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Estimation of the capture efficiency and abundance of Atlantic sea scallops (*Placopecten magellanicus*) from paired photographic–dredge tows using hierarchical models

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Abstract: The efficiency of survey gear is an important measure that can be used to estimate the absolute scale of populations in assessment models. We develop a general hierarchical model for estimating the efficiency of a New Bedford-style sea scallop (*Placopecten magellanicus*) survey dredge from paired dredge and Habcam camera system tows. Habcam data for each tow consist of multiple images that give information on within-tow variability of scallop density. The model accounts for these multiple observations as well as the possibility of differences between the true densities in dredge and Habcam pairs due to the pairs not covering exactly the same ground. We fit several models with alternative assumptions to observations on Atlantic sea scallops and compare the relative performance using Akaike's information criterion. The best performing model estimated higher dredge efficiency on fine substrates than on coarse ones (approximately 0.40 and 0.27, respectively). Our results inform the scale of annual abundance estimates from dredge surveys and reduce uncertainty in the sea scallop stock assessments.

Résumé : L'efficacité des engins de relevé est une importante mesure pouvant être utilisée pour estimer l'ampleur absolue de populations dans des modèles d'évaluation. Nous élaborons un modèle hiérarchique pour estimer l'efficacité d'une drague de relevé de type New Bedford pour le pétoncle géant (*Placopecten magellanicus*) à partir de traits de la drague et d'un système de caméra Habcam jumelés. Les données du système Habcam pour chaque trait consistent en de multiples images qui fournissent de l'information sur la variabilité de la densité de pétoncles au sein d'un même trait. Le modèle tient compte de ces multiples observations ainsi que de l'éventualité de différences entre les densités réelles obtenues des paires de drague et Habcam du fait que les zones couvertes ne sont pas exactement les mêmes. Nous avons calé plusieurs modèles reposant sur différentes hypothèses sur des observations relatives aux pétoncles géants de l'Atlantique et comparé leur performance relative à l'aide du critère d'information d'Akaike. Le modèle qui donne les meilleurs résultats estime une efficacité de la drague plus grande sur des substrats fins que sur des substrats grossiers (d'environ 0,40 et 0,27, respectivement). Nos résultats fournissent de l'information sur la magnitude des abondances annuelles estimées tirées de relevés à la drague et réduisent l'incertitude dans les évaluations des stocks de pétoncles géants. [Traduit par la Rédaction]

Introduction

Absolute scale of fish stock abundance is determined in stock assessment models by estimating catchability of relative abundance indices (Megrey 1989; Arreguín-Sánchez 1996). Most stock assessments estimate absolute abundance from annual catch data and an assumed natural mortality rate, but one or more of these sources of information can be highly uncertain, leading to similarly uncertain estimates of absolute scale (Maunder and Piner 2015). An alternative approach is to estimates components of the catchability scalar. The two components of catchability are the efficiency of the survey gear for the species of interest and the proportion of the population available to the survey sampling frame. Estimates of these components immediately translate into absolute abundance and biomass estimates that do not require knowledge of either catch or natural mortality. This is one reason there has been substantial research towards estimation of gear efficiency, including those focused on efficiency (Somerton et al. 2013), availability (Kotwicki et al. 2009), fish behavior (Godø et al. 1999; Bryan et al. 2014), and gear mensuration (Weinberg and Kotwicki 2008). We define efficiency here as the fraction of available fish (which in our case are those in the path of the dredge) retained by the gear, equivalent to availability-selection described by Millar and Fryer (1999).

Efficiency is often studied using paired gear experiments where two gear are fished either concurrently at the same location (such as with a trouser trawl or covered net) or as close together in space and time as possible. The reference gear is often similar to the gear for which efficiency estimation is of interest (Munro and Somerton 2001), but comparisons have also been made using towed camera sleds (Uzmann et al. 1977), remotely operated vehicles (Adams et al. 1995), and manned submersibles (Krieger 1993). When neither gear can be assumed to be fully efficient, the efficiency of one gear relative to the other is estimated (e.g., Fryer et al. 2003; Miller 2013; Kotwicki et al. 2017). However, some studies involve a reference gear that is assumed to be fully efficient, such as direct observation from photographs.

The efficiency of dredge gear has long been of particular interest. Estimation of efficiency has been obtained from depletion studies (e.g., NEFSC 1999; Gedamke et al. 2004, 2005; Rago et al.

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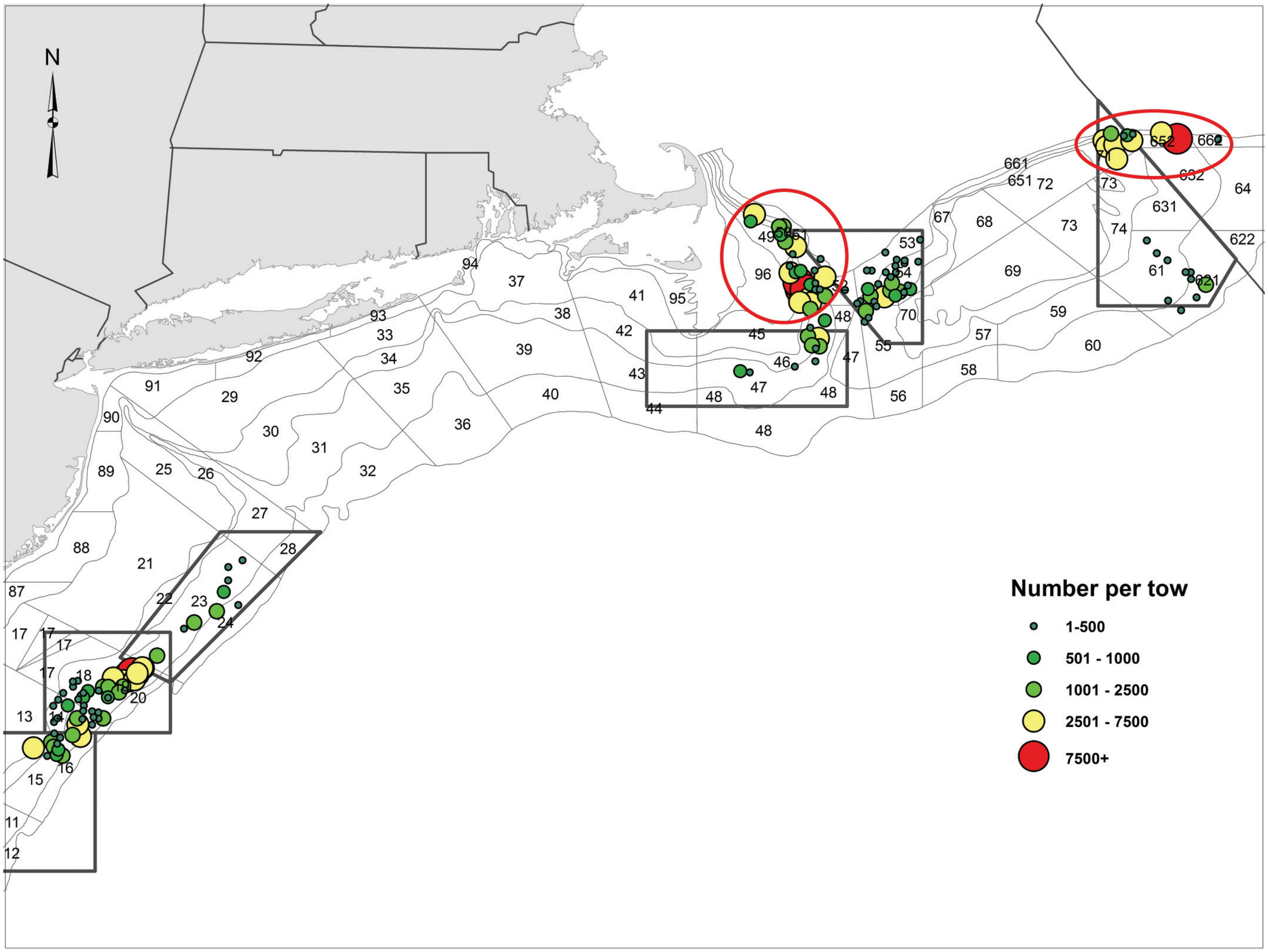
Fig. 1. Locations of 137 stations with dredge and Habcam observations in 2008 and 2009 together with the labelled shellfish survey strata. The red ellipses enclose stations in the coarse sediment strata, and the grey polygons are areas that are either closed long-term to scallop fishing or ones that are rotationally fished (Hart 2003).



