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Contents lists available at ScienceDirect

### **Fisheries Research**



journal homepage: www.elsevier.com/locate/fishres

## Effects of location errors on estimates of dredge catchability from depletion based methods

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#### ARTICLE INFO

Article history: Received 2 October 2012 Received in revised form 24 July 2013 Accepted 25 July 2013

Keywords: Dredge efficiency Chesapeake Bay Blue crabs Callinectes sapidus Depletion methods Population estimates

#### ABSTRACT

Depletion-based methods are used to estimate the catchability of a research dredge survey for blue crabs (*Callinectes sapidus*) in Chesapeake Bay. The experimental design relies on the ability to repeatedly sample the same area, but experiments have not been conducted to determine the effects of sampling location error on catchability estimates. We conducted a simulation study to evaluate the effects of sampling location of crabs in an area and repeatedly sampled from the area using a range of true values of catchability and four methods to constrain the sampling area: perfect knowledge, buoy deployment, high-accuracy GPS, and consumer-grade GPS. No estimator was best across all scenarios, and in some scenarios no estimator performed particularly well. Error in sampling location error increased. While the Leslie and Rago methods were relatively accurate when location errors were small, the Ricker method performed well when combined with buoys to demarcate the sampling area, and the Rago method performed well with high-accuracy GPS.

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### 1. Introduction

Depletion-based methods are commonly used to estimate catchability (i.e., efficiency) of survey gear, which then allows estimation of absolute density and abundance of organisms in a study area (Leslie and Davis, 1939; DeLury, 1947; Ricker, 1958; Seber, 1982). In traditional depletion experiments the sampling gear is deployed multiple times within the study site, causing the catch per unit effort (CPUE) to decline as a result of decreasing density. Effort and catch are recorded after each sampling event, and the rate of decline in CPUE compared to the amount of removals is used to infer initial abundance or density of the population and catchability. While this approach is particularly appealing because it provides estimates of absolute abundance directly from a survey, it is prone to violations of model assumptions. Most depletion-based methods assume that the population is closed over the timeframe of the depletion experiment, that each animal has an equal probability of capture, and, in some cases, that the location of the sampling gear is known throughout the experiment (Leslie and Davis, 1939;

DeLury, 1947; Rago et al., 2006; Hennen et al., 2012). Small violations of these model assumptions can cause bias in estimates of catchability and abundance (Rago et al., 2006).

Annual blue crab (Callinectes sapidus) abundance in Chesapeake Bay is estimated by adjusting CPUE of the blue crab winter dredge survey for estimated catchability from depletion experiments (Vølstad et al., 2000; Sharov et al., 2003). Winter dredge survey sampling is conducted from December to March when blue crabs are dormant and buried in the sediment (Sharov et al., 2003). For each depletion experiment, a random sampling station is selected in an area of medium to high crab density. Each station establishes a 100 m by 5.5 m (three dredge widths) sampling area, and a vessel tows a 1.8-m-wide Virginia crab dredge over the area at low speed (Vølstad et al., 2000). Three parallel adjacent dredge tows constitute a sample because it is very difficult to repeat a single tow (G. Davis, Maryland Department of Natural Resources, personal communication). Maryland and Virginia use slightly different methods to demarcate the sampling area. In Maryland, the sampling area is marked by four corner buoys, while in Virginia a Global Positioning System (GPS) is used to mark the corners of the sampling area. Both of these methods have some error in the dredging location, but effects of location errors on depletion estimates of catchability are not well understood.

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This study evaluates the performance of three depletion-based catchability estimators under a range of location accuracy, survey design scenarios, and individual variation in catchability scenarios. We conducted a simulation study to approximate catchability experiments for the winter dredge survey of blue crabs in Chesapeake Bay and compared three catchability estimators under a range of scenarios that differed in the true catchability of the gear, the density of crabs in the area, the amount of location error in the sampling, and the amount of inter-individual variation in catchability.

