Spatial variability in distribution and growth of juvenile and adult sea scallops, Placopecten magellanicus (G.), on eastern Georges Bank (Northwest Atlantic).

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Spatial variability in distribution and growth of juvenile and adult sea scallops *Placopecten magellanicus* (Gmelin) on eastern Georges Bank (Northwest Atlantic)

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ABSTRACT: Spatial distribution of juvenile and adult sea scallops *Placopecten magellanicus* (Gmelin) was studied from video-monitored sled-dredge samples in commercial scallop beds of eastern Georges Bank (Northwest Atlantic). Maximum densities of 1 and 2 yr old individuals, as well as of adults, were recorded in the northern area of the study. Abundance of scallops was significantly higher on gravel than on the other sediment types. Scallops appeared to exhibit a Poisson distribution within sediment type. Distribution of juveniles only partly matched that of adults; age 1 individuals were less dispersed than 2 yr olds and adults, and were mainly located on a gravel-pebble deposit in the northern half of the Bank. It is inferred that movements associated with tidal currents occur as the individuals grow older. The relative abundances of pre-recruits and recruits emphasize the impact of fishing activity on size structure. Growth parameters of the von Bertalanffy function would indicate that Lee's phenomenon acts on the population. Age 2 juveniles showed a strong depth-related decrease in shell growth, linked to temperature and probably to food availability. The sampling technique employed has the potential for establishing pre-recruitment indices for use in management of this fishery.

INTRODUCTION

The sea scallop *Placopecten magellanicus* (Gmelin, 1791) supports a valuable fishery throughout its geographic range along the east coast of North America (Posgay 1957). Georges Bank, an offshore bank in the Northwest Atlantic between latitudes 41 and 42° N, normally provides more than 50 % of the landings (Serchuk et al. 1979). Commercial concentrations generally occur at depths of 40 to 100 m (Brown 1987). Since the early 1950's there has been continuous exploitation by both Canada and the United States, with important variations in landings (Sinclair et al. 1985). The establishment of a 200 mile (370 km) fishing zone by both countries (in 1977) increased competitive fishing pressure on the stocks, as respective claims overlapped on the Bank's northeastern corner. As a result of increased fishing effort, the fishery concentrated more on incoming recruitment, and annual harvests fluctuated depending on year-class strength (Brown 1987). Despite the stock-rehabilitation strategy, fluctuations in the exploitable biomass will continue, since environmental factors may generate strong variability in year-class strength even under conditions of high adult spawning abundance (Mohn et al. 1988).

Establishment of pre-recruit (ages 1 and 2) indices would enhance predictive capacity under the enterprise allocation scheme of the Canadian fishery management strategy (Robert & Black 1990). Stock assessment surveys give relative abundance indices only for sea scallops above 35 to 40 mm shell height, i.e. in their third year of life (Serchuk & Wigley 1986). Furthermore, several aspects of the species' early life history are still poorly understood. Larval dispersion patterns have been recently studied on the Bank (Tremblay & Sinclair 1990), but quantitative data on post-larvae and

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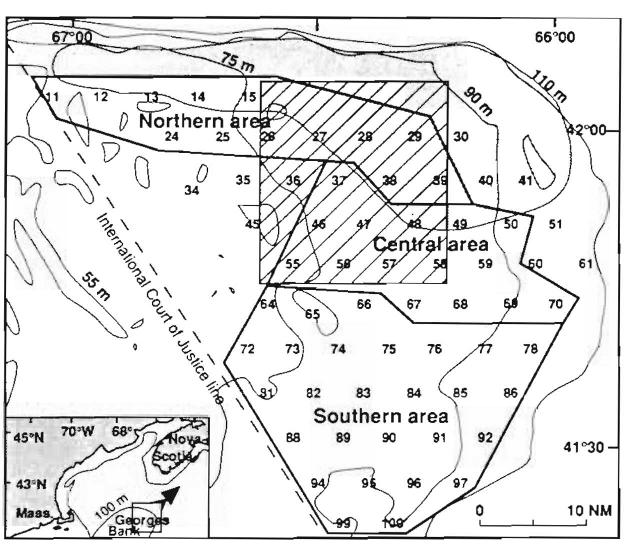
juveniles younger than age 3 are rare (Larsen & Lee 1978). Settlement patterns and distribution-regulating factors on the Bank are not well understood; some post-larvae have been found byssally attached to hydrozoans, amphipod tubes and sand grains, but they accounted for a small proportion of the individuals collected (Larsen & Lee 1978). Growth of the early benthic stages seems to be highly variable, since mean sizes at the first and second rings range from 1 to 8 mm and from 18 to 25 mm, respectively (Merrill et al. 1966, Merrill & Posgay 1967, Larsen & Lee 1978, Posgay 1979a, Serchuk et al. 1979, Mohn et al. 1988). Decreasing shell growth with increasing depth has been reported for adults by Posgay (1979b), but neither spatial variations in juvenile growth nor growth-regulating factors have been established for Georges Bank.

This study presents the first published data on distribution, abundance and growth of juvenile sea scallops on the Canadian side of Georges Bank. The specific objectives were to locate the distribution areas of ages 1 and 2, to define growth characteristics and spatial variations within the Bank, and to examine distribution- and growth-regulating factors using published data on the Bank's environment and on behaviour patterns of post-larvae and juveniles. The study also evaluates the impact of fishing activity on the size structure and growth parameters of the population, and the potential of the sampling technique for estimating pre-recruit abundance.



Sampling area of age 2 sea scallops, according to a grid design

Fig. 1. Location of stations sampled with the AQUAREVE III in August 1989 on Georges Bank (Northwest Atlantic). Shaded area: pebble gravel deposit, as outlined in Lough et al. (1989). The sampling area was divided into 3 zones (northern, central and southern) to calculate mean densities of sea scallops. Age 2 scallops were also collected with a research scallop dredge to determine spatial variability in juvenile growth. NM: nautical miles