2006), from comparisons between dredge catches and densities obtained from photographs or divers (e.g., Dickie 1955; Caddy 1971; Giguère and Brulotte 1994; Beukers-Stewart et al. 2001), or from recaptures of tagged animals (e.g., Dickie 1955; Dare et al. 1993). Paired tow experiments between lined survey dredges and unlined New Bedford-style dredges have indicated that the lined dredges have reduced efficiency on larger scallops compared with unlined gear (Serchuk and Smolowitz 1980; NEFSC 2004; Yochum and Dupaul 2008).

The purpose of this paper is to estimate the efficiency of a lined New Bedford-style survey dredge for Atlantic sea scallops (*Placopecten magellanicus*), based on paired dredge–Habcam underwater camera tows. Surveys for the Atlantic sea scallop using this lined dredge have been conducted off the coast of the United States since 1979 (Serchuk and Wigley 1986; Hart and Rago 2006). In typical paired tows studies, the pairs consist of a single catch observation from each gear type. In our case, each Habcam tow can be hundreds or thousands of individual images that give information on within-tow variability of scallop density, which would not be available from the catch of conventional fishing gear. We develop a general hierarchical model that can employ this additional information, compare relative performance of a set of specific models, assess the statistical behavior of the estimators for the best performing model, and apply dredge efficiency estimates to make annual absolute abundance estimates for Atlantic sea scallops.

Methods

Study areas

A total of 137 paired dredge–Habcam tows were collected in the summer of 2008 and 2009 off the coast of the northeast US in the Mid-Atlantic Bight (MA) and Georges Bank (GB); we include in the latter region the Great South Channel and Nantucket Shoals (Fig. 1). Station depths averaged about 66 m and ranged from 38 to 113 m. We divided the survey strata where the paired sampling occurred into those areas with mostly fine substrate habitats (sand, silt, mud) and those with primarily coarser substrate habitats (gravel, cobble, rocks, boulders). Fine substrate habitats are predominant in all of the MA strata (13, 14, 15, 18, 19, 23, and 24) and some of the GB strata (46, 47, 53, 54, 55, 61, 67, and 621), whereas coarse substrate habitats are common only on portions of GB (strata 49, 50, 51, 52, 71, 651, 652, 661, and 662). There were a total of 99 stations in fine substrate strata (of which 50 stations were in the MA) and 38 in coarse substrate strata.

Dredge sampling

Dredge samples were collected on the R/V *Hugh R. Sharp* using a 2.44 m wide New Bedford-style scallop dredge with 5.1 cm rings

Fig. 2. On the left is a high-density scallop survey dredge catch, and on the right is an example photo from the paired Habcam tow. These observations are from a station in the Elephant Trunk area off of Deleware Bay in the Mid-Atlantic Bight (the middle polygon of the Mid-Atlantic region in Fig. 1).

and a 3.8 cm mesh liner as part of the annual Northeast Fisheries Science Center (NEFSC) scallop survey (Fig. 2, left panel), which uses a random stratified design (Serchuk and Wigley 1986; Hart and Rago 2006). Tows targeted 15 min on the bottom at a speed of 7.04 km·h^{-1}. Dredge sensors indicate that the dredge typically started fishing a little before the nominal start of the tow. However, dredge sensor data were not available for all the dredge tows utilized in this study. A regression was developed to estimate the actual distance the dredge was fishing Z_i at station i from the nominal tow distance Z_{ni} (time between when the winch was locked and when haulback began times mean vessel speed) and water depth Y_i based on 110 tows where dredge sensor data were available (R^2 = 0.68, both predictors significant with $p < 0.001$; NEFSC 2014):

$$(1)\qquad Z_i = -0.0388 + 1.061Z_{ni} + 0.001484Y_i$$

This relationship was used to estimate tow distance for all dredge catches in our study. Dredge swept area, A_{Di}, was thus estimated by multiplying the dredge width (2.44 m) by the tow distance Z_i.

Habcam sampling

A towed camera system, "Habcam v2", was deployed near the paths of the dredge stations; in many cases, multiple Habcam tracks were made parallel to the dredge tow. This system is an underwater vehicle containing an Uniq Vision digital still camera, four machine vision strobes, an Imagenex 881a side-scan sonar, and other instruments that are controlled from the vessel via a fiber-optic cable (Howland et al. 2006). The system was towed between 9 and 11 km·h^{-1} from the F/V *Kathy Marie*, with the camera taking about 6 photos·s^{-1} (Fig. 2, right panel). The dredge tracks were visible on the side-scan sonar and was used to assure that the Habcam tow path was close to, but not exactly on, the dredge track. About 1 out of 10 of the photos that were collected were manually annotated, where all observed live scallops were noted and measured. The distance between annotated photographs was roughly 5 m. Altitude, pitch, roll, and yaw sensors aboard were used to calculate the field of view (FOV) of each image so that scallop density (number of scallops/FOV) could be estimated for each photograph and tow. The median number of annotated images per station was 380 and ranged from 60 to 4024 (interquartile range = 270).

Observation models and parameter estimation

At stations $i = 1, \ldots, n$, we observe the number of scallops captured by the dredge N_{Di} and the number in each of $j = 1, \ldots, n_i$ Habcam images N_{Hij} (all mathematical notation is defined in Table 1). All scallops in the photographs are assumed to be detected by the annotators, and the area A_{Hij} of the sea floor in the field of view in each image is known. We assume the number of scallops observed in each Habcam image j is Poisson-distributed with mean

$$(2)\qquad E(N_{Hij} \mid \delta_{Hij}, A_{Hij}) = \delta_{Hij}A_{Hij}$$

given the density in the Habcam image δ_{Hij}. We consider two different models for the densities in Habcam images at a given station. The first simply assumes that the densities within a station are equal for all Habcam images: $\delta_{Hij} = \delta_{Hi}$. The second assumes that the Habcam densities are gamma-distributed

$$(3)\qquad \delta_{Hij} \mid \delta_{Hi} \sim \mathrm{G}(\delta_{Hi}, s_{Hi})$$

with station-specific mean δ_{Hi} and shape parameter s_{Hi}. In the former model, the counts in the Habcam images, $N_{Hij} \mid \delta_{Hi}$, are still conditionally Poisson-distributed, whereas they are negative binomial-distributed in the latter model with mean

$$E(N_{Hij} \mid \delta_{Hi}) = \delta_{Hi}A_{Hij}$$

and variance

$$V(N_{Hij} \mid \delta_{Hi}) = E(N_{Hij} \mid \delta_{Hi})\left[1 + \frac{E(N_{Hij} \mid \delta_{Hi})}{s_{Hi}}\right]$$

For models where Habcam densities are assumed to be gamma-distributed within a station, two approaches are considered: the shape parameter is assumed constant across stations $s_{Hi} = s_H$, or the station-specific shape parameters themselves are gamma-distributed

$$s_{Hi} \mid s_H \sim \mathrm{G}(s_H, s_{s_H})$$

Table 1. Definition of terms.

