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Efficiency estimates from depletion experiments for sedentary invertebrates: evaluation of sources of uncertainty in experimental design

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ABSTRACT

Between 1997 and 2011, The National Marine Fisheries Service conducted 50 depletion experiments to estimate survey gear efficiency and stock density for Atlantic surfclam (*Spisula solidissima*) and ocean quahog (*Arctica islandica*) populations using commercial hydraulic dredges. A model formulated for this purpose, the Patch Model, was used to estimate gear efficiency and organism density. The range of efficiencies estimated is substantial, leading to uncertainty in the application of these estimates in stock assessment. A simulation protocol was developed to examine sources of uncertainty in Patch Model estimates. Analysis of simulations showed that uncertainty in the estimates of gear efficiency from depletion experiments was reduced by higher numbers of dredge tows per experiment, more tow overlap in the experimental area, a homogeneous as opposed to patchy distribution of clams in the experimental area, and the use of gear of inherently high efficiency. Stock density was of lesser importance, though still contributing to estimated uncertainty. Simulations suggest that adapting the experimental protocol during the depletion experiment by adjusting tow number and degree and dispersion of tow overlap may substantively reduce uncertainty in the final efficiency estimates. Simulations also suggest that the pattern of population dispersion in the experimental area is, and will likely remain, an important source of uncertainty, which may, however, be mitigated by updating experimental design during the course of the experiment.

1. Introduction

The ocean quahog (*Arctica islandica*) and the Atlantic surfclam (*Spisula solidissima*) support substantial fisheries on the northeast U.S. continental shelf. Hydraulic dredges are the commercial gear exclusively used by the commercial fishery and for the stock assessment survey. Ocean quahogs are reputed to be the longest-lived non-colonial marine species (Butler et al., 2013) - they are certainly the most abundant of the very-long-lived species - and, on the U.S. East coast continental shelf, are typically found offshore in deep water, between 30 m and 220 m (NEFSC (Northeast Fisheries Science Center), 2017b) with life spans exceeding 250 years (Pace et al., 2017). The Atlantic surfclam has a lifespan of about 30 years and is found in more inshore waters, typically between 8 and 66 m depth (NEFSC (Northeast Fisheries Science Center), 2017a). They coexist with ocean quahogs along their offshore range boundary that approximately follows the 15 °C summer bottom water temperature isotherm (NEFSC (Northeast Fisheries Science Center), 2017b; Powell et al., 2020). Surveys conducted in the 2000s show evidence that a range shift is occurring as the western North Atlantic warms, with surfclams invading deeper water, presently often occupied by ocean quahogs, throughout the mid-Atlantic region (Hofmann et al., 2018; Powell et al., 2020).

The ability to accurately estimate abundance from the National Marine Fisheries Service (NMFS) ocean quahog (*Arctica islandica*) and Atlantic surfclam (*Spisula solidissima*) stock assessment surveys benefits from empirical estimates of the efficiency of the survey dredge (NEFSC (Northeast Fisheries Science Center), 2003; Powell et al., 2007). However, efficiency is a key source of uncertainty in stock assessments. Efficiency estimates are notoriously variable (Vølstad et al., 2000; Powell et al., 2007; Hennen et al., 2012; Morson et al., 2018) at least in part because little is known about how experimental variables can influence the efficiency of a dredge. Gear efficiency is defined as the probability that an organism in an area intersected by the dredge will be caught (Hennen et al., 2012). Efficiency estimates have been obtained for a range of dredge types, including oyster dredges (Powell et al., 2007; Morson et al., 2018), crab dredges (Vølstad et al., 2000; Bohrmann and

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Christman, 2012; Wilberg et al., 2013), and scallop dredges (Beukers-Stewart and Beukers-Stewart, 2009; Lasta and Iribarne, 1997). These are all dry dredges designed to harvest epibenthic animals. In contrast, hydraulic dredges are designed to harvest infaunal clams by using water pressure to liquefy the sediment, thereby penetrating deeply into the sediment and exhuming the clams (Da Ros et al., 2003; Hauton et al., 2007; Meseck et al., 2014). Hydraulic dredges are efficient in comparison to dry dredges (Thórarinsdóttir et al., 2010).

A typical hydraulic dredge is a large rectangular box constructed of steel bars evenly spaced apart mounted on skids and towed along a seabed (Lambert and Goudreau, 1996; Meyer et al., 1981). A cutting blade in front of the dredge digs into the sediment as high-pressure water is pumped through a series of jets from a manifold, serving to liquefy the sediment, thus permitting the dredge to be towed with little resistance through the surficial sediment and thereby increasing the catchability of the target bivalve species (Gilkinson et al., 2003). Parker (1971) provides a historical account of the development of hydraulic dredges in the surfclam fishery.

Despite the increased focus on quantitative stock assessments in recent years and the industrial success of the hydraulic dredge, gear efficiency is still an uncertain parameter that is affected by many variables, including spatial characteristics such as the size frequency of clams in the population and the patchiness of clams in the benthos. Little is known about exactly how these factors might cause variation in efficiency estimates for hydraulic dredges.

Depletion experiments are commonly used to estimate gear efficiency and density of the target organism in the benthos (Leslie and Davis, 1939; Skalski et al., 1983; Lasta and Iribarne, 1997; Gedamke et al., 2005; Wilberg et al., 2013). Depletion experiments consist of deploying the gear multiple times in a target area, allowing the catch per tow to decline as a result of decreasing organism density. This rate of decline is used to estimate gear efficiency and the initial abundance of the organism.

A series of depletion experiments was conducted between 1997 and 2013 by academic and industry collaborators on commercial and survey vessels to estimate the efficiency of the commercial clam dredges and infer the efficiency of the National Marine Fisheries Service survey dredge (NEFSC (Northeast Fisheries Science Center), 2010c, 2013). The depletion experiments were carried out at locations specified in Appendix 3 of NEFSC (Northeast Fisheries Science Center) (2017a).

The Patch Model (Rago et al., 2006) was developed to analyze depletion experiments and estimate gear efficiency, stock abundance, and dispersion of organisms in a target area. The Patch Model has been important in informing stock assessments of commercially exploited populations of Atlantic surfclam, ocean quahog, monkfish (*Lophius americanus*) and Atlantic sea scallop (*Placopecten magellanicus;* (NMFS (National Marine Fisheries Service), 2009; NEFSC (Northeast Fisheries Science Center), 2010b, 2010a). Hennen et al. (2012) examined the performance of the Patch Model under a range of conditions and found that uncertainty in dredge position and distribution of dredge tow overlap in the experimental area were important contributors to the uncertainty in estimates of dredge efficiency.

The correction for dredge efficiency continues to be a primary source of uncertainty in the estimation of stock abundance for both clam species. In this study, we extend the analytical approach of Hennen et al. (2012) to develop metrics that can be used to guide retrospective evaluation of the effectiveness of experimental design of previous depletion experiments and to proffer an improved experimental design for future dredge efficiency estimates. To do so, a simulation protocol (Hennen et al., 2012) is implemented to test Patch Model efficiency estimates under a variety of conditions involving experiment methodology and dispersion and density of the target species to ascertain the characteristics of depletion experiments that contribute to the accuracy of efficiency estimates.

2. Materials and methods

2.1. The Patch Model

The Patch Model estimates capture efficiency (the probability of capture of an organism intersected by the dredge), and density of organisms in the target area (numbers per m^2) by tracking the relative depletion (reduction in catch) over the tow series. Capture efficiency is theoretically a measurable characteristic of the gear. Here, we examine the influence of the number of tows in an experiment, the distribution of organisms in the benthos, the density of organisms in the benthos, the degree of overlap of the multiple dredge tows conducted during the experiment, and the influence of the inherent ('true') efficiency of the gear on the uncertainty in the estimate of dredge efficiency obtained from the experiment.

Simulated depletion experiments follow a typical in-field experimental design used for actual depletion experiments conducted using hydraulic dredges designed to capture surfclams and ocean quahogs. A long rectangular area is chosen, on average about 10 dredge widths wide (25−38 m), and 400−800 m (1200−2400 ft) long. For the simulations described herein, the box dimension was taken as 960m × 45m, the narrow dimension being about 12 times the width of the present survey dredge. A series of overlapping dredge tows are taken across the selected area, with the dredge hitting bottom at one of the short edges of the rectangle and being retrieved at the other short edge. Ideally, the dredge is towed over the same ground multiple times while covering the majority of the demarcated area. The experiment requires the assumption that all catches are random samples and that no transport of organisms into or out of the study site occurs during the experiment (Leslie and Davis, 1939). The tow paths, catch, and fishing effort are recorded for each tow. Over a series of tows, the catch per tow will decrease; this rate of decline is proportional to the efficiency of the dredge (Hennen et al., 2012). For example, if the rate of decline is rapid, the dredge is highly efficient.

