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Accuracy of the Patch model used to estimate density and capture efficiency in depletion experiments for sessile invertebrates and fish

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The Patch model is used to analyse depletion experiment data for sessile invertebrates and fish that do not randomize after sampling. Simulations indicate that density and capture efficiency estimates were useful under realistic conditions for Atlantic surfclam (*Spisula solidissima*) and many other sessile demersal species. Density estimates were generally biased low by position-data errors, whereas efficiency estimates were relatively unbiased. A new "hit" matrix method improved the accuracy of efficiency estimates, reduced the variability for efficiency and density estimates, and simplified assumptions about the movement of organisms after sampling. Depletion tows should be spaced to cover the entire study area and to intersect in areas where densities are not low. Model estimates can be made for individuals fully or partially selected by the sampling gear, and information about size selectivity is useful. Patch-model estimates can be used to calculate swept-area abundance or biomass, estimate catchability coefficients for survey or catch per unit effort data, form prior distributions used in stock assessment models, and estimate efficiency for other types of sampling gear.

Keywords: catchability, gear efficiency, invertebrates, Patch model, stock assessment.

Introduction

Depletion experiments have been used to estimate abundance or density of animals and to estimate catchability coefficients for sampling gear (Leslie and Davis, 1939; DeLury, 1947; Ricker, 1975). In traditional fisheries depletion studies, mobile gear such as trawls and dredges are towed repeatedly within a study site. The fishing effort and catch are recorded after each tow as the abundance and the catch per unit fishing effort (cpue) declines. Initial density (before sampling) of organisms in the study area and catchability are estimated from the rate at which cpue or log cpue declines as fishing effort or catch increase. The key assumptions are that all catches are random samples and that there is no movement in or out of the study area (Leslie and Davis, 1939; DeLury, 1947). The assumption of random sampling implies that the organisms remaining in the study site mix after each tow.

During the years 1995–2008, the Northeast Fisheries Science Center (NEFSC) developed techniques for carrying out depletion experiments for sessile or nearly sessile animals that may have complex spatial distributions and do not mix after sampling. Experiments for sessile organisms differ from traditional depletion experiments because detailed position data are collected during each tow and because the relative positions and overlap between tows are important parts of the experimental design (Rago *et al.*, 2006). Depletion experiments were conducted for commercially exploited stocks of Atlantic surfclam (*Spisula solidissima*; NEFSC, 2010a), ocean quahog (*Arctica islandica*; NEFSC, 2009), Atlantic sea scallop (*Placopecten magellanicus*; NEFSC, 2010b), and monkfish (*Lophius americanus*; NEFSC, 2010c). These species accounted for $458 million in ex-vessel revenues during 2010, and Patch-model estimates are important in their stock assessments (NMFS, 2010).

Rago *et al.* (2006) extended the Leslie and Davis (1939) approach and developed the spatially explicit Patch model for analysing depletion experiment data for sessile organisms. Expected cpue in the Patch model is conditioned on the initial density of organisms and the removals by previous depletion tows in the area swept during each tow. In particular, if a large fraction of a tow was in previously fished territory, then the cpue should be low. If a large fraction of a tow was in unfished territory, then the cpue should be high. The final tow in a depletion experiment with a high cpue is interpretable and provides useful information to the Patch model if the tow sampled mostly unfished territory. In contrast, the Leslie and Davis (1939) and DeLury (1947) models assume that expected cpue declines with each tow.

Following Rago *et al.* (2006), we estimated capture efficiency instead of catchability, and density (numbers m^{-2}) instead of abundance in this study. Capture efficiency is defined as the probability of capture (between 0 and 1) for an organism fully selected by the sampling gear, which is located in front of, above, or in the sediments below the area swept by the gear (Thorarinsdóttir *et al.*, 2010). Efficiency should not be confused with size selectivity, which describes the fishing power for target organisms of different sizes. In contrast, catchability is a scaling factor that converts survey indices or cpue to abundance or fishing effort to fishing mortality. Capture efficiency and catchability are related because $q = ae/A$ and $e = Aq/a$, where q is the catchability, a the area swept by the sampling gear, e the capture efficiency, and A the spatial domain of the estimates (Paloheimo and Dickie, 1964). Capture efficiency is useful in experimental work because it is a measurable characteristic of sampling gear, has meaningful bounds, and is independent of the area swept or experimental domain. Similarly, abundance and density are closely related.

Patch-model estimates can be used in several ways for stock assessment work. Capture efficiency estimates can be used to form prior distributions for catchability parameters in stock assessment models (Somerton *et al.*, 1999; NEFSC, 2009, 2010a, b). If the depletion experiment was conducted where initial density is near average for the stock, then survey and cpue catchability parameters can be estimated directly (Paloheimo and Dickie, 1964). Depletion studies can be used to estimate capture efficiency for survey gear not used in the depletion experiment. NEFSC (2009, 2010a) carried out "setup" tows next to depletion sites, using a relatively small survey dredge with relatively low capture efficiency before depletion experiments were carried out by an efficient commercial dredge. Efficiency of the survey dredge was estimated as s/D_0, where s is the survey density (catch by the survey dredge/area swept) and D_0 the Patch-model initial density estimate.

The purpose of this paper is to test rigorously the accuracy of Patch-model estimates by simulation under a wide range of conditions and to refine sampling and analytical approaches. We estimate accuracy of model estimates and characterize conditions that cause poor estimates. Rago *et al.* (2006) and NEFSC (2010a) tested the model under a limited range of spatial distributions and other conditions. Our analysis is based on 20 depletion experiments for Atlantic surfclam carried out before 2008, but test conditions are wide enough to include most other sessile demersal invertebrates and fish.

Material and methods

The actual depletion studies for surfclams in NEFSC (2010a) were carried out using commercial clam fishing vessels in all but one case, and at locations identified during triennial NEFSC clam surveys (NEFSC, 2010a). Clam fishing vessels are ideal because commercial dredges are large (2.4–3.7 m blade width), efficient (median capture efficiency 0.79 for surfclams), and can be controlled precisely (Murawski and Serchuk, 1989). The commercial vessel makes repeated tows in the same location, usually along a north–south or east–west axis, until catches fall to <20% of initial levels. The catch in bushels of clams is recorded at the end of each tow. Length data and counts of clams per bushel are collected every third tow and used to compute catch length composition and catch numbers.

