J. Northw. Atl. Fish. Sci Sci., Vol. 13: 83–99

Statistics of Reproduction and Early Life History Survival of the Georges Bank Sea Scallop (*Placopecten magellanicus*) Population

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Abstract

In a spatial analysis of the Georges Bank sea scallop (*Placopecten magellanicus*) population, variables of population reproduction and abundance are calculated from Canadian and USA research survey size-frequency data. Using commercial catch as a scaling factor to obtain absolute estimates, the time averages of harvestable-sized population numbers and meat-weight biomass, annual recruit numbers, and egg production were calculated from 1977 to 1988 for five principal subregions of Georges Bank. Average survival from egg to age 2 was obtained directly.

Incorporating recent field sampling measurements of larval densities in the water column, survival and thus natural mortality was estimated for egg to larva and larva to age 2 juvenile. The size-specific fecundity vector was also employed in a lifetime egg production-per-recruit analysis. Detailed error analysis of the scaling coefficient and sensitivity analysis of potential error due to gear selectivity were combined into confidence intervals for the estimated population statistics.

Introduction

The Georges Bank sea scallop (*Placopecten magellanicus*) population supports the third most valuable fishery in Atlantic Canada, worth approximately $100 million to Canada and the USA. As with all renewable resources, the processes of population reproduction are crucial to successful management. Detailed studies of sea scallop reproduction have included in particular: the annual reproduction cycle (Naidu, 1970; Robinson *et al.*, 1981; Beninger, 1987; MacDonald and Thompson, 1986a; Shumway *et al.*, 1988), fecundity (Langton *et al.*, 1987), and feeding (Cranford and Grant, 1990; Shumway *et al.*, 1987); the effect on growth (Wildish and Kristmanson, 1988; MacDonald and Thompson, 1985a, 1988) and reproductive output (MacDonald and Thompson, 1985a, 1985b; MacDonald *et al.*, 1987; Barber *et al.*, 1988) in response to changing environmental conditions; of spawning (Posgay and Norman, 1958) and larval development (Culliney, 1974); vertical distribution (Tremblay and Sinclair, 1990a) and vertical migration (Silva and O'Dor, 1988; Balch, MS 1990; Tremblay and Sinclair, 1990b) of larvae in the water column; of settlement (Merrill and Edwards, 1976; Dadswell and Sinclair, MS 1989) and long-term population trends (Dickie, 1955; Dow, 1977; Caddy, 1979). These are summarized in reviews by MacKenzie (MS 1979), Young-Lai and Aiken (1986) and Caddy (1989).

In general it is known that Georges Bank scallops spawn in the early autumn, releasing large numbers of eggs into the water column, where the larvae, feeding on phytoplankton, grow through four stages in a period of roughly 4–6 weeks before settlement. Recruitment to five discrete subregions of the bank (Fig. 1) from sources of egg production is determined by the drift trajectories of pelagic

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larvae and the survival rates after settlement, within and between subregions. The pattern of residual currents, characterized by a tidally driven clockwise gyre (Greenberg, 1983) which retains water most tightly above the bank during scallop spawning in early autumn (Butman *et al.*, 1987), and direct measurements of daily tidal motion (Butman and Beardsley, 1987), and of the spatial distribution of adult beds (Robert and Black, 1990) and larvae (Tremblay, MS 1991; Tremblay and Sinclair, 1988) above the Canadian part of the bank, imply that two of the subregions, the Northern Edge and the Northeast Peak, are occupied by a single subpopulation. The three other subregions are occupied by spatially separated subpopulations (Fig. 1). A study of stock-recruitment relationships within and between the same subregions of Georges Bank studied here (McGarvey *et al.*, 1992) suggests these subpopulations may be connected reproductively through larval transport.

As noted by Sinclair *et al.* (1985), the persistence of aggregations year after year in the same general locations, even under intense harvesting, suggests that the spatial distribution of scallop beds is determined by the local persistence of hydrographic features, gyres, upwellings, mixing and other tidally driven current patterns which affect temperature, primary productivity, bottom flow rates and larval retention in these favourable habitats. The spatial processes of the Georges Bank scallop fishery were investigated by Caddy (1975) using a detailed model. Postulating stochastic annual recruitment with historical success probabilities in each 10' square area, Caddy confirmed that the intense levels of exploitation directed towards aggregations of high abundance, in particular on the Northern Edge, diminish the sustained yield, in part at least, by excessively rapid removal of younger scallops. Time-averaged spatial analysis is valuable for identifying distributions of population reproduction and abundance in relation to physical conditions especially geographically stable features of the marine environment.

Yearly scallop population surveys have been carried out since 1977 on Georges Bank by the Canadian Department of Fisheries and Oceans in Halifax and the USA National Marine Fisheries Service in Woods Hole. Using data from these surveys for 1977–88, we generated time–averaged estimates of variables of population reproduction. These include recruitment, egg production, and abundance for the five subregions of Georges Bank (Fig. 1). The results yield a spatial breakdown of the demographics of the scallop populaton on the bank. In

