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Is beach-spawning success for capelin, *Mallotus villosus* (Müller), a function of the beach?

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We postulate that the variation in capelin, *Mallotus villosus* (Müller), egg concentration among spawning beaches in eastern Newfoundland is a function of beach characteristics. This hypothesis is explored by examining relations between egg concentration and beach characteristics among 15 beaches located around the perimeter of Conception Bay. Beaches ranged in mid-tide area from 300 to 8000 m^2, in shore-normal orientation from 20 to 330°, in median grain size from 2.4 to 11.3 mm, and in egg concentration from 360 to 4380 cm^{-2} mid-tide zone. Variations in beach sediment grain-size distributions were captured by variations in the overall rate constant (k) and inflection point (I) of the logistic equation fitted to the cumulative percentage grain-size distributions. Beach orientation explained 57% of the variation in egg concentration among beaches. Orientation and k explained 61% and additional exploratory models explained 80–86% of the variation. Our findings build upon previous reports that describe the significance of the physical environment on the early life history of capelin and provide a quantitative method for classifying the spawning habitat of beach-spawning capelin.

Keywords: beach sediments, beach-spawning, capelin, latitude, orientation, spawning.

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Introduction

Ripe female capelin, *Mallotus villosus* (Müller), spawn with attendant males over the exposed intertidal zone of gravel beaches during June and July in the coastal areas of the Northwest Atlantic (Templeman, 1948). The negatively buoyant eggs remain adhesive for ~2 h after exposure to water (Fridgeirsson, 1976) and adhere to the beach substratum. The fertilized eggs incubate and develop in beach sediments, at depths of up to 20 cm (Taggart and Leggett, 1987b). The hatched larvae are eventually dispersed from the substratum into the ocean during wind-driven increases in wave turbulence and the mixing of beach sediments, and the corresponding increase in water temperature associated with water-mass replacement (Frank and Leggett, 1981a,b; Taggart and Leggett, 1987a).

The "selection" of spawning beaches by capelin is postulated to be some function of beach grain size (Hart and McHugh, 1944; Templeman, 1948; Velikanov, 1984, 1988). Templeman (1948) examined four capelin spawning beaches and noted the most spawn on beaches with grain sizes in the diameter range 2–25 mm; he observed limited or no spawn on beaches where the nominal grain size exceeded 20 mm. Grain sizes in the range 1–4 mm have been reported as suitable substratum for capelin spawning in deep water off Iceland (Thors, 1981). Pitt (1958) reported a grain-size range of 0.5–2.2 mm for capelin spawning on the Southeast Shoal of the Grand Bank, although the estimates were based on particles adhering to capelin eggs found in haddock (*Melanogramus* sp.) stomachs. Spawning substrata at shallow (12–18 m) and deep (35–70 m) spawning locations off northern Norway have grain sizes in the range 5–15 mm (Bakke and Bjorke, 1973). Pacific capelin spawn most heavily on particle sizes in the range 1–5 mm (Hart and McHugh, 1944). Velikanov (1984) reported that capelin eggs along the southern reaches of Aniva Bay in the

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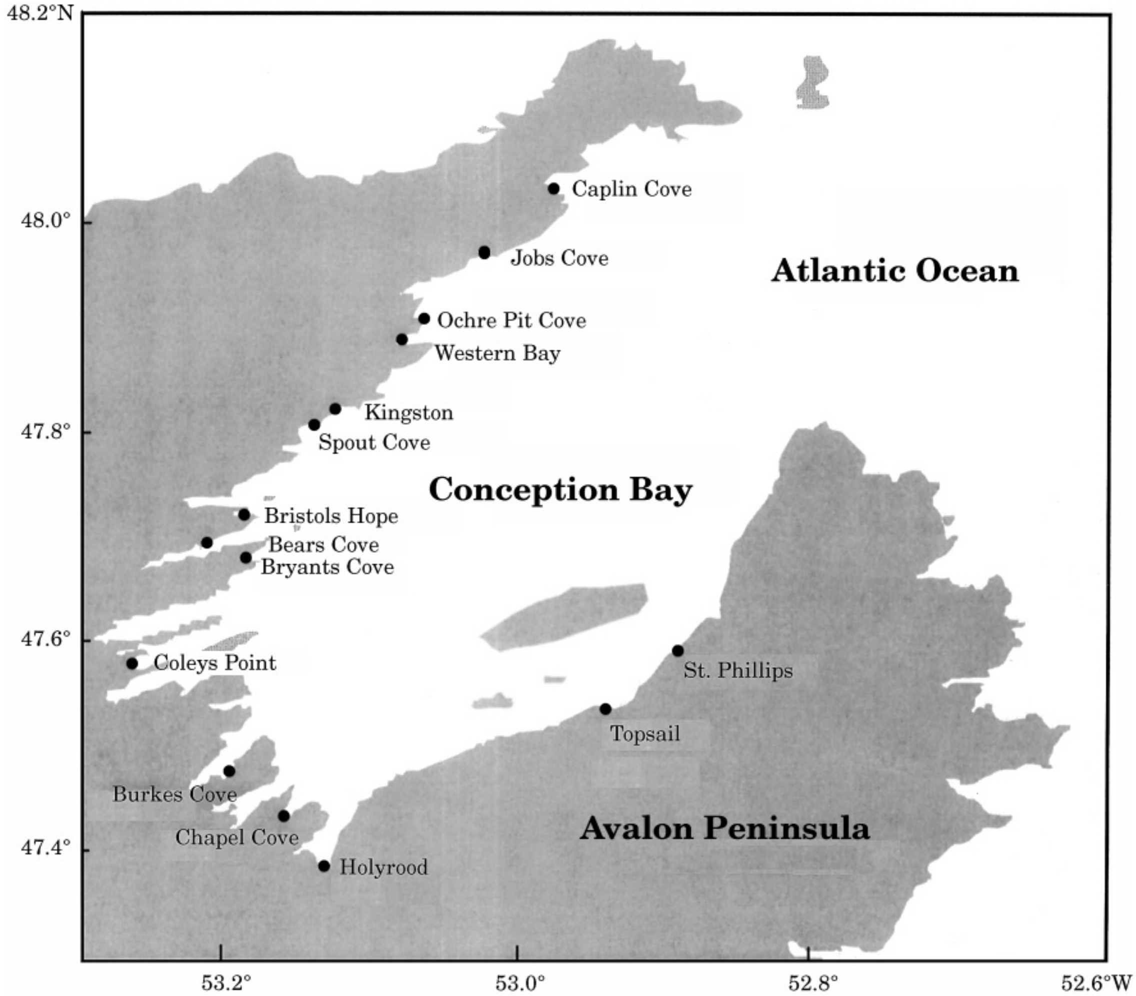