Position data are collected continuously on the ship during depletion tows and used as a proxy for the position of the centre of the dredge during fishing (the dredge track). The area swept by each tow is calculated as the distance towed times dredge width. Loran-C position data were collected by hand on ship every 30 or 60 s (roughly 30 or 60 m intervals) during early surfclam depletion experiments. Global positioning system (GPS) data were collected automatically every 2–10 s during recent experiments. Position data from depletion studies contain unknown amounts of error attributable to the rate at which position data were recorded (because intermediate positions are calculated by linear interpolation) and changes in the relative position of the ship and dredge as a result of currents, weather, sea state, and other factors.

The study site is the spatial domain of inference in a Patch-model analysis. It is defined geometrically after an experiment is completed as the smallest rectangular area that contains all the tows. The sites used here have axes orientated north–south and east–west. Study sites vary in size and shape depending on clam density (low densities may require longer tows) and the spatial pattern of the tows. Depletion tows in an experiment overlap where dredge paths cross. A particular point in a study site may be contacted by the dredge zero to n times, assuming n depletion tows.

In Rago *et al.* (2006) and most previous analyses (NEFSC, 2010a), the study site is subdivided into relatively small square cells whose width is twice the width of the dredge (cells are typically 3.7–7.3 m wide). Expected cpue from the Patch model for depletion tow i in a depletion study is $E(C_i) = a_i^* D_0$, where D_0 is the initial density (Rago *et al.*, 2006). The effective area swept a_i^* is the total area swept (m^2) discounted for cells hit by the dredge during previous tows:

$$a_i^* = ea_i \sum_{j=1}^{i} f_{i,j}(1 - e\gamma)^{j-1} \quad (1)$$

where e is the capture efficiency, and $f_{i,j}$ is the fraction of cells hit by the dredge j times. The fractions $f_{i,j}$ are the components of the square $n \times n$ "hit" matrix, with one row vector for each of the total n depletion tows in an experiment and one column for cells hit 1 to n times. Each row of the hit matrix sums to 1 ($\sum_{j=1}^{i} f_{i,j} = 1$) because the row represents an entire tow. The third tow in a hypothetical depletion experiment with five total tows, for example, may have crossed ten cells, of which seven were contacted for the first time, one for the second time, and two for the third time, and the corresponding row in the hit matrix would be {0.7, 0.1, 0.2, 0, 0}.

In standard practice, γ in Equation (1) is the ratio of the dredge width and cell size, so is the fraction of a cell assumed swept when the dredge contacts the cell (NEFSC, 2010a). The definition of γ can be expanded to include indirect effects of fishing during depletion experiments attributable to the displacement of clams from the study site or clams destroyed by the dredge but not caught (Rago *et al.*, 2006). However, γ is confounded with efficiency e in Equation (1), and potential indirect effects are difficult to estimate. Rago *et al.* (2006) proposed that cells be twice the dredge width ($\gamma = 0.5$), based on probable errors in position data and the accuracy of hit-matrix calculations. In testing the original hit-matrix approach, we used cells of the same width as the simulated dredge ($\gamma = 1$), based on improved accuracy in density and efficiency estimates in preliminary simulations.

Following Rago *et al.* (2006), parameters in the Patch model were estimated assuming that the observed cpue for each tow was from a negative binomial distribution with mean equal to the expected value for catch in numbers $E(C_i)$ and variance $\sigma_i^2 = E(C_i) + E(C_i)^2/k$, where k is a dispersion parameter estimated in the model, and $E(C_i)$ and σ_i^2 change with each tow. The negative binomial distribution is often used in the analysis of benthic invertebrates because it accommodates zero or highly variable catches through aggregated spatial distributions (small k; Elliot, 1977). It becomes the Poisson distribution when k is large, to accommodate random spatial patterns.

The negative log likelihood minimized while estimating parameters is:

$$-LL(k, D_0, e|C_i, a_i^*) = k\sum_{i=1}^{l}\left(\log\left(1+\frac{D_0 a_i^*}{k}\right)\right) + \sum_{i=1}^{l} C_i\left(\log\left(\frac{D_0 a_i^*}{D_0 a_i^* + k}\right)\right) \qquad (2)$$

where the combinatorial used to define the negative binomial probability distribution is a constant and was omitted. Patch-model input data for each tow consist of the observed catch (dependent variable), area swept, and one row from the hit matrix. The negative binomial distribution is defined for integer data, but the negative log-likelihood accommodates the real-valued (non-integer) cpue data collected during depletion experiments if the combinatorial function is omitted. We estimated the transformed parameters $\log(D_0)$, $\text{logit}(e)$, and $\text{logit}(k/50)$, where $\text{logit}(x) = \ln(x/(1-x))$ for x between 0 and 1, so $e \in (0, 1)$, $D_0 > 0$, and $k \in (0, 50)$.

Hit matrix

Patch-model analysis depends on how the study site and position data are represented spatially when the hit matrix is formed. Rago *et al.* (2006) assumed that organisms remaining in a cell hit by the dredge mixed randomly within the cell between tows (this assumption becomes less important as cell size decreases). Assumptions about dredge and cell size are important because the algorithm counts all cells intersected (hit) by the track line as though they were swept completely by the dredge and ignores cells that were actually contacted by the dredge but did not intersect the track line. If cells are smaller ($\gamma > 1$) or larger ($\gamma < 1$) than the dredge, then the area swept may be underestimated or overestimated. The fraction of the total area swept during tow i that was hit j times ($f_{i,j}$) is estimated from the ratio of the total number of cells hit j times by the end of the tow divided by the total number of cells hit during the tow. We developed a simpler algorithm for forming the hit matrix that eliminates the need to specify cell size, effectively eliminates γ from Equation (1) if there are no indirect effects, and more accurately calculates proportions of the area swept in the hit matrix.

The new hit-matrix method counts closely spaced and evenly distributed points instead of cells. We used points 10 cm apart, less than the length of a large surfclam. The dredge path between two position observations is represented as a rectangle (distance between positions × width of the dredge), and closely spaced points inside the rectangle are counted as hits. The new method approximates $f_{i,j}$ as the ratio of the total number of points hit j times by the end of the tow divided by the total number of points hit during the tow (Figure 1). Study site boundaries are set as in the original method.