MATERIALS AND METHODS

Study sites and sampling technique. The field work was carried out on the RV 'E.E. Prince', between 23 and 29 August 1989, from 41°23'30" to 42°03'30" N and from 65°56'30" to 67°02'30" W (Fig. 1). The bottom-sampling gear used was the AQUAREVE III (Application QUAntitative d'un Rabot Epibenthique avec contrôle Vidéo de l'Echantillonnage; Thouzeau & Hily 1986), adapted from gear developed for sampling *Pecten maximus* (L.) juveniles (Thouzeau & Lehay 1988, Thouzeau 1989). The AQUAREVE (Fig. 2) works like an epibenthic sled-dredge, sliding on the bottom (tow speed 1 to 1.5 knots) while its knife slices the upper 5 cm of sediments. The working of the dredge is monitored via an underwater video camera (LVC-480 CCD B&W Cohu camera, with 100° diagonal view field) mounted on the sled and turned toward the opening of the box. While in operation, instantaneous picture transmission to the ship allows the tow to be stopped before the box overfills, and the dredging efficiency to be controlled. Two external video lights (2 × 250 W, 110 V, model VLS-400) spotlight the mouth of the dredge. Distance travelled on the bottom is measured by an odometric wheel; the sensor is a magnetic switch linked to an impulse counter (1-unit increase for each odometer wheel revolution) on board. In spite of a resonance artifact due to the magnet, the odometer gives a precise estimate of tow length, as the double impulses are easily detected on the counter. The opening of the dredge is 1.0 m wide × 0.4 m high. The collecting box is a rectangular steel box drilled with regularly spaced holes of 10 mm diameter; a box closing device adapted from Aldred et al. (1976) triggers when the sled leaves the bottom. The sled is towed by an electromechanical cable (steel-armoured cable, reference no. A300813, Rochester Co., Culpeper, Virginia, USA; single co-ax, 11 single conductors, belt and steel armor in a double layer with right and left helix). Electronic equipment on board includes: (1) power supplies for the camera (12 V DC), the detector (24 V DC) and the lights (0 to 110 V AC); (2) a 9 in. (23 cm) monochrome monitor (OVM-9E); (3) a video cassette recorder and (4) an impulse counter.

Once on board, the samples were washed, sorted (mechanical sorting table; grid with 10 mm diameter holes), and preserved in 70 % ethanol (juveniles) or frozen (−5 °C; adults).

Targeted fauna and sampling design. Megabenthic animals retained by the 10 mm holed grid – specifically 1 yr old *Placopecten magellanicus* – were the targeted fauna. In August, Georges Bank age 1 scallops were expected to measure about 15 mm in shell height (Merrill et al. 1966, Serchuk et al. 1979, Mohn et al. 1988). Loss of some of the smallest juveniles (< 10 mm)

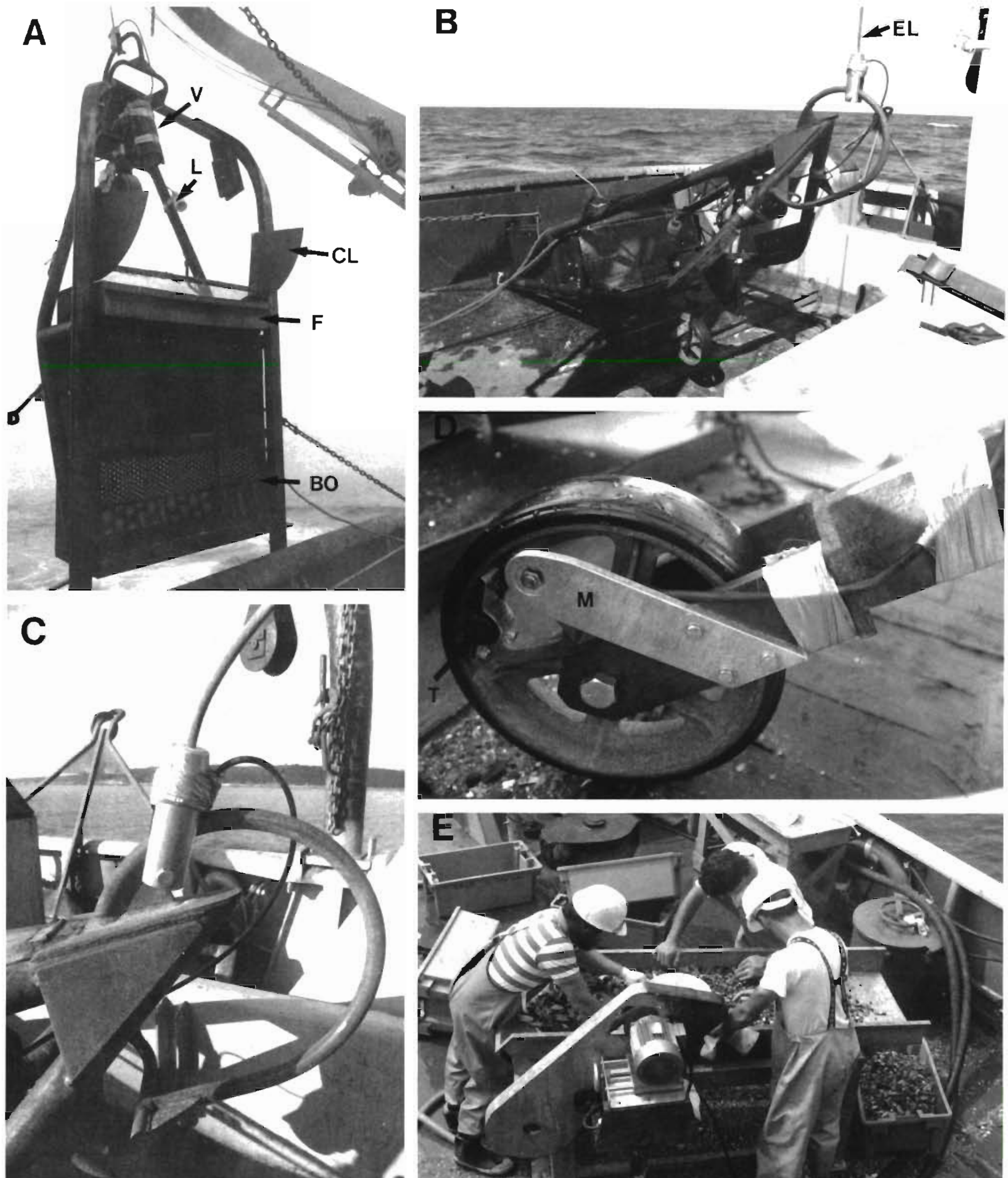


Fig. 2. AQUAREVE III sampling gear. (A & B) Sled-dredge structure. BO: collecting box; CL: box closing device; EL: electromechanical cable; F: straight-edge knife; L: video light; V: video camera. (C) Stainless steel towing bullet with wirelock cement. (D) Odometric wheel. M: magnetic switch plate; T: trigger. (E) Sorting table

was expected, due to dredge selectivity. Hole diameter could not be decreased, however, because of the duration of the sorting process.

A 2-dimensional systematic lattice sampling scheme (Frontier 1983) was used because little was known about the distribution and behaviour of sea scallop post-larvae and juveniles (see Larsen & Lee 1978, Melvin et al. 1985, Caddy 1989). Furthermore, sediment types in the sampling area are not well described (Lough et al. 1989). Thirteen latitudinal transects were initially defined, spaced 4 nautical miles apart. Sampling stations were located at 4.5 nautical mile intervals along these lines. The 110 m isobath was defined as the outer limit of the sampling area, since *Placopecten magellanicus* rarely occurs in deeper waters, and usually not in commercial quantities (Posgay 1979a). The stations were positioned in alternate rows (Fig. 1) so that the distance between them was maximum; this avoids redundancy and information gaps, as may occur with a random sampling design (Frontier 1983). Of 99 potential stations within the 110 m isobath east of the International Court of Justice (ICJ) line, operational constraints due to bottom type, time available, and inclement weather reduced coverage to 65 stations (Fig. 1). A total area of 1776 m^2 was sampled. Mean sample size was 25.1 m^2 (SD = 9.4 m^2), with a range of 11 to 50 m^2 according to sediment type.