2.2. Patch Model estimates of efficiency

The Patch Model inputs are the tow series of area swept, the observed catch, and the hit matrix. The spatial domain in the model is defined as the smallest rectangular area that contains every tow in the experiment. Typically, this is marginally smaller in the short dimension and longer in the long dimension than the original specified rectangular area as vessels shy away from the lateral boundaries as they tow, and inaccuracy in dredge deployment and retrieval routinely extends tows across the narrow ends of the box. Any particular point in this domain can be touched by the dredge 0 to n times after n tows. The rectangular area is subdivided into a grid of points that is used to calculate the hit matrix which records the number of times any point was contacted by the dredge.

The backbone of the Patch Model is the ability to calculate the catch per tow, the density of organisms in the area after each tow, and the cumulative catch for any tow from the initial conditions of the experiment. The equation

$$E(c) = e\left(\frac{a}{A}\right)N \quad (1)$$

describes the expected catch in a sample from a closed population given e, the probability of capture of an individual given an encounter with the dredge, $\frac{a}{A}$, the area swept by the tow divided by the total area, and N, the number of individuals in the population in the defined area. Substituting q for $e\left(\frac{a}{A}\right)$ and adding the elements of time and space allows for the calculation of expected catch in any tow i given initial density and the cumulative catch from previous samples, T_{i-1}:

$$E(C_i) = q(N_0 - T_{i-1}) \tag{2}$$

Rago et al. (2006) incorporated the fraction of cells in the defined area that were hit by the tow, the hit matrix, into the equation, giving the expected catch per unit effort (CPUE) for depletion tow i as

$$E(C_i) = (EAS_i)D_o \tag{3}$$

where D_0 is the initial density of the target organism in the area, and EAS is the effective area swept for each tow i, the total area swept (m^2) by the dredge in tow i taking into account points hit by the dredge in previous tows. EAS is calculated as:

$$EAS_i = ea_i \sum_{j=1}^{i} f_{i,j}(1 - e\gamma)^{j-1}. \tag{4}$$

where e is capture efficiency, a_i is the area swept by tow i, $f_{i,j}$ is the fraction of cells hit by the dredge j times, and γ is the ratio of dredge width and cell size, or in other words, the fraction of the cell the dredge swept. Rago et al. (2006) and NEFSC (Northeast Fisheries Science Center) (2010c), subdivided the study sites into small square cells about twice the width of the dredge. Hennen et al. (2012) set γ to 1 by reducing the cells to points, which results in improved accuracy and precision of efficiency estimates.

A negative binomial distribution is used to describe the distribution of catch, as it accounts for extra variation in observed catches and can take into account catch from previous tows when estimating catch in tow i. This method uses the cumulative spatial pattern of animal removals to define the probability of capture and expected catch per tow. The negative binomial distribution of catch can be expressed as a function of D_o (initial density of organisms), K (the dispersion parameter), and EAS (the effective area swept in tow i) (Rago et al., 2006): thus,

$$Pr\left(C_i|D_0, K, EAS_i\right) = \left(\frac{K}{D_0(EAS) + K}\right)^K \left(\frac{D_0(EAS)}{D_0(EAS) + K}\right)^{C_i} x\prod_{j=1}^{C_i} \frac{K+j-1}{j} \tag{5}$$

The log likelihood function gives the likelihood of the dispersion parameter, initial density, capture efficiency, and fraction of the cell hit, given the data for catch and area swept.

$$LL(D_0,\ k,\ e,\ \gamma \mid Ci,\ EAS_i) = k\sum_{i=1}^{I}(\log(k) - \log(D_0(EAS) + k)) + \sum_{i=1}^{I}(\log(D_0(EAS)) - \log(D_0(EAS) + k)) + \sum_{i=1}^{I}\sum_{j=1}^{Ci}\log(k + j - 1) - \sum_{i=1}^{I}Ci! \tag{6}$$

Rago et al. (2006) utilized the hit-matrix approach to simulate the number of clams caught in the dredge in each tow. In our presentation, the fractions $f_{i,j}$ are part of a square $n \times n$ hit matrix consisting of one row vector for each depletion tow and one column vector for each cell hit at least once. Each row represents an entire tow, thus the cells in a single row always sum to 1. Organisms remaining in a cell that was hit by the dredge are assumed to be mixed randomly within the cell after each tow. Hennen et al. (2012) changed the definition of the hit matrix, using points 10 cm apart rather than a grid pattern. The redefined $f_{i,j}$ is the ratio of the number of points hit j times by the end of each tow divided by the total number of points hit during the tow.

2.3. Patch Model simulation protocol

Synthetic depletion experiments were generated using a defined distribution of clams with a given density and a set of dredge tow paths across the defined experimental area. The Simulation Model allows the dredge with an assigned efficiency to catch clams in its path. The Patch Model uses the catch per tow data generated from the simulated depletion experiment to estimate gear efficiency, clam distribution, and clam density in the area. The Simulation Model allows for various inputs to be treated as predictors of model performance by examining the effects of initial stock abundance, distribution, and fishing behavior on stock removal and Patch Model efficiency estimates.

The Simulation Model allows for the adjustment of factors, some of which are normally unalterable or difficult to evaluate in designing an actual field experiment. Normally, the distribution and density of organisms on the bottom is unknown, although test tows in the area of interest might provide some information as to the uniformity of clam distribution. Dredge tow paths can be partially, but not completely, controlled as tide and wind conditions affect vessel performance. The number of tows required is not known *a priori*.

In this study, the Simulation Model was specifically used to evaluate how the number of tows and amount of tow overlap in an experiment, the distribution and abundance of organisms, and the inherent gear efficiency affect the efficiency estimates using the Patch Model. Positional uncertainty of the dredge is also an important consideration. It was evaluated in detail by Hennen et al. (2012) and is consequently not included in the present simulation series. A complete block design was implemented to support statistical analysis. Blocks included 4 levels of clam distribution (a relatively uniform distribution (no patches: NP), clams distributed in vertical bands (P), clams distributed primarily in the lower half of the area (HP), and clams distributed in a triangular wedge (T)) (see depictions in Fig. 1), 3 numbers of tows per simulation (10, 20, 40) (Fig. 2), 3 levels of clam density (0.75, 1.5, and 3 clams m^{-2}) (Fig. 3), and 3 levels of inherent gear efficiency (0.2, 0.6, and 0.9) (Fig. 4). Fifty simulations were run for each set of the 4 blocked variables, 108 tetrads of block variables in total, each followed by a Patch Model estimation of efficiency and density. In total, 5400 simulations were conducted for this study. Henceforth, each simulated depletion experiment will be called a simulation, and a set of 50 simulations for 1 tetrad of block variables will be called an experiment.

For each experiment, 50 sets of tow paths were randomly generated for each tow number (50 tow paths were generated with 10 tows, 50 tow paths with 20 tows, and 50 tow paths with 40 tows), using the *runif* function in R (R Core Team, version 3.6.0). The same set of tow paths was used for every experiment with the same number of tows. The tow paths were generated by randomly generating a start point (x_o,y_o) and an end point (x_1,y_1) at the short ends of the rectangle (e.g., Fig. 1) and linearly interpolating the tow path between the 2 points. The rectangular experimental area was kept constant at 960 × 45 m.

The depletion rectangle was populated with clams by placing clams randomly at position coordinates within the target area as specified from a multivariate normal distribution using the *mvrnorm* function in R (R Core Team, version 3.6.0). The four distributions used are shown in Fig. 1. The number of organisms in the area is determined by the density level specified for the experiment. The overall density of clams for each distribution was maintained the same, but the dispersion of clams was varied in order to have different local densities. As an example of how this was done, the P distribution (vertical bands in Fig. 1) comprises 4 vertical bands, each with 25 % of the total density of clams in the area. The remaining dispersion patterns were developed with an equivalent approach, including the HP pattern and the T pattern. Catch was