Simulation experiments

Simulations were based on position data from 20 actual depletion experiments for Atlantic surfclam conducted from 1997 to 2005 with different numbers of tows, study site sizes and shapes, tow patterns, and position data collection frequencies (examples in

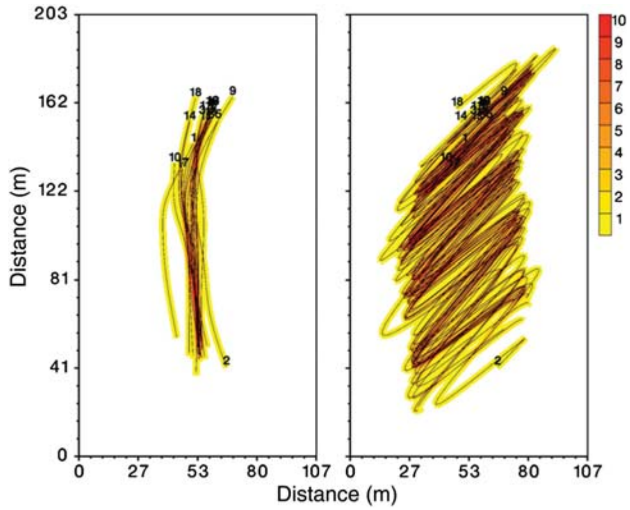

Figure 1. Position data from a true surfclam depletion experiment (18 tows) with no errors (left) and with maximum simulated errors ($\omega = 25.0$ m, $\lambda = 36.0$ m, right). The order of each tow is indicated at the end of each track line. The colour scale indicates how many times a point was contacted by the dredge based on the new hit-matrix approach.

Figure 1). The original dredge width, tow order and direction, and intervals for collecting position data in each experiment were preserved. Experimental sites ranged from 1 to 66000 m^2, and there were 4–40 depletion tows per experiment. Position data collected as degrees latitude and longitude were converted to distance (m) from the southwest corner of the experimental site before analysis (Lambert, 1942). The raw position data were smoothed before previous Patch-model analyses (NEFSC, 2010a), and the smoothed data were used in simulating track lines. Dredge tracks were assumed to follow straight lines between smoothed positions in simulations to preserve the differences in position data sampling between sites.

The number of clams caught during a simulated tow was based on the true position of the simulated dredge and an algorithm similar to the new method for hit matrices. The tow path was represented by a series of rectangles as long as the distance between position observations and as wide as the dredge. Any clam inside a rectangle was hit by the simulated dredge. A uniform random number between 0 and 1 $U(0, 1)$ was drawn for each clam hit by the dredge to determine if it was caught. The clam was added to the catch and removed from the simulated population if the random number was less than or equal to the true simulated capture efficiency. Catch data were simulated without errors because errors in catch data are believed to be relatively minor in actual depletion experiments. Capture efficiency was assumed to be the same for all simulated clams in the study, and size selectivity was ignored (see Discussion).

We studied the effects of four categorical and six continuous test variables on the accuracy of Patch-model estimates. The categorical variables were experimental site number (sites A–S), position errors (on or off), hit-matrix calculation method (original or new), and orientation (perpendicular or parallel; see below). Continuous variables were initial clam density (n m^{-2}), dredge capture efficiency, standard deviations in north–south and east–west clam positions (patchiness of the resource), and the amplitude and wavelength of sinusoidal errors in position data (see below).

Locations of simulated clams in each study site were determined using random numbers from two independent normal distributions with means at the centre of the site. The standard deviation for each normal distribution was calculated as the product of a uniform random number $U(0.1, 1)$ multiplied by the length or width of the site (Table 1, Figure 2). Large standard deviations correspond to random spatial distributions, and small standard deviations correspond to aggregated spatial distributions. Random locations were selected until the density of the simulated clams within the study site reached the target level. Random positions outside the site were discarded.

The orientation of clam spatial distributions relative to the direction of depletion tows might affect Patch-model performance. Sites were therefore categorized as parallel (or perpendicular) if the standard deviation in the direction of the tows and the long axis of the site was larger (or smaller) than the standard deviation along the other axis perpendicular to the direction of the tows.

Table 1. Test variables used in Patch-model simulation.

Variable	Observed range	Sampling distribution
Continuous variables		
Initial density (D_0, n m^{-2})	0.13–0.68	$U(0.01, 4)$
Efficiency (e)	0.35–0.99	$U(0.1, 1)$
Errors in position data		
Amplitude (ω, m)	<6 m	$U(0.01, 0.5)$
Angular frequency (γ, radians position observation^{-1})	n.a.	$U(0.1, 10)$
Spatial position of clams (x, y coordinates in m)		
Standard deviation (σ, m)	n.a.	$U(0.1, 1)$
Coordinate	n.a.	$N(0, \sigma^2)$
Categorical variables		
Site	19 choices	Multinomial
Position errors	Yes/no	Bernoulli
Hit-matrix method	Old/new	Bernoulli

Observed ranges are from actual depletion studies and Patch-model estimates for surfclam. Sampling distributions are for random numbers used to choose values for simulated test variables. Random numbers for continuous text variables were from either uniform U (lower bound, upper bound) or normal N ($\mu = 0$, σ) distributions. Random numbers for categorical test variables were either multinomial or Bernoulli distributions with equal probability for each possible outcome. n.a., not available or not applicable.

Simulated position data errors were introduced by adding sinusoidal error terms to either the latitude or the longitude associated with each recorded position:

$$E_{i,j} = \omega \sin(\lambda i), \tag{3}$$

where $E_{i,j}$ is the error in the jth position observation for tow i (m), ω the amplitude of the error (m), and λ the analogous to angular velocity (radians between position observations). The direction of the simulated errors was always perpendicular to the longest dimension of the site and the general direction of tows. Bounds for ω and λ were chosen to mimic various patterns in real data (Figure 2). For example, a low angular frequency and moderate amplitude reproduce errors produced by a GPS unit placed high on a ship that is rolling in high seas. A high angular frequency and moderate amplitude would mimic consistent errors perpendicular to the movement of the ship caused by strong tidal currents.

The amplitude (ω) in simulated position errors was based on a uniform random number $U(0.1, 1)$ multiplied by the distance along the smaller axis of the site and bounded between 0 and 25 m, based on residuals around the splines used to smooth the original position data from real depletion experiments (Table 1). It was necessary to truncate the amplitude of the simulated errors at 25 m to preserve some semblance of the original tow pattern. The angular frequency (λ) was a uniform random number $U(1, 10)$, which translates to wavelengths between 36 and 360 m (Table 1).