Figure 1. Chart (N latitude, W longitude) of the Avalon Peninsula and Conception Bay, Newfoundland, showing the location of 15 capelin spawning beaches along the perimeter of Conception Bay.

Sakhalin region (western Pacific) were spawned on grain sizes in the range 0.25–10.0 mm; however, spawning was more common on “coarse-grained sand” in the range 0.5–1.0 mm. Farther north in Aniva Bay, spawning was most concentrated on grain sizes of 2–10 mm (Velikanov, 1988).

Taggart and Nakashima (1987), using three samples (one from each of three tidal zones) collected at each of 16 beaches around Conception Bay in 1983, reported that egg concentrations were near maximal at beaches with a N to NE orientation and that the beaches appeared to be grouped by latitude. However, definitive conclusions could not be reached. First, egg concentrations may have been underestimated because the presence of capelin egg shells (7–63% of egg volume in the mid-tide zone) and large numbers of pre-emergent larvae in the samples imply substantial hatching at all sites prior to sampling. Second, because only one sample was collected per tidal zone, the data may have been too limited to estimate beach-specific intertidal egg concentration. These limitations, the apparent influence of beach orientation, and the absence of grain-size distribution data for the beach substrata were partly responsible for the study we report here.

Additional prompting arose from our postulation that physical factors are quantitatively related to the suitability of beaches as spawning sites – if measured through the magnitude of egg deposition (i.e. spawn concentration). This follows from observations that physical (hydrological and meteorological) factors appear to act in concert in determining capelin egg development, and subsequent larval emergence and survival among beaches across a large geographic range (Frank and Leggett, 1981a,b). Such relatively coherent conditions over large scales cannot explain the degree of variation in egg concentration observed among beaches

Table 1. Shore-normal orientation, latitude, total mid-tide area, average core-sampling depth, number of core samples (n), average areal capelin egg concentration and total abundance estimates, and egg development stage (% early, eyed, and dead) for mid-tide areas, with means and medians, for 15 spawning beaches (and identifier codes) along the perimeter of Conception Bay, Newfoundland, sampled in June 1987.

							Egg				
Beach	Date sampled	Orientation (°true)	Latitude (°N)	Mid-tide area (m^2)	Core depth (cm)	n	Concentration (eggs cm^{-2})	Abundance ($\times 10^{10}$)	Early (%)	Eyed (%)	Dead (%)
Bears Cove (BE)	24 June	110	47.703	1138	12.7	4	2884	3.28	40.3	33.1	26.7
Bristols Hope (BH)	24 June	60	47.720	1220	16.7	3	2066	2.52	46.0	25.6	28.4
Bryants Cove (BR)	23 June	55	47.675	1462	16.4	3	4379	6.40	60.9	10.6	28.5
Burkes Cove (BU)	29 June	305	47.463	462	9.2	3	647	0.30	26.4	59.3	14.3
Caplin Cove (CA)	25 June	45	48.027	2090	12.7	2	4068	8.50	75.5	3.6	21.0
Chapel Cove (CH)	29 June	30	47.437	2184	14.6	3	949	2.07	8.0	56.8	35.3
Coleys Point (CO)	28 June	50	47.577	4320	12.8	4	737	3.18	11.6	58.7	29.8
Holyrood (HO)	30 June	40	47.388	336	17.5	3	1550	0.52	0.0	76.0	24.0
Jobs Cove (JO)	25 June	175	47.972	1430	15.9	2	2111	3.02	53.1	32.2	14.9
Kingston (KI)	27 June	145	47.825	7980	13.8	4	2771	22.10	38.1	43.5	18.5
Ochre Pit Cove (OC)	26 June	20	47.912	1557	14.5	3	1601	2.49	76.3	11.3	12.4
Spout Cove (SC)	28 June	90	47.820	4094	15.2	3	2005	8.21	21.4	34.2	44.4
St Phillips (ST)	30 June	325	47.592	675	14.3	2	389	0.26	39.0	38.4	22.8
Topsail (TO)	30 June	330	47.543	2527	13.8	4	361	0.91	51.4	30.1	18.5
Western Bay (WB)	26 June	45	47.883	3651	12.8	5	2347	8.57	42.2	26.7	31.1
Mean	27 June	122	47.702	2342	14.2	3	1924	4.82	39.4	36.0	24.7
Median	27 June	60	47.703	1557	14.3	3	2005	3.02	40.3	33.1	24.0

Table 2. Descending order of sediment sorting screen mesh sizes and geometric mean sizes of retained beach sediments (mm and Phi scale; Φ).

Screen mesh size		Geometric mean size retained	
mm	Φ	mm	Φ
>63.00	—	—	—
31.50	− 5.00	44.55	− 5.50
16.00	− 4.00	22.45	− 4.50
8.00	− 3.00	11.31	− 3.50
5.60	− 2.50	6.69	− 2.75
4.00	− 2.00	4.73	− 2.25
2.80	− 1.50	3.35	− 1.75
2.00	− 1.00	2.37	− 1.25
1.40	− 0.50	1.67	− 0.75
1.00	0.00	1.18	− 0.25
0.71	0.50	0.84	0.25
0.50	1.00	0.60	0.75
0.36	1.50	0.42	1.25
0.25	2.00	0.30	1.75
<0.25	—	—	—

at the relatively small geographic scale represented by Conception Bay. Given the qualitative evidence suggesting a beach sediment size structure and spawning relation outlined above, we hypothesized that variation in capelin egg concentration among spawning beaches is some function of beach characteristics. We explore this hypothesis by examining egg concentration and beach sediment characteristics among 15 capelin spawning beaches of different orientation along the perimeter of Conception Bay, Newfoundland.