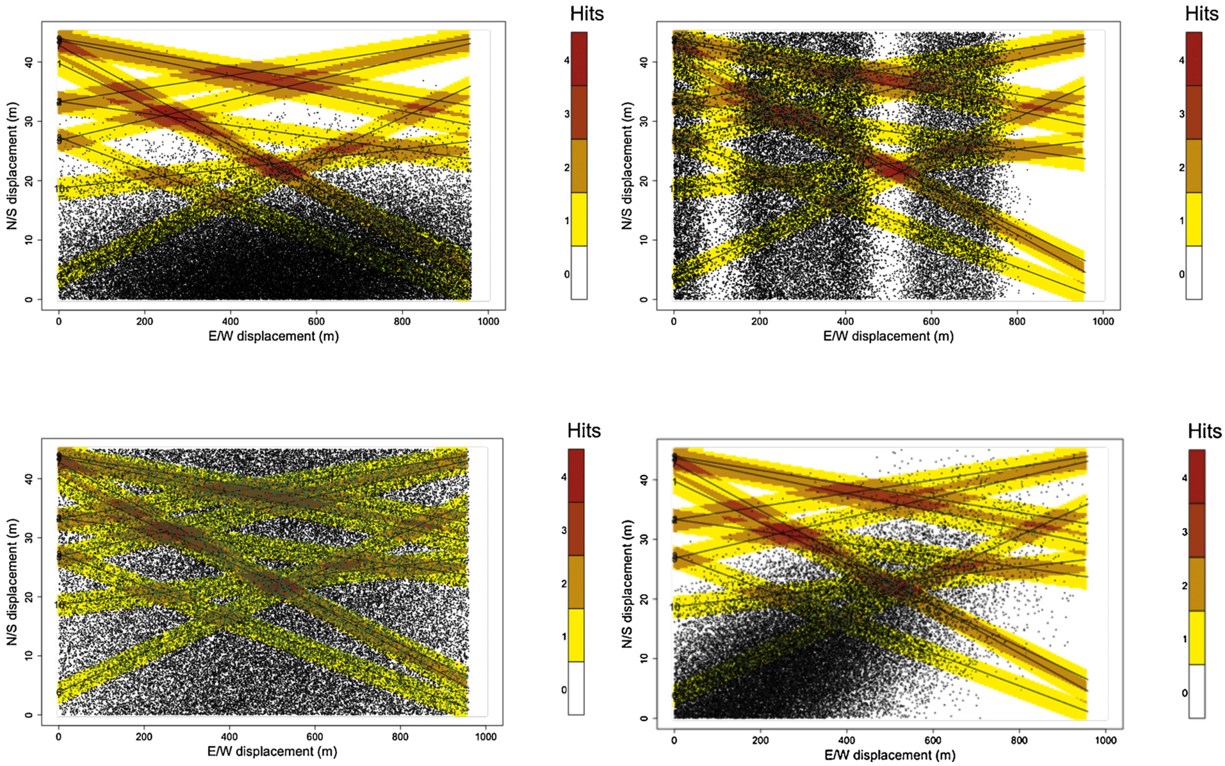

Fig. 1. The different clam distributions with dredge tow paths, the straight colored lines, passing through the area. Colors denote the amount of overlap (number of hits) in the dredge paths. Dots are clams. Top left: a biased clam distribution with highest densities in half the area (HP). Top right: clams distributed in even vertical bands (P). Bottom left: not-patchy, clams distributed relatively uniformly (NP). Bottom right: clams distributed in a triangle wedge from south west to north east across the area (T).

simulated by a series of Bernoulli trials, in which organisms were removed within the towpaths with a probability of capture equal to the assigned efficiency of the dredge. When an organism is encountered by the dredge, a uniform (0,1) random number is drawn. If that number is less than the assigned efficiency value, the organism is considered captured and removed from the area. If the number is greater than the true efficiency, the organism is not captured, and it remains in the area.

2.4. Statistics

An important evaluation of the simulation is the difference between the estimated efficiency obtained from the simulation and the true efficiency declared for the simulation. In the ideal case, the Patch Model would return the same efficiency it was given. The error in the efficiency estimate is designed to identify how closely the model was able to do that. The percent error in efficiency was calculated from the Patch Model estimate of efficiency, *EstEff*, and the inherent efficiency specified, *TrueEff*, as:

$$Error = \frac{EstEff - TrueEff}{TrueEff}(100). \tag{7}$$

The coefficient of variance (CV) was calculated as the standard deviation of the efficiency estimate divided by the mean of the efficiency estimates by the Patch Model from the log likelihood equation (Eq. 6):

$$CV = \frac{\sigma}{m}(100). \tag{8}$$

Type III SS ANCOVAs were used to analyze main effects and interaction effects of tow number, clam distribution, clam density, and degree of tow overlap on the Patch Model error in the efficiency estimates, and the CV CV of the efficiency estimate for simulations. Comparisons were conducted using ANCOVAs explicitly with the following models. Six ANCOVAs were conducted for all 5393 simulations, using the error and CV metrics in Patch Model efficiency estimates as dependent variables, each partitioned by the true efficiency declared for the simulation (0.2, 0.6, 0.9) (Table 1). The independent variables were clam distribution, clam density, and number of tows, producing 3 main effects and 4 interaction effects. Six ANCOVAs also were conducted using the error and CVs in Patch Model efficiency estimates for the 1799 simulations with 10 dredge tows, identically partitioned by the true efficiency declared for the simulation (Table 2). The independent variables are clam distribution, clam density, and EAS. Including EAS in a series of separate ANCOVAs at different levels of tow number is necessary because EAS is only comparable across experiments with the same number of tows and with the same true dredge efficiency (Eq. 4). Six ANCOVAs with the same dependent and independent variables were conducted on simulations with 20 tows and with 40 tows (Table 3).

To evaluate the overlap in tows for each simulated experiment, the effective area swept (EAS) was calculated for each tow. The EAS measures the amount of untouched ground over which the dredge was towed for each tow (Eq. 4). A lower EAS indicates that more of the dredge tow path passed over ground that had been swept by the dredge in previous tows. Effective area swept per tow will decrease as the number of tows increases.

Estimated Marginal means (EMmeans, also known as Least Squared means) (Lenth, 2016) were used post-hoc to identify where significant differences occurred within the ANCOVAs.

3. Results

3.1. Effects of tow number per simulation, clam density, and clam distribution on efficiency

Simulations with higher numbers of tows and more even distributions of clams produce more reliable efficiency estimates. Clam density does not influence the accuracy of the efficiency estimate, but it can

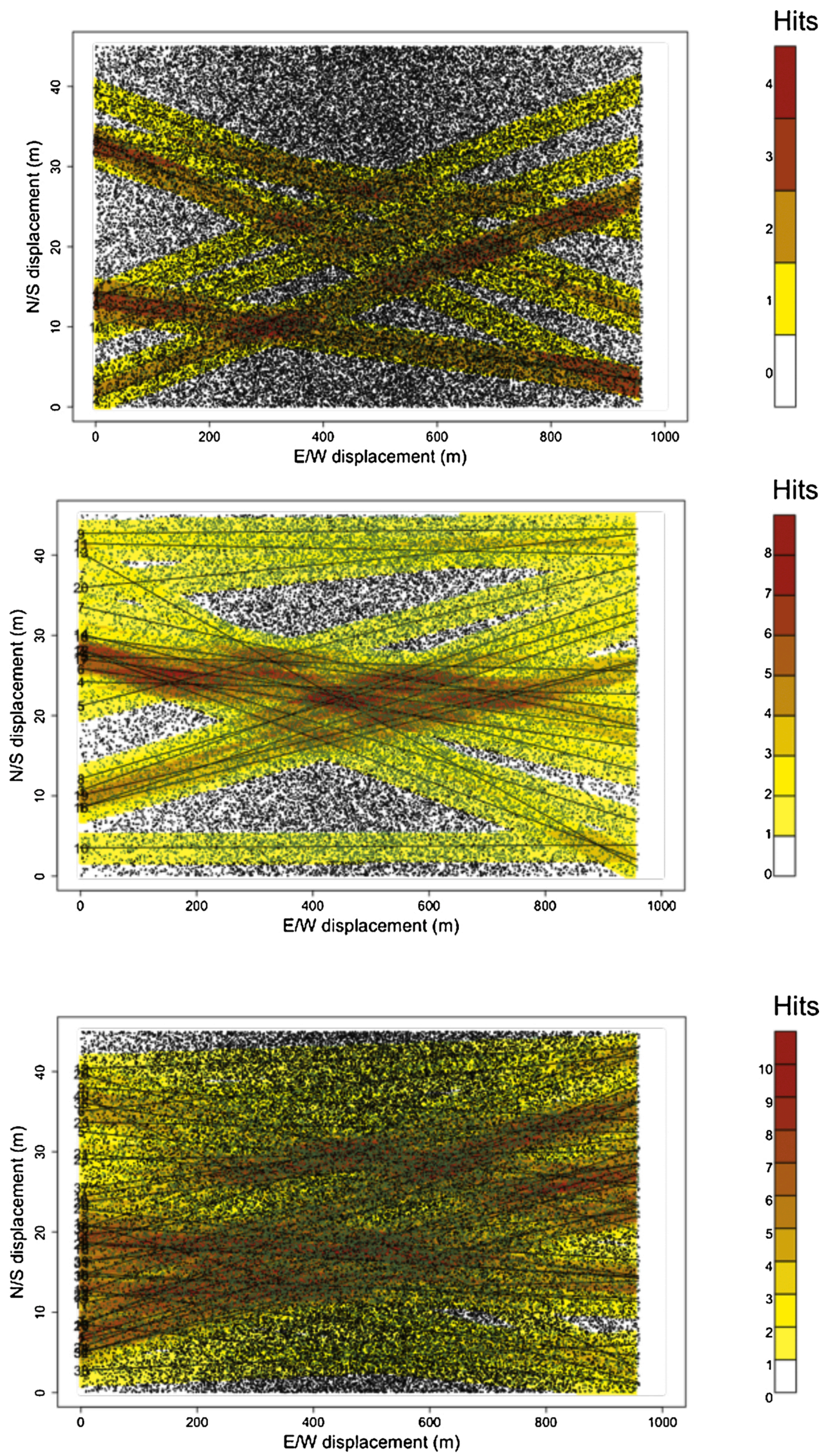

Fig. 2. From top to bottom; an example using the NP distribution of the number of tows per simulation: 10, 20, and 40. The straight colored lines are dredge tow paths; colors denote the amount of overlap in the dredge paths. The dots are the clams.