Experimental design and statistics

Values for each test variable were chosen independently at the outset of each simulation, to approximate a balanced factorial experimental design and facilitate statistical analysis (Table 1). The range of test variables in simulations was substantially wider than the ranges in real depletion experiments (Table 1; NEFSC, 2010a). All simulations (the full range of test variables) were analysed to determine when the Patch model performed poorly. A

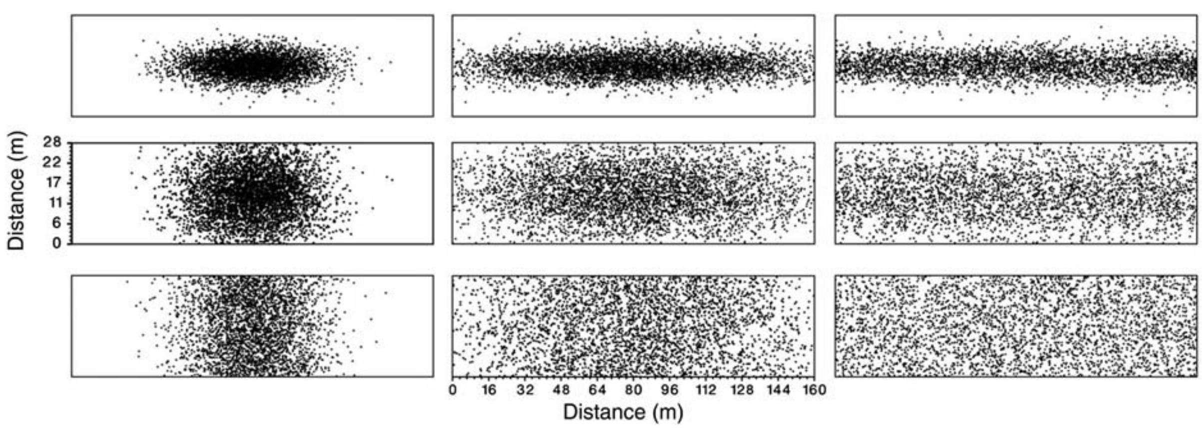

Figure 2. Example random bivariate normal distributions for the spatial position of clams in simulated depletion experiments. The mean vertical and horizontal positions are the centre of the site. Standard deviations for the distributions were 0.1, 0.25, or 0.75 times the length or the width of the site. The density of simulated clams is 1.0 clam m^{-2} in each panel and points show the position of one simulated clam. Simulated sites are populated with clams by drawing random numbers for the horizontal and vertical position of a clam until the desired density level is reached. Random positions outside the site are discarded.

Table 2. Summary statistics for relative errors in simulated Patch-model density and efficiency estimates based on all simulations, simulations with realistic test variables for Atlantic surfclam, two hit-matrix methods, and with and without positional errors.

	Quantile							
Variable	**5%**	**10%**	**25%**	**Median**	**75%**	**90%**	**95%**	**IQR**
All simulations								
Density	−0.64	−0.564	−0.474	−0.217	0.012	0.197	0.369	0.486
Efficiency	−0.327	−0.23	−0.091	−0.046	0.288	0.625	0.916	0.379
Simulations with realistic conditions only								
Density	−0.539	−0.483	−0.348	−0.131	0.026	0.179	0.342	0.374
Efficiency	−0.227	−0.149	−0.05	0.035	0.207	0.472	0.656	0.257
Hit-matrix method with realistic conditions only								
Density								
Old	−0.504	−0.447	−0.310	−0.099	0.087	0.258	0.418	0.396
New	−0.539	−0.483	−0.348	−0.131	0.026	0.179	0.342	0.374
Efficiency								
Old	−0.346	−0.278	−0.169	−0.048	0.115	0.345	0.506	0.284
New	−0.227	−0.149	−0.050	0.035	0.207	0.472	0.656	0.257
Positional errors with realistic conditions only								
Density								
Off	−0.169	−0.116	−0.046	0.028	0.130	0.324	0.494	0.176
On	−0.558	−0.513	−0.408	−0.245	−0.065	0.093	0.242	0.342
Efficiency								
Off	−0.217	−0.150	−0.069	−0.013	0.029	0.080	0.124	0.098
On	−0.230	−0.149	−0.035	0.091	0.300	0.564	0.739	0.335

$n = 73\,030$ for simulations under realistic conditions, and there were $n = 138\,167$ total simulations.

subset of simulations with test variables within bounds from real depletion experiments was extracted and used to evaluate accuracy under realistic conditions.

The accuracy of Patch-model estimates was measured by relative error statistics ($(\hat{\theta} - \theta)/\theta$), where $\hat{\theta}$ was the estimated value of the parameter and θ was the simulated true value. Medians were used to characterize the central tendency, and interquartile ranges (IQRs) were used to characterize variability among groups of simulations, because estimates had skewed distributions.

Deviance tables based on linear models with a relative error as the dependent variable were used to determine which of the categorical and continuous variables had statistically significant ($p \leq 0.05$) effects on the accuracy of estimates. Variables tested included each categorical and continuous test variable, and a number of two- and three-way interactions judged potentially important based on experience with the Patch-model and preliminary analyses. Linear models for deviance table analyses were fitted by sequentially adding main effects and interactions. Explanatory variables were judged statistically significant as they entered the model if they reduced model deviance by at least 5% of the deviance associated with the null (intercept only) model. The deviance table approach may be better than conventional χ^2-tests, which are more sensitive to the order in which explanatory variables are tested (Ortiz and Arocha, 2004). The number of simulations was large and traditional model selection approaches based on the Akaike information criterion resulted in very complicated models in which nearly all covariates and interactions tested were significant. We did not find these models useful, so opted for a more discriminating approach. Estimates with absolute relative errors >90% were categorized as poor. Deviance table analysis based on logistic regression models with a dummy variable for poor estimates as the dependent variable were used to identify statistically significant predictors of a poor estimate.

The simulation model was programmed in FORTRAN 90 using International Mathematics and Statistical Library routines (IMSL, 1989), and the simulated annealing algorithm for parameter estimation can be found in Press *et al.* (1992). The R statistical computing language was used for statistical analyses (R Development Core Team, 2008).