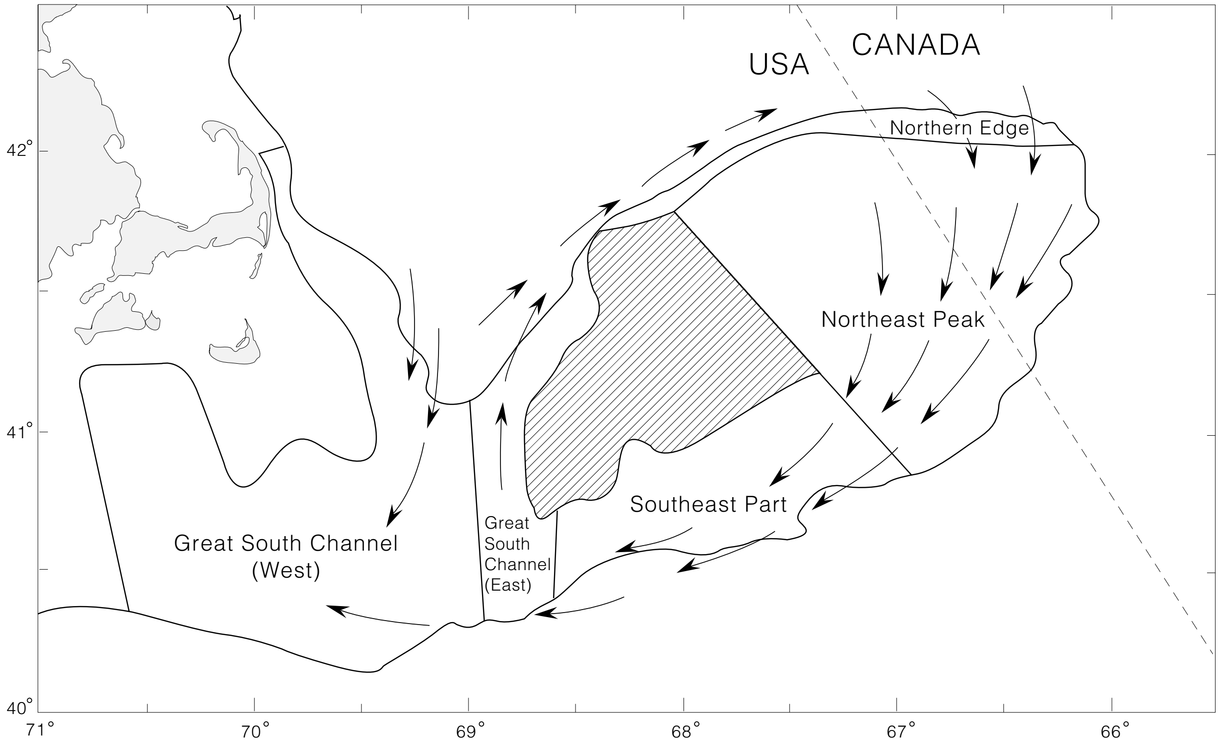

Fig. 1. Georges Bank and its five subregions utilized in a spatial analysis of the sea scallop (*Placopecten magellanicus*) population.

addition, from the recruitment and egg production estimates for the Northern Edge and Northeast Peak subregions combined, we estimated the average survival rate from egg to recruitment (age 2) in that region. Combining this estimate with estimates of peak larval density during spawning from Tremblay (MS 1991) and Tremblay and Sinclair (1990a) for the same area, we also estimated the average survival probability from egg to larva and from larva to age 2.

Materials and Results

Population surveys

In both the Canadian and USA scallop surveys on Georges Bank,a commercial scallop dredge fitted with a small-mesh liner, was towed along the bottom at randomly chosen locations in a stratified sampling design (Serchuk and Wigley, 1986; Mohn *et al.*, 1987; Robert and Black, MS 1990). Canadian and USA data were combined (Serchuk and Wigley, 1986) and the stratified numbers-per-tow were calculated (Cochran, 1977) within each subregion. Size frequencies of numbers of scallops per tow were obtained for size classes of 0–5, 5–10, 10–15 mm, etc. for each subregion, for the Northern Edge and Northeast Peak subregions combined, and for Georges Bank overall.

Two previous assessments of variance of the scallop survey data have been undertaken (Serchuk and Wigley, 1986; Mohn *et al.*, 1987) for the USA and Canadian mean numbers-per-tow on the Northern Edge and Northeast Peak, which include 80% of the Georges Bank population. Serchuk and Wigley (1986) specifically considered the years 1982, 1983 and 1984 when both Canadian and the USA surveys were undertaken in these subregions. Correcting for small differences in sampling procedure (the USA survey towing a dredge for 15 min at 3.5 knots, and the Canadian survey towing identical gear for 10 min at 4.0 knots) by standardizing to equivalent distances towed, Serchuk and Wigley found good agreement, both in total and size-specific number-per-tow (see Fig. 6 in Serchuk and Wigley, 1986). The Canadian survey in this area (which lies in Canadian waters) included 2 to 3 times as many tows overall, averaging 193 *versus* 86 USA survey sets per year. Annual sample sizes for the combined data averaged around 70 000 scallops captured and measured for shell height (Serchuk and Wigley, 1986).

The two surveys differed primarily in stratification scheme. The USA survey employs simple random sampling in fixed strata drawn along depth contours (Cochran, 1977) while tow locations in the Canadian survey are directed towards areas of higher catch as reported by the Canadian commercial fishery (Robert and Jamieson, 1986; Mohn *et al.*, 1987) and on this basis the sampling strata were redrawn yearly. Mohn *et al.* (1987), comparing their relative variance improvements on a simple unstratified mean number-per-tow, found no significant advantage accruing to either stratification design.

Standard errors of the survey data, calculated by two different methods from the study of Serchuk and Wigley (1986), are presented in Appendix 1. Indicated confidence intervals for derived population statistics are calculated by methods detailed in Appendix 2.

Biomass, population and recruitment

To obtain absolute population numbers from survey numbers-per-tow, total catch was employed as a scaling factor. This procedure, detailed in Appendix 3, is summarized as follows: From the average annual catch (1977 to 1988) and an independent estimate of average fishing mortality, we derived the average total number of scallops of fishable size in the Georges Bank population. This estimate from the fishery was divided by the analogous survey statistic (the average numbers-per-tow of all commercial sizes (≥80 mm) for all of Georges Bank from 1977 to 1988) to generate a scaling coefficient, α (Appendix 3) used to transform the survey numbers per tow into scallops per m^2. α was then employed to derive population statistics for all subregions and for Georges Bank overall.

Specifically, the matrix of survey number-per-tow data, {NPT(YR,HT); YR = 1977, HT = 0–185 mm}, rescaled by α, yielded the average adult population,

$$\overline{\text{POPULATION}} = \frac{1}{12} \sum_{\text{YR} = 1977}^{1988} \left[\sum_{\text{HT} = 80}^{185 \text{ mm}} \alpha * \text{NPT(YR,HT)} \right]$$

and the average recruitment,

$$\overline{\text{RECRUITS}} = \frac{1}{12} \sum_{\text{YR} = 1977}^{1988} \left[\sum_{\text{HT} = 30}^{60 \text{ mm}} \alpha * \text{NPT(YR,HT)} \right]$$

as densities per m^2 in each region (Table 1). These densities, multiplied by areas, yield population totals (Table 2).

TABLE 1. Average sea scallop (*Placopecten magellanicus*) population densities (per m^2) for the five subregions of Georges Bank. Biomass, measured as adductor muscle weight and population numbers are the sums for commercial–size scallops, ≥ 80 mm. Recruit values are adjusted by GS_{best} (Appendix 2, Fig. 4) to consider likely gear selectivity at smaller sizes. The unadjusted value and a likely upper value based on GS_{high} are included in brackets.

