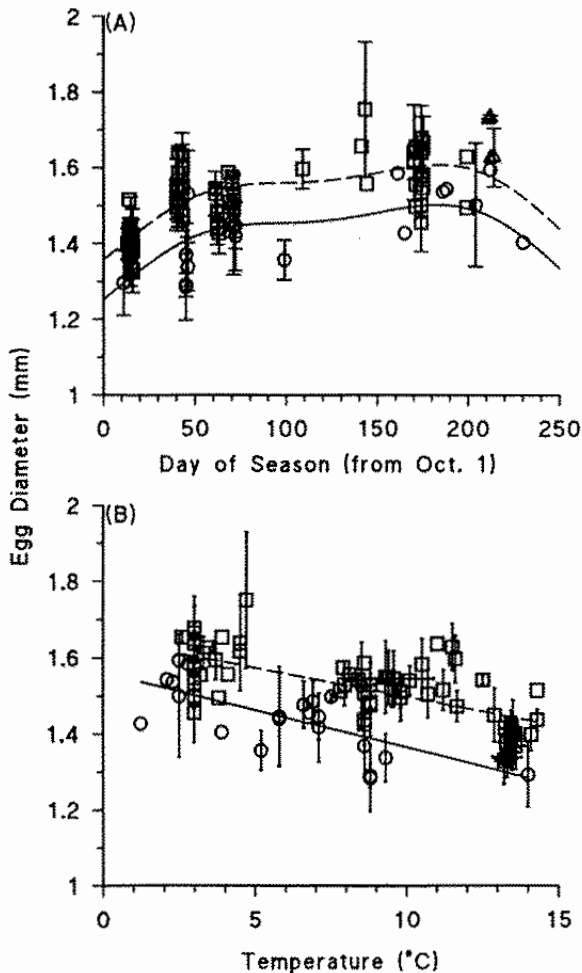
Table 3. ANCOVA of mean diameter of eggs (mm) from the i th station from the j th season collected on the r th day of that season, Φ_{ijr} , with year, μ_j (year was coded as a dummy variable with 1991–1992 = 0 and 1992–1993 = 1) and average 0- to 30-m water temperature of that station, τ_{ijr} .

Source	df	SS	F	p
Egg diameter				
Equality of slopes				
Year	1	0.11	5.33	0.023
Temperature	1	0.21	43.72	<0.001
Year \times temperature	1	0.0034	0.74	0.39
Error	83	0.39		
Equality of adjusted means				
Year	1	0.21	45.37	<0.001
Temperature	1	0.32	68.41	<0.001
Error	84	0.39		
SL				
Equality of slopes				
Year	1	0.00019	0	0.95
Temperature	1	6.05	107.6	<0.001
Year \times temperature	1	0.014	0.25	0.61
Error	83	4.66		
Equality of adjusted means				
Year	1	0.069	1.24	0.27
Temperature	1	10.61	190.56	<0.001
Error	84	4.67		

years. An earlier extensive ichthyoplankton survey conducted in this area during 1979–1981, the Scotian Shelf Ichthyoplankton Programme (SSIP), also documented prolonged spawning over a similar period (Brander and Hurley 1992). However, the SSIP data suggest a strongly bimodal spawning distribution, with a weaker peak in November and a stronger peak in April–May (Brander and Hurley 1992). We did not find evidence for a strongly bimodal spawning distribution. Moreover, in our data the autumn spawning was clearly stronger than the spring event. An otolith-based birth date frequency analysis similarly suggests a dominant autumn spawning (M.G. Meekan, Université Laval, Laval, QC, personal communication). The decline in strength of the spring cohort appears not to be a local phenomenon. In an elegant analysis of length at age 1 data from standard trawl surveys, Frank et al. (1994) show evidence for a decline in the spring cohort over the entire western Scotian Shelf from 1984 onwards. Thus, it is unlikely that our data reflect a shift in spawning location instead of a change in spawning effort.

We found substantial variability in cod egg and larval hatching sizes. Egg diameters varied by over 46% from 1.19 to 1.88 mm, and larval SLs varied by 84% from 2.4 to 6.1 mm. Egg size varied seasonally. Several features of this relationship are of importance. The overall seasonal pattern was dome shaped with smaller eggs occurring both early and late in the season. We suggest that this pattern results from the effects of the strong temperature signal on the shelf. Indeed variation in ambient temperature explains 52% of the variation in egg diameter. However, the finding of significantly different intercepts in the ANCOVA