combine with an irregular clam distribution to increase the uncertainty in the efficiency estimate. At an inherent efficiency of 0.6, clam distribution, tow number, clam density, and their pairwise interaction terms significantly affected the error in efficiency estimates (Table 1). At inherent efficiencies of 0.9 and 0.2, significant effects of clam distribution, tow number and their interaction on the error in efficiency were retained, but clam density no longer exerted a significant main effect nor did any of its pairwise interactions.

At inherent efficiencies of 0.9 and 0.6, clam distribution, tow number, and their interaction terms significantly affected the CV of efficiency estimates (Table 1). At an inherent efficiency of 0.2, the main effects of clam distribution and tow number still strongly influenced the CV of efficiency estimates, whereas the interaction term was barely significant.

EMmeans analysis showed that significantly different error in efficiency estimates are primarily associated with low tow numbers, lower inherent efficiency levels, and more irregular clam distributions (Fig. 5). The efficiency estimates from the triangle (T) and half area (HP) clam

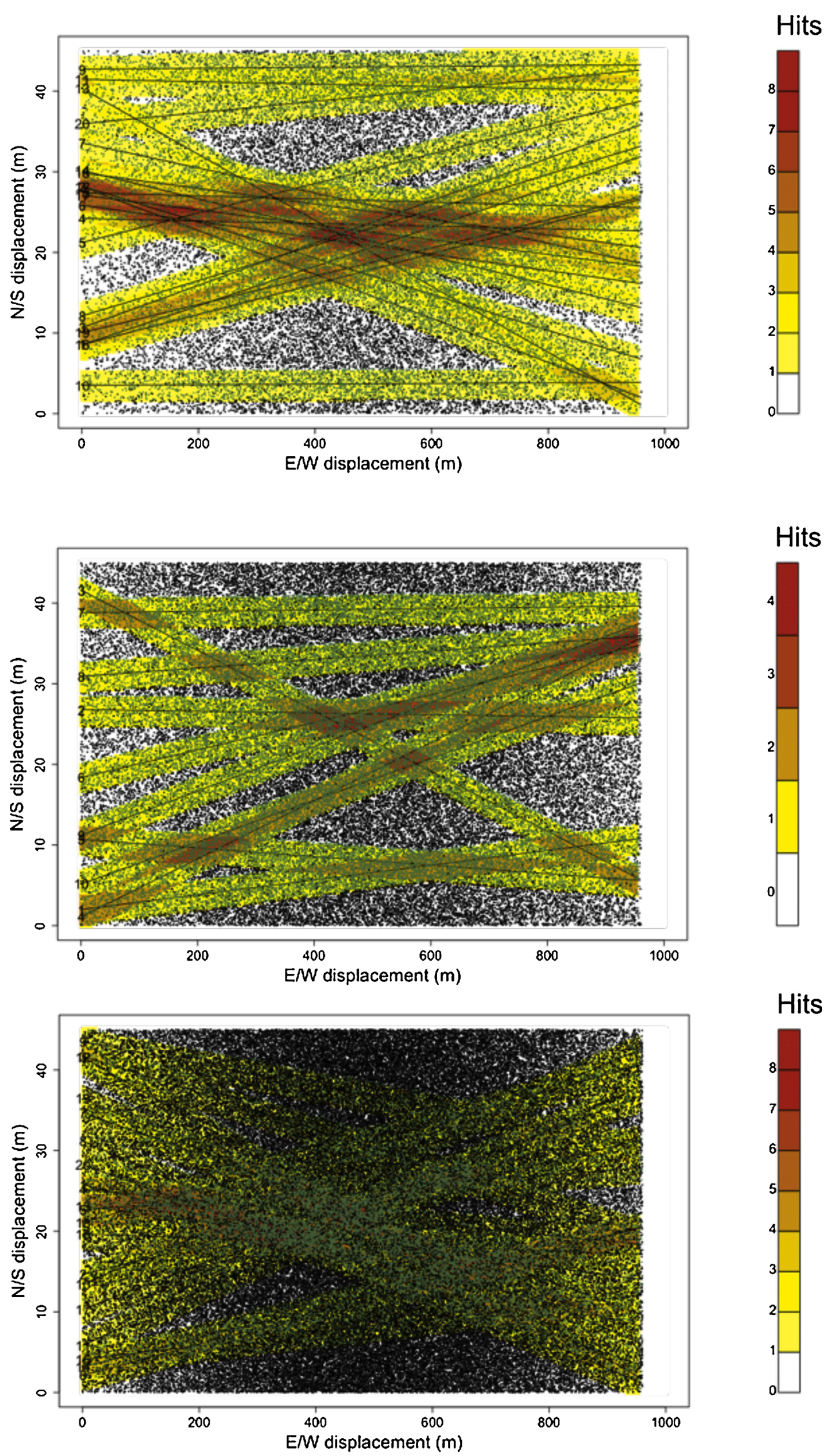

Fig. 3. From top to bottom; an example using the NP distribution of the different levels of clam density: 0.75, 1.5, and 3 clams m^{-2}. The straight colored lines are the dredge tow paths; colors denote the amount of overlap in the dredge paths. The dots are the clams.

distributions are typically significantly different from the efficiency estimates from the non-patchy (NP) and vertical banded (P) clam distributions. In the same vein, experiments run with 10 tows per simulation had more variability in the efficiency estimates than experiments run with 20 and 40 tows per simulation. The error in efficiency estimates at 10 tows per simulation was much higher than the error in efficiency estimates at 20 and 40 tows per simulation, and significant differences existed in the T and HP distributions for experiments with 10 tows, 20 tows, and 40 tows per simulation at all true efficiency levels. In contrast to the T and HP distributions, the EMmeans for the error in efficiency estimates for the NP and P distributions were not significantly different across differing tow numbers and efficiency levels.

The error in efficiency estimates varied significantly among density levels at an efficiency of 0.6, as density exerted a significant main effect at this efficiency level (Table 1, Fig. 6). This result, however, was due to only a single experiment, that one being the set of simulations with the T (triangle) clam distribution, 20 tows per simulation, and 1.5 clams m^{-2}.