Region	Area (km^2)	Biomass density ($g\ m^{-2}$)	Population density (m^{-2})	Recruit density (m^{-2})
Northern Edge	1 475	2.91	0.172	0.877 [0.809, 2.796]
Northeast Peak	15 582	1.32	0.0739	0.280 [0.247, 0.914]
Southeast Part	6 304	0.29	0.0118	0.012 [0.011, 0.036]
South Channel (Eastern)	3 838	0.44	0.0170	0.015 [0.013, 0.043]
South Channel (Western)	12 444	0.33	0.0175	0.071 [0.065, 0.219]
Northern Edge & Northeast Peak (combined)	17 057	1.49	0.0847	0.339 [0.304, 1.098]
Georges Bank (total)	39 643	0.79	0.0431	0.168 [0.151, 0.543]

TABLE 2. Average sea scallop (*Placopecten magellanicus*) population totals for the five subregions of Georges Bank obtained by multiplying the absolute densities from Table 1 by the area of each subregion.

Region	Area (km^2)	Biomass (mt)	Population (millions)	Recruits (millions)
Northern Edge	1 475	4 291	254	1 293 [1 193, 4 124]
Northeast Peak	15 582	20 599	1 152	4 357 [3 856, 14 240]
Southeast Part	6 304	1 840	74	76 [70, 226]
South Channel (Eastern)	3 838	1 682	65	56 [50, 166]
South Channel (Western)	12 444	4 082	218	888 [808, 2 728]
Northern Edge & Northeast Peak (combined)	17 057	25 498	1 440	5 784 [5 180, 18 730]
Georges Bank (total)	39 643	31 467	1 710	6 679 [5 986, 21 540]

The vector of weight (g) versus height (mm) {WT(HT)}, taken from Serchuk and Wigley (MS 1986),

$$WT = EXP(-11.7656) * (HT)^{3.1693},$$

was used to calculate average adductor muscle meat-weight biomass, per m^2, for harvestable size scallops ≥80 mm:

$$\overline{BIOMASS} = \frac{1}{12} \sum_{YR = 1977}^{1988} \left[\sum_{HT = 80}^{185\ mm} \alpha * NPT\ (YR,HT) * WT(HT) \right]$$

Egg production

The average number of eggs produced by females in each size class, {EGGS(HT)}, was derived from measurements in Newfoundland by MacDonald and Thompson (1985b) of average gonad weight loss during the spawning season. Their results from the 10 m depth sampling location at Sunnyside in 1982 were chosen for use here as a proxy for Georges Bank. Comparing sea scallops from this study site with samples from the open sea off New Jersey and from inshore populations at St. Andrews, New Brunswick and Sunnyside 30 m depth, (MacDonald and Thompson, 1988) revealed gamete production as a function of age to be about average at Sunnyside 10 m depth among the sites sampled.

Spawned biomass as a function of shell height, the relationship originally measured in their field study of MacDonald and Thompson, was obtained from their published curves of gamete energy production as a function of age, 1985b, fig. 1). Age was converted back to shell height, and energy to weight (g) of spawned gonad biomass, using the relationships,

$$\mathrm{HT} = 176.5\,(1 - \exp\left[-0.19 * (\mathrm{AGE} - 0.55)\right]),$$

and

$$1 \text{ g dry-weight of eggs} = 26 \text{ kjoules}$$

provided by MacDonald and Thompson (1985a, 1985b).

Finally, total eggs-per-female (Table 3) was estimated from gonad weight change during the spawning season using the conversions

$$1 \text{ egg} = 1.6 \times 10^{-7} \text{ g wet weight},$$

and

$$4.0 \text{ g wet weight} = 1.0 \text{ g dry weight}$$

TABLE 3. Estimated egg-per-female for sea scallops (*Placopecten magellanicus*) from MacDonald and Thompson (1985b) for an inshore Newfoundland population, measured as the average difference in gonad weight before and after spawning. Numbers of eggs in the third column are rescaled values of the estimated weights of spawned gonad biomass shown in the second column.

Shell height size class (mm)	Estimated gonad weight change per female (g dry-wt)	Estimated eggs per female (millions)
0–45	0.0	0
45–50	0.1	2.50
50–55	0.18	4.50
55–60	0.26	6.50
60–65	0.33	8.25
65–70	0.43	10.75
70–75	0.54	13.50
75–80	0.69	17.25
80–85	0.87	21.75
85–90	1.09	27.25
90–95	1.37	34.25
95–100	1.7	42.50
100–105	2.09	52.25
105–110	2.54	63.50
110–115	3.06	76.44
115–120	3.65	91.24
120–125	4.33	108.40
125–130	5.09	127.24
130–135	5.95	148.72
135–140	6.91	172.72
140–145	7.99	199.76
145–150	9.19	229.76
150–155	10.53	263.24
155–160	12.03	300.76
160–165	13.71	342.76

derived by assuming that eggs are spherical, neutrally buoyant and 67 micrometers in diameter (Langton *et al*., 1987).

Further evidence that the fecundity of the Sunnyside population at 10 m in 1982 is representative, is the agreement with data from the Gulf of Maine (Langton *et al*., 1987) also presented in Fig. 2. The fecundity curves for the two populations are particularly close at sizes below 120 mm which encompasses the majority of scallops in the heavily fished population of Georges Bank (Fig. 3).

The size-specific population densities and fecundities yielded the average yearly egg production per m^2 for each region (Table 4):

$$\overline{\text{EGGS}} = \frac{1}{12} \sum_{\text{YR} = 1977}^{1988} \left[\sum_{\text{HT} = 40}^{170 \text{ mm}} \alpha \; \frac{1}{2} * \text{NPT(YR,HT)} * \text{EGGS(HT)} \right] .$$

The factor of 1/ 2 inside the sum expresses the observed 1:1 sex ratio (MacKenzie, MS 1979).

Multiplying $\overline{\text{EGGS}}$ by the area of Georges Bank yielded the integrated total size-specific egg production of the Georges Bank population (Fig. 3a). The peak at 95–100 mm occurs where scallops, mostly of age 4, are fully recruited and egg production is substantial.

Fecundity per recruit

Sinclair *et al*. (1985) addressed the importance of fecundity-per-recruit, in addition to the meat-weight yield-per-recruit, for maintaining a viable spawning stock, and showed that lower fishing mortality or a delayed age of first capture increased average gonad size. Caddy (1989) reiterated the importance of fecundity-per-recruit, citing the example of the notably successful scallop aquaculture in Mutsu Bay, where regular and abundant spatfall is assured by a dense spawning biomass.