Fig. 4. Characteristics of individual cod eggs. (A) Seasonal change in egg diameter (station mean \pm SD). Symbols without associated errors indicate only one egg collected. Symbols are: Δ , 1990–1991; \circ , 1991–1992; \square , 1992–1993 cohorts. The 1990–1991 data are shown for comparison, but were not used in analyses. Regression estimates of seasonal pattern in egg diameter, derived from Eq. 2 (see text) for 1991–1992 is a solid line and for 1992–1993 is a broken line. (B) Relationship between egg diameter (station mean \pm SD) and mean 0- to 30-m temperature. Symbols as in A. Fitted regression, derived from ANCOVA after evaluating equality of slopes, is $\Phi_{ij} = 1.59 - 0.016\tau_{ij} + 0.12\mu_j$, $r^2 = 0.52$, $n = 86$, $p < 0.001$.



results indicates that temperature cannot be the sole mechanism influencing egg diameters. There was some evidence of bimodality in egg diameter, with the later (spring) mode exhibiting larger predicted maximum egg sizes. The presence of the two peaks may reflect the historical bimodal spawning pattern. Alternatively, the bimodal pattern may be a statistical artifact of the temporal distribution of our collections, especially given the lack of bimodality in the SL data.

Our data do not exhibit the simple declining seasonal egg size reported for Northeast Atlantic cod by Knutsen and Tilseth (1985). We suggest the difference between the pattern in the Northwest and Northeast Atlantic reflects

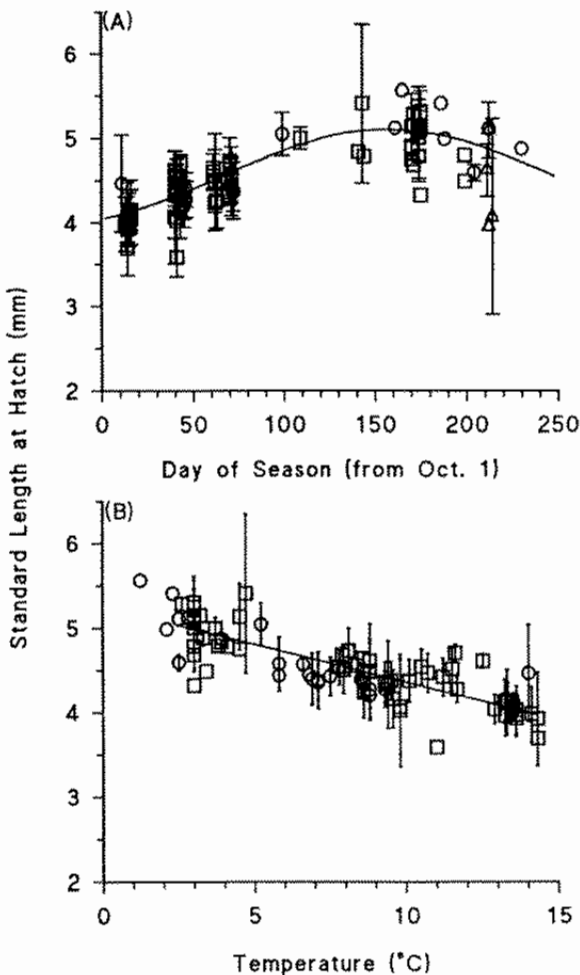
the lengths of the two spawning seasons. In Scotian Shelf waters cod spawn over 6 months, in temperatures between 1 and 14°C. In Northeast Atlantic waters, the duration of spawning is reduced to the spring period only when water temperatures are increasing from their minimum to approximately 5°C (Ellertsen et al. 1989; Hessen and Rijnsdorp 1989). Thus, the seasonal pattern of egg diameter for Northeast Atlantic cod may simply represent the descending arm of the entire seasonal pattern for Scotian Shelf cod.

Page and Frank (1989) provide data on cod incubation times as a function of temperature. Their data suggest that for cod eggs on the Scotian Shelf incubation times vary from 8 to 42 days at 14 and 1°C, respectively. This fivefold difference in incubation time may have important implications for egg survival and recruitment, particularly given the apparent reduction of the historically dominant spring spawned cohort. If egg survival is related negatively to incubation time, the survival from the autumn spawning peak that now prevails could be dramatically inferior to that which has occurred historically.

Egg and larval sizes were positively correlated. However, the relationship is not simple. The strength of correlations varied widely from cruise to cruise. In general correlations became weaker as sample sizes increased. These correlations ignore seasonal effects. When we removed seasonal effects, egg diameter explained 30% of the variation in larval SL. Laboratory studies suggest that egg size is highly correlated with larval hatching size (Miller et al. 1988). However, this expectation is derived from analyses based upon group means. The r^2 we obtained, 30%, is not markedly different from that derived from an analysis of capelin conducted at the individual level (Chambers et al. 1989). Furthermore, traditional studies that have reported higher r^2 have commonly exposed the eggs to a constant temperature, and the data are often derived from restricted brood stocks (R.C. Chambers Huntsman Marine Laboratory, St. Andrews, NB, personal communication). In contrast, in the field, individual eggs from different females co-occur and are exposed to a variable temperature regime. We suggest this acts to uncouple egg and larval size. For example, while we observed significant inter-year differences in egg diameters, we failed to detect this effect in the larvae that hatched from these eggs. Thus, a given size of larvae was produced by different egg sizes in the 2 years we studied in detail. Together, these genetic and environmental factors should increase the expected variance in the egg size – hatching size relationship and lead to a lower correlation coefficient.