Material and methods

Study site and sampling

The Conception Bay and Avalon Peninsula region (Figure 1) has crenulated coastlines and shorelines composed of unmetamorphosed clastic sediments and volcanics with minor carbonate constituents (Forbes, 1984). The paraglacial sediments that dominate the region are difficult to characterize because they are drawn from heterogeneous, multisourced, and polycyclic sediments with varying amounts of sand, gravel, and cobble (Church and Ryder, 1972). In a coastal environment, these deposits are reworked by wave and tidal action into coastal barriers that have a variety of depositional forms, including gravel ridges, spits, bars, beach ridge plains, and transverse lag shoals (Church and Ryder, 1972). The beaches typically found among the embayments along the coastline of the Avalon Peninsula are primarily barrier beaches or pocket (bayhead) accumulations, and beach-face samples collected throughout the coastal regions of Newfoundland have average grain sizes ranging from 0.14 to 290 mm (Forbes, 1984).

We collected 48 samples of beach sediments and attached eggs that were distributed among 15 barrier- and pocket-type spawning beaches around Conception Bay (Figure 1, Table 1). Beach orientation (° true)

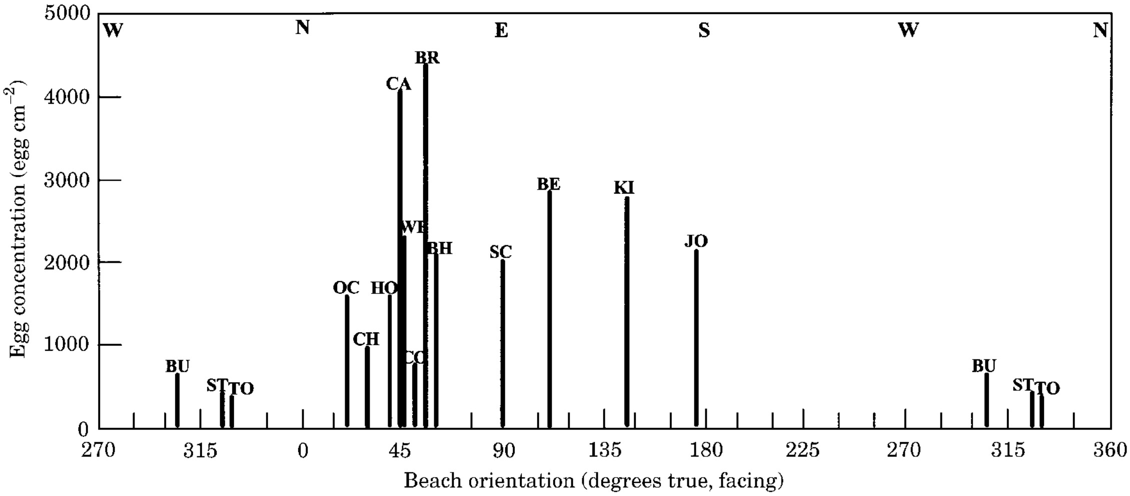

Figure 2. Histogram showing variation in capelin egg concentration among 15 spawning beaches (identifier codes above estimates are listed in Table 1) as a function of beach orientation along the perimeter of Conception Bay, Newfoundland. Note that the north-through-west estimates are displayed at both ends of the linear compass-rose representation.

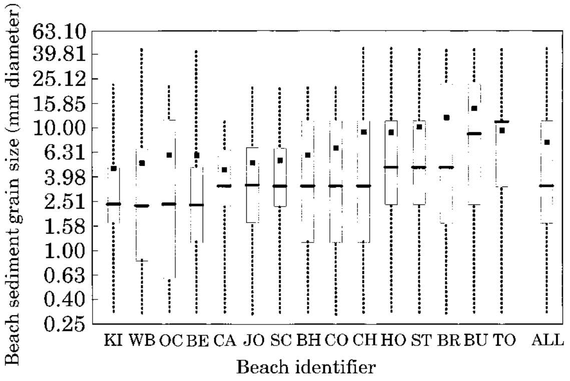

Figure 3. Box-and-whisker summary of sediment grain size (geometric mean, mm) distributions for each of 15 capelin spawning beaches (identifier codes listed in Table 1) along the perimeter of Conception Bay, Newfoundland, and for all (ALL) beaches, showing the 1st and 3rd quartiles (lower and upper margins of the rectangles), the median size-class (solid bar; based on geometric mean size), the mean size (solid square), and size range (limits of the broken line).

was determined from hydrographic charts and aerial photographs, and was measured normal to the beach. Sampling was between 23 and 30 June 1987 and commenced immediately following the seasonal maximum (16–21 June) in capelin spawning in the region in that year, as determined from aerial surveillance of spawning aggregations (Nakashima, 1988) and periodic inspections of some beaches. All samples were collected in the mid-tide (MT) zone (area between the high- and low-tide water marks), and during low tide, to maximize the sampling of several beaches in a short period. Mid-tide sampling (only) was partly related to logistics and partly determined by the assumption that sampling the mid-tide area does not affect estimates of egg concentration for this type of study (Taggart and Nakashima, 1987).

The area of the MT zone on each beach was estimated using length and width measurements made when samples were collected. The number of samples collected at each beach depended on a qualitative inspection of the egg distribution in the MT zone and consisted of visually examining the concentration of eggs in sequential "grabs" of beach sediments along the length of the MT zone. Two qualitative and relative indices were employed: HC (high concentration) and LC (low concentration). When patterns of egg abundance were judged relatively heterogeneous, the MT zone was stratified into HC and LC areas (each measured), and a sediment core sample was collected haphazardly within each stratum. Only one beach, Caplin Cove, had a relatively uniform egg distribution and was sampled at two different locations within the MT zone.