Comparisons of CVs among the different tow numbers and clam

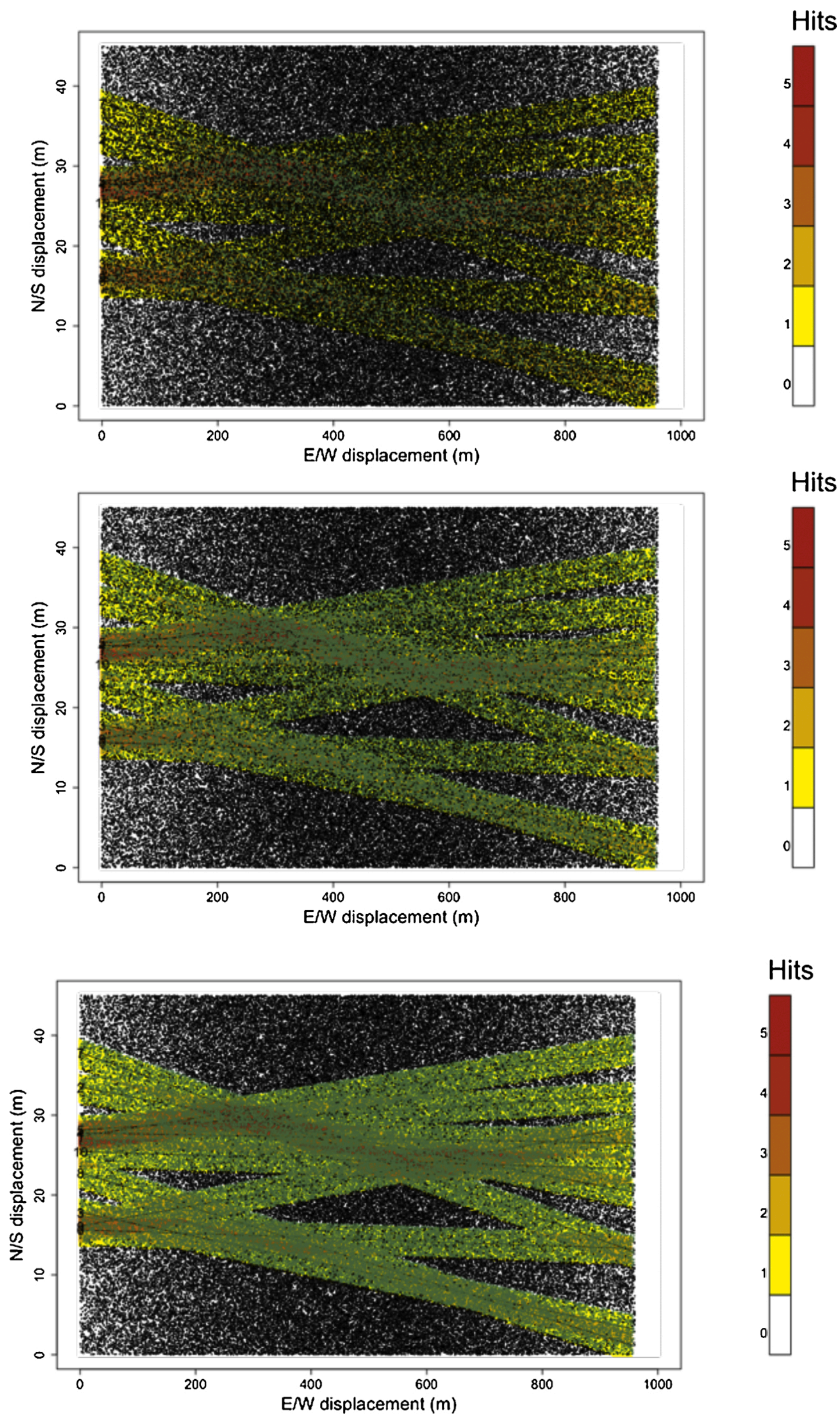

Fig. 4. From top to bottom; an example using the NP distribution with a density of 3 clams m^{-2} for 3 levels of true gear efficiency, 0.2, 0.6, and 0.9. Green dots are caught clams, black dots are uncaught clams.

distributions for each declared true efficiency using EMmeans are shown in Fig. 7. At an inherent efficiency of 0.9, the EMmean for CVs for the experiment with the T (triangular wedge) clam distribution and 10 tows was significantly different from all other CV EMmeans. At an inherent efficiency of 0.6, experiments with 10 tows, the T and HP (half of the area) clam distributions did not differ significantly from each other but each differed significantly from all other CV EMmeans. At an efficiency of 0.2, the T and HP experiments with 10 tows have CVs that are no longer significantly different from the HP experiment with 20 tows. None of the experiments conducted with 40 tows per simulation had significantly different CVs.

3.2. *Effect of dredge tow overlap on Patch Model efficiency estimates*

The mean effective area swept (EAS) per tow was calculated for each simulation as an estimate of the degree of overlap amongst dredge tows (Fig. 8). Because clam density and clam distribution exerted significant interaction effects with tow number, density and distribution are evaluated further in ANCOVAs with simulations with the same number of tows, in addition to EAS. At lower tow numbers, dredge overlap and clam distribution significantly affected the error in efficiency estimates. At all inherent efficiency levels for experiments with 10 tows, clam distribution and the interaction between clam distribution and EAS

Table 1
P values from Type III SS ANCOVA conducted on the error and coefficients of variance (CV) in Patch Model efficiency estimates for 5393 simulations. Columns are the true efficiency levels subdivided by the response type. Rows are the parameters tested: clam distribution, clam density, and number of tows in each simulation. Only significant (a<0.5) results are shown, non-significance is denoted by a dash (-).

Efficiency	0.2		0.6		0.9	
Response	Error	CV	Error	CV	Error	CV
Distribution	<0.0001	<0.0001	<0.0001	0.002	0.006	0.006
Density	–	–	<0.0001	–	–	–
Tow Number	<0.0001	<0.001	<0.0001	<0.0001	<0.0001	<0.0001
Distribution x Density	–	–	<0.0001	–	–	–
Density x Tow Number	–	–	–	–	–	–
Distribution x Tow Number	<0.0001	0.046	<0.001	<0.001	<0.0001	<0.0001
Density x Distribution x Tow Number	–	–	–	–	0.017	0.0165

Table 2
P values from Type III SS ANCOVA conducted on the error and coefficients of variance (CV) in Patch Model efficiency estimates for 1799 simulations with 10 tows. Columns are the true efficiency levels subdivided by the response type. Rows are the parameters tested: clam distribution, clam density, and effective area swept (EAS) in each simulation. Only significant (a<0.5) results are shown, non-significance is denoted by a dash (-). Results of the 40-tow case are shown in Table 3. Simulations with 20 tows per simulation are not shown because no significant main or interaction effects were observed.

10 Tows Per Simulation						
Efficiency	0.2		0.6		0.9	
Response	Error	CV	Error	CV	Error	CV
Distribution	<0.0001	–	<0.0001	–	<0.0001	0.024
Density	–	–	–	–	–	–
EAS	0.025	–	–	0.006	<0.001	–
Distribution x Density	–	–	–	–	–	–
Density x EAS	–	–	–	–	–	–
Distribution x EAS	<0.0001	–	<0.0001	–	<0.0001	–
Density x Distribution x EAS	–	–	–	–	–	–

Table 3
P values from Type III SS ANCOVA conducted on the error and coefficients of variance (CV) in Patch Model efficiency estimates for 1798 simulations with 40 tows. Columns are the true efficiency levels subdivided by response type. Rows are the parameters tested: clam distribution, clam density, and effective area swept (EAS) in each simulation. Only significant (a<0.5) results are shown, non-significance is denoted by a dash (-). Results of the 10-tow case are shown in Table 2. Simulations with 20 tows per simulation are not shown because no significant main or interaction effects were observed.

40 Tows Per Simulation						
Efficiency	0.2		0.6		0.9	
Response	Error	CV	Error	CV	Error	CV
Distribution	–	–	–	–	–	–
Density	–	–	–	–	0.011	0.033
EAS	–	–	–	–	–	–
Distribution x Density	–	–	–	–	0.002	0.006
Density x EAS	–	–	–	–	0.013	0.038
Distribution x EAS	–	–	–	–	0.06	–
Density x Distribution x EAS	–	–	–	–	0.003	0.008

exerted significant effects on the error in efficiency estimates (Table 2). EAS as a main effect was also significant at true efficiencies of 0.2 and 0.9. In contrast, EAS did not exert a significant main effect on the error in efficiency estimates at an inherent efficiency of 0.6, indicating that the amount of tow overlap did not significantly affect the error in the efficiency estimates for these simulations. No significant main or interaction effects were observed with simulations with 20 tows. Consequently, the statistical results for 20 tows were not provided in tabular form. At an inherent efficiency of 0.9, experiments with 40 tows produced a significant main effect on the error in efficiency for clam density, and all interactions exerted significant effects (Table 3). As in the case with 20 tows, in contrast, no main effects or interaction terms were observed at inherent efficiencies of 0.6 and 0.2 with 40 tows. The distribution of effects of response variables changes between low and high tow numbers. At low tow numbers, EAS is an important metric. At high tow numbers, the important variables are the density and distribution of clams in the area, which then are only important at high defined dredge efficiencies. This pattern is not observed elsewhere in the simulations. A possible explanation for this pattern is that, at high defined dredge efficiencies and high tow numbers, the dredge passes over the same ground multiple times and quickly depletes these overlapping areas of clams. To the degree that tows later in a depletion experiment pass over empty ground, the error in efficiency estimates will increase leading to the counterintuitive result that uncertainty increases under high efficiency-high tow number conditions.

The CVs of the efficiency estimates were evaluated to determine if the CVs were significantly affected by the same factors that significantly affected the error in efficiency estimates. Higher CVs were observed with 10 tows than with 20 and 40 tows for all efficiency levels (Fig. 7). At an inherent efficiency of 0.9, simulations with 10 tows produced a significant main effect for clam distribution on the CV of the efficiency estimates. The EAS exerted a significant main effect at an inherent efficiency of 0.6. No main effects or interaction terms proved to be significant with an inherent efficiency of 0.2 (Table 2). For simulations with 20 tows, no variable produced a significant effect on CV nor were any interaction terms significant. Experiments with 40 tows exhibited significant main effects and interactions only when the inherent efficiency was set at 0.9. In this case, clam density and most pairwise interactions were significant (Table 3).