Several samples of age 2 sea scallops were also collected during the annual stock assessment survey (17 to 22 August 1989), to determine spatial variability in juvenile growth. Use of a research scallop dredge allowed a greater sample size to be obtained, compared to the sled-dredge. Samples were collected within a grid of 64 stations (8 latitudinal transects, 8 stations per line; Fig. 1).

Data analyses. Shell height of sea scallops, i. e. the maximum distance between the dorsal (hinge) and ventral margins (Seed 1980), was recorded to the nearest 0.1 mm using vernier calipers. Individual ages were estimated by interpreting external growth rings on the shells, after removing epibionts (Stevenson & Dickie 1954, Merrill et al. 1966). This technique is fairly reliable for scallops up to age 7, although disturbance or shock marks between annual rings might lead to age overestimates (Krantz et al. 1984, Tan et al. 1988).

The effect of sediment type on spatial distribution of sea scallops was investigated using the methods discussed in McCullagh & Nelder (1989). The number of scallops caught in each tow was expressed as number per m^2. A preliminary plot of the total number of scallops per m^2 indicated that the mean number for each sediment type was proportionate to the associated variance, implying that the Poisson distribution would be a reasonable model for the random effects in the data; that is, the number of scallops per m^2 (y_{ij}) was assumed to exhibit a Poisson distribution within a given sediment type, so that $y_{ij} \approx P(\lambda_i)$, where i indexes sediment type, j indexes sample number and λ_i is the mean for the ith sediment type. If the mean numbers of scallops per m^2 do differ over i then the distribution of y_{ij}, ignoring the effect of sediment, is a mixture of Poisson distributions which is indistinguishable from a negative binomial distribution. The equality of means across sediment type was tested using an analysis of deviance (McCullagh & Nelder 1989) and parameter estimates were obtained using GLIM (generalized linear interactive modelling) software (Payne 1985). The expected number of scallops per m^2 was expressed as an exponential function of sediment type. The exponential ensures that the predicted number of scallops is ≥ 0. Note that we are assuming the distributions of scallops to be Poisson at the m^2 level, and therefore the total count obtained from the dredge represents a sum of Poisson random variables. Given that the distribution of the sum of Poisson random variables is also a Poisson (Johnson & Kotz 1969), then adjusting by a constant to the m^2 level should still yield a Poisson-distributed random variable.

The von Bertalanffy function was fitted to shell growth data according to the Gaschütz procedure (Gaschütz et al. 1980). This allows weighting of the data according to the number of individuals per age-class, and estimation of the coefficient of determination. Mean shell heights for each age-class were estimated using the equation: $H_t = H_\infty[1 - e^{-k(t-t0)}]$, where H_t = shell height at time t, H_∞ = mean asymptotic shell height, k = the Brody growth coefficient and t_0 = time when shell height equals zero. Sea scallops were assigned a biological birth date of 1st October of the year in which they were born (Posgay 1959). Thus, 12 mo old juveniles are referred to as age 1 individuals in this study. Spat were assigned a settlement date of 1st December, to calculate average growth rates.

The depth-related size frequency distributions of age 2 juveniles were compared using a 1-way analysis of variance (unbalanced designs; SYSTAT package, Systat, Inc., Evanston, Illinois, USA).

RESULTS

Spatial distribution

The sampling area (Table 1) was divided into 3 main zones (Fig. 1), based on sediment type and location. Gravel and pebbles (particle size 2 to 15 mm and 15 to 64 mm respectively, similar to the scale in Buchanan & Kain 1971) were observed in the northern area; sand mixed with gravel was observed in the central part, and sand in the southern half. Mean densities were calculated for

Table 1. Benthic sampling stations, total numbers of scallops *Placopecten magellanicus* caught and mean density per station (ind. $10m^{-2}$) of ages 1, 2, and 3 to 7. Samples were collected on eastern Georges Bank (Northwest Atlantic) between August 23 and 29 1989. MS: medium sand; CS: coarse sand; MiSe: mixed sediments; G: gravel; P: pebbles; R: cobbles and boulders; BB: biogenic bottom (admixture of gravel, sands and polychaete tubes); (•) indicates sand dunes (sand waves and megaripples). See Fig. 1 for stations

Stn no.	Depth (m)	Sediment type	Area sampled (m^2)	Total scallops caught	Density		
					Age 1	Age 2	Age 3+
11	57	CS	17	6		0.6	3.0
12	58	CS	11	2			1.9
13	66	MiSe	17	10		1.2	4.9
14	66	P + G	14	21	3.7	5.9	5.2
15	71	G	24	22	2.9	3.3	2.9
24	62	P + G	26	35	5.4	5.0	3.1
25	66	G + R	15	14	2.8	4.1	2.1
26	79	MiSe	19				
27	77	G	14	35	6.2	10.3	7.6
28	77	G	17	22	3.6	7.9	1.2
29	77	G + P	18	2			1.1
30	84	BB	20				
34	66	•CS	11	1	0.9		
35	66	MiSe	23	1		0.4	
36	73	•MiSe	14				
37	82	MiSe	17	3		1.1	0.6
38	75	G + P	14	15	6.6	2.2	2.2
39	77	G + P	15	34	11.7	0.7	11.0
40	84	MiSe	9	1			1.2
41	91	BB	12				
45	68	MiSe	34				
46	75	CS	36	4		0.3	0.8
47	80	R	44	1			0.2
48	80	G	29	26	2.8	1.0	5.2
49	80	G + R	22	17	2.7	2.2	2.7
50	90	MiSe	14	9		5.0	1.5
51	88	•MiSe	17				
55	77	CS	27	2			0.7
56	75	P + R	34	12	0.6	1.5	1.5
57	77	G	18	8	1.1	0.6	2.9
58	80	MiSe	17	9	0.6	0.6	4.3
59	82	MiSe	15	1			0.7
60	91	•MS	30	2	0.3		0.3
61	101	•MS	18	1			0.5
64	66	•MS	51				
65	69	•MS	27				
66	75	MS	24				
67	80	MS	27	7		1.1	1.5
68	84	G	36	15	0.6	1.7	2.0
69	91	MS	20	4		0.5	1.5
70	90	MS	50	6			1.2
72	60	•MS	31				
73	68	•MS	31				
74	75	MS	35				
75	79	MS	51	9		0.4	1.4
76	84	MS	48	2		0.2	0.2
77	91	MS	32	1	0.3		
78	88	MS	23	1	0.4		
81	77	MS	34				
82	79	MS	30				
83	82	MS	26				
84	82	MS	29	3		0.3	0.7
85	90	MS	34				
86	91	MS	23				
88	82	MS	29				
89	86	MS	55	1			0.2