A steel sediment corer (6.5 cm internal diameter) was used to collect samples. The corer was manually "drilled" into the beach sediments to the greatest depth possible (limited by the strength of the operator) and core depth was measured using a calibrated plunger inside the corer. Each core sample was fixed with a 4% (vol:vol) formalin:seawater solution buffered with sodium borate to protect the eggs from deterioration. Egg concentration and development rate were assumed to be vertically homogeneous within the beach sediments (cf. Frank and Leggett, 1981b).

Processing of eggs and sediments

Capelin eggs were separated from beach sediments by rinsing each sample with freshwater over a 250 µm mesh

Table 3. Statistical parameters of sediment particle-size distributions for 15 capelin spawning beaches (as coded in Table 1) along the perimeter of Conception Bay, Newfoundland. Included are the rate constant (k) and the inflection point (I) from the logistic fit to the cumulative percentage distribution as well as the mean, standard deviation (s.d.), coefficient of variation (CV), median (Med), skew (Skew), kurtosis (Kurt), 1st and 3rd quartiles (Q_1, Q_3), inter-quartile range (IQR), and the 5th, 90th, and 95th percentiles (P_5, P_{90}, P_{95}).

Beach	k	I	Mean (mm)	s.d. (mm)	CV	Med (mm)	Skew	Kurt	Q_1 (mm)	Q_3 (mm)	IQR (mm)	P_5 (mm)	P_{90} (mm)	P_{95} (mm)
BE	3.54	0.30	6.01	9.47	157.62	2.37	2.80	7.89	1.18	4.73	3.55	0.60	22.45	22.45
BH	2.87	0.38	6.01	6.89	114.59	3.35	1.47	0.99	1.18	11.31	10.13	0.43	22.45	22.45
BR	2.53	0.60	12.23	15.36	125.64	4.73	1.33	0.26	1.67	22.45	20.78	0.60	44.55	44.55
BU	2.42	0.82	14.50	15.22	105.03	9.00	1.05	− 0.25	2.37	22.45	20.08	0.60	44.55	44.55
CA	5.15	0.50	4.53	3.12	68.87	3.35	0.97	0.10	2.37	6.69	4.32	0.84	11.31	11.31
CH	2.54	0.44	9.28	12.77	137.57	3.35	1.85	2.42	1.18	11.31	10.13	0.43	22.45	44.55
CO	2.67	0.49	6.85	7.22	105.46	3.35	1.20	0.23	1.18	11.31	10.13	0.43	22.45	22.45
HO	3.60	0.53	9.21	10.22	111.03	4.73	1.98	3.96	2.37	11.31	8.94	0.84	22.45	22.45
JO	4.37	0.45	5.12	4.97	97.07	3.35	1.97	4.10	1.67	6.69	5.02	0.60	11.31	11.31
KI	5.16	0.34	4.62	5.20	112.52	2.37	2.25	4.75	1.67	4.73	3.06	0.84	11.31	22.45
OC	2.46	0.21	5.92	7.31	123.45	2.37	1.41	0.66	0.60	11.31	10.71	0.30	22.45	22.45
SC	4.68	0.47	5.45	5.16	94.70	3.35	1.94	3.67	2.37	6.69	4.32	0.84	11.31	22.45
ST	4.25	0.62	10.25	11.40	111.25	4.73	1.81	2.73	2.37	11.31	8.94	1.18	22.45	44.55
TO	3.41	0.83	9.55	8.14	85.20	11.31	1.58	3.85	3.35	11.31	7.96	0.60	22.45	22.45
WB	3.20	0.23	5.25	7.56	143.96	2.37	2.94	10.67	0.84	6.69	5.85	0.43	11.31	22.45
Mean	3.52	0.48	7.65	8.67	112.93	4.27	1.77	3.07	1.76	10.69	8.93	0.64	21.68	26.86
Median	3.41	0.47	6.01	7.56	111.25	3.35	1.81	2.73	1.67	11.31	8.94	0.60	22.45	22.45

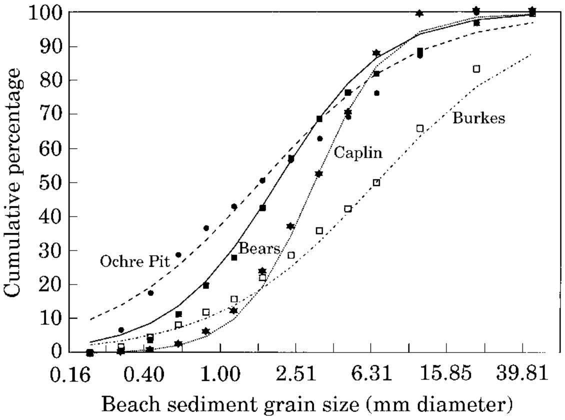

Figure 4. Examples from Ochre Pit Cove (solid circle, dashed curve), Bears Cove (solid square, solid curve), Caplin Cove (star, dotted curve), and Burkes Cove (open square, dash-dot curve) beaches that typify the range in observed (symbols) and fitted (lines) cumulative percentage sediment grain size (geometric mean, mm) distribution among a collection of 15 capelin spawning beaches along the perimeter of Conception Bay, Newfoundland. Coefficients of determination between the observed and fitted distributions using the logistic function are all >0.98.

screen, followed by submersion in a 2% (by weight) KOH solution for 24–36 h. Separated eggs were subsequently washed from the sediments, decanted, and collected on a 250 µm mesh screen.

Egg abundance was estimated by subsampling the decanted eggs with a 10-chamber whirling vessel. The entire sample was sequentially fractionated until the number of eggs per chamber was reduced to ~2500. Eggs from two randomly selected chambers were counted and averaged (Nakashima, 1987). Average egg concentrations (eggs cm^{-2}) among beaches were estimated using sediment-core egg concentration weighted by beach stratum area and core depth, and were log-transformed to normalize the data (Taggart and Nakashima, 1987).