δ_i	Mean density of scallops at station i
δ_{Di}	Mean density of scallops in the area sampled by the dredge at station i
δ_{Hi}	Mean density of scallops in area sampled by the Habcam at station i
δ_{Hij}	Density of scallops in the area of Habcam observation j at station i
θ	Generic parameter
$\rho_{\delta i}$	Correlation parameter for the bivariate gamma distribution of mean Habcam and dredge densities at station i
$\bar{a}_h$	Mean swept area of dredge tow in stratum h
A_h	Area of stratum h
A_{Di}	Area sampled by the dredge at station i
A_{Hij}	Area in Habcam observations j at station i
$\bar{C}_h$	Mean catch per dredge tow of scallops in stratum h
H_0	No substrate effects
H_1	Two-level (fine and coarse) substrate covariate defined by stratum attribute
H_2	Three-level (Mid-Atlantic fine, Georges Bank fine, Georges Bank coarse) substrate covariate, which includes region with H_1
n	No. of stations with dredge and Habcam observations
n_i	No. of Habcam observations at station i
N_h	Abundance of scallops in stratum h
N_{Di}	No. of scallops captured by the dredge at station i
N_{Hij}	No. of scallops in Habcam observations j at station i
q_h	Efficiency of the dredge in stratum h
q_i	Efficiency of the dredge at station i
$s_{\delta i}$	Shape parameter for gamma distribution describing variation in either δ_{Hi} or δ_{Di} at station i
s_H	Mean shape parameter for gamma distributions describing variation in δ_{Hij} at each station
s_{Hi}	Shape parameter for gamma distribution describing variation in δ_{Hij} at station i
s_{s_H}	Shape parameter for gamma distributions describing variation in s_{Hi} across stations
$\boldsymbol{X}_{\theta i}$	Covariate vector for station i defined by assumed substrate effect (H_0 to H_2) on parameter θ
Y_i	Depth at station i
Z_i	Actual dredge tow distance at station i
Z_{ni}	Nominal dredge tow distance at station i
RD_i	Relative differences of a parameter estimate $\hat{\theta}_i$ and the true parameter value θ
$\mathrm{RB}(\hat{\theta})$	Relative bias of a parameter estimator $\hat{\theta}$

with mean s_H and shape parameter s_{s_H}. The former corresponds to an assumption that the coefficient of variation (CV) of the densities observed in images at each station is constant across stations, and the latter allows the CV to differ among stations. For stations where s_{Hi} is large relative to $E(N_{Hij}\,|\,\delta_{Hi})$, the distribution of Habcam image observations is closer to Poisson.

Conditional on the density of scallops available to the dredge at a given station δ_{Di}, we assume the number of scallops captured by the dredge is Poisson-distributed with mean

$$E(N_{Di}\,|\,\delta_{Di}, A_{Di}) = q_i\delta_{Di}A_{Di} \tag{4}$$

where A_{Di} and q_i are the (known) dredge swept area at station i and the efficiency of the dredge at station i (cf. Paloheimo and Dickie 1964; Millar 1992; Lewy et al. 2004).

The dredge efficiency q_i, densities δ_{Di}, and the mean densities δ_{Hi} for Habcam observations at a given station are not all estimable as fixed effects. Estimation of dredge efficiency requires some assumption regarding the relationship of dredge and Habcam densities both within and across stations. We assume a bivariate gamma distribution described by Moran (1969) for the dredge and mean Habcam densities (δ_{Di} and δ_{Hi}) available to the observations at each station (see Appendix A). The distribution is a function of the means and shape parameters for the marginal gamma distributions and a correlation parameter ($-1 \le \rho_{\delta i} \le 1$) that defines the relationship of dredge and Habcam densities within a station. The densities at a given station are independent when $\rho_{\delta i} = 0$ and equal when $\rho_{\delta i} = 1$. We assume the means ($E(\delta_{Di}) = E(\delta_{Hi}) = \delta_i$) and shape parameters ($s_{\delta i}$) of the dredge and Habcam densities at each station are equal. When densities for Habcam observations within stations are gamma-distributed (eq. 3), the numbers in the Habcam images conditional on δ_{Hi} are negative binomial, which provides some computational efficiency in parameter estimation. Similarly, the dredge counts are marginally negative binomial-distributed because of the conditional Poisson assumption with the gamma-distributed densities. In all models, the correlation of Habcam and dredge observations is defined by $\rho_{\delta i}$.

Table 2. Substrate effect assumptions for dredge efficiency (q_i), mean station density (δ_i), and bivariate gamma shape and correlation parameters ($s_{\delta i}$, $\rho_{\delta i}$, respectively), and distributional assumptions for station-specific Habcam densities (δ_{Hij}) and variation of Habcam densities (s_{Hi}) in each of the models fitted to dredge and Habcam observations.

Model	q_i effects	δ_i effects	$s_{\delta i}$ and $\rho_{\delta i}$ effects	δ_{Hij}	s_{Hi}	n_p	ΔAIC
M_1	H_0	H_0	H_0	δ_{Hi}	—	4	9739.8
M_2	H_0	H_0	H_0	$G(\delta_{Hi}, s_{Hi})$	s_H	5	1380.6
M_3	H_0	H_0	H_0	$G(\delta_{Hi}, s_{Hi})$	$G(s_H, s_{s_H})$	6	129.7
M_4	H_1	H_0	H_0	$G(\delta_{Hi}, s_{Hi})$	$G(s_H, s_{s_H})$	7	131.4
M_5	H_0	H_1	H_0	$G(\delta_{Hi}, s_{Hi})$	$G(s_H, s_{s_H})$	7	53.3
M_6	H_0	H_0	H_1	$G(\delta_{Hi}, s_{Hi})$	$G(s_H, s_{s_H})$	8	39.2
M_7	H_0	H_1	H_1	$G(\delta_{Hi}, s_{Hi})$	$G(s_H, s_{s_H})$	9	13.4
M_8	H_1	H_1	H_1	$G(\delta_{Hi}, s_{Hi})$	$G(s_H, s_{s_H})$	10	9.1
M_9	H_1	H_1	H_2	$G(\delta_{Hi}, s_{Hi})$	$G(s_H, s_{s_H})$	12	12.8
M_{10}	H_1	H_2	H_1	$G(\delta_{Hi}, s_{Hi})$	$G(s_H, s_{s_H})$	11	0.0
M_{11}	H_2	H_1	H_1	$G(\delta_{Hi}, s_{Hi})$	$G(s_H, s_{s_H})$	11	8.3
M_{12}	H_2	H_2	H_1	$G(\delta_{Hi}, s_{Hi})$	$G(s_H, s_{s_H})$	12	0.8

Note: $G(a,b)$ denotes a gamma distribution with mean a and shape parameter b. The number of fixed effects estimated by maximum marginal likelihood is n_p.

Scallop density and dredge efficiency may vary with benthic habitat (Thouzeau et al. 1991). We evaluated whether dredge efficiency, mean density, and variation of densities between stations differed between the coarse and fine substrates (H_1, a factor with two levels) and whether it also depended on region of the fine substrate (H_2, a factor with three levels: Georges Bank coarse (GB,C), Georges Bank fine (GB,F), and Mid-Atlantic fine (MA,F)). Models with these assumptions were compared with a simpler model with no effects of substrate (H_0). We also conducted preliminary analyses with proportion of fine or coarse habitat at each station based on observations from that station in the Habcam images, but this continuous covariate performed poorly compared with the categorical covariates.