Results

Density estimates were biased low by ~20% in all simulations with positional errors, but efficiency estimates had relatively low bias under most conditions (Table 2). Considering all simulations, the median relative error was −0.217 (IQR, −0.474 to 0.012 = 0.486) for density, and −0.046 (IQR −0.091 to 0.288 = 0.379) for efficiency (Table 2, Figure 3). Based on realistic simulations only, the median relative error was −0.131 (IQR −0.348 to 0.026 = 0.374) for density, and 0.035 (IQR −0.05 to 0.207 = 0.257) for efficiency (Table 2, Figure 3). The Patch model failed to converge in just 2 of 56 613 (0.0004%) simulations.

The new hit-matrix method reduced the median relative error in efficiency estimates from realistic simulations, but increased the median relative error for density estimates (Table 2, Figure 3). The new hit-matrix method reduced the IQR of both efficiency and density estimates. Positional errors increased median relative errors substantially (Table 2, Figure 4). Sites with parallel orientations had less error than those with perpendicular orientation (Figure 4).

True efficiency, amplitude, and wavelength of positional errors, site and all two-way interactions with site, were significant predictors of the relative error for density. The sign of parameters in linear models indicated that density estimates were more accurate at high efficiency, low amplitude, and longer wavelengths. The same test variables with the addition of the two-way interaction between efficiency and amplitude and three-way interactions among site, true efficiency, and amplitude were significant for relative errors in efficiency. Relative errors in density and efficiency estimates differed markedly among sites (Figure 5)

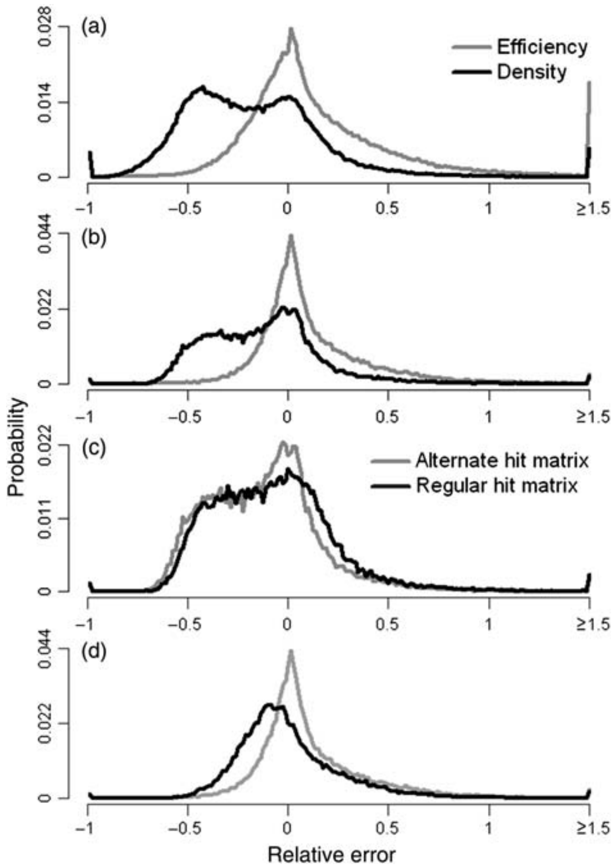

Figure 3. Probability distributions in relative errors in simulated Patch-model estimates based on all simulations (a), simulations with realistic test conditions (b), and showing the differences between hit-matrix methods in relative errors in density (c) and efficiency (d) estimates, based on realistic test conditions.

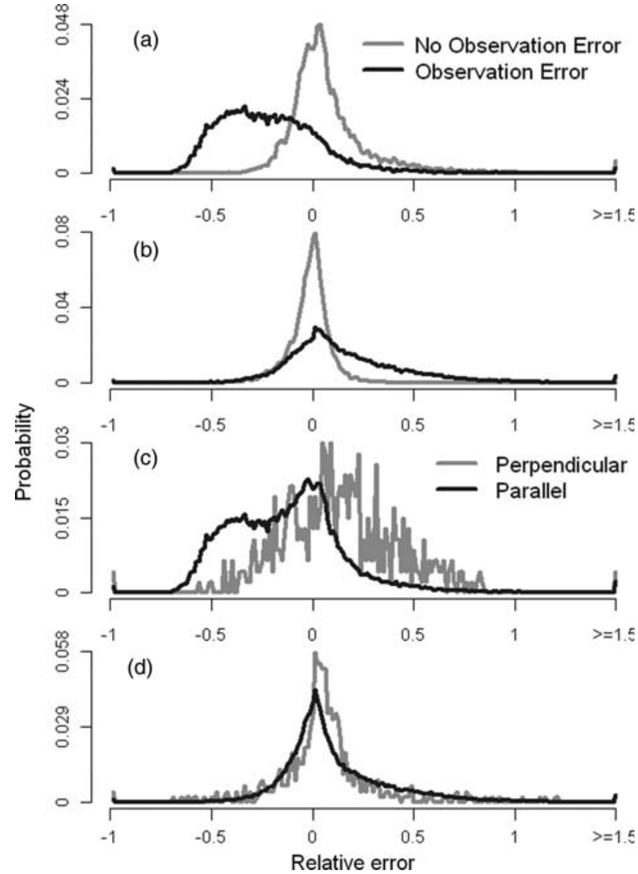

Figure 4. Probability distributions for relative errors with and without position errors based on simulations using realistic test conditions, in estimated density (a) and efficiency (b), and showing differences in simulations with parallel and perpendicular orientations based on simulations with realistic test conditions in density (c) and efficiency (d).

Tow orientation was not significant in predicting relative errors, but there were relatively few (2.3% of all simulations) perpendicular cases, so this result is uncertain. Most of the simulated sites were long and narrow, so variances in the location of simulated clams were likely to be larger in the direction parallel with track lines.

Additional simulations ($n = 138\,167$, including 81 554 additional runs) were used to predict the probability of poor estimates in linear models and deviance table analysis because poor estimates were relatively uncommon. Considering all simulations, there were 9402 runs (7%) with poor estimates. Of these, 24% had poor density estimates, 84% had poor efficiency estimates, and 9% had poor density and efficiency estimates. Poor estimates were about one-third as common (3% of cases) using the new hit-matrix method only.

