Optimal estimation of catch by the continuous underway fish egg sampler based on a model of the vertical distribution of American plaice (*Hippoglossoides platessoides*) eggs

P. Pepin, K. A. Curtis, P. V. R. Snelgrove, B. de Young, and J. A. Helbig

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We investigate how the vertical stratification of the water column (specifically density) affects predictions of the catch of American plaice eggs (*Hipploglossoides platessoides*) from a fixed-depth sampler [the continuous underway fish egg sampler (CUFES)] relative to the integrated abundance in the water column measured in bongo tows. A steady-state model of the vertical distribution of fish eggs coupled with a simple model of the vertical profile of eddy diffusivity (i.e. mixing) is applied. Key model parameters are estimated through optimization of a one-to-one relationship between predicted and observed catches fit, using a generalized linear model with a Poisson, negative binomial, or gamma error structure. The incorporation of data on the vertical structure of the water column significantly improved the ability to forecast CUFES catches when using Poisson or negative binomial error structure, but not using a gamma distribution. Optimal maximum likelihood parameter estimates for eddy diffusivity and egg buoyancy fell within the range of expected values. The degree of uncertainty in the parameterization of eddy diffusivity suggests, however, that greater understanding of the forces that determine the vertical profile of mixing is critical to achieving strong predictive capabilities. The inverse problem of predicting integrated abundance from CUFES catches did not benefit from the environmental-driven model because of the high uncertainty in the catches from the CUFES.

Keywords: American plaice, biophysical modelling, catchability, fish eggs, sampling, survey design, uncertainty, vertical distribution.

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P. Pepin, K. A. Curtis and J. A. Helbig: Fisheries and Oceans Canada, PO Box 5667, St John's, NL, Canada A1C 5X1. K. A. Curtis and P. V. R. Snelgrove: Ocean Sciences Centre and Department of Biology, Memorial University of Newfoundland, St John's, NL, Canada A1C 5S7. B. de Young: Department of Physics and Physical Oceanography, Memorial University of Newfoundland, St John's, NL, Canada A1B 3X7. Correspondence to P. Pepin: tel: +1 709 772 2081; fax: +1 709 772 4105; E-mail: pepinp@dfo-mpo.gc.ca

Introduction

The application of ichthyoplankton survey data in egg-production models (Lasker, 1985; Alheit, 1993; Armstrong *et al.*, 2001) provides a fishery-independent approach to the estimation of stock abundance. The strategy can be particularly advantageous in cases where variability in the catchability of adult fish impedes the ability of fishery and research vessels to provide consistent indices of abundance. Surveys of fish eggs provide an absolute measure of abundance, because gear avoidance is non-existent and the retention efficiency of plankton nets can be estimated precisely (Lo, 1985). However, survey design and precision represent key challenges in the study of marine plankton because currents move the population while it is being surveyed (Helbig and Pepin, 1998) and because the resolution of patchiness usually requires a sampling frequency difficult to achieve (Lo *et al.*, 1997, 2001). The measurement of animal abundance at sea generally represents a compromise between the sampling frequency and the spatial extent of collections.

Measurements of the abundance of marine plankton, and therefore also production and mortality rates, require consistent sampling of the population through the range of environmental conditions encountered in the region of interest. Sampling devices must consequently supply an estimate of abundance over the water column in which the eggs occur, which is typically accomplished with oblique or vertical tows using ring nets or bongo nets. Nonetheless, the collection of vertically integrated net samples has important logistical constraints that limit the resolution and precision of a survey: the ship must be slowed or stopped on station in order to collect the sample, only a limited number of sampling sites can be occupied during a survey, and laboratory processing is time-consuming and costly. An alternative approach is provided by the continuous underway fish egg sampler (CUFES) (Checkley *et al.*, 1997), which allows uninterrupted sample collection from a fixed depth (e.g. 3 m) as well as onboard processing while the ship is underway. The resulting higher spatial resolution can be more effective at delineating and characterizing the spawning distribution (Lo *et al.*, 2001), but because eggs are distributed non-uniformly in the water column, CUFES must be calibrated with traditional samplers such as a bongo or CalVET (Smith *et al.*, 1985) net, in order to estimate the total number of eggs present. The ratio of the egg concentration at 3 m to the mean concentration over the entire water column is affected, however, by hydrographically and meteorologically induced variations in the vertical distribution of eggs (Boyra *et al.*, 2003; Pepin *et al.*, 2005; Petitgas *et al.*, 2006; Curtis *et al.*, in press). As environmental conditions vary with space and time, the calibration will also vary. One would expect variations in catch ratio over seasonal and storm time scales that reflect changes in water column stratification and wind-induced turbulence, as well as spatially in coastal areas as a result of upwelling. Precision is also an issue with CUFES, because of the substantially smaller volume of water sampled by CUFES relative to traditional bongo net samplers (Pepin *et al.*, 2005).

In order to obtain accurate estimates of abundance from fixed-depth samplers while minimizing the number of samples collected for intercalibration, two issues must be addressed: the accurate modelling of the vertical distribution of fish eggs with respect to variations in the physical environment and the comparison of observed and predicted catches using a model with an appropriate variance structure. The former requires accurate model formulation and knowledge of model parameters and variables, and the latter requires understanding of the repeatability of the sampling devices. The question is whether predicting changes in catchability provides a statistically significant improvement over predictions based on a constant catch ratio.

The vertical distribution of fish eggs is determined by the balance between egg buoyancy and the vertical profile of density and mixing (Sundby, 1983, 1991; Westgård, 1989; Anderson and de Young, 1995). The mean proximity to the surface of positively buoyant eggs increases with increasing buoyancy of the eggs and reduced mixing. Egg density is generally measured experimentally using density-gradient columns (Coombs, 1981), and the density profile of the water column can be readily measured using conductivity–temperature–depth (CTD) profilers, so estimation of the vertical profile of egg buoyancy is relatively straightforward. Specification of vertical mixing is far more difficult. The most common approach is to parameterize turbulent mixing in terms of a vertical eddy diffusivity [$K_v(\mathrm{m^2\,s^{-1}})$], and a wide variety of formulations have been applied to account for the influence of winds, density stratification, currents, and other environmental influences (Kantha and Clayston, 2000; Boyra *et al.*, 2003; Curtis *et al.*, in press).

In general, the physics of the upper layer suggests that K_v should depend on wind stress, convection induced by night-time cooling, and the vertical profile of density. In addition, within the upper 5 m or so (i.e. within the zone sampled by CUFES), mixing generated by waves breaking as well as Langmuir circulation can also be important. Here we use a modified form of Umoh and Thomson's (1994) model for K_v that depends on the wind stress and the density profile. This model was successfully applied by Mathieu and deYoung (1995) to several years of hydrographic data from Station 27, a nearby long-term monitoring site that is representative of oceanographic conditions over a broad geographic region which includes the study site (Petrie *et al.*, 1992; Ouellet *et al.*, 2003).

In addition to dependence on local environmental conditions, gear intercalibration is also affected by the precision of the samplers. Van der Lingen *et al.* (1998) and Pepin *et al.* (2005) found that replicate sample variances of the CUFES, the CalVET net, and bongo samplers were directly proportional to the mean local concentration, suggesting that the probability distribution of catches approximated a Poisson process, i.e. individuals/eggs were randomly distributed throughout the sampled volume. However, this conclusion is in contrast with studies where negative binomial (Downing *et al.*, 1987; Pace *et al.*, 1991, Cyr *et al.*, 1992; Pepin and Shears, 1997; Power and Moser, 1999) and gamma (Myers and Pepin, 1990; Hesler *et al.*, 2004) error distributions were found to be better descriptors of the variability in catches of insects, plankton, and fish. Pepin *et al.* (2005) suggested that variations in environmental conditions or differences in the movement or advection of animals within the different studies could be the cause of the different estimates of the underlying error distribution. If so, we would expect that an accurate model of the environment–animal distribution relationship should lead to a better precision in estimated abundance and provide insight into the most appropriate error distribution for the survey. We would thus achieve the appropriate balance between uncertainty in physical process and local abundance.