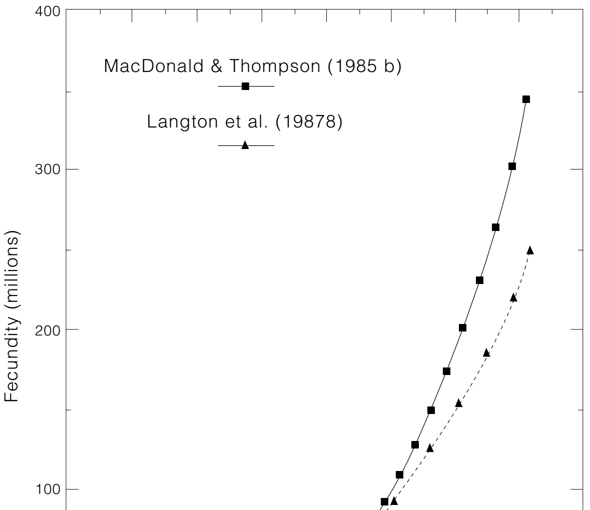

Fig. 2. Average numbers of eggs-per-female released in annual spawning as a function of size. Fecundities of sea scallop (*Placopecten magellanicus*) used in this study were derived from MacDonald and Thompson (1985b) from their 1982 Sunnyside, Newfoundland, 10 m depth sampling location. The fecundities reported by Langton *et al*. (1987) for an inshore Maine population are plotted for comparison.

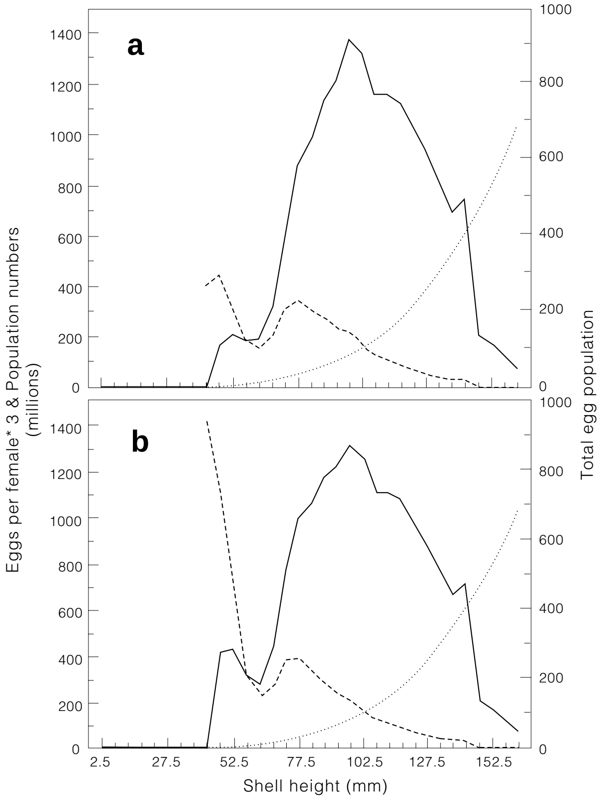

Fig. 3. (**a**) Eggs-per-female rescaled upward by a factor of 3 (dotted), total population numbers (dashed), and their product, the total numbers of eggs produced (solid), by size class for the Georges Bank sea scallop (*Placopecten magellanicus*) population. (**b**) The same quantities but with population numbers adjusted by GS_{high} (Appendix 2, Fig. 4) to compensate for lower survey gear selectivity at smaller sizes.

The fecundity curve derived above allowed us to calculate lifetime egg production per age 2 recruit employing the following simplifying assumptions.

We averaged out variability of recruitment and the patchiness of scallop aggregations, which Caddy (1975) explicitly considered in yield-per-recruit investigations. Fixing F = 0.8, we assumed the population had reached a stable age distribution. Natural mortality was taken as 0.1 (Dickie, 1955; Merrill and Posgay, 1964; MacDonald and Thompson, 1986b). The fecundity vector, derived above with size as the independent variable, was transformed (with a reduction in reliability) into fecundity with age. The ranges of shell height size assigned to ages 2, 3, and 4 were based on the observed peaks in the survey height-frequency data and for older ages on the size-age relationship of Serchuk *et al.*, (1979). At present, scallops are fully exploited by age 4. We therefore considered two knife-edged fishing strategies: case A, in which F = 0 for ages 2–3 and F = 0.8 for ages 4+, and case B, in which F = 0 for ages 2–5, and rises to F = 0.8 for ages 6+. That is, we assume meat-count restrictions were tightened so that fishing was delayed until age 6, the general recommendation of most previous authors who undertook yield-per-recruit analysis (Posgay, 1979; Sinclair *et al.*, 1985). Case B yielded a large increase over case A: each age 2 recruit released 2.9 times the number of eggs in an average lifetime before capture. Previous analysis of yield-per-recruit predicted an increase of 1.4–1.6 in the harvested meat weight per recruit (Posgay, 1979; Sinclair *et al.*, 1985). The greater increase in egg production compared with yield-per-recruit is due to the fact that delaying harvest by 2 years allows two additional spawnings, releasing considerably more eggs with every additional year in age, while the benefits of a larger meat are obtained only once, at harvest.

Early life history natural mortality

MacDonald and Thompson (1985b) and Langton *et al.* (1987) measured the average change in gonad weight of scallops during spawning and supposed, as we do, with additional histological examination of the spent gonads, that most of that weight change represents eggs released. Since many of those eggs may not be viable and many viable ones may not get fertilized, Table 4 represents maximum average egg production. Bearing this in mind, for the Northern Edge and Northeast Peak, the total number of eggs produced (Table 4) divided by the best estimate of total recruits yielded a survival rate from “potential” egg to age 2,

$$L\text{ (egg to age 2)} = 1.26 \times 10^{-7}$$

of one in ten million. For a steady state population, the reciprocal of this quantity is equal to the total lifetime egg production of an average age 2 female.

Given information about the density of larvae in the water column, we subdivided this survival (or equally, mortality) estimate into egg to larva and larva to age 2. Tremblay (MS 1991) and Tremblay and Sinclair (1990a) measured larval density at locations crossing the Northern Edge and Northeast Peak with pump and bongo net sampling at various depths. Timing their cruises with annual spawning, they observed peak densities of 500–2 000 per m^3 in the first week of October, most concentrated above or at the pycnocline around 30 m depth. These closely match observations (Ventilla, 1982) of 1 200 per m^3 for maximum larval density of a closely related species, the Japanese scallop (*Patinopecten yessoensis*), but are roughly a full order of magnitude greater than the *Placopecten magellanicus* larval densities reported for the Bay of Fundy (Tremblay and Sinclair, 1988). Depth integrating bongo net larval densities, and averag-

TABLE 4. Egg production by sea scallops (*Placopecten magellanicus*) for the 5 subregions of Georges Bank, obtained by multiplying the survey data by eggs-per-female at size and averaging over the years 1977 to 1988.