We assessed variation in developmental stage and viability of eggs among samples to ensure that our concentration estimates were not unduly biased by variations in egg development among beaches that might lead to a "loss" of eggs through differential hatching (Taggart and Nakashima, 1987). At least 50 eggs from each core sample were placed in Stockard's solution (Bonnet, 1939), examined, and classified as dead (opaque or in arrested development), in early development (stages I–IV, as described by Fridgeirsson, 1976; generally associated with the first 6 d of development), or eyed embryo. Extremely advanced development within a sample was recorded if pre-emergent (hatched) larvae were present.

The egg-free sediments were oven-dried (80 ± 1°C) for ~16 h, cooled, and weighed (±0.1 g). Each sample was sorted using an ordered series of sieving screens (Table 2) mounted in a Ro-Tap® sediment shaker for 10 min. The grain-size distribution of the sediments from each sample was determined after sorting by estimating the proportional representation, by weight, of 13 geometric mean size fractions retained among 15 different screens (Table 2) arranged in descending Φ and $\frac{1}{2}\Phi$ intervals (Krumbein and Pettijohn, 1938). The geometric mean size is the arithmetic diameter (mm) calculated geometrically from the screen sizes limiting the particular size fraction retained. As the potential size distribution is continuous and two-tailed, sediments in the first and last size-class (>63.0 and <0.25 mm) were not used because no sediments were retained by the >63.0 mm screen (the beach corer was limited to a 65 mm diameter) and the last sorting screen (0.25 mm) passed <1% of the total dry weight of sediments in the <0.25 mm grain size.

Data analysis

We employed two methods to describe the sediment grain-size distribution for each beach quantitatively, because these sediments are difficult to characterize (Church and Ryder, 1972). Both methods were applied to the within-beach average size distribution compiled from the beach-specific core samples. First, we calculated moments (mean, skew, kurtosis), quartiles, interquartile ranges, and percentiles of the proportional distribution of the geometric mean diameters. These parameters are frequently employed by sedimentary petrologists to describe structure (Krumbein and Pettijohn, 1938). We also used a least-squares method to fit iteratively (r^2 maximization) a logistic curve to the cumulative percentage in each size-class (P) derived from Ricklefs (1967), such that

$$P = \frac{100}{1 + e^{-k(D-I)}} \qquad (1)$$

where k is the logistic rate constant (proportional to the overall rate of increase), D the logarithm of the geometric mean sediment diameter of each size-class, and I is the inflection point. No correlation was observed between k and I ($n=15$, $r^2=0.006$).

Our analysis was exploratory and multivariate (SAS® 8.02; SAS Institute Inc., Cary, NC, USA). We examined the various beach morphometrics (geographic variables and sediment distribution parameters) to identify those that best explained the variation in egg concentration among the 15 spawning beaches. Because beach orientation is a constrained and circular variable (0–360°), we employed a simple trigonometric transformation that provided sinusoidal continuity and symmetry:

$$Or = \cos^{2\alpha}\left[\frac{(\theta + \varphi)}{2}\right] \qquad (2)$$

Table 4. Spearman rank correlation coefficients (right of diagonal) and significance probabilities (left of diagonal) for capelin egg concentrations (Lc; $\log_{10}$ egg cm^{-2}) and the four uncorrelated ($\alpha=0.05$) independent "beach" variables (underscored): latitude (Lat), transformed orientation (Or), and the constant (k) from the logistic fit to sediment grain-size distribution, and skew (Skew) of the distribution; and potentially collinear independent variables: median (Med), 95th (P_{95}), 90th (P_{90}), and 5th (P_5) percentiles and the standard deviation (s.d.) of the particle distributions used in model development. Coefficients and probabilities for variables considered significantly correlated are denoted by an asterisk*.

	Lc	Lat	Or	k	Skew	Med	P_{95}	P_{90}	P_5	s.d.
Lc	—	0.6202*	0.6154*	0.2753	0.1841	− 0.5407*	− 0.3543	− 0.3341	0.0454	− 0.3056
Lat	0.0136*	—	0.2127	0.4071	0.0643	− 0.6262*	− 0.6631*	− 0.6855*	− 0.0315	− 0.7464*
Or	0.0146*	0.4466	—	0.1555	0.1644	− 0.4098	− 0.2359	− 0.1884	− 0.0779	− 0.2735
k	0.3208	0.1320	0.5800	—	0.4179	− 0.1888	− 0.5692*	− 0.7786*	0.7338*	− 0.6357*
Skew	0.5113	0.8199	0.5581	0.1212	—	− 0.4543	− 0.1489	− 0.4557	0.1279	− 0.0571
Med	0.0374*	0.0125*	0.1293	0.5004	0.0889	—	0.3983	0.5444*	0.3366	0.4655
P_{95}	0.1951	0.0071*	0.3974	0.0268*	0.5963	0.1414	—	0.7198*	− 0.0360	0.8753*
P_{90}	0.2236	0.0048*	0.5014	0.0006*	0.0878	0.0359*	0.0025*	—	− 0.2405	0.8241*
P_5	0.8722	0.9113	0.7826	0.0018*	0.6497	0.2199	0.8987	0.3878	—	− 0.0871
s.d.	0.2680	0.0014*	0.3240	0.0109*	0.8397	0.0804	<0.0001*	0.0002*	0.7576	—

where Or is the transformed beach orientation, θ is the beach orientation (° true), φ allows for rotation to some new reference direction (° true), squaring ($\cos^2$) keeps the transform positive, and α is a "shaping" parameter for the function, where $\alpha>1$ narrows the peak and broadens the trough and $\alpha<1$ does the opposite. We set $\alpha=1.0$ because we had no *a priori* reasons for "shaping" the distribution, and set $\varphi=90°$ to reflect the direction of the dominant fetch and prevailing wind related to maximum open-ocean wind-driven wave turbulence, and the generation, mixing, and sorting of beach sediments.