The suite of models (Table 2) were compared using Akaike's information criterion (AIC). First we fit models with increasing complexity. The first three models assumed no substrate effects on any parameters (H_0). Model M_1 assumed no variation in the densities observed in Habcam images at each station, M_2 allowed these densities to be gamma-distributed, and M_3 further allowed the scale parameter of the gamma distribution also to be gamma-distributed among stations. Given the comparisons of AIC for these three models, further models built on M_3 and included differences between fine and coarse substrates (H_1) for efficiency (M_4), mean density (M_5), and variability in densities (M_6). We also used AIC to evaluate subsequent inclusion of H_1 effects in each of these efficiency and density components of the model (M_7–M_8). Finally, models M_9–M_{12} allowed further complexity by also including differences between fine substrates in the MA and GB regions

(H_2). Note that the observations with levels C and GB,C are the same because there are no strata defined as coarse substrates in the MA region.

The actual parameters estimated for efficiencies, densities, and shape parameters were on log scale, and those for the correlation of dredge and Habcam densities at a given station were on a logit scale bounded at –1 and 1. The models were fit by maximizing a Laplace approximation of the marginal likelihood of the dredge and Habcam observations using the Template Model Builder package in R (Kristensen et al. 2016; R Core Team 2015). Standard errors of back-transformed parameters are constructed by application of the delta method to covariances of the actual parameter estimates from the inverted Hessian matrix. The AIC we used for comparing model performance is based on this maximized marginal log-likelihood and the number of fixed effects parameters.

We used the dredge efficiency estimates from the best performing model to convert dredge catches in the NEFSC dredge surveys from 1979 to 2017 and derive annual estimates of absolute abundance for sea scallops. Some of the sampling in the most recent years was done by the Virginia Institute of Marine Science using identical gear and protocols as the NEFSC survey (Rudders 2015). The estimated absolute abundance N_h in stratum h is

$$\hat{N}_h = \frac{\bar{C}_h A_h}{\bar{a}_h \hat{q}_h} \quad (5)$$

where A_h is the area, $\bar{C}_h$ is the mean catch, $\bar{a}_h$ is the mean dredge swept area, and $\hat{q}_h$ is the estimated efficiency in stratum h based on any estimated effects of habitat in the stratum. The estimated total absolute abundance over the surveyed area is simply the sum of the abundance estimates in each stratum. For consistency, only regularly surveyed strata in the MA and US GB were included in the abundance estimates. These estimates exclude, in particular, a large number of scallops that have been observed since 2013 in the southern portion of the Nantucket Lightship Closed Area outside the regular strata set.

Simulation study

We also performed a simulation study to evaluate the accuracy of parameter estimation from the model with the lowest AIC value. Assuming the parameter estimates from this model as the true values, we simulated 1000 data sets and fit the same model to each data set. Relative bias of parameter θ was evaluated using the estimator

$$\widehat{\mathrm{RB}}(\hat{\theta}) = \frac{\hat{\theta}}{\theta} - 1 = \frac{1}{m}\sum_{t=1}^{m}\frac{\hat{\theta}_t}{\theta} - 1$$

where $\hat{\theta} = \sum_{t=1}^{m}\hat{\theta}_t/m$ and $\hat{\theta}_t$ is the estimate from simulated data set t. We also report the standard error of the relative bias estimate

$$\mathrm{SE}[\widehat{\mathrm{RB}}(\hat{\theta})] = \frac{1}{\sqrt{m}\theta}\sqrt{\frac{\sum_{t=1}^{m}(\hat{\theta}_t - \hat{\theta})^2}{m-1}}$$

based on m successful fits.

Results

The swept areas for dredge tows are generally much greater (mean = 5094 m²) than the combined areas of all the annotated Habcam photos at each station (mean = 313 m²; Table 3). Variation of dredge swept area relative to the mean (CV = 0.07) was much less than that for Habcam observations (CV = 1.17). Dredge tow swept areas were slightly greater in coarse strata on GB than the fine substrate strata, but the swept areas were more consistent (lower CV) in the fine substrate areas. Mean areas of all Habcam observations at a given station ranked similarly by substrate type to the dredge swept areas, but there was substantial variability in the areas observed by the Habcam.

Table 3. Mean and coefficient of variation of swept areas at each station for dredge and Habcam observations in all areas combined and by region and substrate category.

	Dredge		Habcam	
	Mean	CV	Mean	CV
All	5094	0.07	313	1.17
GB,C	5239	0.10	359	0.95
GB,F	5129	0.06	303	0.71
MA,F	4949	0.04	288	1.69

Note: GB,C: Georges Bank coarse substrates; GB,F: Georges Bank fine substrates; MA,F: Mid-Atlantic fine substrates.

Allowing variation in densities among Habcam observations and variation in the CV of the densities among stations (M_3) performed better than simpler models (M_1 and M_2) based on AIC (Table 4). Models that included effects of H_1 (just differences between coarse and fine substrates) on dredge efficiency, mean densities at each station density, and variation of mean densities across stations all provided better performance than simpler models without these effects on one or more of these components (M_8 versus M_3–M_7). Further differentiating between fine substrates in GB and MA regions was only important for mean densities at a given station (M_{10}).

Based on the best performing model M_{10}, the estimated dredge efficiency was greater in fine substrates (0.4) than in coarse substrates (0.27). Estimated mean density was greatest in GB coarse substrates (>2 m^{-2}), but mean density in GB fine substrates (~0.3 m^{-2}) was less than that in MA fine substrates (~0.7 m^{-2}). The precision of the estimated densities and dredge efficiencies was lower in coarse sediments due to fewer observations there (density: CV ~ 0.21 for GB coarse versus CV ~ 0.15 for MA and GB fine substrates; efficiency: CV ~ 0.15 for coarse versus CV ~ 0.05 for fine). Correlation estimates for mean densities at each station for the two gears were higher in fine substrates (0.95) than in coarse substrates (0.76; Fig. 3).

Of the 1000 attempted fits of model M_{10} to simulated data sets, 22 failed to provide estimates. The relative bias for estimates from the 978 successful fits was negligible (<2%) for all parameters except the shape parameters s_δ in both substrate types (6% and 3% in coarse and fine substrates, respectively) and shape parameters for Habcam densities within stations: s_H (2%) and s_{s_H} (11%; Table 5).

Using the habitat-specific estimates of dredge efficiency in the stratified absolute abundance estimates of sea scallops (eq. 5), the sea scallop population has increased from less than 2 billion in 1979–1981 to more than 10 billion (Fig. 4). The increase in total population size is due to similar increases in both the MA and GB populations. Dredge and stock assessment model estimates of biomass were generally similar from 1979 to 2004 (for details of the assessment model, see Hart et al. 2013 and NEFSC 2018). The dredge estimates (as well as optical surveys) were consistently greater than the model estimates during 2005–2012, likely due to underestimation of mortality in the stock assessment model. In the last 3 years, the model estimates (and those from optical surveys) have been considerably above those from the dredge, which may be due to reduced dredge efficiency in areas of extraordinary densities (up to hundreds per square metre).