Longitudinal variance in spatial distribution, sites, and all two-way interactions involving sites were statistically significant predictors for poor density estimates (Figure 6). The probability of a poor density estimate declined as efficiency and longitudinal variance increased. Efficiency, amplitude of position errors, sites, and the interaction between amplitude and site were statistically significant predictors of a poor efficiency estimates. Poor efficiency estimates were more common when efficiency was low and position errors had large amplitude.

Discussion

Simulation results indicate that depletion studies and the Patch model give useful estimates of initial density and capture efficiency under a range of simulated conditions wide enough to include Atlantic surfclams, ocean quahogs, and many other sessile or nearly sessile demersal species. However, there are a number of factors to consider in designing depletion studies and interpreting results from any single study. Differences in accuracy among sites should be expected as a result of variability in the spatial distribution of organisms and depletion tow characteristics, including the number of tows and overlap among tows. Our experience indicates that differences between species should be expected too. For example, Patch-model estimates are more accurate for Atlantic surfclams than for ocean quahogs, because the latter are found in deeper water, which increases errors in position data and because they burrow deeper into sediments so that capture efficiency is reduced.

High capture efficiency increased the accuracy of efficiency estimates because depletion caused by repeat sampling was easier to distinguish from sampling variability in the same way that steep slopes are easier to estimate accurately in linear regression. Density estimates were more accurate too, because tows over virgin ground had catch rates nearly equal to initial density.

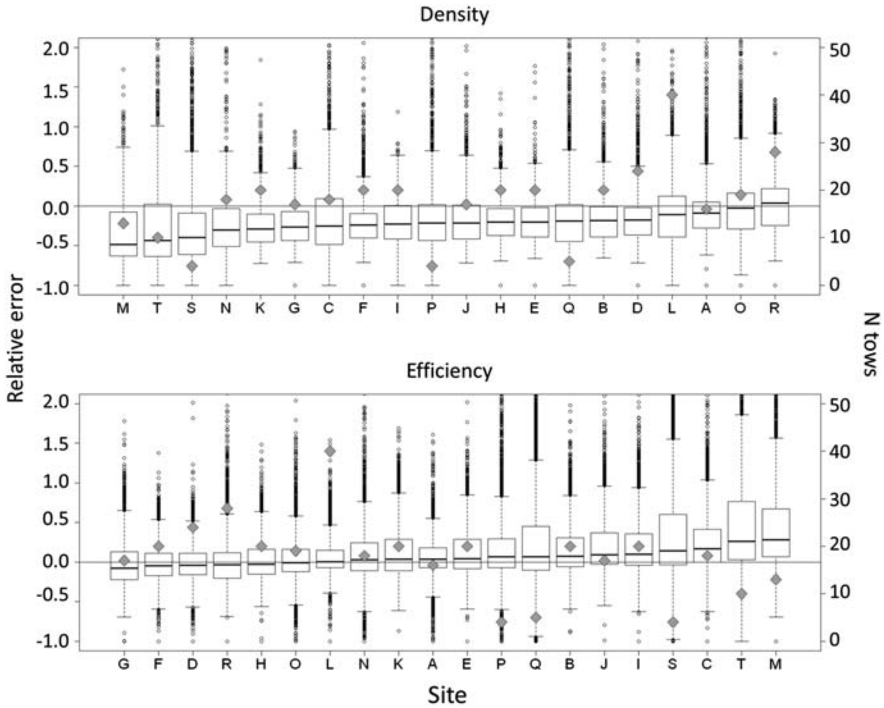

Figure 5. Boxplots showing distributions of relative errors in initial density (top) and capture efficiency (bottom) by site, based on all Patch-model simulations. Diamonds are the number of tows taken at each site. Simulations with relative errors >2 are not shown to enhance readability.

Based on medians and IQRs for relative errors, the new hit-matrix approach increased the accuracy of efficiency estimates under realistic test conditions (Table 2, Figure 3). The new method is advantageous in that it is not necessary to select a cell size that balances the realism of small cells against positional errors or to assume that clams not captured mix randomly within cells after sampling. The new approach is computer-intensive, but easier to program.

One useful approach to dealing with unavoidable uncertainties is to conduct a series of depletion studies and to use the distributions of Patch-model estimates to identify outliers, to quantify variability, and to determine the central tendency for a species or stock as a whole. NEFSC (2009, 2010a) use the medians of 24 sets of Patch-model estimates for surfclams and 20 sets for ocean quahogs to form prior distributions for survey catchability parameters in stock assessment modelling.

In forming prior distributions for stock assessment, it is important to remember that the central tendency of depletion experiment results may be biased if ideal experimental sites are chosen to minimize contact with rocks or other features that reduce dredge efficiency. There are two types of bias to be concerned about: bias in estimates from individual depletion experiment, and bias generated by applying depletion experiment results to the larger stock area. For example, density estimates from depletion studies with clam dredges may be biased low if substrata prevent the capture of clams along the edges of rocks. An example of the second type of potential bias might arise if prior distributions for catchability were based on efficiency estimates from depletion studies in ideal habitats, then applied to larger stock areas that include substantial amounts of rocky areas that are not clam habitat. NEFSC (2009, 2010a) reduced the second type of bias by adjusting for the amount of clam habitat within a stock area. It is useful to conduct multiple experiments over a wide range of sites that may, as a whole, better represent conditions across the entire suitable habitat within a stock area.

The realism of simulated clam distributions is difficult to judge precisely, because no empirical data are available. However, the overall range of variability in simulated clam distributions includes the range observed in real surfclam depletion experiments. The accuracy of negative binomial dispersion parameter k estimates was not evaluated because the negative binomial distribution was not used in modelling simulated spatial patterns. Estimates of k from the Patch model are, however, indirectly related to the spatial distribution of clams and tow distance. In particular, k should be higher with less spatial variability, and lower with more spatial variability, because $k = \mu^2/(\sigma^2 - \mu)$, where μ and σ are the mean and the variance of the negative binomial distribution. As tow distances increase and more area is sampled, the central-limit theorem guarantees that variance in catch data will decrease (higher k), and *vice versa*. Tows in the same experiment typically have similar lengths and swept-areas ($\bar{a}$). The negative binomial parameters μ and k can be expressed based on the area swept as $\mu^* = \mu/\bar{a}$ and $k^* = k/\bar{a}$, with $C/\bar{a} \sim NB(\mu^*, k^*)$, where C is the expected catch based on the model. Estimates of k^* are comparable among depletion experiments because the effects of differences in the area swept are removed. Distributions of k^* in simulations included the distribution of k^* from real surfclam depletion studies.