	Egg production	
Region	Total (10^{15} eggs)	Density (millions of eggs per m^2)
Northern Edge	8.10	5.49
Northeast Peak	36.60	3.35
Southeast Part	3.19	0.51
South Channel (Eastern)	2.90	0.76
South Channel (WSestern)	7.56	0.61
Northern Edge & Northeast Peak (combined)	45.75	2.68
Georges Bank (total)	55.95	1.41

ing across all sample sites on the Northeast Peak during the week of peak larval density, Tremblay (MS 1991) reported mean densities of 20 000 in 1986 and 16 800 in 1987, yielding an average of 18 400 per m^2.

We arbitrarily assumed that the fraction of total larvae present in the water column at the time of peak sampling represented half of the total spawned ±0.25. Wide dispersal of larvae which survive was unlikely due to currents which retain them above the Bank. The measurements of Tremblay (MS 1991) in regions off the edge of Georges Bank, are 1 to 4 orders of magnitude lower, confirming this assumption that most of the larvae spawned are still above the Bank at the time of sampling. A similar synchrony of spawning, in time, is evident in the significant reductions in larval abundance, factors of 3–5, in these regions 1 week later (Tremblay, MS 1991).

Employing the estimates of egg production and recruitment density, the survival, L, of "potential egg" to larva in the most productive waters above the Northern Edge and Northeast Peak is therefore

$$L(\text{eggs to larva}) = (36\,800\ m^{-2}) / (2.68 \times 10^{6}\ m^{-2}) = 0.014$$

with a confidence interval (Appendix 2) of -75% below to +80% above this best estimate. The survival probability from a larva to age 2 recruit is

$$L(\text{larva to age 2}) = (0.339\ m^{-2} / (36\,800\ m^{-2}) = 9.2 \times 10^{-6}$$

with a -78% to +261% confidence interval. This assumes that the larvae found in dense concentrations above the Northeast Peak originated from eggs spawned in the combined area of the Northeast Peak and the Northern Edge, and that those larvae successfully settle in that region. This is likely, based on the persistence of these populations (Sinclair *et al.*, 1985; Caddy, 1989), on stock-recruitment evidence (McGarvey *et al.*, 1992), and on the much lower levels of population abundance in neighbouring areas.

We further partitioned mortality for the egg to larva,$M_{E\text{-}L}$, and the subsequent development from larva to age 2 juvenile, $M_{L\text{-}2}$, stages. Assuming that the larvae sampled by Tremblay and Sinclair (1990a) averaged 17± 5 days old, and that the age 2 recruits were 700 days old (because the survey cruises were in August and peak spawning occurs in mid-September on Georges Bank; M. J. Tremblay, Halifax Fisheries Research Laboratory, Dept. of Fisheries and Oceans, Halifax, Nova Scotia, pers. comm.), we obtained average daily mortality rates for these two stages of scallop development:

With constant mortalities $M_{E\text{-}L}$ and $M_{L\text{-}2}$,

$$N_L = N_E \exp(-M_{E\text{-}L} * 17)$$

and

$$N_2 = N_L \exp(-M_{L\text{-}2} * 683),$$

yielding

$$M_{E\text{-}L} = 0.25\ \text{day}^{-1}$$

and

$$M_{L\text{-}2} = 0.016\ \text{day}^{-1}$$

with confidence intervals of -35% to +35% and -6% to +22%, respectively.

Discussion

Investigations of scallop distribution now provide population density (as harvestable biomass or population numbers) averaged over four space scales:

1. All of Georges Bank.
2. In the five subregions of Georges Bank, which vary in density over a factor of 10.
3. Among computer-drawn contours in maps constructed from both survey and commercial catches (Robert and Black, 1990). Densities on these scales of roughly 1' square range over a factor of 200, with the greatest variation among the youngest age group (age 3).
4. Direct observations of adult densities in typical scallop beds lie in the range of 1 to 6 per m^2 (MacDonald and Thompson, 1986b; Naidu, MS 1969; Caddy, 1968 and 1970; Dickie, 1955), roughly 20–100 times the Georges Bank average.

Population estimates obtained using cohort analysis of data from port sampling of the commercial fleet by Robert and Black (1990) yielded a 1977–88 average of 1 200 million for ages 3+ in Canadian waters. This may be compared with the value obtained in this study of 1 440 million for scallops 80 mm and larger in the Northern Edge and Northeast Peak which includes a large area of less densely populated scallops outside Canadian waters. On the other hand, ≥80 mm probably leaves off some age 3 scallops, judging from the age 3 peak in the original size-frequency data. Thus, employing different data and using two independent methods, the two population estimates effectively agree.

Average meat-weight biomass density on the Northern Edge is 3 times higher than the Northeast

Peak. This explains the higher fishing intensity in that region than all others (Caddy, 1975). More intense fishing, in turn, explains the lower biomass (i.e. weight) per individual of 2.91/0.172 (Table 1) or 16.9 g per average scallop of 80 mm in size or greater, compared with the less intensively fished Southeast Part, where the higher average meat weight of 24.6 g per individual almost certainly reflects a longer average lifespan. Values for other regions are 17.9 g per ≥80 mm individual in the Northeast Peak, 25.9 g in the eastern South Channel, and 18.9 g in the western South Channel.

The rescaling coefficient, α, which transforms numbers-per-tow into numbers-per-m^2, may be useful with other applications of the research survey data. A value of α could be obtained for chosen years or areas employing a method like that detailed in Appendix 3.

Recruitment is defined as total scallops captured between the sizes of 30 and 60 mm. If 40 mm is an accurate cutoff for the lower capture rate of smaller scallops by the survey gear, an assumption compatible both with published gear investigations (Dickie, 1955; Caddy, 1972) and with the mesh size of the nylon liner chosen specifically for capturing smaller scallops (1.5" or 38.1 mm), then the underestimate of age 2 recruitment due to variation in capture rate with size is small, and compensating for this bias yielded only a 10% increase. On the other hand, the size range where capture rates are significantly lower probably does not extend to 100 mm as we assume in GS_{high}, so the upper limits of ~220% higher than the best estimates, based on the assumption of GS_{high}, are likely to be exaggerated.