Spearman rank correlation matrices of all beach metrics were examined to identify potential relations among them, to assist in the selection of variables for multivariate modelling, and to minimize the potential for multi-collinearity effects in model development. Model selection was based on multivariate linear regression, employing criteria to maximize explained variance, to reduce Mallow's Cp statistic (as described in Hocking, 1976), and to maintain significant ($p\sim0.05$) F-values in the model and model variables, and variables with reasonable power ($1-P$; type-II error). The potential for collinear effects among model variables was assessed by the size of the correlation coefficients among the explanatory variables (Chatterjee and Price, 1977) and by the diagnostics of Belsley *et al.* (1980).

Results

Beaches and egg deposition

There was a high degree of variation in egg deposition and in the characteristics of the 15 beaches sampled. The beaches encompassed a wide range in orientation (20–330°), and varied in MT area from 336 to 7980 m^2 (Table 1). Areal egg concentration among the beaches varied over two orders of magnitude from as few as ~400 eggs cm^{-2} at Topsail to as many as ~4400 eggs cm^{-2} at Bryants Cove (Table 1). Egg concentration was generally higher among the NE- through SE-facing beaches and lowest among the N- through W- and S-facing beaches (Figure 2). Estimates of total egg deposition among beaches ranged over two orders of magnitude, from 2.6×10^9 at St Phillips to 2.2×10^{11} at Kingston, and reflected, to some degree, the variation in beach area (Table 1).

Examination of the egg samples showed that the proportion of dead eggs at the time of sampling varied from 12 to 44%, averaged 25% (Table 1), and was not correlated with time (day of sampling). The proportion of eggs in the early and eyed stage ranged from 0 to 76%. The eyed stage was most frequently observed among beaches sampled later (e.g. Chapel Cove, Burkes Cove, Holyrood), and an overall ~47% of the variation in the eyed stage was explained by time (increasing at ~5.8% d^{-1}). Early eyed stages decreased at approximately the same rate. This likely explains why pre-emergent larvae were observed in only 3 of the 48 samples (one each at Spout Cove, Topsail, and St Phillips). Consequently, all beaches were represented by samples that exhibited little or no evidence of hatching. We therefore assume that the beach-specific estimates of egg concentration are not unduly biased by egg losses incurred through differential hatching or emergence of larvae among beaches.

Sediments

There was a high degree of variation in the sediment grain-size distribution in the MT zone of the various beaches. The overall grain size was 7.65 mm, ranging from an average of 4.6 mm at Kingston to 14.5 mm at Burkes Cove (Figure 3, Table 3). Relatively narrow inter-quartile ranges that define well-sorted sediments were found among beaches that also exhibited a range in

Table 5. Linear regression models, (a) excluding and (b) including latitude, that describe the areal concentration of capelin eggs among 15 spawning beaches around the perimeter of Conception Bay, Newfoundland, as a function of transformed beach orientation (Or) and latitude (Lat), the logistic rate constant (k) fitted to the beach-specific grain-size distributions, with the standard deviation (s.d.) and the 90th (P_{90}) and 5th (P_5) percentiles of the distributions. The coefficient of determination (r^2) and as adjusted for d.f. (adj-r^2), with the significance of the model (based on F-values and Mallow's Cp statistic) and the power (in parenthesis) of each contributing variable, are provided.

(a) Regression models excluding latitude	r^2	adj-r^2	Model	Or	k	P_{90}	P_5
Log_{10} (egg cm^{-2}) = 0.88312 Or + 2.55744	0.57	0.54	0.0011	0.001 (0.971)	—	—	—
Log_{10} (egg cm^{-2}) = 0.86015 Or + 0.06813 k + 2.33353	0.61	0.55	0.0035	0.0016 (0.961)	0.3016 (0.169)	—	—
Log_{10} (egg cm^{-2}) = 0.98397 Or + 0.15867 k + 0.01254 P_{90} + 1.65574	0.68	0.59	0.0047	0.0008 (0.985)	0.0864 (0.405)	0.1550 (0.287)	—
Log_{10} (egg cm^{-2}) = 0.85289 Or + 0.44324 k + 0.02565 P_{90} − 1.06856 P_5 + 1.14184	0.81	0.73	0.0014	0.0009 (0.986)	0.0069 (0.862)	0.0124 (0.782)	0.0285 (0.636)

(b) Regression models including latitude	r^2	adj-r^2	Model	Lat	Or	s.d.	k	P_{90}
Log_{10} (egg cm^{-2}) = 0.70324 Lat + 0.72479 Or − 30.87785	0.72	0.68	0.0004	0.0244 (0.944)	0.0022 (0.657)	—	—	—
Log_{10} (egg cm^{-2}) = 1.23608 Lat + 0.80072 Or + 0.04275 s.d. − 56.71917	0.82	0.78	0.0002	0.0023 (0.948)	0.0004 (0.995)	0.0300 (0.622)	—	—
Log_{10} (egg cm^{-2}) = 0.92615 Lat + 0.86484 Or + 0.11318 k + 0.01855 P_{90} − 42.41051	0.86	0.81	0.0003	0.0045 (0.907)	0.0002 (0.999)	—	0.0850 (0.408)	0.0102 (0.812)

the median size-classes (e.g. Kingston, Caplin Cove, St Phillips, and Topsail). Sediments on other beaches with similar median size-classes were not as well sorted, as illustrated by their relatively broad grain-size distributions (e.g. Ochre Pit Cove, Bristols Hope, and Bryants Cove). Similarly, there was considerable variation in the other moments and parameters of the size distribution among beaches (Table 3). Sediments on beaches such as Bears Cove and Western Bay had highly skewed and kurtotic distributions, while others such as Caplin Cove were more normal. Caplin Cove had the most normal and narrow grain-size distribution (i.e. well sorted), was the only beach that had a relatively uniform distribution of eggs in the MT zone, and exhibited the second highest concentration of eggs among all beaches.