4. Discussion

The simulations show that low tow number, certain patchy distributions, and low effective area swept (EAS) generate the largest deviations in estimated efficiency from the true efficiency. Uniform clam distributions and high tow numbers which also ordinarily generate low EAS (indicating more dredge overlap) routinely conduce highly accurate efficiency estimates. Save for rare occurrences, clam density has no significant influence on the efficiency estimate.

The error in efficiency estimates, the CVs, and the differences in efficiency estimates across all four defining variables - tow number, inherent efficiency, clam distribution, and clam density - indicate that the depletion experiments yielding the most accurate efficiency estimates are those characterized by a high number of tows. No significant differences in CV were observed for simulations with 20 tows and 40 tows, but experiments with 10 tows per simulation were more likely to be distinguished by higher uncertainty (Fig. 7). The error in efficiency estimates, a direct evaluation of the ability of the Patch Model to return a known efficiency, shows the same pattern, with a clear trend towards improved performance as tow number increases. Even at patchy distributions and low densities of clams, the Patch Model is more likely to produce an accurate efficiency estimate with a high number of tows,

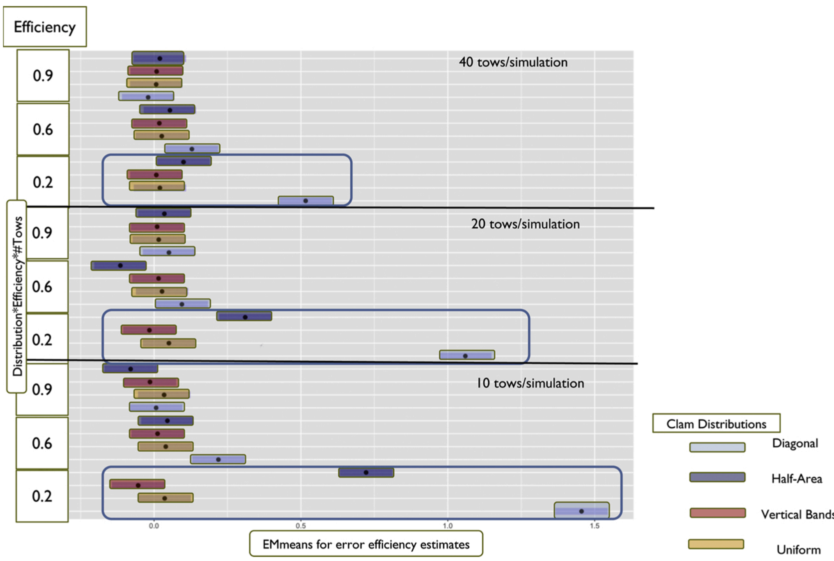

Fig. 5. Plot of estimated marginal means (EMmeans) for error in the estimates of efficiency for groups of simulations conducted under a variety of efficiency levels, tows per simulation, and clam distributions. Each bar is 150 simulations, 50 for each of the 3 density levels, with the corresponding set of parameters. Colors correspond to the distribution of clams. Numbers on the y-axis are the true efficiency levels. Horizontal black bars separate experiments by number of tows per simulation. Blue outlines emphasize the increase in error as the true efficiency decreases and the number of tows per simulation decreases.

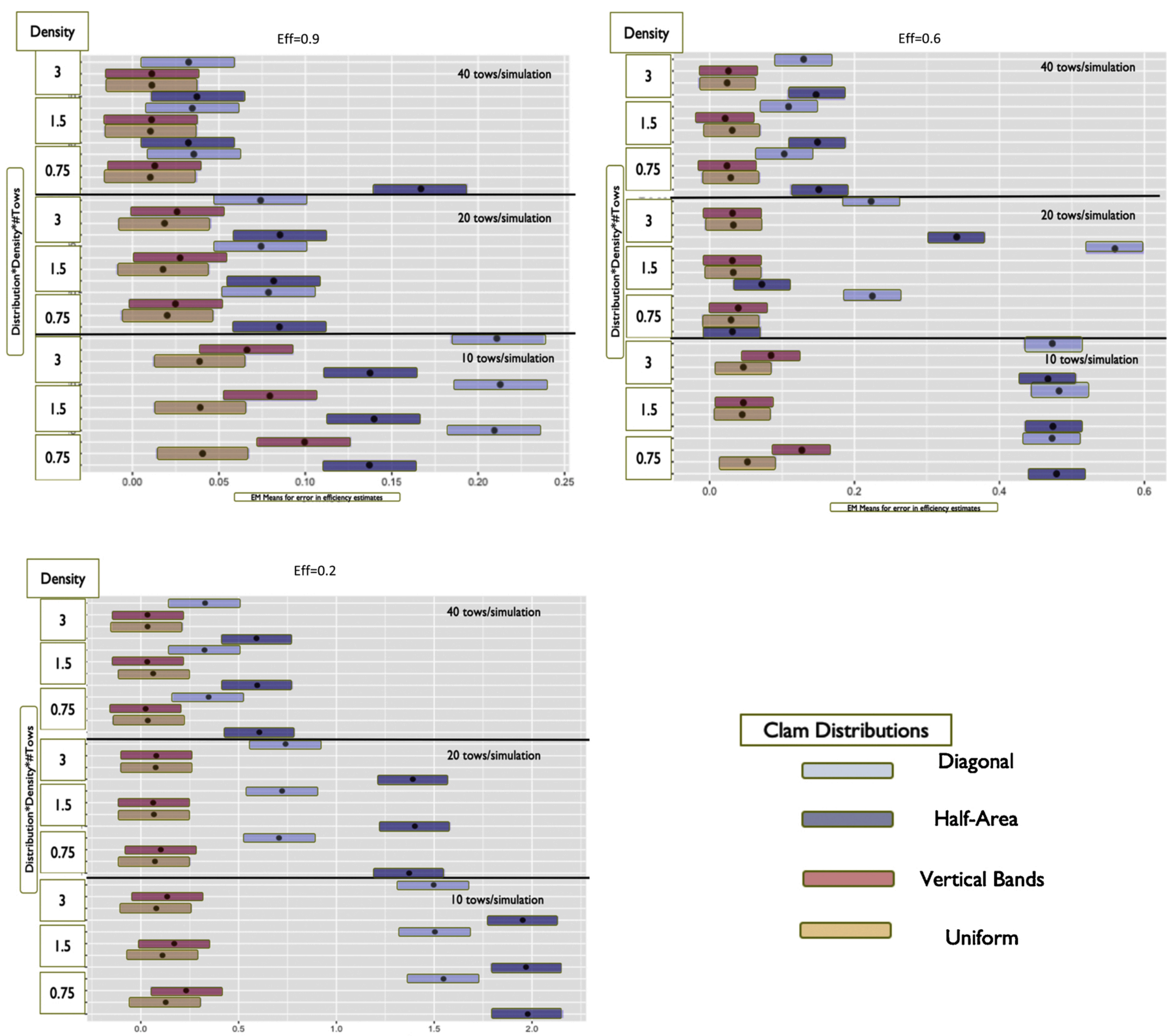

Fig. 6. Estimated marginal means (EMmeans) of the absolute value of the error in efficiency estimates with clam distribution, clam density, and number of tows as variables. Each bar is 50 simulations for each parameter. Top is an efficiency of 0.9, middle is an efficiency of 0.6, and bottom is an efficiency of 0.2. Note the different scales on the x-axis for each efficiency level. Ordinate labels correspond to the distribution-density-number of tows.