Here we use Sundby's (1983) model for the vertical distribution of fish eggs in relation to local hydrographic and wind mixing to intercalibrate a fixed-depth sampler (CUFES) and integrated (bongo) one. We then explore how our ability to forecast CUFES catches varies in relation to estimates of vertical eddy diffusivity and equivalent egg salinity. The model is applied to the pelagic eggs of American plaice (*Hippoglossoides platessoides*) collected in simultaneous samples from the CUFES and a bongo net. We use a generalized linear model to evaluate the relationship between predicted and observed CUFES catches and to assess which error distribution (Poisson, negative binomial, and gamma) is most appropriate to describe the uncertainty in catches once the effect of environmental conditions on the vertical distribution of fish eggs has been taken into account. Finally, we consider the inverse problem of predicting integrated egg abundance (i.e. bongo catches) based on samples obtained at a fixed depth near the surface (i.e. CUFES catches).

Little is known about the spawning of American plaice. Morgan (2003) found that the average depth of spawning on the Grand Banks generally decreased from 140 m for 7 year-old fish to 80 m for 16 year-olds, although younger plaice shifted deeper (210 m) to spawn between 1993 and 1998. There are no direct observations of spawning, but Solmundsson *et al.* (2003) observed limited off-bottom ventures into the water column by spawning plaice (*Pleuronectes platessa*) west of Iceland, a pattern consistent with laboratory observations by Beverton (1964) for North Sea plaice. Eggs are spherical, pelagic, and approximately 2.4 mm in diameter.

Material and methods

Data

Comparative CUFES and bongo surveys were carried out in 2002 within Trinity Bay, a large embayment on the northeast coast of Newfoundland measuring approximately 120 km long by 30 km wide (Figure 1). Near its centre, a deep trench runs parallel to the coast to a maximum depth of 630 m, and a sill at the mouth of the bay has a maximum depth of 240 m. As in most other bays in the region, stratification and upper layer circulation are highly responsive to synoptic wind forcing at periods of 2–6 d (Yao, 1986; Davidson *et al.*, 2001). Southwesterly (out of bay) offshore winds prevail through much of the year and induce upwelling on the western side of the bay. Conversely, periods of onshore (northeasterly) winds reverse the spatial structure of the upwelling.

A total of 12 transects, spaced at 10 km intervals and orientated perpendicular to the main axis of the bay (Figure 1), was sampled

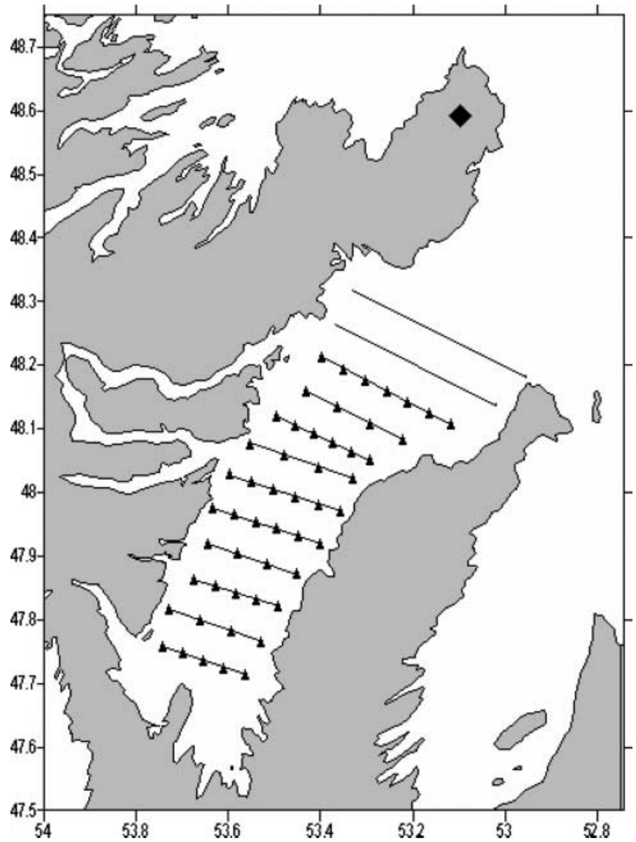

Figure 1. Map of the study area, Trinity Bay (Canada), showing the CUFES transects (lines) and bongo/CUFES sampling locations (triangles). The diamond shows the position of the Bonavista lighthouse weather station.

during six surveys conducted from 28 May to 8 June 2002 aboard CCGS "Teleost", a 63 m research vessel. During all surveys, continuous CUFES samples were collected over intervals of 1 nautical mile while the vessel was steaming at ∼10 knots. Start and end positions were noted using the global positioning system. During three of the surveys (survey 2, 28–30 May; survey 4, 1–3 June; survey 6, 6–7 June), paired bongo and CUFES samples were collected at 47 stations (Figure 1) at a vessel speed of 2–3 knots. Length and duration of each tow varied slightly as a result of variations in the deployment and retrieval rate of the bongo nets (discussed subsequently). The remainder of this paper deals only with the paired samples. Throughout the surveys, current speed and direction were collected at 3 min, 4 m depth intervals using a hull-mounted acoustic doppler current profiler (ADCP) located at a depth of 7 m. Hourly average wind speed and direction were obtained for the Bonavista lighthouse (48°40′N 53°07′W) from the Meteorological Service of Canada. A hydrographic survey of 31 stations throughout the bay was performed on 30 and 31 May 2002 using a Seabird 25 CTD probe.

Bongo nets were 63 cm in diameter and equipped with 505 μm Nitex mesh and a General Oceanics flowmeter and an Applied Microsystems CTD-Plus (Sidney, BC, Canada), which provided real-time measurements of depth, temperature, and conductivity that ensured we were sampling the target depth. Nets were towed obliquely to 75 m at approximately 10–15 m min^{-1} payout, then retrieved at 5–7.5 m min^{-1}. Bongo nets were expected to filter approximately 100–200 m^3 of water. Because of failures in the conductivity probe of the CTD-Plus, some salinity profiles collected during bongo tows had to be estimated using a fourth order polynomial fit to the temperature/salinity data collected during the hydrographic survey at the start of the study.

The CUFES sampler included a submersible pump, concentrator, and sample collector (Checkley *et al.*, 1997). The submersible pump was located 3 m deep and fixed to the hull of the ship by a rigid pipe that housed flexible 9 cm diameter hose. Water was pumped at a calibrated flow rate of 618 l min^{-1} to the concentrator, where particles were concentrated in a flow of 15–20 l min^{-1}. The CUFES sampler, operated simultaneously with bongo net tows, filtered ∼6.4–11.5 m^3 per sample. In order to allow comparisons with bongo net samples, the CUFES concentrator was fitted with 505 μm mesh.

All samples were preserved in 2% buffered formaldehyde. All fish eggs were later sorted and identified to the lowest taxonomic level possible under a dissection microscope. All CUFES and bongo samples were enumerated in full, except for bongo net samples with an excess of 300 eggs of a given species, for which a Motodo splitter was used for subsampling. The development stages of eggs were determined according to the scheme of Markle and Frost (1985).

Egg density

To estimate the equivalent salinity of plaice eggs, we collected ripe-and-running female plaice from the northern Grand Banks during May 2005. Only two ripe-and-running females (F1 and F2) were collected using a Campelen shrimp trawl at depth of 140 m (F1: standard length, 60 cm; location, 46°38.2′N 55°30.3′W) and 80 m (F2: standard length, 37 cm; location, 44°18.6′N 52°13.3′W). The salinity at the depth of capture was 32.51 for F1 at 140 m, and 33.92 for F2 at 80 m, with an average salinity of 33.22 at depth of capture. Eggs were fertilized upon capture with surface water (salinity 32.28), then held at 5°C and kept in separate containers until transport to the laboratory. In all, 26 viable eggs were placed in density gradient columns (Coombs, 1981) and their density was monitored as they developed from stage 2 to early stage 4.