One fact suggests that the uncertainty in recruitment, due to gear selectivity, is not as wide as the large confidence interval of -10% to +250% suggests. The comparison (Appendix 1) of survey numbers-per-tow from independent US and Canadian surveys (Serchuk and Wigley, 1986; Mohn *et al.*, 1987) shows, on average, that survey measures of recruitment yield a 3 times smaller standard error (Appendix Table 1.2), at around 3% for the 12-year average, and are, by that measure, 3 times more accurate than adult population variables. Since the lower gear capture rate primarily affects recruitment sizes only, this suggests that gear selectivity does not alter the consistency of measurement at smaller sizes but does affect the absolute quantities captured in each size class. The two orders of magnitude (3% *versus* 300%) between the precision of the recruitment data and uncertainty of its absolute value reflects uncertainty about the actual trace of the gear selectivity ogive. The relatively highly self-consistent result for recruit numbers, however, seems to suggest that a relatively consistent gear selectivity curve does exist but that it is, as yet, not well defined.

Comparable with our survival estimate of 1.3×10^{-7} for egg to age 2 survival, Vahl (1981) derived a value of 5×10^{-7} for the survival rate of the Iceland scallop, *Chlamys islandica*, from egg to age 4 recruit. Natural mortality was found here to be an order of magnitude lower for larva to age 2 compared with potential egg to larva. This decline in mortality with age in early life history has been widely suspected but not previously documented for *Placopecten*. Combined with the natural mortality estimates for ages 2 and older of MacDonald and Thompson (1986b, Fig. 2), a measure of natural mortality at all ages is obtained. It drops very rapidly from potential egg to age 2 then levels off in a relatively steady parabolic shape at a value around 0.1 for ages 2+, with a minimum in full adulthood (ages 5–11), and rises slowly for ages 11–20.

Acknowledgements

This work was supported by the USA National Marine Fisheries Service, Northeast Fisheries Center, Woods Hole, Massachusetts and the Canadian Department of Fisheries and Oceans, Bedford Institute of Oceanography and Halifax Fisheries Research Laboratory, Halifax, Nova Scotia.

We thank Bob Mohn and Ginette Robert at the Halifax Laboratory who provided survey data, and discussion with John Tremblay stimulated ideas in the estimation of natural mortality.

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Appendix 1. Survey Data Accuracy and Precision

The results of Serchuk and Wigley (1986) allow direct calculation of standard errors of survey numbers per tow by two different methods. The first is to apply the standard theory of stratified sampling (Cochran, 1977) and calculate the standard error for the whole region, based on the standard deviations of the samples (i.e. tows) within each stratum, weighted by their relative areas (Serchuk and Wigley, 1986). These results for 1982, 1983 and 1984 are presented in the first two columns of Table 1.1. The second method is to consider USA and Canadian survey estimates of mean number per tow as independent samples of the mean, a sample size of two. By this method, the standard error (SE) is the standard deviation of this small sample of means. The 95% confidence intervals (CI) by this second method, expressed as percentages of the mean,

$$\mathrm{CI} = 1.96 * \mathrm{SE} * 100 / \left[(\overline{\mathrm{US}} + \overline{\mathrm{CAN}}) / 2\right]$$

are presented in Table 1.2, and the last column of Table 1.1.

The confidence intervals of the 3-year means in both tables are calculated by considering the samples and thus = standard errors from each year to be independent random variables:

$$\mathrm{SE3} = \frac{1}{3}\sqrt{\sum_{\mathrm{YR}=1982}^{1984} \left[\mathrm{SE(YR)}\right]^2} .$$

Confidence intervals for the full 12-year population estimates are obtained by assuming the 3-year means and their standard errors are simply repeated three additional times;

$$\mathrm{SE12} = \frac{1}{4}\sqrt{4 * \mathrm{SE3}^2} = \frac{\mathrm{SE3}}{2}.$$

95% confidence intervals calculated for seven population statistics, are presented in the seven columns of Tables 1.1 and 1.2. In fact, there are just five population variables, since the three columns of Table 1.1 are independent estimates for total mean number per tow, from USA and Canadian surveys (and thirdly from their difference). These represent three measures, by two methods of confidence interval. The lower standard errors for the Canadian versus USA surveys during these years (Table 1.1) reflect the greater number of Canadian tows per stratum. The overall confidence intervals for 12-year averages lie in the range of 5 to 20% of the means, based on the standard deviations of the samples (Table 1.1.). Thus, the close agreement of USA and Canadian means for the four population variables of Table 1.2, ranging from 3 to 9%, was better than expected, considerably enhancing our confidence in the reliability of these data.

The four statistics in Table 1.2 are not defined identically by Serchuk and Wigley (1986) to the population variables estimated in Methods and Results (listed in the bottom row of Table 1, 2). However, the time series of the two forms of each statistic are, in general, very close. As quantified by their correlation over the 12 years 1977 to 1988 on the Northern Edge and Northeast Peak, RECRUITS and number per tow <70 mm ($r = 0.961$, $P = 4\times10^{-7}$, df = 10), BIOMASS and meat weight per tow total ($r = 0.997$, $P = 6\times10^{-8}$, df = 10), and thirdly, EGGS and meat weight per tow ≥70 mm ($r = 0.995$, $P = 6\times10^{-8}$, df = 10), are nearly identical time series, differing by a constant, while yearly adult POPULATION differs slightly from numbers per tow ≥70 mm ($r = 0.846$, $P = 3\times10^{-4}$, df = 10). Moreover, it is not the yearly means, but the uncertainty of the average of the 12 means which is being estimated. Because the variances, and therefore the standard errors of the 12-year averages are likely to differ considerably less than the time series of the means, it is safe to conclude that these confidence intervals (Tables 1.1 and 1.2) are accurate.

One possible bias in this analysis is that it considers only the years 1982–84 when comparisons were possible between USA and Canadian surveys. These were years of relatively low scallop abundance. The general pattern, however, is towards higher precision as abundance increases.This is evident spatially in comparing the means and coefficients of variation in different strata (see Table 4 in Serchuk and Wigley, 1986) and is also expressed temporally in the 3 years analyzed (see Table 3 in Serchuk and Wigley, 1986) insofar as the closest agreement for <70 mm (1982), and ≥70 mm (1984) number per tow occurred in their respective years of highest abundance (Table 1.2). This may suggest that the 12-year averages reported in Methods and Results are more precise than the confidence intervals in Tables 1.1 and 1.2.

Overall, recruitment was not particulary low in these 3 years, the age 2 recruitment peak of 1984 being the second largest between 1977 and 1988. This could, in fact, explain the closer agreement obtained for recruit numbers (3% between US and Canadian <70 mm number per tow counts) compared with the other 3 statistics of Table 1.2.