Rago *et al.* (2006) used likelihood profile analysis to estimate confidence intervals for Patch-model estimates, which were useful in understanding the precision and covariance of estimates from individual datasets. Our analysis focuses on variability among experiments and test conditions. In practice,

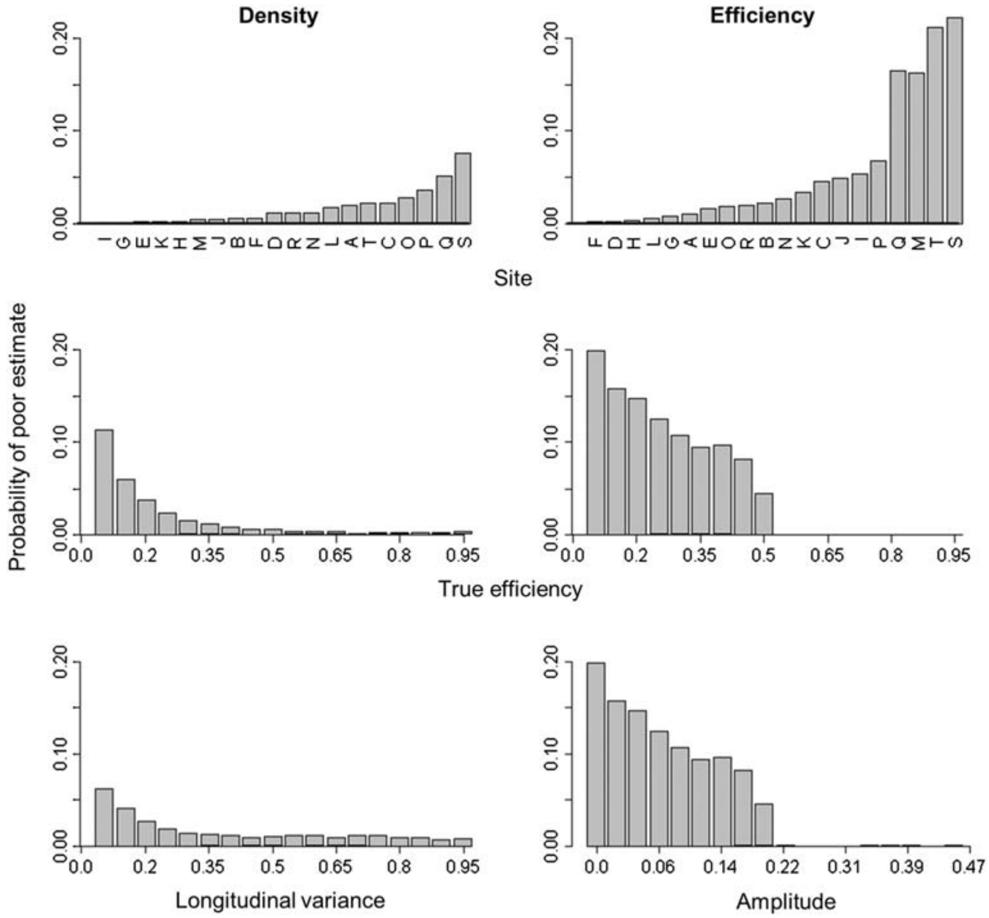

Figure 6. Probability of poor density (left) or poor efficiency (right) estimates for statistically significant predictor variables based on deviance table analyses.

the variance in Patch-model estimates among sites exceeds the statistical variance of estimates from individual experiments.

Information on size selectivity may be important in analysing depletion experiments (NEFSC, 2010a; Thorarinsdóttir *et al.*, 2010). Capture efficiency and size selectivity of the dredge are confounded in Patch-model estimates unless the data are restricted to size groups fully selected by the dredge or the catch data are adjusted for selectivity effects. The statistical effects of including partially recruited sizes are difficult to predict and probably depend on the particular experiment.

Incompletely selected size groups can be omitted from catch data to simplify Patch-model analysis if a selectivity curve or related information is available (NEFSC, 2009, 2010a). If no information about selectivity is available and commercial fishing gear is used in depletion experiments, then Patch-model estimates will be for the fishable stock (Thorarinsdóttir *et al.*, 2010). If survey gear with a small mesh liner is used for the depletion experiment, then the density of organisms selected by the survey dredge may approximate the density of commercially fishable size groups (when these are adjusted for selectivity of the commercial gear; NEFSC, 2000).

Size composition data might be included in the Patch model so that the selectivity curve could be estimated at the same time as other model parameters, possibly using selectivity estimates from other studies as prior distributions. This is an important area for future research. Size compositions, like expected catch, for a particular tow will depend on the relative amounts of virgin and previously sampled the area swept during a tow. In particular, previously fished areas should have different size compositions (fewer large animals) on average than unfished areas. Size data were collected from only a subset of tows (typically 3–4 per experiment at about every fifth tow) during NEFSC surfclam and ocean quahog depletion studies, because of time constraints. Estimation of size selectivity within the Patch model may be difficult with existing limited size sampling, and because changes in size data may be difficult to interpret without considering the area swept and size data from previously unsampled tows.

The interaction between efficiency and site in linear-model analysis was significant in predicting the relative error in both efficiency and density estimates. Under low dredge-efficiency conditions, the number of depletion tows and tow pattern become more important. With low efficiency and few depletion tows, or with tows that had limited spatial overlap, there was not enough information in simulated depletion data to determine whether the density was high and efficiency low, or if density was low and efficiency moderate. Difficulties in simulations with low efficiency were reduced in sites where there were many tows or substantial spatial overlap.

There was a relationship between the accuracy of density estimates and highly clumped spatial distributions that were or were not intersected by most of the depletion tows. Under these conditions, density estimates were biased high if tows fully sampled the centre of the site where the simulated clam aggregations were located, because the tows tended to measure density within the aggregation. In contrast, tow patterns that missed, or partially sampled the centre of the site where the clams, were concentrated resulted in density estimates that were biased low because areas of lower density were sampled preferentially.