Table 1 (continued)

Stn no.	Depth (m)	Sediment type	Area sampled (m^2)	Total scallops caught	Density Age 1	Density Age 2	Density Age 3+
90	88	MS	32	1			0.3
91	86	MiSe	15	2		1.3	
92	97	MS	26	3		0.8	0.4
94	90	MS	15	2			1.3
95	91	MS	24	3	0.8		0.4
96	88	MS	40	1			0.3
97	104	MS	39				
99	88	MS	24	1			0.4
100	90	MS	14				

Table 2. *Placopecten magellanicus.* Spatial variability in abundance of sea scallops on Georges Bank. Densities (per 10 m^2) are given as mean ± SD. The different zones are outlined in Fig. 1

Age-class	Northern area	Central area	Southern area
Age 1	3.60 ± 3.36	0.41 ± 0.52	0.04 ± 0.16
Age 2	3.43 ± 3.18	0.95 ± 0.97	0.11 ± 0.29
Ages 3 to 7	3.86 ± 2.80	1.82 ± 1.36	0.21 ± 0.37
Total	10.9 ± 7.10	3.18 ± 2.25	0.37 ± 0.52

each zone (Table 2). The remaining stations had either sand dunes (Stns 34, 36, 51, 60, 61), rocks (Stns 35, 45, 47, 56) with cobbles (64 to 256 mm particle size) and boulders (> 256 mm), or biogenic bottom (Stns 30, 40, 41; sediment consisted of an admixture of sands, gravel and tubes of the polychaete *Filograna implexa*). The distribution of *Placopecten magellanicus* (Fig. 3) showed maximum adult densities (age 3+) in the northern area, intermediate values in the central zone within the 75 to 110 m depth range, and low values in the southern area (Table 2). Age 1 and 2 juveniles exhibited patterns similar to those of the adults, but were less dispersed (few individuals in the southernmost stations). Juveniles were mainly found on gravel (0.88 to 1.65 ind. m^{-2}) at depths from 62 to 91 m. Furthermore, the small-scale distribution of age 1 in the northern half of the Bank was clearly related to sediment type. In a given area, juvenile sea scallops were more abundant on gravel beds than on mixed sandy bottoms (Stns 14, 15, 24, 25 vs Stns 11, 12, 13, 26, 34, 36; Stns 28, 29, 38, 39, 48, 49 vs Stns 37, 50, 51, 58, 59, 60; Figs. 1 & 3). Low densities of age 1 juveniles were found at rocky stations (35, 47, 56), but not on biogenic bottom.

Results of the analysis of deviance to evaluate the statistical significance of sediment type are given in Table 3. The theory of generalized linear models is

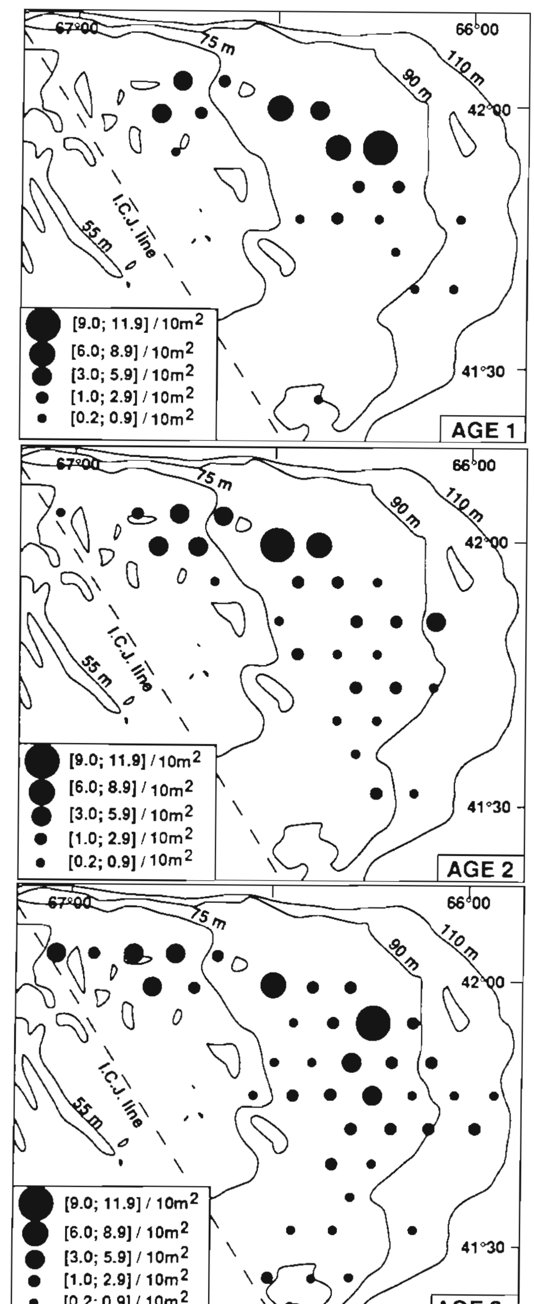


Fig. 3. *Placopecten magellanicus.* Distribution of sea scallops (ages 1, 2, and 3 to 7) on eastern Georges Bank. Samples were collected with the AQUAREVE III in August 1989, and catches were standardized to numbers of individuals per 10 m^2 (upper and lower limits shown for each symbol size)

based on the measure of the discrepancy between observations and the fitted values from a model, calculated from the logarithm of the ratio of the respective likelihoods as deviance (McCullagh & Nelder 1989). The significance of the amount of deviance explained by sediment type was assessed by a χ^2 test; sediment type did explain a significant portion of the deviance (Table 3a). The parameter estimates (Table 3b) indicate

Table 3. Results of fitting a Poisson model to the frequency distribution of the total number of sea scallops *Placopecten magellanicus* caught in each tow of the sled-dredge AQUAREVE III. Variables as follows: Mean = Grand mean; Sediment = bottom sediment type; the p-level refers to a χ^2 statistic; Mixed = mixed sediments; Coarse = coarse-grain sand; Gravel = gravel-pebble deposit; Cobbles = cobbles and boulders plus biogenic bottoms; Medium = medium-grain sand

(a) Analysis of deviance for Poisson error with log link:

Model	First difference in deviance	df	p-level	Scale
Mean				0.6379
+ Sediment	28.32	4	<0.0001	0.2084

(b) Parameter estimates for final model: Mean+Sediment:

Parameter	Estimate	Standard error
Mean	−1.819	0.507
Mixed-Coarse	0.163	0.589
Gravel-Coarse	1.926	0.521
Cobbles-Coarse	−0.546	0.900
Medium-Coarse	−1.152	0.621