We estimated the average density over the entire development period for each egg, excluding data from late stage 4 eggs because of significant increases in density close to hatching. Very few stage 4 eggs were taken during the surveys.

The equivalent salinity S_{egg} for buoyancy determination was estimated as

$$S_{egg} = (1 - ps) * S_{column} + ps * S_{sw},$$

where S_{column} is the species-specific equivalent salinity of the egg measured in the density gradient column, S_{sw} the sea surface salinity, and ps the ratio of the perivitelline space to the total egg volume, which for American plaice is 0.75 (30–40% of diameter) (Froese and Pauly, 2006). Egg salinity is the primary determinant of density, because the thermal expansion coefficient in pelagic fish eggs is similar to that of water (Coombs *et al.*, 1985).

Model

The vertical distribution of fish eggs in the water column is determined by their buoyancy and the vertical distribution of turbulent mixing. Sundby (1983) developed a steady-state model based on the underlying principle that the vertical velocity of the eggs is dependent on the density difference with the surrounding medium ($\Delta\rho = \rho_e - \rho_w$, where the subscripts e and w refer to the density of eggs and seawater, respectively) and the diameter of the egg. These variables are then used in the Stokes equation:

$$w = \frac{1}{18} g d^2 \, \Delta\rho \nu^{-1}, \tag{1}$$

where w is the terminal velocity (m s^{-1}) of the egg of diameter d (m), g the gravitational acceleration (m^2 s^{-1}), and ν the molecular viscosity (kg m^{-1} s^{-1}), which is dependent on the salinity and temperature of the water. Assuming stationary conditions and neglecting horizontal gradients, the vertical distribution of fish eggs can be described using the reduced diffusion equation

$$K_v \frac{\partial C_z}{\partial z} - w C_z = 0, \tag{2}$$

where K_v is the vertical eddy diffusivity (m^2 s^{-1}), C_z the concentration of fish eggs (m^{-3}), and z the depth (m). The solution to Equation (2) is

$$C_z = C_a \, \exp\left\{ - \int_z^0 \frac{w}{K_v} \, dz \right\}, \tag{3}$$

where a is a reference depth, typically the surface. We treat w/K_v as a piecewise constant over a fixed interval (z_i, z_{i+1}), so that the water column can be partitioned into 1−m intervals and numerically integrated (Westgård, 1989).

The average relative concentration expected to be measured by the CUFES sampler is estimated by integrating Equation (3) over a 1 m interval centred at the pump's location (3 m). The expected catch is determined by multiplying by the volume filtered. The average expected relative concentration of the bongo sample is estimated by numerically integrating Equation (3) from 0 to 75 m, i.e. summing estimates at discrete 1 m intervals and dividing by the depth of the tow:

$$\hat{\bar{C}}_{0-75} = \frac{1}{75} \sum_0^{75} C_a e^{(w/K_v)(z-a)} \Delta z, \tag{4}$$

where each depth stratum is centred over a 1 m interval.

We specified the vertical profile of K_v based on a modification of the formula in Umoh and Thompson (1994) and Umoh *et al.* (1995), which relates K_v to the vertical density profile and wind stress:

$$K_v = K_w \bar{W}_{24}^2 e^{-z/\delta} (1 + \alpha N^2)^{-1}, \tag{5}$$

where K_w is an adjustable time scale for wind mixing (s), $\bar{W}_{24}^2$ the average squared wind speed over the 24 h prior to occupying the station (m^2 s^{-2}), z the depth (m), δ the e-folding depth scale (m), α a constant (s^2), and N^2 the Brunt–Väisälä frequency, a measure of stratification. This formulation is a modification of earlier diffusivity parameterizations (e.g. Henderson-Sellers, 1982) in which K_v depends explicitly on the Richardson number, which itself depends on velocity shear. Although we have some information on the spatial variation in shear from the hull-mounted ADCP from which the Richardson number can be calculated, the data exclude the top 14 m of the water column, and extrapolation through this depth is uncertain. The main advantage of Equation (5) is that it does not depend on current shear. This approach is quite reasonable in an average sense (Mathieu and deYoung, 1995), but probably has limitations when applied locally and for specific times.

Analysis

Our objective was to determine the degree to which Sundby's (1983) model of the vertical distribution of fish eggs can improve the relationship between the CUFES and the bongo sampler, which was evaluated using the model

$$f(E(Y)) = \gamma + \beta X + \varepsilon, \tag{6}$$

where X is the CUFES catch predicted from our estimate of $\hat{\bar{C}}_{0-75}$ from the bongo tow and multiplied by the volume filtered by CUFES, $E(Y)$ the expectation for the observed CUFES catch, γ the intercept, β the slope of the relationship estimated using a generalized linear model, and ε is either Poisson, negative binomial, or gamma error structure. We set the intercept γ to zero, because an accurate environmentally driven model should pass through the origin. Equation (6) was evaluated using SAS procedure GENMOD and a log-link function for all three error structures, i.e. $f(\bullet)$ corresponds to logarithm. Sundby's (1983) model was used to predict the vertical distribution of eggs based on local hydrographic and wind conditions, from which we derived relative estimates of the concentration at 3 m and the average concentration over the 0–75 m interval to generate a catch ratio. This catch ratio was then multiplied by the integrated average concentration ($\hat{\bar{C}}_{0-75}$) from the bongo nets, which was taken as the "true" estimate of local abundance, assuming that all depths were sampled equally. The optimal fit between projected and observed CUFES catches was evaluated using the residual deviance goodness-of-fit criterion. Our expectation is that, with the most appropriate error distribution, the optimal solution to Equation (6), based on predictions from the combined environmental models, should follow a one-to-one relationship, i.e. $\beta = 1$, within the known range for parameters ρ_e and K_w.

We investigated the ability of the combined models [Equations (1)–(4)] to predict CUFES catches over a range of egg buoyancies (ρ_e) and an adjustable time scale for wind mixing (K_w) for the three different error structures. We set the diameter of the eggs to 2.4 mm, the e-folding scale (δ) to 85 m, based on the analysis of Umoh *et al.* (1995), and the value of α to 500. Exploratory analysis revealed the overall results to be insensitive to variations in α over a range of 300–800.

A jackknife estimate of variation in the slope and residual deviance was calculated for the optimal parameter set to assess the influence of any single observation on model fit. To determine the relative influence of variations in wind stress and water column density profile on the ability to predict CUFES catches with the environmentally driven model, we completed three sets of 500 permutations of the data inputs to the model. In each randomization, the physical input(s) (i.e. wind, vertical density profile, or both) was (were) randomly and independently assigned to each CUFES/bongo pair, without replacement, and used to predict CUFES catches using the optimal parameter set. Residual deviance was used to assess the influence of wind and hydrographic conditions on predictive ability.

We also investigate the inverse case where CUFES catches combined with the environmental model were used to predict

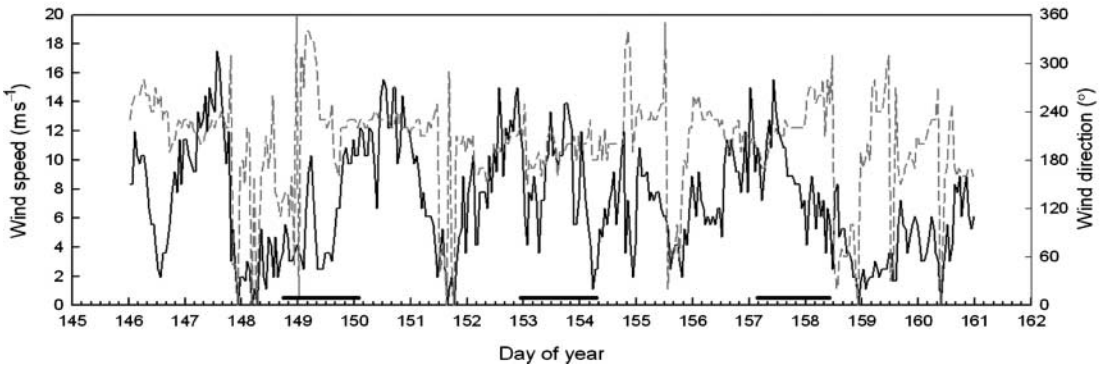

Figure 2. Bonavista lighthouse wind speed (solid black line) and direction (dashed grey line). Bold lines at the bottom of the panel indicate the bongo/CUFES survey periods.

integrated bongo catches using Poisson and negative binomial error structures.