### 2. Methods

### 2.1. Simulation design

Our study simulated the distribution of blue crabs in a sampling area (grid) and repeatedly sampled the grid with different true catchabilities and amounts of location error to generate data sets. Three methods for estimating catchability were applied to the data sets, and estimates were compared to the true values to characterize bias and accuracy. We implemented four location accuracy scenarios: perfect accuracy, the buoy method, the Wide Angle Augmentation System (WAAS)-enabled GPS unit method (*i.e.*, high accuracy GPS), and non-WAAS-enabled GPS unit method (*i.e.*, low accuracy or commercial grade GPS; Witte and Wilson, 2005). We also simulated three levels of crab density (high –  $0.5 \text{ m}^{-2}$ , medium -  $0.1 \text{ m}^{-2}$ , low -  $0.05 \text{ m}^{-2}$ ) and five levels of true catchability (0.1, 0.3, 0.5, 0.7, 0.9). Additionally, we evaluated the effect of inter-individual vulnerability to the dredge by drawing catchability values for each individual from beta distributions. For each dataset, we applied the Leslie, Ricker, and Rago catchability estimators (Leslie and Davis, 1939; Ricker, 1958; Rago et al., 2006). We simulated 500 data sets for each of the scenarios.

In the perfect location accuracy scenario no errors were introduced into the simulated dredge path. In the buoy method scenario the four corners of the sampling area were marked with buoys to visually guide the dredge paths. The first buoy is placed, and the second is placed relative to the first by measuring 5.5 m along the length of the vessel. Consumer grade GPS is then used to measure 100 m perpendicular to the first two buoys, and the third buoy is placed. The final buoy is placed by measuring 5.5 m along the length of the boat, as for the second buoy. The buoy method, used by the Maryland Department of Natural Resources (MDNR), should result in accurate placement for the width of the sampling area with GPS error potentially occurring for the length of the sampling area.

The low and high accuracy GPS scenarios use GPS waypoints to mark the corners of the sampling area. Non-WAAS enabled and WAAS-enabled GPS units were assumed to have a standard deviation (SD) of 7.1 and 0.54 m for the low and high accuracy scenarios respectively, based on a study of the perpendicular error in GPS locations when conducting a transect (Witte and Wilson, 2005). The low accuracy GPS scenario simulates the current dredge survey method used in Virginia and the high accuracy GPS scenario simulates what might be possible with a survey grade GPS system. Because these methods use GPS units with less than perfect accuracy and no visual signs to keep dredges within the sampling area boundaries there is potential error in both the length and width of the sampling area as well as the dredge location relative to the target sampling area.

### 2.2. Simulation model

The simulated sampling area was populated by randomly placing crabs in a grid. Grid cells were 0.18 m<sup>2</sup>, based on the carapace width of an adult male crab, and only one crab could occupy each



**Fig. 1.** Example for applying location error in the dredge survey simulation. The initial *x* and *y* coordinates of a tow were randomly drawn depending on the scenario, and the length of the tow was random with a mean of 100 m. Length and width of the dredge tracks are not to scale.

cell. Crabs were placed throughout the grid by randomly selecting grid cells without replacement until the desired number of crabs was placed in the grid, resulting in a random distribution of crabs throughout the grid. The number of crabs placed in each grid was determined by the three crab density levels. The size of the grid over which crabs were distributed was substantially larger than the target sampling area to allow for location error to result in sampling outside of the target area.

#### 2.3. Sampling model

Three potential location errors (starting *x*, starting *y*, ending *y*) were possible for each tow (Fig. 1). We assumed that relatively little error is derived from the side-to-side and diagonal movement of dredge tows. Therefore, all dredge tows followed straight paths, were parallel to one another, and were parallel to the boundaries of the intended sampling area. Three parallel adjacent tows constitute a sample to mimic the approach conducted in Chesapeake Bay for blue crabs (Vølstad et al., 2000).

We included four scenarios of location accuracy for dredge sampling. In the perfect accuracy scenario there was no error in dredge location (Table 1; Fig. 2). For the buoy method, tows were constrained within the sampling area boundaries. Because error could only be toward the inside of the sampling area, half normal distributions were used for the starting *x* location on the two outer tows of a three-tow sample (*i.e.*, all errors were positive for one side, while all errors were negative on the other). A normal distribution was used for the starting *x* location of the middle tow and for the starting and ending *y* locations. We used an SD of 0.75 m for all location errors in the buoy method. This SD was assumed to represent the accuracy of the dredge location because the buoys could be used to judge the location of the vessel relative to the sampling area, and, therefore, dredge tracks should be relatively accurate. We did not include a larger SD for the length of the sampling area because

#### Table 1

Equations describing location error scenarios. Symbols  $\hat{x}_i$  and  $\hat{y}_{1,i}$  represent the starting x and y coordinates of dredge tow *i*, and  $\hat{y}_{2,i}$  represents the ending y coordinate of the dredge tow (Fig. 1). Symbols without hats indicate the desired starting and ending locations with no errors. The  $\varepsilon$  symbols represent location errors and were all drawn from normal distributions with means of zero and standard deviations ( $\sigma$ ) determined by the scenario. Symbols  $\tilde{x}$  and  $\tilde{y}$  represent the observed locations that are necessary inputs for the Rago method.