TABLE 1.1 95% confidence intervals (CI) of total mean numbers per tow of sea scallop (*Placopecten magellanicus*) on Georges Bank, calculated from Serchuk and Wigley (1986) by two methods, expressed as percentages above and below the mean.

	Calculated from sample variance		Calculated from standard deviation of USA and Canadian means
Year	USA	Canadian	
1982	±36.8	±22.9	±9.1
1983	±45.5	±17.1	±40.9
1984	±62.3	±28.8	±6.9
3-year mean	±40.2	±17.8	±9.3
12-year mean	±20.1	±8.9	±4.6

TABLE 1.2. 95% confidence intervals (CI) of the mean numbers per tow of sea scallops (*Placopecten magellanicus*), derived from Serchuk and Wigley (1986), calculated from the means of the two independent surveys, expressed as percentages above and below the mean. The associated population variables are indicated below.

	Mean number per tow		Mean meat weight per tow	
Year	< 70 mm	≥ 70 mm	≥ 70 mm	Total (all sizes)
1982	±17.4	±4.3	±12.4	±11.0
1983	±27.1	±57.2	±40.5	±40.4
1984	±4.75	±19.2	±38.0	±18.3
3-year mean	±5.8	±18.0	±17.5	±14.3
12-year mean	±2.9	±9.0	±8.7	±7.2
	RECRUITS	POPULATION	EGGS	BIOMASS

Appendix 2: Confidence Intervals

Details of the calculations of confidence intervals are presented here. Uncertainty due to the rescaling coefficient α and due to variation in gear capture probability with size, for the four population variables of Tables 1, 2 and 4 and for the estimates of survival and natural mortality of early stage scallops are considered.

Uncertainty of α

Summarizing, the formula for α is

$$\alpha = \frac{\overline{CA}_{mt} * \overline{MPT} * \exp(\bar{F})}{\bar{D}_{NPT} * AREA}$$

The error in α will arise from error in the 5 input variables:

1. The uncertainty in AREA is negligible.

2. Error in the raw data, in $\bar{D}_{npt,}$ is predominantly due to gear selectivity and is therefore factored into the overall confidence limits below.

3. Because catch restrictions played no role in the USA fishery and have only recently been established in the Canadian fishery and still act rather weakly, reported catch ($\overline{CA}_{mt}$) is likely to be reliable. We may postulate an upper limit of $\delta(CA_{mt}) = 5\%$ for unreported catch. There is no significant probability that reported catch is an overestimate.

4. The limit of 33 meats per 500 g came fully into effect in 1986 (Mohn *et al.*, MS 1989). This meat count was used to estimate the lower bound of the average number of scallops per ton of meat weight harvested ($\overline{MPT}$) over 1977–88. Based on reported smaller average sizes in earlier years (Serchuk, MS 1984; Robert and Black, MS 1990), 40 meats per 500 g was used to estimate the likely upper limit of the average during this period.

5. Average fishing mortality, $\bar{F}$ was calculated from the yearly values of F-at-age obtained by Robert and Black (MS 1990) employing cohort analysis. Weighting the F-at-ages by catch-at-age (Robert and Black, MS 1990) and averaging these yearly means over 1977–88 yields a value of 0.78 with a standard error of 0.05. Rounding, we set $\bar{F} = 0.8$ and, choosing confidence intervals on the safe side, set the uncertainty as $\delta\bar{F} = \pm 0.2$.

Since the information sources for the last three input variables are different, the errors are independent. Applying the standard theory of error propagation (see Taylor, 1982, p. 177), the error of α, $\delta\alpha$, in terms of these three sources of uncertainty is

$$\pm\delta\alpha = \sqrt{\left[\frac{\delta\alpha}{\delta\bar{F}} \cdot \left|\pm\delta\bar{F}\right|\right]^2 + \left[\frac{\delta\alpha}{\delta\overline{CA}_{mt}} \cdot \left|\pm\delta\overline{CA}_{mt}\right|\right]^2 + \left[\frac{\delta\alpha}{\delta\overline{MPT}} \cdot \left|\pm\delta\overline{MPT}\right|\right]^2}$$

The resulting upper confidence limit is 27% above the best estimate of α. The lower bound of uncertainty is smaller, at 16% below.

Gear selectivity

A number of studies of gear selectivity have been undertaken (Dickie, 1955; Caddy, 1972; Smolowitz and Serchuk, MS 1988) but the range of reported variation is high for different bottom types (Caddy, 1968; Smolowitz and Serchuk, MS 1988). Most experiments have investigated the capture and selection rates of the commercial dredge but no accurate measure of gear selectivity has been found (Smolowitz and Serchuk, MS 1988). Here we apply one reasonable measure and one more extreme measure of gear selectivity in order to determine the general sensitivity of the population estimates to this source of error.

The size selectivity studies of Dickie (1955) and Caddy (1972), for the survey gear which includes a 1.5" nylon liner inside a commercial scallop drag, suggest that scallops above 40 mm are retained. If we neglect the effect of the behavior change for scallops above around 100 mm when they stop swimming as an escape mechanism from both predators and the scallop drag (Caddy 1968), a reasonable "best estimate" of survey gear size selectivity can be obtained. Noting that in surveys virtually no scallops below 20 mm in size are captured, taking 40 mm as the asymptote of the best estimate above which a constant capture efficiency is assumed, and letting the gear selection ogive rise linearly from 20 to 40 mm, we obtain one reasonable curve of survey gear selectivity called GS_{best}, plotted in Fig. 4. Recruitment numbers (Tables 1 and 2), derived employing GS_{best} are taken as the best estimates.

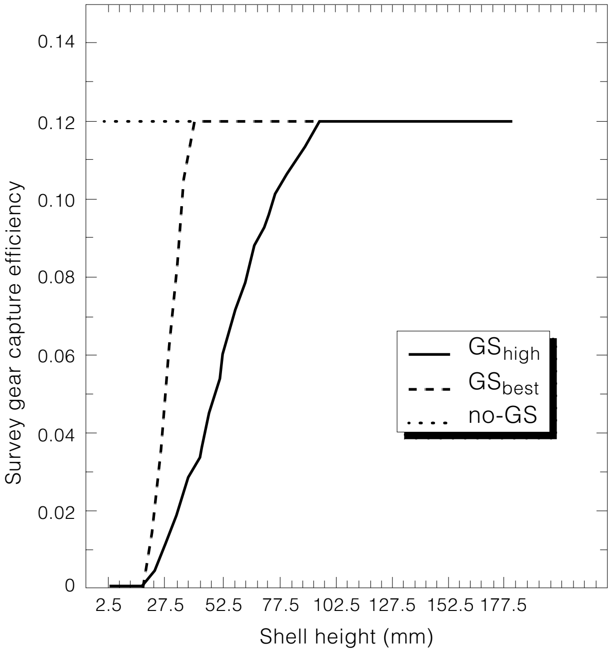

Fig. 4. Derived gear selectivity-at-size (GS_{best}), intermediate between the uniform capture efficiency implicit when gear selectivity is not considered (no-GS), and the gear selectivity curve (GS_{high}) employed here in analyzing maximum likely sensitivity to this source of error for sea scallops (*Placopecten magellanicus*).