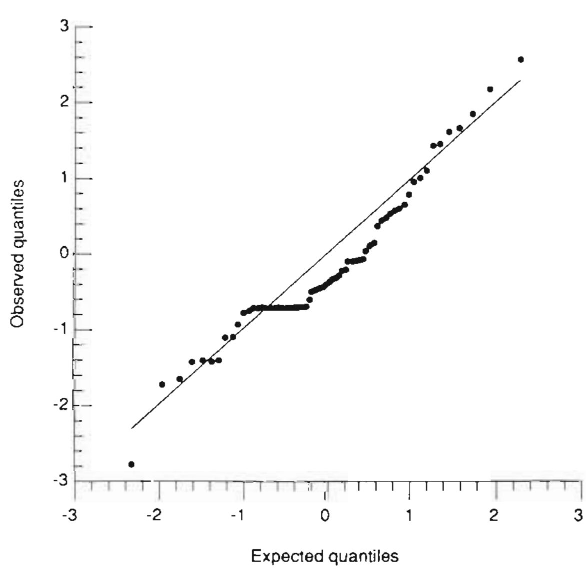


Fig. 4. *Placopecten magellanicus*. Quantile-quantile plot of scaled deviance residuals from the Poisson model for sea scallops (ages 1 to 7) caught with the AQUAREVE III in August 1989. Catches were standardized to numbers of individuals per m^2

that the sediment effect was mainly due to more scallops being found on gravel than on coarse-grain sand. Differences between the other sediment types and coarse sand were much smaller. All the differences are expressed on a logarithmic scale.

The distribution of deviance residuals should be approximately normal if the random component of the model is reasonably similar to patterns in the data (Pierce & Schafer 1986). The quantiles of the scaled deviance residuals (McCullagh & Nelder 1989) from

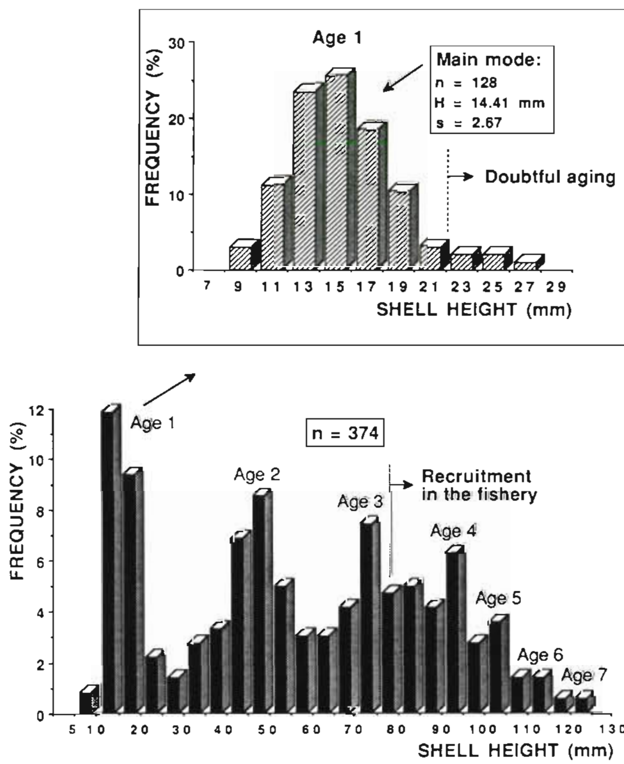


Fig. 5. *Placopecten magellanicus*. Size-frequency distribution of sea scallops sampled with the AQUAREVE III on Georges Bank (23 to 29 August 1989). Size distributions are shown for all year-classes sampled and age 1 individuals (detailed). Age at recruitment also indicated. n: number of scallops; H: mean shell height; s: standard deviation

Table 4. *Placopecten magellanicus*. Mean shell height per age-class (plus 95 % confidence intervals, CI) of sea scallops collected with the AQUAREVE III on Georges Bank (August 23 to 29 1989)

Age-class	No. of individuals	Mean shell height (mm)	SD	95% CI
1	98	14.39	2.71	13.94–14.88
2	112	44.52	7.82	43.05–45.99
3	81	72.00	6.06	70.66–73.34
4	50	89.52	3.85	88.43–90.61
5	21	101.71	2.53	100.56–102.86
6	9	112.00	2.74	109.89–114.11
7	3	121.00	1.41	116.71–125.29

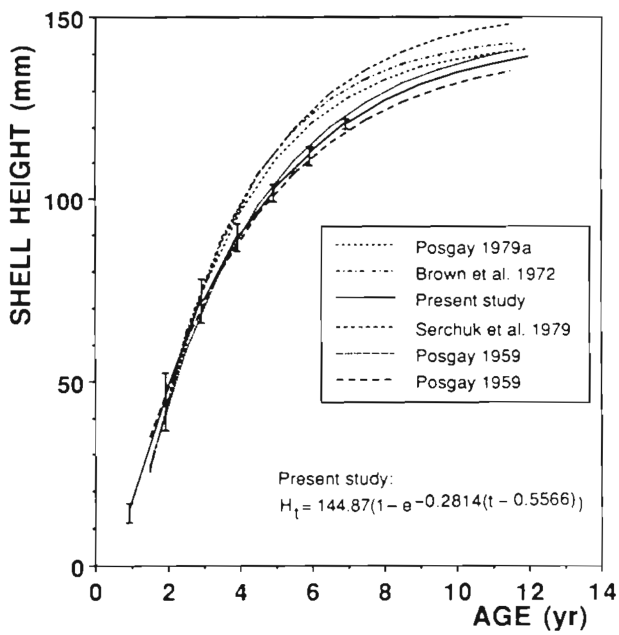


Fig. 6. *Placopecten magellanicus.* Age-specific shell heights fitted to von Bertalanffy equations for sea scallop populations from Georges Bank, according to different studies. Mean height and 95 % confidence intervals are added to the growth curve from the present study

Table 5. *Placopecten magellanicus.* Parameters of the von Bertalanffy equations describing shell height (H, mm) as a function of age (yr) in sea scallops from Georges Bank. Data fitted to the equation $H_t = H_\infty[1 - e^{-k(t-t_0)}]$, where H_t = height at age t; H_∞ = mean asymptotic height; k = Brody growth coefficient; t_0 = a parameter representing time when $H_t = 0$. n: no. of observations

Source	H_∞	k	t_0	n
Posgay (1959)	146.5	0.30	1.32	426
Posgay (1959)	141.8	0.28	1.00	254
Posgay (1962)	148.9	0.26	1.0	NK
Brown et al. (1972)	145.5	0.38	1.50	NK
Posgay (1979a)	143.6	0.37	1.00	7000
Serchuk et al. (1979)	152.46	0.3374	1.4544	NK
Present study	144.87	0.2814	0.5566	374

the model were compared with expected quantiles from a normal distribution (Fig. 4). Deviations from the normal appear to be slight, and therefore we can assume that the Poisson distribution is a reasonable model for the random component.