Method	X	<i>y</i> <sub>1</sub>	<i>y</i> <sub>2</sub>	Distributions
Perfect	$\hat{x}_i = x_i$	$\hat{y}_{1,i} = y_1$	$\hat{y}_{2,i} = y_2$	
Buoy	$\hat{x}_i = \begin{cases} x_1 +  \varepsilon_{x,i}  \\ x_2 + \varepsilon_{x,i} \\ x_3 -  \varepsilon_{x,i}  \end{cases}$	$\hat{y}_{1,i} = y_1 + \varepsilon_{y_1,i}$	$\hat{y}_{2,i} = y_2 + \varepsilon_{y_2,i}$	$\varepsilon_{x,i}, \varepsilon_{y_1,i}, \varepsilon_{y_2,i} \sim N(0, \sigma = 0.75)$
High accuracy GPS	$\hat{x}_i = x_i + \varepsilon_{x,i}$	$\hat{y}_{1,i} = y_1 + \varepsilon_{y_1,i}$	$\hat{y}_{2,i} = y_2 + \varepsilon_{y_2,i}$	$\varepsilon_{x,i}, \varepsilon_{y_1,i}, \varepsilon_{y_2,i} \sim N(0, \sigma = 0.54)$
Low accuracy GPS	$\hat{x}_i = x_i + \varepsilon_{x,i}$	$\hat{y}_{1,i} = y_1 + \varepsilon_{y_1,i}$	$\hat{y}_{2,i} = y_2 + \varepsilon_{y_2,i}$	$\varepsilon_{x,i}, \varepsilon_{y_1,i}, \varepsilon_{y_2,i} \sim N(0, \sigma = 7.1)$
Rago method errors	$\tilde{X}_i = \hat{X}_i + \varepsilon_{x,i}$	$\tilde{y}_{1,i} = \hat{y}_1 + \varepsilon_{y_1,i}$	$\tilde{y}_{2,i} = \hat{y}_2 + \varepsilon_{y_2,i}$	$\varepsilon_{x,i}, \varepsilon_{y_1,i}, \varepsilon_{y_2,i}$ distributed according to the scenario.

preliminary simulations indicated that catchability estimates were much less sensitive to error in the length of the sampling area (ylocations) than the x locations. For the high and low accuracy GPS scenarios, we used normal distributions for the starting x, starting y, and ending y locations. We used SDs of 0.54 m and 7.1 m for the WAAS-enabled GPS unit and the non-WAAS-enabled GPS unit scenarios, respectively (Witte and Wilson, 2005). The location errors altered each of the demarcated dredge tow areas from their intended path (Fig. 1), based on the SD of the location accuracy. We simulated the catch of each dredge tow by randomly sampling crabs within the tow with a probability of capture equal to the catchability of the scenario for the constant catchability experiments and equal to the individual catchability for the individual variability experiments. Individual catchability for each crab was drawn from a beta distribution with means equal to the levels of the constant catchability scenarios and an SD of 0.1 (Fig. 3). When a crab was encountered, a uniform (0, 1) random number was drawn. If that number was less than the catchability for the crab, the crab



Fig. 2. Examples of dredge paths under each of the levels of accuracy: (a) no error – perfect, (b) buoy method, (c) waypoint method with WAAS-enabled GPS, and (d) waypoint method with consumer-grade GPS. The gray shading indicates the number of times an area was sampled.

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**Fig. 3.** Probability density (f(q)) of individual catchability for the variable catchability scenarios. Each of the scenarios followed a beta distribution with a standard deviation of 0.1. Numbers on the plot indicate means of the beta distributions.

was considered captured and removed from the grid. An experiment ended when no crabs were caught in a three-tow sample or when six three-tow samples had been conducted. Only experiments that resulted in at least two positive samples were used in subsequent analyses.

#### 2.4. Estimation models

We applied three estimation models to each data set. The Leslie method estimates catchability based on a linear regression of catch in each three-tow sample against the cumulative catch that occurred prior to the sample (Leslie and Davis, 1939; Seber, 1982):

### $y_i = qP_0 - qK_{i-1}$

where  $y_i$  is the catch at tow *i*,  $K_{i-1}$  is the cumulative catch to tow *i*-1, *q* is the catchability coefficient, and  $P_0$  is the initial population size (Vølstad et al., 2000).