To evaluate the uncertainty in recruit numbers derived with this choice of gear selectivity ogive, a second gear selectivity vector, GS_{high} (Fig. 4), is chosen which is likely, on the basis of the studies of Caddy (1972) and Dickie (1955) to somewhat overestimate the lower capture rate at smaller sizes. At the other extreme, we obtain a lower confidence bound on our recruit estimate by simply neglecting gear selectivity and calculating recruit numbers directly from the survey numbers per tow at all sizes ("no-GS" in Fig. 4). The lower and upper bounds thus derived are presented in brackets below the best estimate for recruit numbers in Tables 1 and 2. To obtain overall recruitment confidence intervals, we choose the widest variation among the various subregions and obtain deviations of -11% and +220% for the contribution due to gear selectivity.

Population, biomass and egg production are unchanged by the GS_{best} survey gear ogive since scallops 40 mm and less are not counted in their summation. The GS_{high} ogive yields estimates which are 4.5% higher for biomass and population numbers and which are unchanged for egg production. These GS_{high} fractional deviations are employed directly in the overall confidence intervals obtained below.

Confidence intervals of population statistics

Because absolute population and density are rescaled using total catch, any size-uniform error in the survey data will not affect the final population estimates, leaving the two important sources of uncertainty due to survey gear selectivity and α. We cannot presume that these two sources of error are independent since commercial gear selectivity, implicit in α through commercial catch and meat weight per ton, is also significant and may generate bias which has a positive covariance with survey gear selectivity. For the three adult population statistics, we therefore employ the formula (see Taylor, 1982, p. 178) for the combined errors of these two sources which make no assumptions of independence. The combined fractional error (i.e. the percentage deviation) in the case of non-independence is simply the sum of the fractional errors (Taylor, 1982).

The confidence bounds of +27% and -16%, derived for α above, are due specifically to the three factors in α that are independent of the survey, and so may be factored out of the double summations which define the four population statistics. Since α is a simple multiplicative factor, the combined errors due to both α and gear selectivity are the sums of the two percentages. The resulting overall confidence intervals are -16% and +27% for BIOMASS, -16% and +27% for POPULATION, -16% and +31.5% for EGGS, and -27% and +250% for RECRUITS.

Since the commercial and survey gear selectivity act at different scallop size ranges (<~40 mm *versus* <~80 mm), and since most of the error in α is not due to gear selectivity, this covariance is probably small, so the resulting confidence intervals for these population statistics are probably wider than need be.

Two additional sources of uncertainty, in the eggs-per-female-at-height (Fig. 2) and meat-weight-at-height vectors, are probably small compared to the two principal sources of error described above, especially at the truncated size ranges (Fig. 3) typical of this heavily exploited population, and can therefore be neglected.

Confidence intervals of survivals and natural mortalities

No assumption of independence was made in calculating the confidence bounds for L(egg to age 2) which are therefore simply the sums of the percentage confidence bounds (Taylor, 1982) for egg production and recruit numbers. For the survivals in the two stages, L(egg to larva) and L(larva to age 2), independence was assumed between the larval counts of Tremblay (MS 1991) and our estimates of recruitment and egg production.

Similarly, the confidence intervals for natural mortalities are calculated assuming independence in the uncertainties of the independent variables specified above, namely pelagic larval counts, egg production or recruitment estimates, average age of sampled larvae, and fractions of the total present during the week of peak larval abundance. A formula is therefore employed analogous with that used to calculate the uncertainty in α.

Appendix 3. Scaling Survey Numbers to Density

The calculation of the scaling coefficient, α, which transforms the survey measure of abundance, numbers per tow, into absolute numbers per m^2, proceeded as follows: the time series (Mohn *et al.*, MS 1989; New England Fishery Management Council, MS 1982) of annual commercial catch for all of Georges Bank was averaged over the years 1977 to 1988 yielding:

$$\overline{CA_{mt}} = 11\,635 \text{ mt.}$$

From catch in metric tons, the total number of harvested scallops was derived using knowledge of the meat-count restrictions limiting average harvest size in this fishery. In 1986, a limit of 33 meats (i.e. scallops) per 500 g was instituted (Robert and Black, MS 1990). Canadian commercial catch-at-size data during these years (Mohn *et al.*, MS 1989) suggests that this limits harvested scallops to be roughly 80 mm shell height or greater. Assuming 33 scallops per 500 g of harvested biomass, the number of scallops captured $\overline{CA}$ in an average year was

$$\overline{CA} = 768\,500\,000.$$

Employing the value $\overline{F} = 0.8$ (Robert and Black, MS 1990, New England Fishery Management Council, MS 1981), the average size, $\overline{N}$, of the Georges Bank scallop population was estimated.

Given

$$\overline{CA} = \overline{N} \exp(-\overline{F}),$$

$$\overline{N} = 1.71 \times 10^9 \text{ scallops}$$

of 80 mm shell height and greater.

We define a constant, α, which rescales the survey density, expressed as number per tow, D_{npt}, into units of scallops per m^2, D_{m^2};

$$\overline{D}_{m^2} = \alpha * D_{npt}.$$

Total population equals density times area,

$$\overline{N} = \overline{D}_{m^2} * \text{AREA},$$

yielding the formula for α in terms of the two population averages,

$$\alpha = \overline{N} / (\overline{D}_{npt} * \text{AREA}).$$

The area of Georges Bank (excluding the shallow central region not included in this study), is

$$\text{AREA} = 39\,643 \times 10^6 \text{ m}^2.$$

The average number per tow, $\overline{D}_{npt}$, for scallops 80 mm and greater, calculated directly from the survey data,

$$\overline{D_{npt}} = \frac{1}{12} \sum_{YR=1977}^{1988} \left[\sum_{HT=80}^{185 \text{ mm}} NPT(YR,HT) \right]$$

is found to be

$$D_{npt} = 64.7,$$

yielding

$$\alpha = 0.0006663.$$