Table 4. Parameter estimates for the best performing model (M_{10}) with standard errors in parentheses.

q_i	δ_i	$s_{\delta i}$	$\rho_{\delta i}$	s_H	s_{s_H}
0.27 (0.04) (C)	2.08 (0.44) (GB,C)	0.61 (0.11) (C)	0.76 (0.07) (C)	3.57 (0.62)	0.93 (0.18)
0.40 (0.02) (F)	0.33 (0.05) (GB,F)	0.75 (0.09) (F)	0.95 (0.01) (F)		
	0.70 (0.11) (MA,F)				

Note: Parameters denoted with (C) and (F) are specific to observations from coarse and fine substrates, respectively, and GB and MA denote Georges Bank and Mid-Atlantic, respectively.

Fig. 3. Estimated station densities for dredge and Habcam observations in Mid-Atlantic fine substrates (circles), Georges Bank fine substrates (triangles), and Georges Bank coarse substrates (+ symbols) from model M_{10} in Table 2.

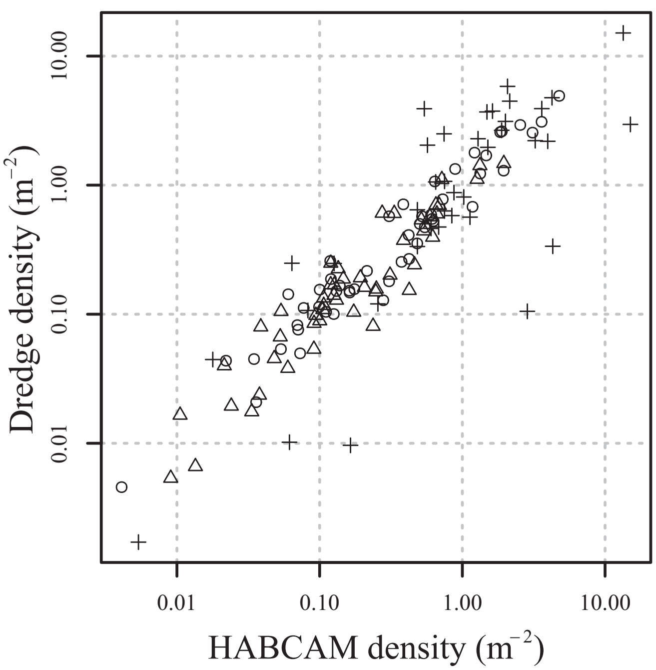


Table 5. Relative bias of parameter estimates and standard error of the relative bias from estimates provided by 978 simulated data sets with parameters specified from the best performing model M_{10} in Table 2.

Parameter	Value	Relative bias	SE
q_i (C)	0.27	0.0190	0.0055
q_i (F)	0.40	0.0005	0.0013
δ_i (GB,C)	2.08	−0.0144	0.0066
δ_i (GB,F)	0.33	0.0034	0.0051
δ_i (MA,F)	0.70	0.0074	0.0051
$s_{\delta i}$ (C)	0.61	0.0569	0.0060
$s_{\delta i}$ (F)	0.75	0.0322	0.0040
$\rho_{\delta i}$ (C)	0.76	−0.0109	0.0031
$\rho_{\delta i}$ (F)	0.95	0.0015	0.0004
s_H	3.57	−0.0187	0.0052
s_{s_H}	0.93	0.1064	0.0052

Discussion

The estimates of dredge efficiency from our study allow direct estimation of annual absolute abundance from the NEFSC sea scallop dredge survey. Estimation of absolute abundance from surveys is rare because it typically requires a strong assumption about gear efficiency, but it is made possible here by the nature of the Habcam observations and the relatively sedentary nature of the population. More caution is warranted when using gear efficiency estimates to infer absolute abundance for more mobile marine populations, such as most commercially important fish stocks, because the availability of the population to the gear may be less than complete.

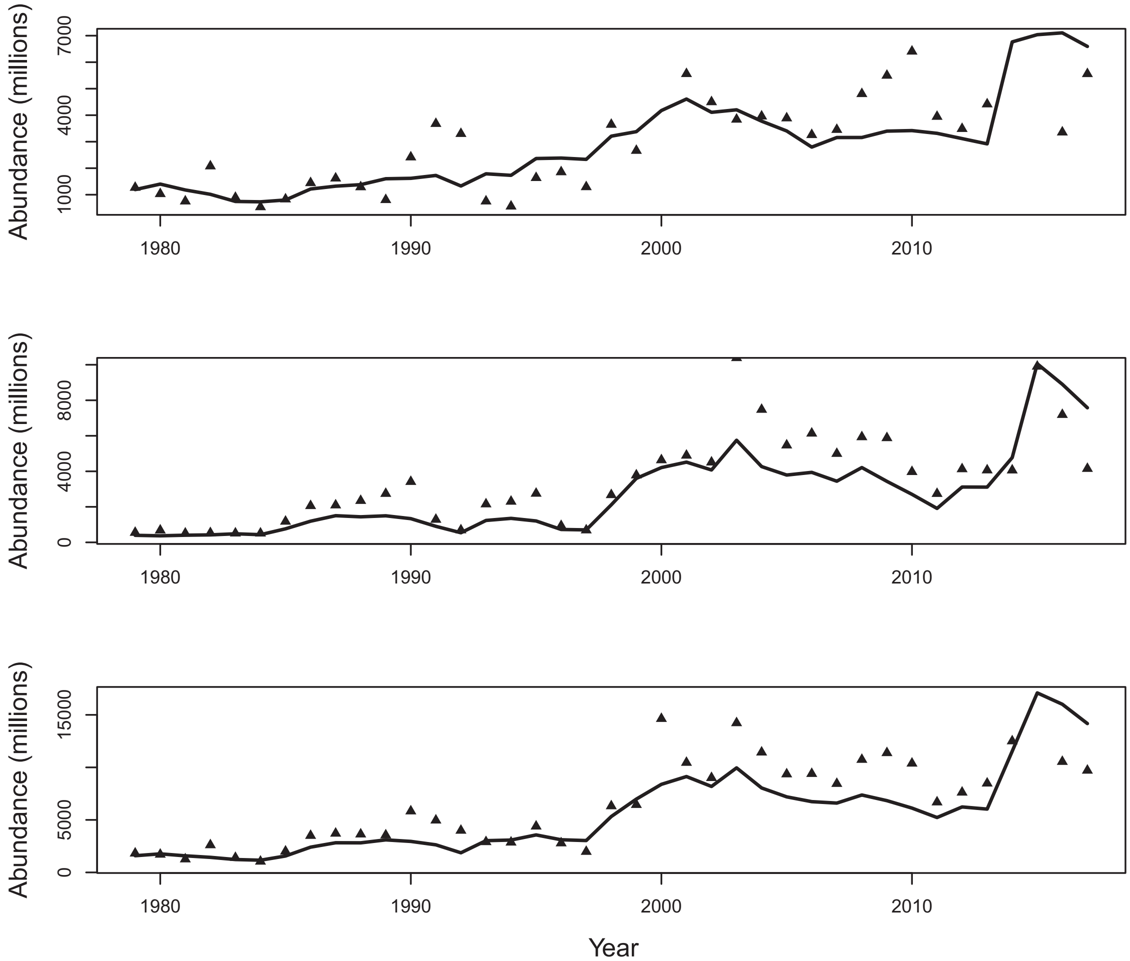
When availability to the gear is not an issue, and an estimate of efficiency and an annual index of abundance are available, there are two general ways to include this information in a stock assessment model with other data sources to estimate a larger set of attributes of the assessed population. The first approach would be to use the annual absolute abundance estimates as calculated here and defining the catchability to equal one. The alternative approach would be to use the unscaled indices and define the catchability to be equal to the efficiency estimated from the paired gear study. In either case, however, it is necessary to propagate the uncertainty of the dredge efficiency estimates into the stock assessment model. The US sea scallop size-based stock assessment model uses the latter approach and takes into account the uncertainty by using a Bayesian prior (or likelihood penalty) for survey efficiency, based on this study (NEFSC 2014). Whichever of the two approaches to incorporating efficiency information in a stock assessment model provides the best statistical performance should be explored further.