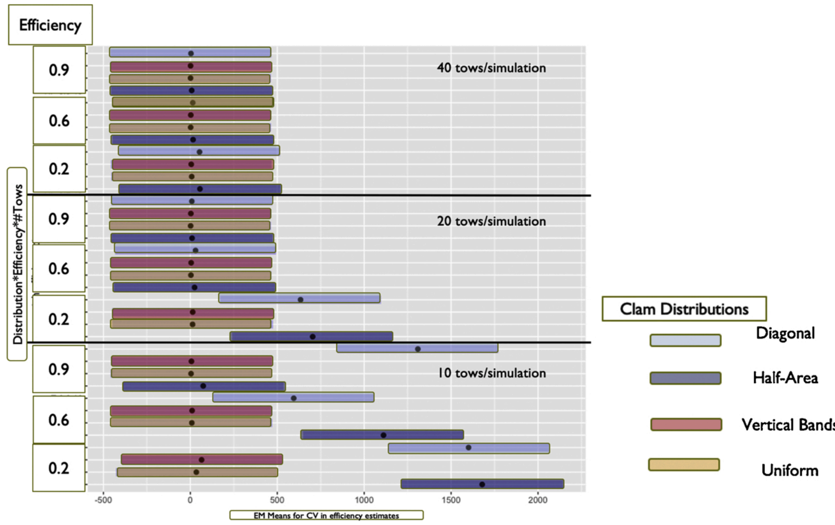

Fig. 7. Estimated marginal means (EMmeans) of the CVs of the efficiency estimates of simulated depletion experiments with clam distribution, clam density, and number of tows as variables. Each bar is 150 simulations, 50 for each clam density level. The figure is divided vertically by the number of tows in each simulation (from top to bottom: 40, 20, 10). Ordinate labels correspond to the distribution of clams – true efficiency – number of tows per simulation.

thus tow number is a controlling variable capable of mitigating the influence of conditions inducing uncertainty (Figs. 6 and 8). Simulation results show little improvement in the accuracy of efficiency estimates between experiments with 20 and 40 tows, especially at relatively uniform densities of clams in an area, but the differential becomes apparent when certain highly biased clam distributions are present.

A metric describing the error in efficiency estimates is more informative for understanding the causes of variation in efficiency estimates than is the CV. Unfortunately, while the convenience of assigning an inherent efficiency for a dredge in a simulated depletion experiment is appreciated, that luxury is not afforded to fisheries scientists during a field depletion experiment. Thus, the error estimate used here, while valuable in assessing the results of simulations, is not available as a metric for distinguishing reliability in efficiency estimates for field experiments. The Patch Model outputs include an efficiency estimate obtained from the maximum likelihood estimate and a corresponding standard deviation for the estimate. For a field experiment, the CV is the only option for quantifying the accuracy of the Patch Model efficiency estimate.

True clam density rarely had a significant effect on the CV, error in efficiency estimates, or the efficiency estimates themselves. The few significant results are associated with clam distributions in which clam density varies strongly across the narrow dimension of the depletion domain and how these distributions interact with tow path overlap in the areas with clams, rather than an inherent effect of clam density overall. Generally, a hydraulic dredge should be equally efficient over a wide range of clam densities. The simulations support this expectation.

Effective area swept (EAS) provided useful information in describing the likely error in efficiency estimates at 10 tows per simulation. Tow overlap significantly affected outcomes at low tow number. At 20 or 40 tows per simulation, the error in the efficiency estimate is not significantly affected by the degree of tow overlap. Thus, EAS and tow number provide the equivalent expectations about the quality of a depletion experiment assuming that the vessel operator is limited in their ability to carefully determine tow location and direction. In field experiments, tow location and tow linearity are commonly controlled as the experiment proceeds (NEFSC (Northeast Fisheries Science Center), 2007); thus, we did not simulate patterned distributions of dredge tow paths in this study.

This analysis confirms findings from Hennen et al. (2012) that under low dredge-efficiency conditions, the number of tows per simulation and the amount of overlap in the dredge tow paths significantly affect the error in efficiency estimates to a greater degree than they do for gear with inherently high efficiency or being operated under conditions facilitating higher efficiency use. Table 2 shows that at 10 tows per simulation the distribution of clams and the degree of dredge overlap quantified by the EAS significantly affect the error in the efficiency estimates, but this is not the case at 20 and 40 tows. Across all efficiency levels, the most error in the efficiency estimates is observed at low tow numbers.

Higher error values are seen when clam distributions are less uniform across the domain of the experiment. This is true across all efficiency conditions and numbers of tows per experiment, with the highest error values observed under combinations of low tow numbers per experiment, low inherent efficiency, and strongly non-uniform clam distributions. When clams are irregularly distributed across the depletion rectangle and the number of tows is low, the dredge tows may overlap multiple times in an area with low clam density, biasing the efficiency estimate. Increasing tow number counteracts this problem by encouraging a more even dredge tow overlap throughout the area. Given this, the fact that EAS did not significantly affect error or CV in efficiency estimates at higher numbers of tows per simulation is not surprising.

However, even experiments with 40 tows can occasionally produce poor results. For example, one set of 50 simulations with 40 tows per simulation, a clam distribution biased towards the lower half of the depletion area with a clam density of 0.75 m^{-2} produced higher error and CV values than other 40-tow experiments with the same clam density and distribution. (Fig. 9). Here, by chance, a high amount of dredge overlap in the portion of the domain with low clam density produced inaccurate efficiency estimates. This occurs, in this case, because efficiency will be overestimated when density is underestimated (see Eqs. 5 and 6). If the tows happened to cluster in the lower portion of the depletion area where most of the clams are, density would have been overestimated and efficiency underestimated. The tendency for outliers to occur is seen across simulations with all tow numbers, with increasing frequency as tow number declines, but is most pronounced with the HP clam distribution. In this case, the upper half of the experimental area has very few clams, generating a higher likelihood for tow overlap to occur in the low-density portion of the domain. Simulations show that the effect of patchiness is only pronounced when the patchiness is orthogonal to the short dimension of the depletion domain, thereby reducing the probability that a tow will fairly sample the range of patchiness in the domain.

Simulations suggest that a good depletion experiment can be

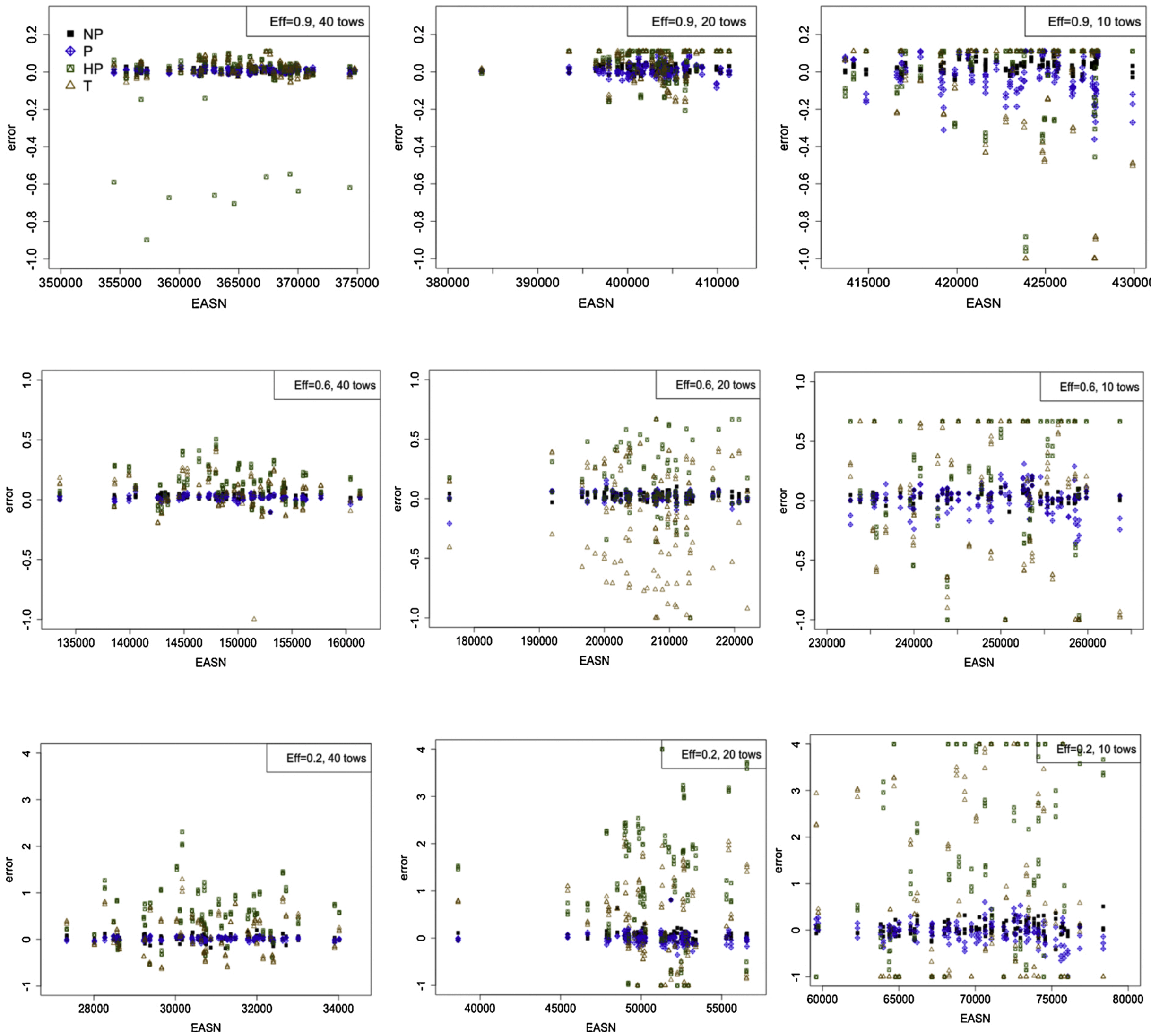

Fig. 8. Error in efficiency estimates as a function of EAS. Plots are orientated into columns based on the number of tows per simulation: 40 tows (left), 20 tows (middle) and 10 tows (right). Plots are oriented into rows by efficiency levels: 0.9 (top), 0.6 (middle), 0.2 (bottom). Plot points are different for each clam distribution, a legend is provided at the top left of the figure. Thus, the upper left plot provides results for 40 tows per simulation and an inherent efficiency of 0.9. Note that the ordinate range varies substantially by row.