Size-frequency distribution and shell growth rate. Size of sea scallops collected with the sled-dredge ranged from 9 to 122 mm in shell height (Fig. 5). This corresponded to 7 age-classes (Table 4), of which age 1 (26.2 %) and age 2 (29.9 %) made up 56 % of the total. Mean shell height of 1 yr olds in August was 14.4 ± 2.67 mm. The height ranged from 8 to 22 mm for the main mode, with few larger individuals (5.1 %).

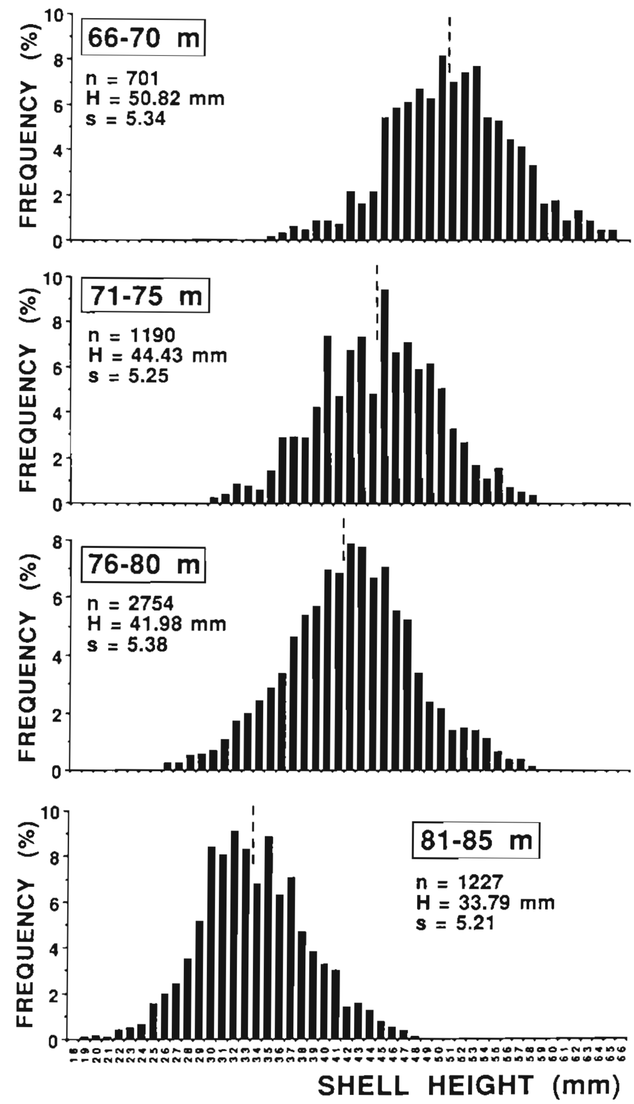


Fig. 7. *Placopecten magellanicus.* Size-frequency distribution of 2 yr old sea scallops with respect to depth, on Georges Bank. Samples were collected during the stock assessment survey (17 to 22 August 1989). n: number of scallops; H: mean shell height; s: standard deviation

Growth parameters of the von Bertalanffy function (Fig. 6) are H_∞ = 144.87 mm, k = 0.2814 and t_0 = 0.5566. The von Bertalanffy model provides a good fit to the shell data (r^2 = 0.998). The present growth curve is the only one from Georges Bank (results from previous studies shown in Table 5 and Fig. 6) using data for age 1 scallops.

Spatial growth variations. Up to 5872 2 yr old sea scallops collected during the stock assessment survey were measured to determine spatial variability in juvenile growth. Shell height histograms plotted against 4 depth ranges (Fig. 7) show that mean shell height varied with depth. A mean size reduction of 33.3 % was observed between the shallowest (65 to 69 m) and the deepest (81 to 85 m) waters. The 4 depth-

Table 6. *Placopecten magellanicus*. Comparison of size-frequency distributions of 2 yr old sea scallops according to depth. Distributions were fitted by pairs and tested with Pearson and likelihood-ratio chi-square statistics (99 % probability level)

Depths fitted (m)	Pearson's chi-square	Likelihood-ratio chi-square	df	Tabulated chi-square (99 % p.l.)	Probability
65–70/71–75	471.37	508.99	26	45.64	0.000
71–75/76–80	231.16	229.62	30	50.89	0.000
76–80/81–84	1485.31	1616.47	22	40.29	0.000

related distributions were compared with a 1-way analysis of variance (test of differences in the mean height at each depth), after the homogeneity of variances was tested (Cochran test in Winer 1971). According to Winer (1971) and Underwood (1981), a small departure from homogeneity of variances (calculated value of C= 0.257; critical value= 0.250, for $k = 4$ and df = ∞) does not seriously affect the sampling distribution of the F statistic. Variations in shell height were significant (99 % probability level), with respect to depth (F-ratio = 1541.71 > 3.78 for df1 = 3, df2 = 5867). As the second (70 to 75 m) and third (75 to 80 m) depth ranges showed smaller differences for mean shell height and variance, the height distributions were compared by pairs (test of differences in the distribution of height). Fitted distributions were tested with both Pearson and likelihood-ratio chi-square statistics (frequencies <5 combined). Calculated values of chi-square (Table 6) indicate that all the differences in size-frequency distribution were significant (99 % probability level).

DISCUSSION

Sampling efficiency

The rate at which *Pecten maximus* juveniles were caught with the AQUAREVE technique was evaluated using SCUBA (Thouzeau & Lehay 1988). The device was more than 80 % efficient under good weather conditions. Depths on Georges Bank did not allow such a controlled experiment for *Placopecten magellanicus*. Fishing dredges trigger an avoidance response when disturbing a scallop bed (Caddy 1968, Thomas & Gruffydd 1971, Stephens & Boyle 1978). Compared to *Pecten maximus, Placopecten magellanicus* may tend to avoid the sled-dredge more, since it usually does not live recessed in the sediment and is a better swimmer. Sea scallops approach optimum hydrofoil shape for low-aspect body ratio (Hoerner 1975, Dadswell & Weihs 1990); an average swimming speed of 0.48 m s^{-1} (up to 0.80 m s^{-1}) has been reported (Caddy 1968, Dadswell & Weihs 1990). Thornbun & Gruffydd (1979) established that, of 4 scallop species tested, *P. magellanicus* was the most hydrodynamically suited for swimming.

The efficiency of the sled-dredge might vary depending on individual sizes, since medium-sized *Placopecten magellanicus* (40 to 80 mm shell height) are the best swimmers (optimal hydrodynamic characteristics; Dadswell & Weihs 1990). Larger and smaller sea scallops swim not only at lower velocities but also at lower relative velocities (no. of body lengths s^{-1}). During the tows, several individuals were observed (on the video) swimming away from the dredge and at times escaping the sampling box. Scallops moving out of the path of the dredge could not be seen, because of the camera's orientation. However, any escape from the collecting box during hauling to the surface was prevented by the box closing device.