Since 2013, extraordinarily high densities of sea scallops have been observed (10–300 m^{-1}) in certain portions of the Elephant Trunk area in the MA and the Nantucket Lightship Closed Area. Preliminary comparisons of dredge and optical survey data in these high density areas suggest that the dredges may operate at reduced efficiencies at these densities, possibly due to the dredge filling up before the end of the tow. In such cases, the efficiency estimates presented here may be overestimates in areas of very high densities. However, the model could be further generalized to allow effects of the unknown but estimated density at each station on the dredge efficiency, and we could compare the statistical performance with that of the simpler models we considered in this paper.

Estimates from our and other recent studies have indicated that efficiency of New Bedford-style scallop dredges is greater than was earlier thought (Caddy 1971). The dredges used in Caddy (1971) were towed at a slower speed than in normal survey or commercial operations, likely leading to reduced efficiency (Gedamke et al. 2004). Our efficiency estimates for *P. magellanicus* by New Bedford-style dredges are considerably higher than those estimated for Digby dredges (Dickie 1955; Giguère and Brulotte 1994). This is consistent with Bourne (1966), who, in comparative gear experiments, found the New Bedford-style dredge to be more than twice as efficient as the Digby dredges. They are also at the upper end of efficiency estimates of dredges fishing for the scallops *Pecten* spp. (Mason et al. 1979; McLoughlin et al. 1991; Dare et al. 1993; Beukers-Stewart et al. 2001; Fifas et al. 2004). *Pecten* spp. are more recessed in the sediment than *Placopecten*, and thus it is not surprising that the catchability of *Pecten* is lower.

Our efficiency estimates of the lined survey dredge can be used to infer the efficiency of commercial scallop gear by combining it with paired tow experiments between the survey and commercial scallop dredges. Analysis of 104 paired tows between the survey dredge and a commercial New Bedford-style dredge with 89 mm rings indicated that the survey dredge was about 62.2% as efficient as the commercial dredge (NEFSC 2004). Dividing our estimates of

Fig. 4. Estimates of US sea scallop abundance in the Mid-Atlantic (top), Georges Bank (middle), and total (bottom) from the NEFSC scallop dredge survey expanded by efficiency estimates (triangles) and from the latest assessment of sea scallops (line) (NEFSC 2018).



efficiency of the survey dredge by 0.622 indicates that this type of commercial dredge has efficiencies of about 0.39 and 0.64 on coarse and fine sediments, respectively. This can be compared with independent estimates of efficiency of the 89 mm commercial dredge from depletion studies: 0.41 (NEFSC 1999), 0.427 (range: 0.355–0.525; Gedamke et al. 2004), and 0.54 (range: 0.41–0.54; Gedamke et al. 2005). These estimates are all intermediate between our estimates in coarse and fine sediments and were conducted in the southeastern portion of GB that has predominately sand substrate with small patches of gravel, cobble, and boulders, as well as large sand waves, which may reduce efficiency. Thus, our estimates are consistent with those from these other studies.

Currently, the US sea scallop fishery uses dredges with 102 mm rings. Paired tows between the survey dredge and 102 mm ring dredges indicates that the survey dredge is about 56% as efficient as this commercial gear (Yochum and Dupaul 2008). Thus, the efficiency of commercial gear with 102 mm rings is about 0.43 on coarse sediments and 0.71 on fine sediments.

Commercial dredge efficiency has important implications for estimating the levels of incidental fishing mortality of scallops (i.e., noncapture mortality induced by the fishing process). For example, Caddy (1973) observed that at least 11% of the scallops remaining in the dredge path suffered incidental fishing mortality. Because he estimated dredge efficiency at about 15% (Caddy 1971), he concluded that roughly the same numbers of scallops were killed by incidental fishing mortality as were captured. However, the higher commercial dredge efficiencies estimated here and in other more recent studies imply that incidental fishing mortality rates are much less than the direct mortality due to capture (Hart 2003).

Dredge sensors indicate that the dredge angle during fishing tends to be fairly stable in fine sediments, but is more variable in coarse sediments, likely due to the harder and more irregular bottom. This may at least partially explain why gear efficiency is higher in fine substrates; similar results have been reported in several other studies (e.g., Dickie 1955; Dare et al. 1993; Giguère and Brulotte 1994; Currie and Parry 1999).

Simulations suggest that the best performing model (M_{10}) gave slightly biased estimates of the shape parameters defining variability in mean densities among stations ($s_{\delta i}$), densities of Habcam observations within stations (s_H), and shape parameters among stations defining variability Habcam observations within stations (s_{s_H}). Maximum likelihood estimation of variance parameters can be non-negligibly biased when they are not greatly informed by the data. Since these shape parameters in part define the variance of the dredge and Habcam observations, restricted maximum likelihood may provide less biased estimation of these parameters if desired.

Cadigan and Bataineh (2012) used a model similar to ours to simulate data and evaluate performance of alternative estimators of relative catch efficiency, except that they assume that the gamma-distributed components of the expected value for the observations are the catch efficiencies rather than the densities available to each gear at a given station. They also assume that these gamma-distributed efficiencies for each gear are independent and there is a single observation for each gear. They found poor performance of the estimator for the relative catch efficiency when their estimation model matched the simulation model. The difference between their findings and ours is likely due to the correlation of our densities (rather than being independent) on which the dredge and Habcam observations are based, the multiple observations available for the Habcam at each station, and the larger number of total stations (137 rather than 50).

Estimating variation in densities for both Habcam and dredge observations and in dredge efficiencies among stations simultaneously is infeasible in typical paired gear experiments, as was previously discussed. However, some insight on the relative importance of the between-station variability in densities and efficiencies can be gained from the correlations we estimated for the bivariate gamma random effects. Consider the random station-specific density for dredge observations to instead represent random station-specific efficiencies. Under this assumption, the other station-specific density for Habcam observations is the density for both dredge and Habcam observations. In this case, we would expect the correlation of these station-specific random effects estimated in our model to be zero because the variation in dredge efficiency between stations should be unrelated to the variation in density between stations. However, the models we fit estimate the correlation of these random effects to be quite high (0.76 in coarse substrates or 0.95 in fine substrates). In reality, of course, these paired random effects incorporate both sources of variation, but the high correlations suggest that between-station variation in densities is a larger factor than between-station variation in efficiencies.

Correlation of the densities observed by the Habcam and dredge is determined by several factors, including the distance between the dredge tow and the Habcam observations and the degree of uniformity of the distribution of scallops. It is plausible that scallops are more aggregated in coarse substrates, which would explain the lower observed correlation in these habitats. It is also possible that the lower correlation in coarse substrates may be related, at least in part, to increased variability of efficiency.

Although we were unable to use a continuous measure of substrate type (i.e., the proportion of coarse or fine substrate) to inform dredge efficiency in preliminary analyses, we think further explorations would be useful. Many of the station-specific values of the covariate occurred at the bounds of zero and one, and a log-linear model of this covariate is a poor assumption for effects on efficiency or densities. An alternative measurement of this rugosity that avoids these bounds might perform better. However, nonlinear effects are still likely to be important to consider. An effective continuous measure of substrate type could also explain variation in efficiency between stations and separate it from variation in densities.