characterized as having a high number of tows, between 20 and 40, with dredge paths that overlap multiple times, but distributed evenly throughout the studied area. Multiple tows in an experiment reduce the likelihood that the dredge paths will overlap multiple times exclusively over ground with low densities of clams when the domain is characterized by aggregated clam distributions. The influence of clam distribution is sufficiently pervasive that it could be beneficial to have potential sites for depletion experiments evaluated remotely by divers or video to get an understanding of how clams are distributed in space. Of course, such a capability may reduce the need for the depletion experiment. A recent analysis used Habcam camera system tows along with dredge tows to estimate abundance of sea scallops, for example (Miller et al., 2019), and Thórarinsdóttir et al. (2010) employed divers to ascertain the efficiency of hydraulic clam dredges in shallow water.

Comparison of simulated depletion experiments to in-field depletion experiments is difficult because little empirical data will be available in the field to guide experimental design. The range of variability in the simulated clam distributions and densities includes the range observed in the field surfclam and ocean quahog experiments summarized in NEFSC (Northeast Fisheries Science Center) (2017a, 2017b), supporting the validity of the simulated experiments. Depletion experiments are costly and time consuming at sea. In-field experiments of 20 or more tows typically take 10–20 h of continuous sampling and place an inordinate burden on the captain and the scientific crew. Accordingly, experimental design aimed at limiting the number of tows to the degree possible is critical. Unfortunately, tow number dominates the determinants of error in efficiency estimates and the secondary but also critical effector, clam dispersion, is inherently difficult to observe. Clam density is of little consequence, but inherent gear efficiency is consequential. Hydraulic dredges, being inherently high efficiency gears, limit that degree of consequence, thus placing emphasis on tow number and the degree of tow overlap in experimental design.

Gear efficiencies are influenced by a wide number of relatively uncontrollable factors such as depth, sediment type, bottom current force, sea state, etc. These add uncertainty that cannot be easily constrained. Yet, a correction for gear efficiency is frequently the largest correction factor in determining true abundance from the survey index. A variety of gear calibration methods have been used, including diver quadrat sampling (Powell et al., 2007; Thórarinsdóttir et al., 2010; Morson et al., 2018), hydraulic patent tongs (Chai et al., 1992; Mann et al., 2004), and video (Giguére and Brulotte, 1994), all of which are highly efficient sampling methods in shallow water or for epibenthos. Options are

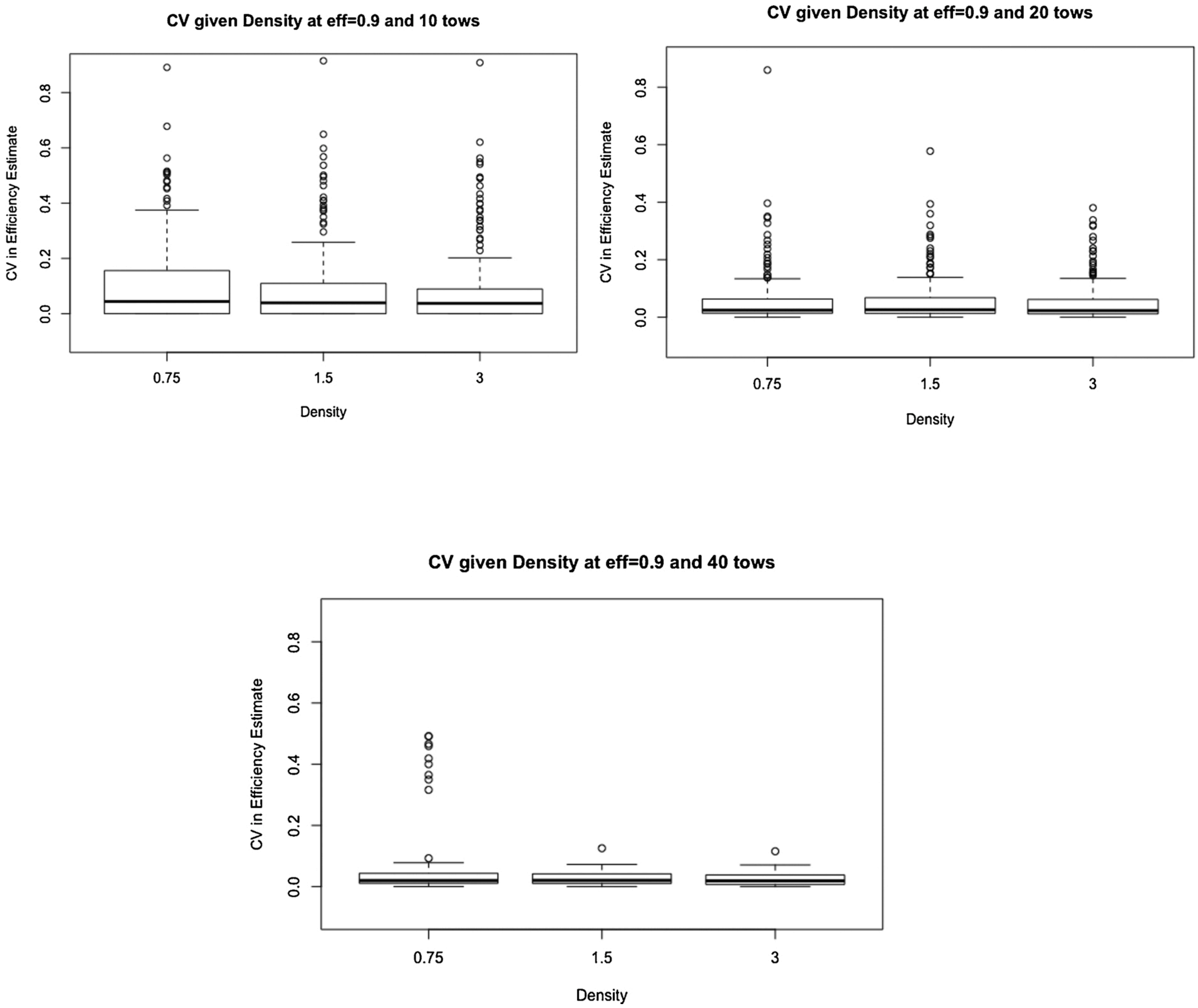

Fig. 9. Boxplots for the coefficient of variance (CV) in efficiency estimates as a function of clam density for 1798 simulations with inherent efficiencies of 0.9. The bottom and top borders of the box represent the first and third quartile. The whiskers represent the 10th and 90th percentiles. Extreme outliers have been deleted for clarity.

limited for infauna on the continental shelf, however, with the depletion experiment being a method of choice. Thus, attention to reducing uncertainty in depletion experiments is important.

Given attention to a reasonable dispersion of tows in the depletion rectangle, how many tows are enough for a depletion experiment to produce an accurate efficiency estimate? Certain metrics may inform this decision during the depletion experiment, assuming that data collected are evaluated using the Patch Model continuously during the experiment. Of greatest use may be the trends in CV and EAS to measure the uncertainty of the dredge efficiency estimate and the amount of dredge overlap as the depletion experiment continues. Adjustments in tow number are readily made on the fly and EAS can be modified at least to some degree by controlling tow location relative to the existing hit matrix that can be updated with each succeeding tow. Preliminary simulation work suggests that adapting the experimental protocol during the depletion experiment may substantively reduce uncertainty in the final efficiency estimate.

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CRediT authorship contribution statement

Leanne M. Poussard: Software, Investigation, Formal analysis, Writing - original draft, Visualization. **Eric N. Powell:** Conceptualization, Software, Formal analysis, Validation, Resources, Writing - review & editing, Funding acquisition. **Daniel R. Hennen:** Software, Formal analysis, Resources, Writing - review & editing.

Declaration of Competing Interest

The authors reported no declarations of interest.

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