Distributional variations were most easily described by the parameters of the logistic fit to the cumulative distribution (Table 3), and examples of the variations typical among beaches are illustrated in Figure 4. Bimodal or multimodal distributions (e.g. Ochre Pit Cove) result in a relatively slow rate of increase ($k=2.46$; Table 3) and a low inflection ($I=0.21$; Table 3). Fine-skewed size distributions (e.g. Burkes Cove) result in an equally low rate of increase ($k=2.42$) and a higher inflection ($I=0.82$). Caplin Cove, the well-sorted beach, shows a typically normal distribution with a relatively high rate of increase ($k=5.15$) and a median inflection point ($I=0.50$). Differences observed in the logistic fit to Bears Cove beach sediments (moderate k and low I) are explained by a slight bimodality and a coarse skew.

Not surprisingly, there was a high degree of correlation among many of the sediment grain-size distribution parameters that limited (from a parsimonious perspective) the number of potential variables for use in the multivariate analyses. Therefore, we initially focused on the four variables (Table 4) that were not correlated among themselves (i.e. latitude and beach orientation, and k and skew parameters from the grain-size distributions). Beach orientation (Or) alone accounted for 57% ($p=0.001$) of the variation in egg concentration (Table 5, Figure 5a). The most significant bivariate model ($p<0.001$) employed latitude and Or to explain as much as 72% of the variation in egg concentration among beaches (Table 5, Figure 5e), followed by Or and the rate constant, k, that explained 61% ($p=0.004$) of the variation (Table 5, Figure 5b). The skew parameter did not contribute to explained variance in any meaningful way.

Further exploratory analysis revealed that the addition of the 90th percentile from the sediment size distributions resulted in a significant reduction in Mallow's Cp statistic and a significant model ($p=0.005$) that explained 68% of the variation in egg concentration (Table 5, Figure 5c). Finally, the addition of the 5th percentile led to a further reduction in Mallow's Cp and a highly significant model ($p=0.001$) that explained 81% of the variance in egg concentration (Table 5, Figure 5d). However, in these last two 3- and 4-variate models, collinearity diagnostics indicated caution in employing the 5th and 90th percentiles owing to their interdependency with k (Table 4). Nevertheless, the coefficients among the different models are very well behaved (consistent in sign and magnitude; Table 5). Furthermore, the inclusion of the upper and lower percentiles suggest a fine, but significant reduction in residual variance over and above that explained by Or and k, because they capture variation among beaches in the leading and trailing ends of the grain-size distribution where the rate of change in the distribution is typically the greatest (see Figure 4). The signs associated with the percentile parameters are consistent with this interpretation. Finally, it appears that latitude, Or, k, and the 90th percentile do as well or better ($p=0.0003$) than the earlier 4-variable model in explaining ~86% of the variation (Table 5, Figure 5f). Despite the consistency and the well-behaved nature of the parameters among the various models, we are wary of placing too much reliance on the 3- and 4-variable models until these findings are subjected to independent testing.

Discussion

At least 57%, and possibly 80% or more, of the variation in areal estimates of capelin egg deposition on beaches in the mid-tide zone in Conception Bay in 1987 can be explained by simple geographic and physical characteristics of the spawning beaches immediately after spawning is complete. The strong correlation between beach orientation and egg concentration may explain the observation that beaches facing the open ocean in eastern Newfoundland are frequently used for spawning year after year and generally have the highest number of eggs. We propose that there are two types of explanatory models, those that do not incorporate latitude and those that do (Table 5). Our reasoning is that the influence of latitude is likely only applicable in a local sense (i.e. Conception Bay), because the northward progression of beaches along the western perimeter of Conception Bay results in increased exposure to the full fetch of the Atlantic Ocean (Figure 1). This would not necessarily be the case for other bays or coastlines (e.g. along the eastern Avalon Peninsula). This reasoning suggests that models that do not incorporate latitude are superior for general application.

Substratum grain sizes on the barrier and pocket beaches we studied are the result of physical forces related to meteorologically driven wave action, a process that is relatively well understood. For beach-spawning populations such as capelin, local variations in substratum among beaches appear informative when assessing spawning habitat. Rocky headlands adjacent to