Similarly, there may still be a degree of spatial correlation among densities of the Habcam observations even though we used a subsample of the Habcam images at each station. We assumed that the Habcam observations at a station were independent at a station conditional on the station-specific mean Habcam density (δ_{Hi}), but we expect the estimated mean densities and dredge efficiencies to be robust to this assumption. A more general model that accounts for the distances between Habcam images and some approximation of the distance between the dredge and Habcam observations might improve estimation of the variation among the station-specific observations.

There is a some similarity between Habcam observations and those collected visually using submersibles, video camera sleds, and divers (e.g., Richards 1986; Lauth et al. 2004; Hart et al. 2008). If measures of substrate area can be made and individuals are recorded for these alternative visual observations, then the same general method as we used here could be used to estimate efficiency of other sampling gears when the observations are collected together.

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References

Adams, P.B., Butler, J.L., Baxter, C.H., Laidig, T.E., Dahlin, K.A., and Wakefield, W.W. 1995. Population estimates of Pacific coast groundfishes from video transects and swept-area trawls. Fish. Bull. **93**(3): 446–455.

Arreguín-Sánchez, F. 1996. Catchability: a key parameter for fish stock assessment. Rev. Fish Biol. Fish. **6**: 221–242. doi:10.1007/BF00182344.

Beukers-Stewart, B.D., Jenkins, S.R., and Brand, A.R. 2001. The efficiency and selectivity of spring-toothed scallop dredges: a comparison of direct and indirect methods of assessment. J. Shellfish Res. **20**(1): 121–126.

Bourne, N. 1966. Relative fishing efficiency and selection of three types of scallop drags. ICNAF Res. Bull. **3**: 12–25.

Bryan, D.R., Bosley, K.L., Hicks, A.C., and Haltuch, M.A. 2014. Quantitative video analysis of flatfish herding behavior and impact on effective area swept of a survey trawl. Fish. Res. **154**(1): 120–126. doi:10.1016/j.fishres.2014.02.007.

Caddy, J.F. 1971. Efficiency and selectivity of the Canadian offshore scallop dredge. ICES CM-1971/K:25.

Caddy, J.F. 1973. Underwater observations on tracks of dredges and trawls and some effects of dredging on a scallop ground. J. Fish. Res. Board Can. **30**(2): 173–180. doi:10.1139/f73-032.

Cadigan, N.G., and Bataineh, O.M. 2012. Inference about the ratio of means from negative binomial paired count data. Environ. Ecol. Stat. **19**(2): 269–293. doi:10.1007/s10651-011-0186-8.

Currie, D.R., and Parry, G.D. 1999. Impacts and efficiency of scallop dredging on different soft substrates. Can. J. Fish. Aquat. Sci. **56**(4): 539–550. doi:10.1139/f98-194.

Dare, P.J., Key, D., and Connor, P.M. 1993. The efficiency of spring-loaded dredges used in the western English Channel fishery for scallops, *Pecten maximus* (L.). ICES CM 1993/B:15 (REF. K).

Dickie, L.M. 1955. Fluctuations in abundance of the giant scallop, *Placopecten magellanicus* (Gmelin), in the Digby Area of the Bay of Fundy. J. Fish. Res. Board Can. **12**(6): 797–857. doi:10.1139/f55-045.

Fifas, S., Vigneau, J., and Lart, W. 2004. Some aspects of modelling scallop (*Pecten maximus*, L.) dredge efficiency and special reference to dredges with depressor plate (English Channel, France). J. Shellfish Res. **23**(2): 611–621.

Fryer, R.J., Zuur, A.F., and Graham, N. 2003. Using mixed models to combine smooth size-selection and catch-comparison curves over hauls. Can. J. Fish. Aquat. Sci. **60**(4): 448–459. doi:10.1139/f03-029.

Gedamke, T., DuPaul, W.D., and Hoenig, J.M. 2004. A spatially explicit open-ocean Delury analysis to estimate gear efficiency in the dredge fishery for sea scallop *Placopecten magellanicus*. N. Am. J. Fish. Manage. **24**(2): 335–351. doi:10.1577/M02-120.1.

Gedamke, T., DuPaul, W.D., and Hoenig, J.M. 2005. Index-removal estimates of dredge efficiency for sea scallops on Georges Bank. N. Am. J. Fish. Manage. **25**(3): 1122–1129. doi:10.1577/M04-111.1.

Giguère, M., and Brulotte, S. 1994. Comparison of sampling techniques, video and dredge, in estimating sea scallop (*Placopecten magellanicus*, Gmelin) populations. J. Shellfish Res. **13**(1): 25–30.

Godø, O.D., Walsh, S.J., and Engås, A. 1999. Investigating density-dependent catchability in bottom-trawl surveys. ICES J. Mar. Sci. **56**(3): 292–298. doi:10.1006/jmsc.1999.0444.

Hart, A.M., Fabris, F.P., Brown, J., and Murphy, D. 2008. Digital video surveys of abalone (*Haliotis* sp.) stocks by commercial fishers in Western Australia. Fish. Res. **93**(3): 305–314. doi:10.1016/j.fishres.2008.06.002.

Hart, D.R. 2003. Yield- and biomass-per-recruit analysis for rotational fisheries, with an application to the Atlantic sea scallop (*Placopecten magellanicus*). Fish. Bull. **101**(1): 44–57.

Hart, D.R., and Rago, P.J. 2006. Long-term dynamics of U.S. Atlantic sea scallop *Placopecten magellanicus* populations. N. Am. J. Fish. Manage. **26**(2): 490–501. doi:10.1577/M04-116.1.

Hart, D.R., Jacobson, L.D., and Tang, J. 2013. To split or not to split: assessment of Georges Bank sea scallops in the presence of marine protected areas. Fish. Res. **144**: 74–83. doi:10.1016/j.fishres.2012.11.004.

Howland, J., Gallager, S., Singh, H., Girard, A., Abrams, L., Griner, C., Taylor, R., and Vine, N. 2006. Development of a towed survey system for deployment by the fishing industry. *In* IEEE Oceans Conference Proceedings, Boston, September 18–21.

Kotwicki, S., De Robertis, A., von Szalay, P., and Towler, R. 2009. The effect of light intensity on the availability of walleye pollock (*Theragra chalcogramma*)