The Ricker method estimates catchability based on a regression of the natural logarithm of catch from each three-tow sample against the cumulative effort prior to that sample (Ricker, 1958; Seber, 1982). Because zero catches are common in the blue crab dredge experiments, a constant must be added so that the logarithm of catch is defined for zero catches. We added one to each of the catches to replicate the method currently used in the blue crab winter dredge survey,

$$\ln(y_i + 1) = [\ln(1 - q)](i - 1) + [\ln(q) + \ln(P_0)]$$

To account for transformation bias, a correction was included to estimate the catchability for a single experiment,

$$\hat{q} = 1 - \exp\left(\hat{\beta} + \frac{s_{\hat{\beta}}^2}{2}\right)$$

where  $\hat{\beta}$  was the estimated slope in the Ricker method with a variance of  $s_{\hat{\beta}}^2$  (Vølstad et al., 2000).

The Rago model differs from the previous two approaches in that it uses the catch on an individual tow and a measure of how much effort had previously occurred in the area swept by the tow (Rago et al., 2006; Hennen et al., 2012). This method is more complex than the previous two methods in that it requires an estimate of the location of each dredge tow to estimate catchability based on the number of times that location has been previously dredged. The area swept by the dredge for each tow is adjusted to account for overlap with previous tows,

$$a_i^* = qa_i \sum_{j=1}^i f_{i,j} (1 - q\gamma)^{j-1}$$

where  $a_i^*$  is the effective area swept,  $a_i$  is the area swept of tow *i*, and *f* is the fraction of cells dredged *j* times before the *i*th tow. We applied the modification from Hennen et al. (2012) so that the  $\gamma$  parameter was assumed equal to one. The expected catch on tow *i* is calculated as the product of the effective area swept and initial density  $(D_0)$ ,  $y_i = a_i^* D_0$ . The parameters of the model were then estimated by minimizing the negative log likelihood (*LL*) assuming a negative binomial distribution for the catches,

$$-LL = k \sum_{i} \ln\left(1 + \frac{a_i^* D_0}{k}\right) + \sum_{i} y_i \ln\left(\frac{a_i^* D_0}{a_i^* D_0 + k}\right)$$

where k is the dispersion parameter of the negative binomial distribution. Because the Rago method requires information on the track of each tow, we included an additional location error in the x and y directions to represent that the recorded location of a tow differs from its actual location. To simulate this additional location error for a tow, we applied an independent error from the same distribution as the location error (Table 1).

We compared the estimated catchability to the true value to assess accuracy and bias of each estimation method under each scenario. We calculated the median relative error for each scenario to assess the bias of each method:

$$RE = \frac{\hat{q} - q}{a}$$

where *RE* is relative error,  $\hat{q}$  is estimated catchability, and *q* is the true catchability for the scenario. We also calculated the root mean square relative error (RMSRE) to assess accuracy:

$$\text{RMSRE} = \sqrt{\frac{\sum_{N}^{i=1} RE^2}{N}},$$

where *N* is the number of simulations per scenario.

### 3. Results

The location error scenarios resulted in substantially different patterns of locations swept during an experiment (Fig. 2). The perfect accuracy method always used exactly the same dredge paths. Location errors toward the middle of the sampling area were much more likely under the buoy method. Sampled areas often fell outside the sampling area under GPS waypoint approaches, with the non-WAAS-enabled GPS scenario having relatively little overlap among individual dredge tows compared to the other scenarios.

No catchability estimator was best across all scenarios, and in some scenarios no estimator performed particularly well. Location error had a larger effect on the bias of catchability estimators, as indicated by their median relative error, than density or variation in catchability (Figs. 4 and 5). While density did not have a strong effect on the median relative errors, it did affect the range of catchability estimates; estimates in the lowest density scenarios usually had the widest range of estimates for a given level of catchability. Variation in individual catchability had a small effect on the bias and precision of catchability estimates compared to the constant catchability scenario (Fig. 5).