Results

Environmental conditions

Winds were generally south-southwesterly (Figure 2) from 0 to 17 m s^{-1}, but there was considerable variability in wind conditions prior to and during each survey. For the first survey, winds were generally weak (5 m s^{-1}), but they increased to 10 m s^{-1} by the end of sampling. During the second survey, winds averaged $\sim$10 m s^{-1}, whereas winds during the third survey were approximately 12 m s^{-1} at the start of sampling and decreased to 4 m s^{-1} by the end of the survey.

Salinity and temperature throughout Trinity Bay are closely related (Figure 3). Sectional profiles across the minor axis in the central part of the bay indicate that patterns of variation in temperature, salinity, and density mimic each other with low density and high temperature water along the eastern side and high density and low temperature water along the western side.

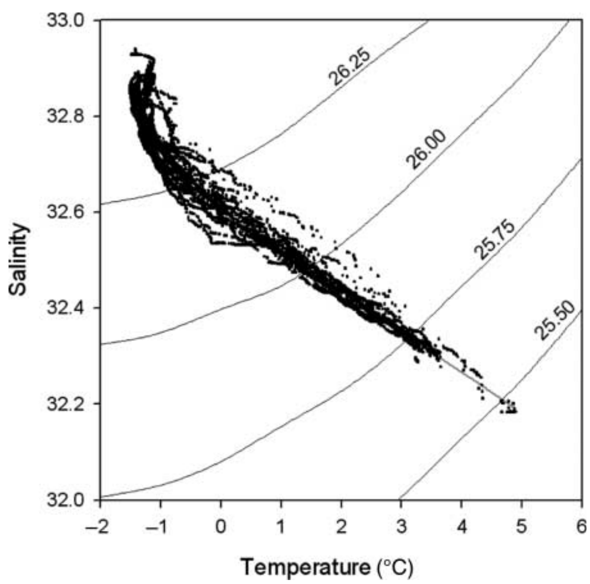

Figure 3. Temperature–salinity plot showing the isopleths for σ_t (density) from the hydrographic survey of Trinity Bay.

The difference in temperature between the sea surface and 75 m, a reflection of the degree of stratification, ranged from 0.5 to 7.5°C. The cross-bay contrast in stratification increased during the course of the three surveys, suggesting intensified upwelling along the western side of the bay over the study period (Figure 4). The intrusion of cold water in the central region of Trinity Bay also led to an increasing along-bay environmental gradient.

Mean salinity of bottom waters at the average depth of spawning for American plaice (80–140 m) (Morgan, 2003) was 32.9, based on the hydrographic survey at the start of the study period.

Egg density

There was considerable variability in the equivalent salinity of eggs (Figure 5). The average observed salinity of eggs in the density column was 30.51 (s.d. = 1.76, $n = 26$), yielding an average equivalent salinity of $S_{egg} = 31.84$ (s.d. = 0.44, $n = 26$), 1.38 salinity units below the average salinity at which the females were captured. At 5°C, this value translates to a density difference of 1.09 kg m^{-3}.

Model

In all, 141 bongo/CUFES sample pairs were collected over the duration of the study, but post-processing errors led to the loss of two samples from the first survey. The variability in the relative concentrations of plaice eggs from the CUFES and bongo samplers increased as the 0–75 m difference in temperature increased (Figure 6); the variance within each 1°C interval increased in direct proportion to the mean catch ratio. The pattern shows that as the degree of stratification decreases, the likelihood of zero catches by the CUFES becomes increasingly important relative to the catches from the bongo nets.

The null deviance is a measure of the association between CUFES and bongo catches without the use of the environmentally driven model (i.e. assuming a constant catch ratio throughout the study region), and it represents a purely statistical relationship between samplers. The best fit between CUFES and bongo catches was achieved by allowing the γ term in Equation (6) to be estimated (i.e. not set to zero). The null deviance for the Poisson, negative binomial, and gamma error distributions were 843, 164, and 64.7, respectively (Table 1). The deviance for different error distributions are calculated with different formulae, so they are not comparable.

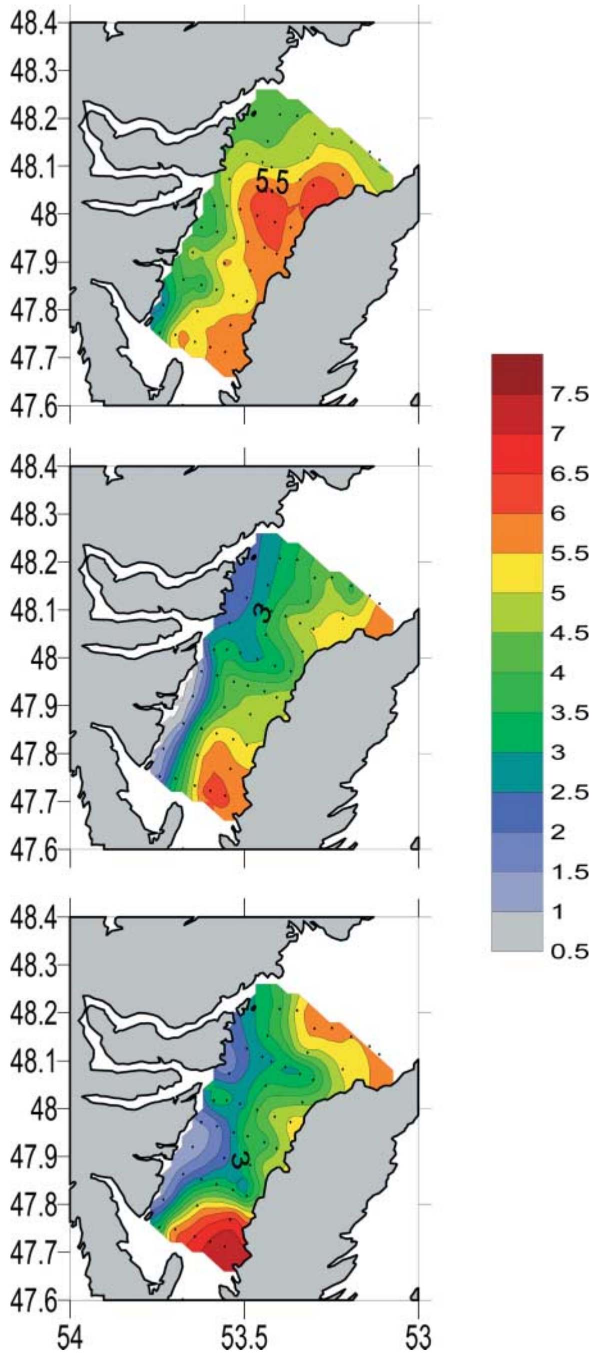

Figure 4. Interpolated map of 0 – 75 m temperature differences (°C) for the bongo/CUFES surveys for 28 – 30 May (top), 1 – 3 June (centre), and 6 – 7 June (bottom panel) 2002.