Accurate estimates of the area swept during depletion tows are important. The time and location where fishing begins and ends may be difficult to determine for sampling gear that is relatively light or deployed in deep water using a slow winch (Weinberg *et al.*, 2002). Inclinometer, depth, and other sensors are mounted on the NEFSC clam survey and commercial dredges used in depletion experiments to determine when and where the dredge was actually fishing (NEFSC, 2010a). Sensors are not as important in shallow water or when using heavy gear that sinks rapidly, such as a commercial dredge deployed by a free spooling winch.

The amplitude of positional errors and sites was a statistically significant predictor of errors in density and efficiency estimates based on deviance table analysis. Sinusoidal position errors with high angular frequencies (short wavelengths) and large amplitudes in simulations caused a negative bias in density because the apparent area swept was exaggerated. In addition, the apparent overlap among tows was reduced so that the observed depletion was attributed to fewer hits than there were in reality, and efficiency estimates were biased high.

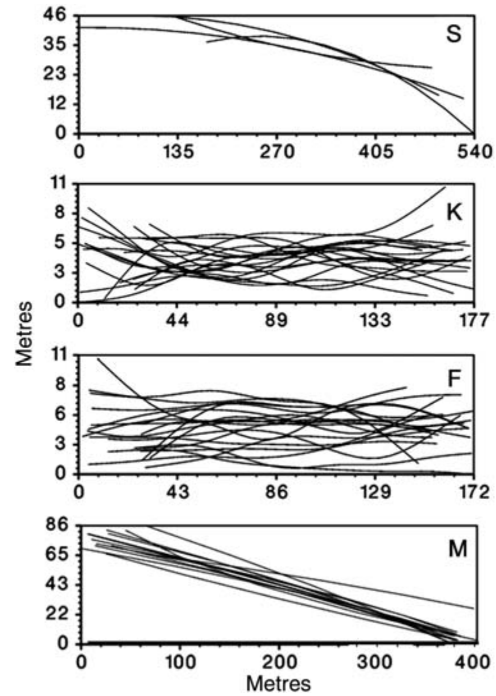

Figure 7. Simulated true track lines for depletion sites that produced poor estimates of density (sites K and F), efficiency (site M), or both (site S).

Poor estimates

Low simulated dredge efficiency was a significant predictor of poor density and efficiency estimates (Figure 6). Lower efficiency reduces information about initial density collected when sampling in unfished territory and reduces the signal-to-noise ratio with repeat sampling. Longitudinal variance (generally perpendicular to the tow paths and the long axis of the site) was significant in predicting poor density estimates because tows tended to miss the simulated clam aggregation when the variance was small (Figure 7). High amplitudes in simulated position errors were associated with poor efficiency estimates, because catches declined with relatively little apparent overlap among tows.

Problems in Patch-model density estimates stemming from aggregated spatial distributions were attributable to differences in density between the site as a whole and the area actually sampled. We arbitrarily based the true density calculation on the area of the entire site. If the area used to determine density was the area actually fished, the Patch model would likely have come closer to an unbiased estimate. Given the constraints imposed by our true density calculation, the ideal experiment would have depletion tows spread out enough to cover the entire site, so catches will reflect abundance across the entire site. Tows should also ideally overlap in areas where there are enough clams to clearly demonstrate depletion effects.

Most sites that consistently had poor density estimates also had poor efficiency estimates. For example, site S was prone to poor density and efficiency estimates because there were only four tows, little overlap among tows, and none of the tows crossed the centre of the site, where density was highest. Therefore, catches were low and not representative of the site (Figure 7). Other sites gave relatively accurate estimates for one parameter but not the other. For example, sites K and F were prone to poor density estimates because large sections of the experimental area, including a portion of the centre of the site, were not well sampled, whereas efficiency estimates were relatively accurate because there was sufficient overlap in tows. Site M gave poor estimates of efficiency in about 10% of simulations, but density was poorly estimated in only ~1% of simulations (Figure 7). The 13 depletion tows passed diagonally through the centre of the site, fully sampling it, which would tend to provide good information for estimating density, but there was relatively little overlap because the site was unusually long and wide (86 × 400 m), and tows were roughly parallel. The overlap that occurred was in one corner of the site, near the maximum distance from the centre of simulated clam aggregations. Although density estimates were relatively accurate because the clam aggregation was thoroughly sampled, efficiency estimates were usually poor because of the lack of overlap in high-biomass areas where the effects of sequential fishing would have been clearer. These results are partly attributable to our decision to place the centre of simulated clam aggregation in the middle of each site, but they clearly illustrate the importance of thoroughly sampling the site and having tows overlap in areas where density is relatively high, when depleting a patchy resource.

Experimental design

Our results demonstrate that it is always better to use sampling gear with high capture efficiency. Based on simulations, depletion studies can be carried out where clam densities are as low as ~0.13 m^{-2}, particularly if the dredge is efficient. At lower densities and with low dredge efficiency, few or no clams were caught during some or all simulated tows, and although density estimates were accurate, efficiency was difficult to estimate.

Long tow distances can be used to compensate for low density, but longer tow distances and larger sites reduce the probability that tows will overlap multiple times, and efficiency estimates may be less accurate as a result. Larger sites may also exacerbate problems attributable to small, highly aggregated spatial distributions.

Positional errors can probably be mitigated by taking GPS readings in calm weather, or near the sea level rather than on a mast above the ship where they are subject to a greater degree of pitch and roll. It may be useful to fish parallel or perpendicular to the prevailing currents such that the relative positions of the ship and dredge are relatively constant. Sensors can be used to determine when the sampler starts and stops fishing. Acoustic positioning techniques for locating towed equipment under water or similar equipment might also be employed to improve the resolution of the location data for sampling gear further. Position data should be collected at relatively short intervals of time and distance.

The area swept is easy to calculate for commercial clam dredges because tow distance and area covered are well defined. Tow distance is easy to measure because free spooling winches allow heavy commercial dredges to sink rapidly and because the winches are powerful enough to lift the dredge off the bottom quickly. In contrast, tow distance is much harder to measure using a smaller and lighter survey dredge deployed using a slower, less powerful winch (Weinberg *et al.*, 2002).

Ideally, the size, location, and approximate density of aggregations would be determined by divers or remote optical methods before a depletion experiment. This information would be useful in choosing the site location, orientation, size, and depletion tow pattern.

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