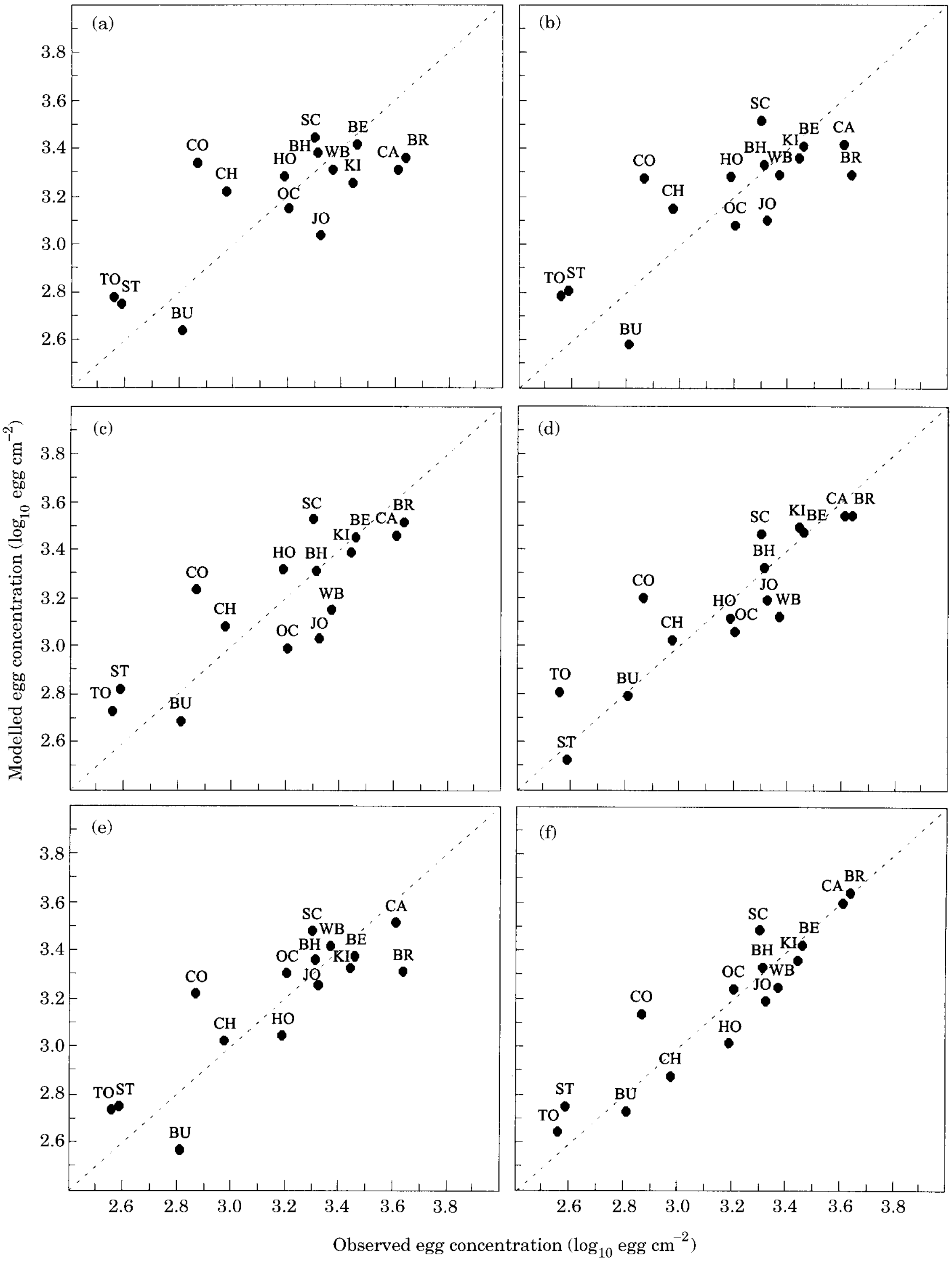

Figure 5. Observed and modelled relationships (expected 1:1 relationship shown on diagonal) for capelin egg concentration ($\log_{10}$ egg cm^{-2}) on spawning beaches along the perimeter of Conception Bay, Newfoundland, explained by (a) beach orientation, (b) beach orientation and k, (c) beach orientation, k, and the 90th percentile of the sediment grain-size distributions, (d) beach orientation, k, and the 90th and 5th percentiles, (e) latitude and beach orientation, and (f) latitude, beach orientation, k, and the 90th percentile. Specific model parameters are provided in Table 5, and beach identifiers associated with each datum are listed in Table 1.

many of the beaches restrict the longshore transport of coastal sediments. Consequently, beach development is strongly dependent on local sediment supply (Forbes, 1984). The exposure to fetch likely has a direct bearing on the grain-size distribution of beaches, and orientation (and latitude, at least locally in Conception Bay) determines exposure to the fetch. Prior to spawning, winds and the resultant wave action serve to sort the beaches; this sorting presumedly provides a suitable substratum for egg deposition and for the subsequent mixing, survival, and development of eggs. Sorting of the beaches from one with a "winter" profile to one with a "summer" profile, gives rise to local jargon of "capelin beach" referring to the fact that the beach is now "ready" (appropriately sorted) for spawning. Beaches are dynamic environments, so the timing of egg deposition on suitable substratum (i.e. well sorted and of suitable size) is likely critical to the retention and development of the adhering eggs. Our results indicate that egg deposition is some function of the direction that beaches face, the optimum being eastwards.

Should we be surprised by the results above? Probably not, given that substratum type influences egg mortality and the survival of emerging larvae in several fish species. Female salmonids apparently "test" the suitability of the substratum in streambeds when digging redds (Chapman, 1988), and during the process the fine sediments (<3.3 mm) are removed. Phillips *et al.* (1975) observed an inverse relation between the concentration of "fines" and the survival of emerging salmonid fry. A large body of literature has shown that the survival of incubating salmonid embryos is a function of grain size and sediment permeability (cf. Chapman, 1988). European grayling deposit their eggs at sites where the substratum permits water circulation sufficient for aeration (Gonczi, 1989), and male yellow perch (in spawning condition) preferentially select sites with a cobble substratum (Robillard and Marsden, 2001). According to Thors (1981), water circulation provides the primary explanation for capelin spawning location offshore, and water temperature and sediment size structure are of secondary importance. Carscadden *et al.* (1989) argued that capelin spawning on the Southeast Shoal required a suitable substratum, but that the final location was a function of bottom water temperature. The results from our analyses show that, for beach-spawning capelin, beach orientation and the size structure of the beach sediments have quantitative and significant influences on spawning success as measured through egg concentration.

The overall medians of the beach-specific grain sizes (means and medians) of sediments from the 15 beaches in this study were 6.0 and 3.4 mm respectively (Table 3), and they compare favourably with the mean and median of 5.4 and 3.1 mm derived using the ranges of sediment grain sizes reported from other circumpolar capelin spawning sites (Hart and McHugh, 1944; Templeman, 1948; Pitt, 1958; Bakke and Bjorke, 1973; Thors, 1981; Velikanov, 1984). This comparison suggests that sediment size distributions suitable for successful capelin spawning are similar across the entire geographic range of the species. Given this similarity, it is reasonable to expect that the models developed here (at least those that do not employ latitude) may be equally applicable across the geographic range.

The total abundance of eggs, beach-specific or otherwise, may be indicative of either spawner abundance (stock size), or the amount of suitable habitat available to retain viable eggs during development in the intertidal zone, or both. Capelin beaches exhibit interannual differences in the abundance of spawn. Velikanov (1984) observed that egg concentrations on capelin beaches in the Sakhalin area were an order of magnitude higher in 1978 than in 1979. We conclude from our results that a significant portion of the variation in egg deposition among beaches in 1987 can be explained by orientation and sediment size structure. Certainly, the overall spawning population size (and likely other unknown factors) will influence interannual variation in spawning deposition. However, we postulate that, if the models presented here have any predictive power, the influence of spawning stock size would appear in the intercept and not among the geographic and sediment parameters. We eagerly await an independent test of model applicability. At the very least, these models offer a quantitative method for classifying the spawning habitat of beach-spawning capelin.

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