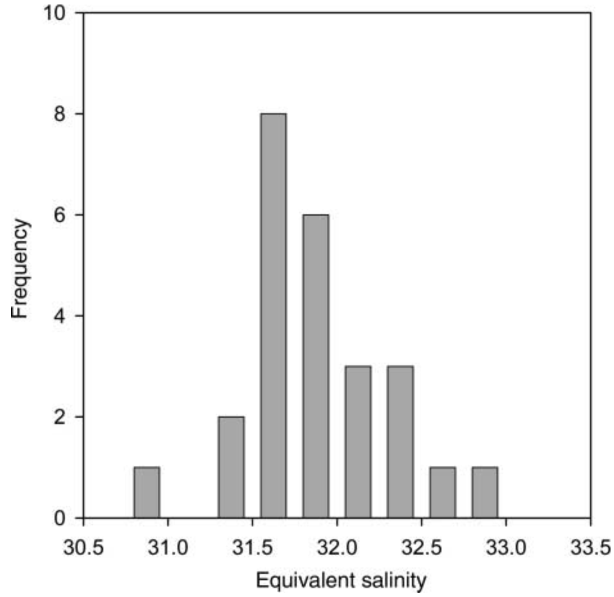

Figure 5. Frequency distribution of equivalent salinity for plaice eggs based on density column measurements in the laboratory.

The residual deviance of predicted CUFES catches with Poisson error decreased exponentially with decreasing equivalent egg salinity and was minimized with a K_w value ranging from 0.0015 to 0.0025 (Figure 7). There is generally a good agreement between predicted and observed CUFES catches (Figure 8). The minimum deviance with $\beta = 1$ was 570, achieved at an equivalent salinity of 31.7 and $K_w = 0.002$, close to the value of 31.5 expected on the basis of our observations of equivalent egg salinity in relation to the salinity at which we expected to find female plaice (32.9). This is a significant improvement over the null deviance. However, the residuals are slightly over-dispersed, possibly because of the lack of independence between the regional distribution of plaice eggs and hydrographic conditions (PP, unpublished data). Beyond these parameter values, there is no significant decrease in residual deviance based on a χ^2 test with three degrees of freedom. If equivalent salinity is restricted to a difference of 0.7, the lower confidence interval of our expected equivalent egg salinity relative to bottom water (i.e. 32.2), a slope of 1 is achieved with $K_w \approx 0.001$ and a residual deviance of 607. Clearly, knowledge of both wind forcing and egg buoyancy has a significant influence on the ability of the model to forecast CUFES catches.

When the error structure is modelled using a negative binomial distribution, predictions from the environmental models show continued decreasing residual deviance with decreasing K_w

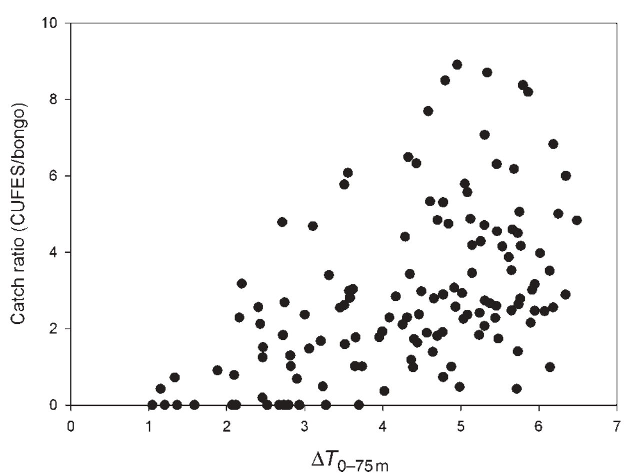

Figure 6. Distribution of CUFES-to-bongo catch ratio in relation to the 0 – 75 m temperature difference at each station during the three surveys.

Table 1. Analytical results of the relationship between CUFES and bongo catches without the use of the environmentally driven model based on fitting an intercept term to Equation (6).

Distribution	γ ($\pm$95% CI)	β ($\pm$95% CI)	Deviance	Scale (s) or dispersion (d) parameter
Poisson	1.63 (1.53–17.2)	0.185 (0.172–0.198)	843.8	1 (s)
Negative binomial	1.31 (1.05–1.56)	0.244 (0.198–0.291)	163.6	0.475 (d)
Gamma	1.54 (1.29–1.78)	0.211 (0.167–0.255)	64.7	2.11 (s)

Confidence intervals (CIs) represent the Wald 95% confidence limits of the parameter estimates. The scale parameter of the Poisson distribution was fixed to 1, and the parameters for the negative binomial and gamma error distributions were estimated by maximum likelihood.

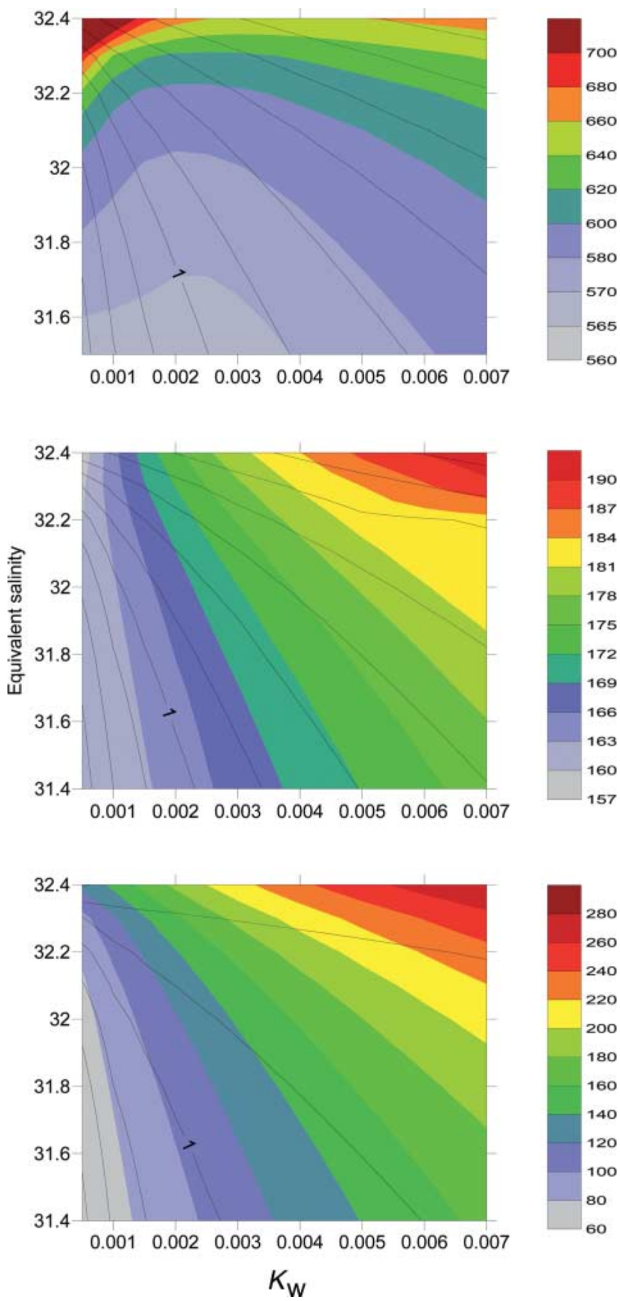

Figure 7. Contour diagram of the residual deviance between predicted and observed CUFES catches based on a Poisson (top), negative binomial (centre), and gamma (bottom panel) error structure. The solid lines represent contours of the value of the slope, β, of the log-linear model [equation (6)], at 0.05 intervals of the slope.

(Figure 7). Maximum-likelihood estimates of the dispersion parameter (k) of the negative binomial distribution range from 0.24 (at low salinity) to 0.28 (at high salinity), for K_w from 0.0005 to 0.005 and salinity values from 31.4 to 32.0. An optimal solution with a one-to-one slope was achieved at an egg salinity slightly over 32.2 and a value of K_w of 0.0005 (Figure 7). There is no significant improvement, based on a χ^2 test (d.f. = 3) when β of 1 is achieved. Moreover, the results are not statistically better than the null model, although for the environmentally driven predictions, we set the intercept to zero, whereas the null model has a statistically significant intercept and a larger dispersion parameter. However, good results are achieved over a wide range of egg buoyancy values (31.4–32.0), suggesting that this variable has relatively little impact on the ability to predict CUFES catches with this error distribution. Although the values of buoyancy are within the range of our laboratory observations and our expectation for K_w, optimal values for these parameter (ρ_e, K_w) are not as distinct as for a Poisson error structure.