In the perfect location scenario with constant catchability, the Leslie and Rago estimators were relatively unbiased, whereas the Ricker method was negatively biased by 5-17%

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**Fig. 4.** Relative error and root mean square relative error (RMSRE) of estimated catchability versus true catchability for three estimation methods (Leslie, Ricker, and Rago) under three density scenarios and four scenarios of location error: perfect (a–c), buoy method (d–f), global positioning system (GPS) waypoint with high accuracy (g–i), and GPS waypoint with low accuracy (j–l). Density is indicated by the color of the box, with white as low density (0.05 crabs m<sup>-2</sup>), dark gray as medium density (0.1 crabs m<sup>-2</sup>), and light gray as high density (0.2 crabs m<sup>-2</sup>). Solid lines indicate the median, the boxes the interquartile range, and the whiskers the 5th and 95th percentiles. RMSRE is indicated on each plot with circles.

(Figs. 4a-c and 5a-c). The difference between the constant catchability and variable catchability scenarios was most evident in the perfect location scenario with the Leslie and Rago estimators having a slightly positive bias across all levels of catchability. For the buoy method scenarios, the bias in the Leslie estimator depended on catchability with positive bias for low catchability scenarios and negative bias for high ones (Figs. 4d and 5d). The Ricker estimator was negatively biased across all levels of catchability, and

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Fig. 5. Relative error and root mean square relative error (RMSRE) of estimated catchability for the scenarios with individual variability in catchability. Panel, color, symbol, and box plot definitions are the same as Fig. 4.

the Rago estimator was approximately unbiased for the lowest level of catchability, but became negatively biased as catchability increased (Figs. 4e, f and 5e, f). In the high accuracy GPS scenario, the Leslie and Ricker estimators had a negative bias between 1 and 40% (Figs. 4g, h and 5g, h). Alternatively, the bias of the Rago estimator changed from positive 40–50% to negative 9–13% as catchability increased (Figs. 4i and 5i). For the non-WAAS-enabled GPS scenario, the Leslie and Ricker estimators had a negative bias between 49 and 98% (Figs. 4j, k and 5g, k). Similar to the GPS scenario with high accuracy, the bias of the Rago estimator changed from positive to negative with increasing catchability (Figs. 4l and 5l). All estimators usually produced more precise estimates as density increased.

The accuracy of the estimators depended on the scenario and estimator, but most estimators had the lowest RMSRE for the high

catchability and high density scenarios (Figs. 4 and 5). For the perfect location scenario, RMSRE decreased with increasing true catchability for all estimators, and was always lowest for the high density scenario. In the buoy scenario, the Leslie and Rago methods performed similarly, but the Ricker estimator had somewhat higher RMSREs at moderate and high levels of catchability. The Rago estimator had lower RMSREs at moderate to high levels of catchability than the Leslie or Ricker estimators for the GPS scenarios with both high and low accuracy (Fig. 4g–i).

### 4. Discussion

Our simulation results indicate that moderate to high levels of error in sampling location generally caused negative bias in catchability estimates from dredge depletion studies. However, the magnitude and sign of the bias primarily depended on the amount and type of location error and the true catchability. Estimators were often positively biased when the true catchability was low and negatively biased when true catchability was high. The higher the degree of location error, the more biased the estimates usually were. This in turn would cause a positive bias in estimates of abundance or density derived from dredge survey data.

The Leslie and Rago estimators had the general property of bias becoming increasingly negative as true catchability increased. Both of these estimators rely on using an approximation of the expected value of a catch on a given tow, which likely causes the observed pattern of bias. The approximation is most appropriate for lower levels of catchability (Gould and Pollock, 1997). While the Ricker method also relies on an approximation for expected catch, its poor performance was likely caused by the constant added to the true catch values to allow for zero catches in the analysis. In additional simulations (not shown), the Ricker method produced biased estimates regardless of the constant applied, unless there were no observed zeros. For any given true catchability, there was an associated constant that would produce an unbiased estimator, but one must know the true catchability in advance. While the addition of constants to allow for a log transformation is widely used, it can produce biased results (Ortiz et al., 2000; Maunder and Punt, 2004). This is a particular problem for the winter dredge survey because the survey attempts to sample until zero catches are observed. Thus, methods that allow for zero catches without transformation should be used when zero catches are frequently observed in the data. Additionally, all of the methods were originally developed for situations in which the population was not completely removed. For example, Ricker (1975) notes that the population should be depleted by at least 30% to obtain quality estimates. Application of a maximum likelihood approach, similar to that in Gould and Pollock (1997), could improve estimates from depletion studies.