Distribution patterns

The main features of scallop distribution in this study were the concentration of sea scallops in the northern half of the Bank and the dispersion of individuals as they grow older (Fig. 3). Physical aggregation at the larval stage, substrate selection at settlement, post-larval differential mortality, or juvenile movement (broader initial distribution and migration to the most suitable areas for survival and growth) may explain these patterns. Settlement is assumed to occur by mid-December on Georges Bank (Merrill & Edwards 1976, Larsen & Lee 1978, Tremblay & Sinclair 1990). In contrast to other pectinid post-larvae (Brand et al. 1980, Orensanz 1986), it seems unlikely that *Placopecten magellanicus* has an obligatory settlement substrate or an obvious preference (Caddy 1973, Naidu & Scaplen 1976, Caddy & Carter 1984). However, sea scallops occur at lower densities on mud than on sand (Caddy 1970, 1989, Langton & Robinson 1990). Experiments on settlement behaviour suggest a general thigmotactic response in pediveligers (Baird 1953, Caddy 1972, Culliney 1974). The attachment of post-larvae to various substrates in nature supports this view; sea scallop spat have been found attached to shells of live *Placopecten magellanicus* (Naidu 1970), shell fragments (Caddy 1968), bryozoans (Baird 1953, Caddy 1972), hydrozoans, amphipod tubes, and sand grains (Larsen & Lee 1978), red algae (Naidu 1970), and metal and wooden navigation buoys (Merrill & Posgay 1967, Naidu 1970, Merrill & Edwards 1976). The present study only partially supports this generalization, since 76.5 % of the 1 yr olds were located on gravel and pebbles and the remainder on sandy bottoms with shell debris. Furthermore, the small-scale distribution of age 1 in the northern half of the Bank was clearly related to sediment type (juveniles more abundant on gravel beds than on mixed sand-gravel bottoms). Ongoing studies confirm this result, since more than 50 % of 19 mo old individuals were found attached to gravel and pebbles in late April 1990 (shell height ranging from 13 to 27 mm).

The fact that juvenile abundance was greatest on gravel might reflect enhanced survival on this bottom type, as suggested by Larsen & Lee (1978) and Castagna & Kraeuter (1977) for *Mercenaria mercenaria*. Gravel might enhance juvenile protection from predation (spat settle predominantly on the underside of gravels or shell fragments; Culliney 1974), allowing sufficient water to surround the individuals while acting as a barrier to epibenthic predators. Pebbles and gravel may also offer a more stable substratum for settlement than does shell debris, in areas where strong tidal currents occur. Since pediveliger larvae are capable of delaying metamorphosis for at least 1 mo and retain their swimming ability (Culliney 1974), they might be able to choose the appropriate substratum for settlement.

Larval drift is a function of the depth-averaged residual current (mixed areas) or of the current above or within the pycnocline (stratified waters) on the Bank (Tremblay & Sinclair 1990). Sea scallop larvae do circulate in the direction of the residual currents but are not spread over the entire Bank (J. Tremblay, Dept of Fisheries & Oceans, pers. comm.). Larval abundance appears to be reduced in the well-mixed area (<60 m), while late-stage larvae are frequently abundant on the Northern Flank. A clockwise circulation occurs around Georges Bank, which requires 33 to 60 d for completion, depending on depth and season (Butman et al. 1982, 1987, Lough & Trites 1989). Given the duration of the larval stage on the Bank (40 to 60 d; J. Tremblay pers. comm.) and regardless of diffusion process, some scallop larvae could be returned to the vicinity of the parental beds at metamorphosis. Other larvae may remain on the shallower part of the Northeast Peak because of lower residual currents (Lough & Trites 1989).

Several studies, mainly performed in inshore areas, indicated an absence of directed population movements or seasonal migrations in adult *Placopecten magellanicus* (Dickie 1955, Posgay 1963, Krantz et al. 1984). However, localized movements were recorded on Georges Bank (8 to 10 km yr^{-1} on average), their direction corresponding with bottom-water residual currents (Posgay 1982, Melvin et al. 1985). In this study, age-classes show different distribution patterns, with a clear drift to the south (age 2) and southwest (age 3+) as the individuals grow older (Fig. 3). The dispersion with age (in an arc, oriented northwest-southeast) supports the hypothesis of current-related dispersion (on a small scale) during the benthic phase. These results agree with previous studies on adult distribution on Georges Bank (Robert et al. 1982, Robert & Black 1990) and in the Gulf of Maine (Serchuk & Wigley 1984). The more localized distribution of age 1 juveniles may be partly explained by their sedentary behaviour (byssal attachment), while the spread of older individuals corresponds to the motile phase (30 to 100 mm shell height; Caddy 1968) with optimal hydrodynamic characteristics (Dadswell & Weihs 1990). The impact of fishing activity on sea scallop dispersion through the capture and release of pre-recruits cannot be assessed here.

Based on the foregoing observations, we suggest that the distribution of juvenile sea scallops is mainly determined by physical processes (advection) during the larval stage and by differential post-larval mortality (according to sediment type) at settlement. Tides and storm events on Georges Bank may give a strong element of temporal variability to the direction and speed of residual currents (Butman et al. 1982). Hence, larval dispersal and settlement areas are likely to vary among years.

On Georges Bank, the higher abundance of sea scallops (especially 1 yr olds) on gravel than on the other sediment types agrees with the spatial distribution of *Placopecten magellanicus* adults in the Gulf of St. Lawrence and Gulf of Maine (Caddy 1970, Langton & Robinson 1990). Scallops appeared to exhibit a Poisson distribution within sediment type in the present study, in contrast to the findings of Langton & Robinson (1990). Age 1 *Pecten maximus* in the Bay of Saint-Brieuc also displayed aggregated distribution at the bay scale, and random distribution within patches (Thouzeau & Lehay 1988, Thouzeau 1989). Differences may be due to the greater size of the sampling units in the present study (≥ 11 m^2, 25.1 m^2 on average) compared to that of Langton & Robinson (1990) (1.24 m^2 quadrats). If the size of sampling units is much larger than the average size of clumps of individuals, and these clumps are regularly or randomly distributed, then the dispersion of the population is apparently random and the non-randomness is not detected (Elliott 1977). Langton & Robinson (1987) established that adult sea scallops in the Gulf of Maine (60 to 88 m depth range) were generally separated by a distance of at least 25 to 60 cm. This cannot be determined for the present study.