When the error structure between predicted and observed CUFES catches is assumed to follow a gamma error structure, the predictive capacity of the environmental models reaches an optimal solution when the effect of the wind is almost negligible ($K_w < 0.0005$) and the equivalent salinity of eggs (ρ_e) is below 31.4 (Figure 7). Moreover, the slope between predicted and observed CUFES catches is well below the one-to-one relationship we expect. The values of both parameters for both the negative binomial and the gamma distributions are near the extremes of what is considered to be realistic.

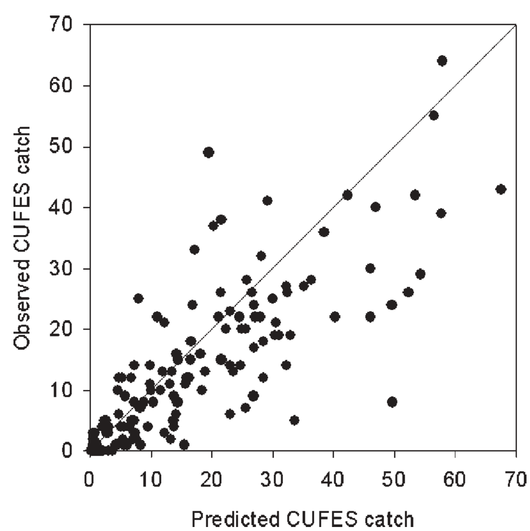

Figure 8. Observed vs. predicted CUFES catches based on the optimal parameter set and a Poisson error structure. The diagonal line represents the one-to-one relationship.

The pattern of residuals using each of the error distributions, based on the optimal parameter set for a one-to-one slope for each of the error distributions, is not ideal, but better overall for the Poisson distribution (Figure 9). For both the Poisson and negative binomial distributions, there is a slight positive trend in the pattern of Pearson residuals in relation to the observed CUFES catches and a slight negative trend in relation to the predicted CUFES catches. There is some indication of an increasing variance at low observed and predicted CUFES catches for the negative binomial distribution. This pattern is even more evident for the gamma distribution. For both the Poisson and negative binomial distributions, there is a trade-off in the pattern of residuals. Parameter values at the low extreme range $\rho_e = 31.4$, $K_w = 0.0005$) produce a more uniform pattern of residuals relative to observed CUFES catches, but yield a stronger negative trend in relation to predicted values.

There was no relationship between residuals and the estimated current shear from 18 to 26 m from the vessel's ADCP, but there was a greater spread in the residuals of the Poisson-fitted model at shear values between 0.007 and 0.01 s^{-1} than at higher levels of shear. This pattern suggests that the prediction of the profile of vertical eddy diffusivity may be poor in regions of low surface current shear and more accurate in regions of high shear, although the density gradient will also play a role in determining mixing potential.

Because the environmentally driven model with Poisson error shows the greatest improvement over the null deviance, we focus here on the use of this error distribution. For the model optimized with the Poisson error structure and $\beta = 1$, a jackknife estimate of β was 1.00 (s.d. = 0.0014) and the residual deviance averaged 568 (s.d. = 7.01). Randomization of environmental data, using the optimal parameter values, resulted in an average residual deviance of 948 when both hydrographic and wind data were varied independently (Figure 10). When only wind data were randomized, the mean residual deviance was 782, and when just hydrographic data were randomized, the mean residual deviance was 818. Therefore, a good knowledge of both wind and hydrographic data is important in predicting the vertical distribution of eggs and the relative catchability of the two gear types.

Because bongo samples typically have a greater proportion of early stage I eggs than CUFES samples (Pepin *et al.*, 2005), we investigated whether the proportion of early stage eggs in bongo samples significantly affected the distribution of residuals from the optimal fit. For both error structures, the Pearson residuals showed a weak negative correlation ($r = -0.16$, $n = 139$) with the proportion of early stage eggs in the bongo net. Although the relationship is statistically significant ($p < 0.05$), it only explained ~3% of the variance, which we consider trivial in predicting CUFES catches based on environmental data.

Inverse case

An obvious, and useful, test of the relation between CUFES and bongo observations is to use the former to predict the latter, an inverse calculation. When we forecast the integrated abundance (bongo net catches) based on surface observations from the CUFES, we find that neither Poisson nor negative binomial error structures yield results that indicate that environmental information is useful in providing an integrated estimate of abundance

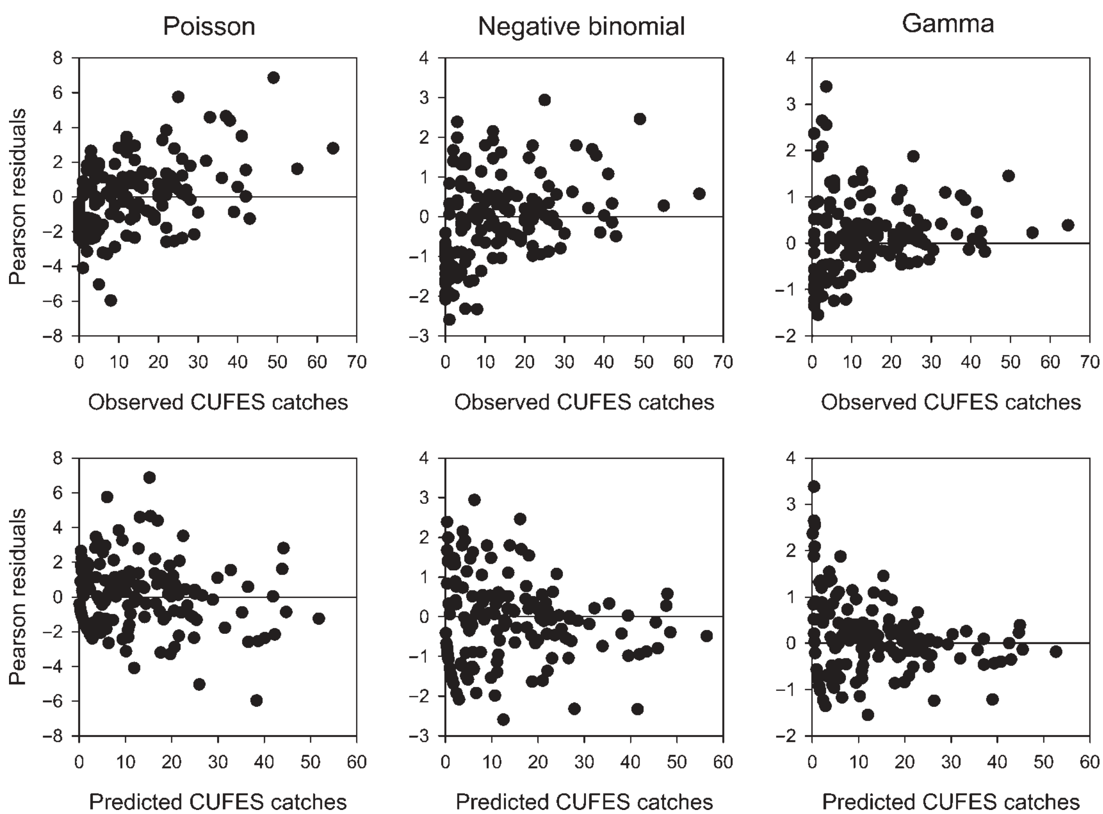

Figure 9. Pearson residuals for Poisson, negative binomial, and gamma generalized linear models in relation to observed (top) and predicted (bottom) CUFES catches.