If cod eggs and larvae are subject to size-dependent processes on the Scotian Shelf, the variation we document may have substantial survival consequences. There are several potential implications of size variability. If egg predation is size dependent, larger eggs may be more vulnerable to predation. Larger eggs also incubate for longer periods (Chambers et al. 1989). Thus, larger eggs will be vulnerable to predators for longer periods than are small eggs. Consequently, larger eggs could experience lower survival than smaller eggs. North Sea cod that are larger at hatching have relatively larger yolks, and improved foraging abilities (Knutsen and Tilseth 1985). Thus, larger larvae may be less restricted in the timing of first feeding and the size of prey eaten. Furthermore, analyses for other

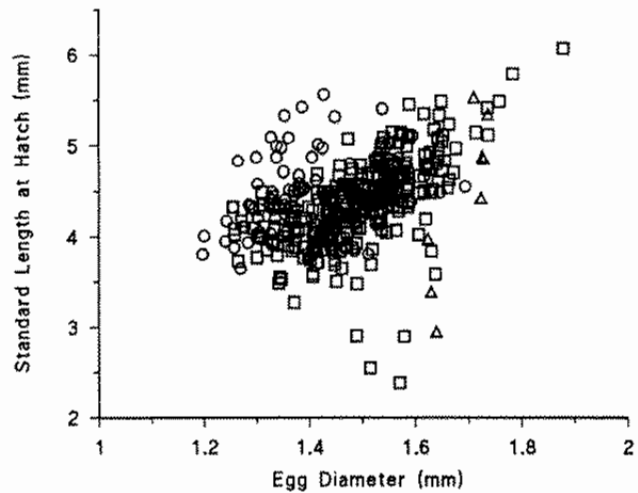
Fig. 5. (A) Seasonal change in standard length (station mean \pm SD) at hatching. Symbols as in Fig. 4. (B) Relationship between SL (station mean \pm SD) and mean 0- to 30-m temperature. Symbols as in Fig. 4. Fitted regression, derived from ANCOVA after evaluating equality of slopes, is $\Phi_{ijt} = 5.2 - 0.091\tau_{ijt}$, $r^2 = 0.70$, $n = 86$, $p < 0.001$.



species based on group mean sizes also suggest such an advantage (Rana 1985; Marsh 1986; Miller et al. 1988). Yet, Chambers et al.'s (1989) analysis of individual-level data conflicts with such an expectation, so it is unclear whether increased size will translate into increased resistance to starvation. Similarly, the effects of increased larval size on vulnerability to predation are unclear. Litvak and Leggett (1992) and Pepin et al. (1992) suggest that small larvae may experience lower overall predation rates. However, once subject to an encounter, larger larvae do have an increased ability to escape (Miller et al. 1988).

What are the implications of our findings for cod recruitment on the Scotian Shelf? The timing of spawning has been suggested as being influenced by the seasonal pattern in productivity on the shelf (Gagné and O'Boyle 1984; O'Boyle et al. 1984; Brander and Hurley 1992). However, these authors differ in the extent to which they attribute the timing of spawning to a match between larvae and potential prey. If spawning is strongly keyed to the abundance

Fig. 6. Relationship between egg diameter and standard length of larvae that hatched from that egg. Data for 3 years are presented, but only data for the last two were used in the analysis. Symbols are as in Fig. 4.



of prey, the reduction in the spring cohort documented here may reflect changes in the ecology of zooplankton on the bank. Alternatively, the change in spawning distribution may reflect underlying changes in the adult population. If the historical bimodality in spawning reflected two separate populations using the bank, the reduction in the spring cohort may result from dramatic changes in one of these two groups. However, if only one population spawns on the bank, the shift in the spawning distribution may reflect changes in the size or age structure of the population. Evidence from DFO groundfish surveys supports the latter possibility (Mohn and MacEachern 1993). These data suggest a dramatic decline in the abundance of older and larger females in the population since the SSIP cruises. This could account for the observed reduction in spring spawning. However, until the spawning biology of these stocks is fully understood, we cannot distinguish between these alternatives.

In summary, we have shown considerable phenotypic variation among individual cod eggs and larvae on the Scotian Shelf. Importantly, we report one of the first examples of longitudinal data collected on individuals caught in the field. The data, thus, represent the first accurate field examination of the initial variability in egg and larval sizes in a population. Our data suggest that there is considerable potential for phenotypic selection among individual cod eggs and larvae of different sizes on the Scotian Shelf. The selection in individual variability has the potential to significantly influence individual survival and possibly the pattern of recruitment in the population.

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