Size structure and growth parameters

Seven age-classes (1 to 7) were sampled in this study, though scallops up to age 12 are caught on Georges Bank (Brown 1987). However, few specimens (1.9% in 1989) over age 7 are caught in commercial scallop dredges (Robert & Black 1990), as for other heavily exploited scallop beds (Langton et al. 1987). Compared to that of recruits (Fig. 5), pre-recruit abundance (ages 1 to 3 = 78 % of total numbers) emphasizes the impact of fishing activity on the size or age structure, even if older individuals might have been underestimated because of their wider dispersion.

Several studies fitting shell growth data to the von Bertalanffy model are available for the Georges Bank area (Posgay 1959, 1962, 1979a, Brown et al. 1972, Serchuk et al. 1979). Asymptotic heights, H_∞, range from 141.8 to 152.46 mm, while k varies from 0.26 to 0.38. Through its geographic range, greater variations are observed for H_∞, from 108.83 mm in the southwestern Gulf of St. Lawrence (Chouinard 1984) to 207 mm on the northeastern coast of Maine (Langton et al. 1987). As pointed out by MacDonald & Thompson (1988), care must be taken when comparing von Bertalanffy derived growth rates from different populations or samples. Comparisons based on the Brody coefficient k are inappropriate when the asymptotic heights or lengths are very different, because k is inversely related to H_∞. Furthermore, k is a growth coefficient and should not be regarded as growth rate per se (Ricker 1975). Asymptotic height in the present study (144.87 mm) is similar to the value of 145.5 mm given by Brown et al. (1972) for Georges Bank. However, k – which determines the steepness of the curve – is much lower in our study (0.2814) than in Brown et al. (0.38). Differences may result from the inclusion of data for ages 1 and 2 in our study (56 % of scallop numbers, versus 0 % in Brown et al.) and from sampling locations in the 2 studies [South Channel and southeastern part of the Bank in Brown et al. (1972); Northeast Peak in the present study]. There may also be some form of 'Rosa Lee's phenomenon' (Ricker 1975) acting on the exploited population, as shown by Chouinard (1984). Heavy fishing would lead the stocks to be mainly composed of slower-growing individuals. These would become available to the fishery at an older age due to size-selectivity of the gear. Further investigations (greater sample size) are needed to validate this hypothesis for the Georges Bank scallop population.

Early growth of sea scallops

The first shell ring of scallops on Georges Bank is formed in March–April (Merrill et al. 1966, Posgay 1979a), at about 6 to 8 mm, although Larsen & Lee (1978) have shown that it may form at a smaller size (0.2 to 2.8 mm). Mean sizes at the second and third rings range from 18 to 25 mm and from 48 to 63 mm, respectively (Merrill & Posgay 1967, Posgay 1979a, Serchuk et al. 1979, Mohn et al. 1988, Caddy 1989). The mean shell height of 1 yr olds in the present study is similar to that reported on the Northern Edge and Peak region of the Bank (Serchuk & Wigley 1984), but lower than that recorded in the shallower waters (23 m) of Cape Cod Bay, Massachusetts (mean height 17 to 18 mm). Faster growth rates are usually recorded for spat held in suspended culture (MacDonald 1986, Dadswell 1989). A mean shell height of ca 22 mm by late August was regularly obtained in Passamaquoddy Bay (southwestern New Brunswick), following fall settlements (Dadswell 1989). An average growth rate of 51.5 µm d^{-1} during the first year of life was found in the present study, compared to 60 to 65 µm d^{-1} in Passamaquoddy Bay (Dadswell 1989).

Scallops 2 yr old exhibited significant variations in shell growth (Fig. 7) over a small depth range (65 to 84 m) in this study. Decreasing shell growth with increasing water depth has been reported in a number of studies from the Bank (Posgay 1979b) and elsewhere (Caddy 1970, MacDonald & Thompson 1985, 1988). The latter showed that growth variations along a depth gradient on a micro-geographical scale were equal to or greater than variations on a latitudinal scale. Growth differences were ascribed to food and temperature conditions, although several studies did not provide quantitative evidence of lower food availability in deeper water. Spatial variations in bottom-water temperature of about 2 °C (60 to 100 m depth range) in summer occur on Georges Bank within the sampling area for juveniles (Dickinson & Wigley 1981, Flagg 1987). Summer temperatures usually decrease from 12 °C at 60 m to 10 °C at 100 m (Flagg 1987), although lower values have been recorded (from 9 to 7 °C; Butman & Beardsley 1987). Depending on the year, the thermocline may persist in fall (up to 6 °C temperature difference) or disappear (Loder et al. 1982, Flagg 1987, Tremblay & Sinclair 1990). According to Posgay (1953), sea scallops grow faster at 10 °C (max. growth rate) than at 12 °C (80 % of max. growth rate) or 8 °C (95 % of max. growth rate). However, larvae are successfully reared in hatcheries at temperatures of 12 to 15 °C (Culliney 1974, Hurley et al. 1987), the upper thermal tolerance limit being about 19 °C (Culliney 1974). Temperatures higher than 15 to 16 °C would be above the optimum for adults in Newfoundland waters (MacDonald & Thompson 1985). Given that bottom-water temperatures and juvenile growth rates are higher at 65 to 70 m than at 80 to 85 m on Georges Bank, high summer temperatures are unlikely to have a detrimental effect on growth within the 65 to 85 m depth range.

Food availability also presents depth-related variations on Georges Bank. A chlorophyll *a* concentration (phytoplankton biomass) of about 8 mg m^{-3} has been recorded close to the bottom at 50 m, versus <4 mg m^{-3} at 80 m and <1 mg m^{-3} at 110 m (Cohen & Wright 1978). Furthermore, a comparable cross-bank gradient from shallow to deep water was found in the size-frequency and species composition of the phytoplankton (O'Reilly et al. 1987). In Gulf of Maine scallop populations, Shumway et al. (1987) showed that gut contents generally reflected food organisms available in surrounding waters (algae 10 to 350 µm in size, pollen grains, ciliates, detritus, bacteria). They concluded that *Placopecten magellanicus* is an opportunistic feeder taking advantage of any food available. On the Bank, one cannot discount the possible importance of particulate organic matter in the benthic boundary layer as scallop food. It cannot be concluded from the present study whether temperature or food availability is the main cause of decreased growth with depth.

This study documents the distribution patterns of sea scallops on Georges Bank and suggests the importance of sediment type for the survival of newly settled post-larvae. These results provide a basis for further investigation into the roles of habitat type, dispersion patterns and food availability in relation to successful recruitment of sea scallops. The study also points out the effect of heavy fishing on size structure, and its likely effect on growth. The strong depth-related decrease in shell growth emphasizes the inadequacy of using only 1 averaged growth curve for the entire Bank. The northern half of Canadian Georges Bank, especially the main pebble-gravel deposit, provides the most appropriate substrata for post-larval settlement and exhibits the highest densities of juveniles. The establishment of pre-recruit indices for incoming year-classes prior to age 3 would require that this area be targeted to collect more individuals.

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