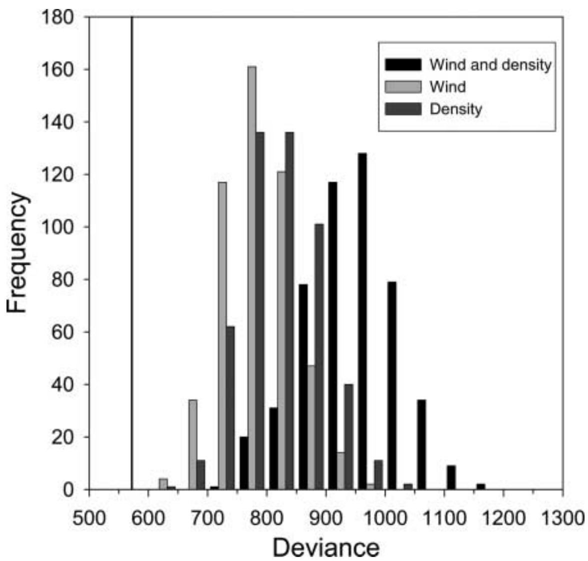

Figure 10. Frequency distribution of residual deviance with Poisson error structure from 500 permutations of wind and hydrographic (density) data independently, wind only, and hydrographic (density) data only. The vertical line indicates the residual deviance based on the optimal predictions with Poisson error.

(Figure 11). Optimum parameter values based on a Poisson error structure indicate that significantly better results are achieved at unrealistically high equivalent egg salinities and wind mixing coefficients, which is in marked contrast to results obtained when trying to predict CUFES catches from integrated measurements of egg abundance. For a negative binomial error structure, there is no significant influence of changes in K_w values on the ability to predict integrated abundance of plaice eggs. For the Poisson error, the pattern of residuals shows evidence of a slight trend with either predicted or observed egg densities, along with over-dispersion. For the negative binomial error, the residuals show greater dispersion at low observed and predicted egg densities.

Discussion

Uncertainty in the repeatability of sampling depends on the patchiness of organisms and how small-scale variations in environmental conditions influence their availability to the gear. Most studies of "local" or within-stratum replicate variance for plankton samplers do not incorporate the effect of environmental variations within a stratum into the estimation of error (Downing *et al.*, 1987; Pace *et al.*, 1991, Cyr *et al.*, 1992; Pepin and Shears, 1997; Power and Moser, 1999; Pepin *et al.*, 2005). Our analysis reveals that, for American plaice eggs in coastal Newfoundland waters, the direct relationship between bongo and CUFES catches, which effectively assumes a constant catch ratio, is very strong. However, the addition of environmental information, in order to refine the predicted catch ratio on a tow-by-tow basis, significantly reduces the residual deviance, particularly when modelled with a Poisson error. It is clear that both wind forcing and water column structure play equally significant roles in the underlying bongo/CUFES relationship, because randomization of either of these input variables results in similar changes in the residual deviance. Incorporation of environmental data also improved the CUFES/bongo relationship with negative binomial and gamma error distributions, but the optimal biological and environmental parameter values were generally at the extremes of what we considered to be realistic.

The regional variations in the physical environmental conditions encountered during this study were relatively limited, with the temperature difference (and hence stratification) over the 0–75 m interval ranging from ~0.5 to 7.5°C. Much larger differences are observed seasonally and spatially during late summer in the region (PP, unpublished data). Therefore, the improvements achieved by modelling the vertical distribution of fish eggs are limited by the restricted environmental conditions, and extrapolation to other times of year requires caution. Nonetheless, the analysis is in general agreement with the findings of Petitgas *et al.* (2006), who investigated the impact of a broader range of environmental forcing (temperature, salinity, tidal and wind forcing), and concluded that knowledge of the physical environment was very important in predicting the vertical distribution of fish eggs. In both studies, a major issue was how to model the profile of eddy diffusivity. Petitgas *et al.* (2006) approached the problem as a dynamic part of a regional circulation model, whereas we chose parameters that were easily measured and that reflected the underlying physics of the upper layer. The success of the parameter fitting applied in this study may be attributed partly to the limited regional variation in forcing. Under a wide range of physical forces, such as those encountered in the Bay of Biscay where haline and tidal forcing vary considerably over the region of interest (Petitgas *et al.*, 2006), the approach applied in this study might have needed to be generalized further. The success of a particular approach may also be affected by the ability to extrapolate among regions, or between observation periods, in a manner that accurately reflects the local dynamics of the system. For example, the optimal parameter estimates for K_w between 0.001 and 0.003 result in a substantial departure of surface eddy diffusivity at low wind speeds from the intercept estimated by Sundby (1983), which was based on estimates from a variety of studies of the vertical distribution of fish eggs. Differences in the relative contribution of tides, freshwater inflow, local topographic steering of winds, and other forcing factors, to the transfer of turbulent energy from the atmosphere through to the water column, will affect the profile of K_v and hence the effect of local winds on the relative comparability of bongo sampler and CUFES. Caution should therefore be taken in the application of general empirical relationships among study sites.

The same rule applies to biological information. As with Petitgas *et al.* (2006), our analysis points to the need for good knowledge on the specific gravity (i.e. equivalent salinity) of fish eggs from the study site and period, in order to forecast the relationship between integrated and fixed-depth samplers. Petitgas *et al.* (2006) noted that the application of a single estimate of egg density for anchovy and sardine in the Bay of Biscay only allowed accurate predictions in one of three studies, possibly as a result of oocyte hydration prior to ovulation. In our study, the optimal equivalent egg density (31.8) was close to that expected based on our preliminary observations of egg buoyancy relative to the water mass in which females spawn (31.5). In contrast, the egg density of American plaice inferred in our previous work (equivalent salinity of 32.2) (Pepin *et al.*, 2005) would have been at the margin of the range of equivalent salinity that improves model predictions based on Sundby's (1983) model, although that value is at the lower confidence limit of our laboratory