Location errors should result in a negative bias in catchability for the Leslie and Ricker methods (Rago et al., 2006). For instance, the Leslie estimator relies on a regression of catch in a tow against cumulative catch up to that tow, and the slope of the regression provides the estimate of catchability. If the depletion experiment is deployed perfectly, catch per tow should decrease as the density of organisms in the sampling area decreases and cumulative catch increases. However, if location errors occur, some portion of the sampling area will be missed during early samples. Eventually these areas that were previously missed will be sampled, resulting in high catches late in the experiment, which exerts substantial leverage on the slope of the regression. The regression slope will be attenuated under these conditions, causing an underestimate of catchability on average.

Dredge survey methods that used pre-deployed buoys to constrain the dredge paths resulted in estimates of catchability that were slightly less biased than methods which relied on high accuracy GPS guidance and much less biased than methods which relied on consumer-grade GPS. Accuracy of catchability estimates increased as the true capture efficiency of the dredge increased in all cases, and the bias of the catchability estimates also tended to be lower as simulated crab density increased, which agrees with previous studies (Seber, 1982; Gould and Pollock, 1997; Gould et al., 1997). In addition to selecting the most unbiased method for estimating catchability, our results highlight the importance of deploying the dredge with high precision to produce accurate estimates of catchability and abundance. Choosing areas of high abundance to conduct catchability experiments also improves performance of the estimators, as long as dredge catchability is the same in areas of high and low crab density.

The Rago et al. (2006) method produced biased estimates of catchability in many scenarios of location error, but the bias changed from positive to negative as the true catchability increased. Hennen et al. (2012) found a three-way interaction between relative error of the catchability estimate and true catchability, error scenario, and dredge path. However, Hennen et al. (2012) concluded that the Rago method produced relatively unbiased estimates of catchability. The disagreement between Hennen et al.'s and our conclusions was probably caused by differences in the aggregation of results. If we aggregate the results of the Rago method over catchability levels, the estimates are approximately unbiased because the negative bias at high catchability balances out the positive bias at low catchability.

The true accuracy of the catchability estimators may have been overestimated in our study because we did not include displacement between the dredge and the vessel, which could cause additional errors in the start and stop locations of the dredge tows. However, this displacement would likely have a minimal effect on our results because it would only affect the error surrounding start and stop locations of each tow. Additionally, preliminary simulations indicated that errors in the length of a dredge tow had a minimal effect on estimated catchability relative to the error introduced when a dredge tow deviates from the intended path. We also assumed that once a dredge pass began the vessel traveled in a straight line and did not wander laterally. Therefore, any lateral error in dredge location would be constant for that tow. Characteristics of the bottom habitat may also affect catchability, causing differences in mean catchability among sites (Vølstad et al., 2000).

The use of buoys to guide the dredge tows, coupled with the Leslie or Rago method (Leslie and Davis, 1939; Rago et al., 2006), or high-accuracy GPS with the Rago method appear to be practical ways to implement catchability experiments for blue crabs in the Chesapeake Bay. Using buoys with the Leslie or Rago method should only require a small correction for the negative bias of the catchability estimate to produce accurate population or density estimates, provided our assumptions about the location accuracy of the buoy method is correct. Under most scenarios with buoys or highaccuracy GPS the Rago method and Leslie method produced similar results in terms of bias and accuracy. The buoy method has the disadvantage that if a buoy is accidentally caught during the experiment, the experiment must be conducted again in a new location. This situation is particularly problematic in deeper waters, in which the location of the buoy may differ from that of its anchor because of currents. However, the Rago method requires that the track of each dredge tow is known and recorded. The winter dredge survey has not recorded the track locations with enough precision (e.g., starting and ending locations of dredge tows were only recorded with precision of  $\pm 10 \text{ m}$ ) to apply the Rago method to historical data. If high-accuracy GPS units were used in future efforts to monitor the dredge tracks, the Rago method would likely have a small negative, correctable bias. For example, the results from our study

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could be used to correct catchability estimates assuming that our location accuracy assumptions are correct. While this approach for correcting bias should be tested before it is applied, it should produce more accurate estimates of catchability. The only high-accuracy GPS scenario where the Rago method performed poorly was at very low catchability (*i.e.*, 0.1). In most cases all methods performed poorly with the low-accuracy GPS, and this combination is not generally recommended.

### Acknowledgments

We thank Tom Miller, Glenn Davis, and Alexei Sharov for suggestions that improved this study. André Punt provided helpful comments on a previous draft of the manuscript. This research was partially supported by NOAA Chesapeake Bay Office, Maryland Department of Natural Resources, Commonwealth of Virginia through funds to Virginia Institute of Marine Science, and the Virginia Marine Resources Commission. This is contribution number 4780 of the University of Maryland Center for Environmental Science.

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