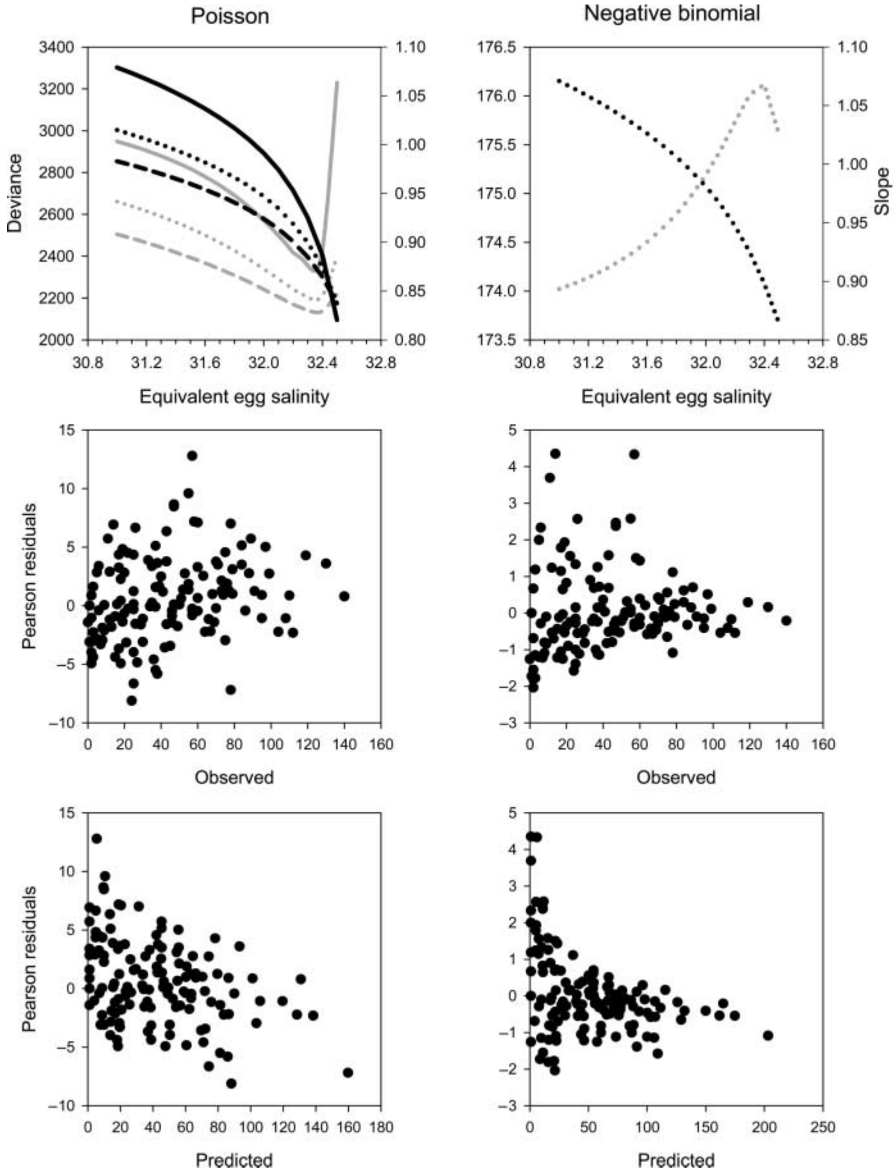

Figure 11. Deviance (left axis) and slope (right axis) of Equation (6) when CUFES catches were used to predict bongo catches based on local environmental conditions (top row), when Poisson (left column) and negative binomial (right column) were used in fitting the relationship in relation to equivalent egg salinity ($\Delta\rho$). Grey lines show the deviance for $K_w = 0.001$ (solid lines), 0.002 (dotted line), and 0.003 (dashed line). Black lines show the corresponding slopes. The four bottom panels show the standardized Pearson residuals in relation to observed (centre row) and predicted (bottom row) catches in the upper 75 m of the water column at values of $K_w = 0.002$ and $\Delta\rho = 31.7$.

observations. Contemporary and possibly regionally stratified egg buoyancy data, or an improved understanding of the factors that drive buoyancy, may prove to be a key requirement for the consistent application of CUFES to egg-production methods.

The predicted/observed CUFES catch relationship based on the Poisson error structure is slightly over-dispersed relative to the nominal variance, possibly through the lack of independence between eggs and their environment. This pattern may arise partly from our assumption of a steady-state vertical distribution of eggs throughout the survey area. There were spatial and temporal variations in the relative proportion of early and late stage eggs during the three surveys (PP, unpublished data), and we know that the CUFES tends to undersample the early stage eggs relative to the bongo sampler (Pepin *et al.*, 2005). Because spawning is likely to take place at average depths of 80–140 m (Morgan, 2003), younger egg stages may not have attained a steady-state vertical distribution. The diffusive time scale to reach equilibrium, set by the depth-range squared over the diffusivity, is very long, many tens of days, although strong mixing, associated with wind forcing, can of course accelerate the process. However, the estimated terminal velocity of plaice eggs (0.3–0.4 mm s^{-1}), based on the model of Coombs *et al.* (2004) for eggs with large perivitelline spaces and assuming that perivitelline fluid has the same density as that of the water in which eggs are spawned, yields an ascent time to the surface from 140 m of 4–6 d. Therefore, most eggs should reach the upper layers rapidly relative to the overall duration of the egg stage. Moreover, our previous observations (Pepin *et al.*, 2005) indicate that few plaice eggs are found deeper than 70 m, most eggs being in the upper 30 m of the water column. The situation where the vertical distribution has not reached a steady state is likely to affect our model-based predictions and lead to clusters of "biological states" that cause inaccuracies in the predicted catches, because of variations in the combination of physical and biological characteristics associated with each sampling site, which can in turn affect the optimal parameter set for prediction of CUFES catches. A more dynamic model of development and environmental history, such as that of Petitgas *et al.* (2006), is needed to address the possible effects of variations in the distribution of developmental stages on the vertical profiles of the eggs. However, we do not currently have the information necessary to address this issue.

The choice of error structure has important implications for our ability to detect the effects of local variations in physical forcing on the relative catches of bongo nets and the CUFES. A Poisson error structure has allowed better evaluation of the environmental influences on relative catches and provided a slightly better distribution of residuals than either the negative binomial or gamma distributions. Generally, the residuals were similarly distributed for Poisson and negative binomial distributions, for which variance increases as some power of the mean, greater than 1, but less than 2. Our inability to effectively contrast the Poisson and negative binomial distributions as models of the error structure in CUFES catches may be caused by the vagaries associated with the use of a single data set that represents a small area sampled over a relatively short time period. There may also be aspects of the processes that affect the vertical distribution, which were not considered in our environmental models. The representation of eddy diffusivity remains a difficult issue in marine modelling, and the representation of egg buoyancy using a single value will not reflect the overall variability among individuals in the population given that there were stage-specific differences in the spatial distribution of eggs (PP, unpublished data). However, our previous observations of replicate variance (Pepin *et al.*, 2005) and the effectiveness of the environmentally driven model to improve residual deviance indicate that the Poisson error structure is likely the more appropriate for contrasting bongo and CUFES catches. The remaining over-dispersion is likely a reflection of unaccounted biological and physical processes.

Taft (1960) and Power and Moser (1999) argued that a negative binomial distribution was probably most appropriate for describing the variance in catches of eggs and larvae by plankton nets, but their analysis did not consider the possible effect of environmental conditions within "strata" in determining the most appropriate error structure to apply. We previously argued (Pepin *et al.*, 2005) that the design of replicate variance studies for plankton collections could easily be contaminated by spatial variability. Sampling should be restricted to the scale typical of an individual tow collected over relatively short time scales in order to avoid the effects of advection across fixed map coordinates. Our previous work showed that the variance of CUFES was directly proportional to the mean, and approximately 20 times greater than that of bongo samplers (Pepin *et al.*, 2005), suggesting that the uncertainty in predicting catches should be dominated by the error in the surface sampler. In other instances, such as the case of CUFES and CalVET, where the variance of both samplers may be more comparable (van der Lingen *et al.*, 1998), the underlying error structure appropriate for the intercomparison of predicted and observed catches will be more skewed (e.g. gamma, log-normal) than for the comparison made here, which was best represented by a Poisson distribution.

The poor performance in predicting integrated abundance from CUFES surface observations based on an environmental model driven by local data suggests that the application of a constant catch ratio would likely be the only approach suitable to deliver an adequate regional estimate of abundance when trying to provide an estimate of integrated abundance based on CUFES observations. Such a catch ratio would need to be derived from comparative tows. However, more important is the need to understand why application of the inverse problem yielded such poor predictive power. Although the forward analysis of predicting CUFES catches from bongo catches and environmental data suggests that both samplers provide accurate estimates of abundance, the precision of bongo nets is approximately 25 times greater than that of the CUFES sampler (Pepin *et al.*, 2005). The greater uncertainty associated with the surface sampler implies that each draw from the local (error) distribution (i.e. a single observation from CUFES) is less likely to be a good reflection of local density than it was when we used the bongo net as our measure of "true" local abundance. As a result, our ability to improve predictions of the more precise integrated sampler was not enhanced by the addition of environmental information, because the overall impact of the latter on the original bongo/CUFES relationship was small relative to the uncertainty of the CUFES as our estimate of local egg abundance.

The potential strength of the CUFES, relative to a grid of widely spaced fixed stations with integrated samplers, lies in the continuity of the observations that can be used to guide integrated sampling (Lo *et al.*, 2001) or to provide a measure of the regional structure in distribution and abundance (Checkley *et al.*, 2000), in much the same manner as one might contrast acoustic and egg production surveys (Hampton, 1996). Consequently, it is the overall estimate of abundance derived from the significantly greater number of CUFES observations, coupled with adaptive sampling, that could provide increased performance in egg-production surveys relative to systematic or random-stratified surveys based on a more limited number of integrated samples. Environmental influences on the relationship of surface-to-integrated abundance estimates could then be useful corrections at a spatial scale, defined by the de-correlation distance in physical conditions identified from the use of geostatistical approaches applied to the CUFES observations (Rivoirard *et al.*, 2000). Parameterization of the environmental influences on vertically integrated and surface catches would have to be derived from the increased accuracy achieved when predicting CUFES catches from bongo or other integrated samplers.

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