to bottom trawl and acoustic surveys. Can. J. Fish. Aquat. Sci. **66**(6): 983–994. doi:10.1139/F09-055.
Kotwicki, S., Lauth, R.R., Williams, K., and Goodman, S.E. 2017. Selectivity ratio: a useful tool for comparing size selectivity of multiple survey gears. Fish. Res. **191**: 76–86. doi:10.1016/j.fishres.2017.02.012.
Krieger, K.J. 1993. Distribution and abundance of rockfish determined from a submersible and by bottom trawling. Fish. Bull. **91**(1): 87–96.
Kristensen, K., Nielsen, A., Berg, C.W., Skaug, H., and Bell, B.M. 2016. TMB: Automatic differentiation and Laplace approximation. J. Stat. Softw. **70**(5): 1–21. doi:10.18637/jss.v070.i05.
Lauth, R.R., Ianelli, J., and Wakefield, W.W. 2004. Estimating the size selectivity and catching efficiency of a survey bottom trawl for thornyheads, *Sebastolobus* spp. using a towed video camera sled. Fish. Res. **70**(1): 27–37. doi:10.1016/j.fishres.2004.06.010.
Lewy, P., Nielsen, J.R., and Hovgård, H. 2004. Survey gear calibration independent of spatial fish distribution. Can. J. Fish. Aquat. Sci. **61**(4): 636–647. doi:10.1139/f04-034.
Mason, J., Chapman, C.J., and Kinnear, J.A.M. 1979. Population abundance and dredge efficiency studies on scallop, *Pecten maximus* (L.). Rapp. Proc.-Verb. Reun. Cons. Int. Explor. Mer, **175**: 91–96.
Maunder, M.N., and Piner, K.R. 2015. Contemporary fisheries stock assessment: many issues still remain. ICES J. Mar. Sci. **72**(1): 7–18. doi:10.1093/icesjms/fsu015.
McLoughlin, R.J., Young, P.C., Martin, R.B., and Parslow, J. 1991. The Australian scallop dredge: estimates of catching efficiency and associated indirect fishing mortality. Fish. Res. **11**(1): 1–24. doi:10.1016/0165-7836(91)90030-J.
Megrey, B.A. 1989. Review and comparison of age-structured stock assessment models from theoretical and applied points of view. *In* Mathematical analysis of fish stock dynamics. *Edited by* E.F. Edwards and B.A. Megrey. Am. Fish. Soc. Symp. 6. pp. 8–48.
Millar, R.B. 1992. Estimating the size-selectivity of fishing gear by conditioning on the total catch. J. Am. Stat. Assoc. **87**(420): 962–968. doi:10.1080/01621459.1992.10476250.
Millar, R.B., and Fryer, R.J. 1999. Estimating the size-selection curves of towed gears, traps, nets and hooks. Rev. Fish Biol. Fish. **9**(1): 89–116. doi:10.1023/A:1008838220001.
Miller, T.J. 2013. A comparison of hierarchical models for relative catch efficiency based on paired-gear data for US Northwest Atlantic fish stocks. Can. J. Fish. Aquat. Sci. **70**(9): 1306–1316. doi:10.1139/cjfas-2013-0136.
Moran, P.A.P. 1969. Statistical inference with bivariate gamma distributions. Biometrika, **56**(3): 627–634. doi:10.1093/biomet/56.3.627.
Munro, P.T., and Somerton, D.A. 2001. Maximum likelihood and non-parametric methods for estimating trawl footrope selectivity. ICES J. Mar. Sci. **58**(1): 220–229. doi:10.1006/jmsc.2000.1004.
NEFSC. 1999. Report of the 29th northeast regional stock assessment workshop (29th SAW): Stock assessment review committee (SARC) consensus summary of assessments. US Dept. Commer., Northeast Fish. Sci. Cent. Ref. Doc. 99-14.
NEFSC. 2004. 39th Northeast Regional Stock Assessment Workshop (39th SAW) assessment report. US Dept. Commer., Northeast Fish. Sci. Cent. Ref. Doc. 04-10b.
NEFSC. 2014. 59th Northeast Regional Stock Assessment Workshop (59th SAW) assessment report. US Dept. Commer., Northeast Fish. Sci. Cent. Ref. Doc. 14-09.
NEFSC. 2018. 65th Northeast Regional Stock Assessment Workshop (65th SAW) assessment report. US Dept. Commer., Northeast Fish. Sci. Cent. Ref. Doc. 18-11.
Paloheimo, J.E., and Dickie, L.M. 1964. Abundance and fishing success. Rapp. Proc.-Verb. Reun. Cons. Perm. Int. Explor. Mer, **155**: 152–163.
R Core Team. 2015. R: a language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria.
Rago, P.J., Weinberg, J.R., and Weidman, C. 2006. A spatial model to estimate gear efficiency and animal density from depletion experiments. Can. J. Fish. Aquat. Sci. **63**(10): 2377–2388. doi:10.1139/f06-121.
Richards, L.J. 1986. Depth and habitat distributions of three species of rockfish (*Sebastes*) in British Columbia: observations from the submersible PISCES IV. Environ. Biol. Fishes, **17**(1): 13–21. doi:10.1007/BF00000397.
Rudders, D.B. 2015. Virginia Institute of Marine Science dredge survey methods report [online]. Available from http://www.cio.noaa.gov/services_programs/prplans/pdfs/ID310_Draft_Product_2-VIMS%20S_Methods%20Review.pdf.
Serchuk, F.M., and Smolowitz, R.J. 1980. Size selection of sea scallops by an offshore scallop survey dredge. ICES CM 1980/K:24.
Serchuk, F.M., and Wigley, S.E. 1986. Evaluation of U.S.A. and Canadian research vessel surveys for sea scallops (*Placopecten magellanicus*) on Georges Bank. J. Northw. Atl. Fish. Sci. **7**: 1–13.
Somerton, D.A., Weinberg, K.L., and Goodman, S.E. 2013. Catchability of snow crab (*Chionoecetes opilio*) by the eastern Bering Sea bottom trawl survey estimated using a catch comparison experiment. Can. J. Fish. Aquat. Sci. **70**(12): 1699–1708. doi:10.1139/cjfas-2013-0100.
Thouzeau, G., Robert, G., and Smith, S.J. 1991. Spatial variability in distribution and growth of juvenile and adult sea scallops *Placopecten magellanicus* (Gmelin) on eastern Georges Bank (Northwest Atlantic). Mar. Ecol. Prog. Ser. **74**: 205–218. doi:10.3354/meps074205.
Uzmann, J.R., Cooper, R.A., Theroux, R.B., and Wigley, R.L. 1977. Synoptic comparison of three sampling techniques for estimating abundance and distribution of selected megafauna: submersible vs camera sled vs otter trawl. Mar. Fish. Rev. **39**(12): 11–19.
Weinberg, K.L., and Kotwicki, S. 2008. Factors influencing net width and sea floor contact of a survey bottom trawl. Fish. Res. **93**(3): 265–279. doi:10.1016/j.fishres.2008.05.011.
Yochum, N., and Dupaul, W.D. 2008. Size-selectivity of the Northwest Atlantic sea scallop (*Placopecten magellanicus*) drege. J. Shellfish Res. **27**(2): 265–271. doi:10.2983/0730-8000(2008)27[265:SOTNAS]2.0.CO;2.

Appendix A. Bivariate gamma distribution

This is the same formulation described by Moran (1969). Let z_1 and z_2 be bivariate standard normal-distributed with correlation parameter $\rho_{\delta i}$

$$f(z_1, z_2) = \frac{1}{2\pi\left(1 - \rho_{\delta i}^2\right)^{\frac{1}{2}}} \exp\left[-\frac{1}{2\left(1 - \rho_{\delta i}^2\right)}\left(z_1^2 - 2\rho_{\delta i} z_1 z_2 + z_2^2\right)\right]$$

and the marginal distributions $F(\delta_{Di}) = F(z_1)$ and $F(\delta_{Hi}) = F(z_2)$, where

$$F(\delta_{Di}) = \int_0^{\delta_{Di}} \frac{u^{s_{\delta i}-1}\exp\left(-u s_{\delta i}\delta_i^{-1}\right)}{\Gamma(s_{\delta i})\left(\frac{\delta_i}{s_{\delta i}}\right)^{s_{\delta i}}} du$$

and

$$F(\delta_{Hi}) = \int_0^{\delta_{Hi}} \frac{u^{s_{\delta i}-1}\exp\left(-u s_{\delta i}\delta_i^{-1}\right)}{\Gamma(s_{\delta i})\left(\frac{\delta_i}{s_{\delta i}}\right)^{s_{\delta i}}} du$$

Then δ_{Di} and δ_{Hi} have a bivariate gamma distribution with the same marginal mean δ_i and variance $\delta_i^2 s_{\delta i}^{-1}$, but correlation defined by $\rho_{\delta i}$. When $\rho_{\delta i} = 0$, δ_{Di} and δ_{Hi} are independent, and when $\rho_{\delta i} = 1$, δ_{Di} and δ_{Hi} are equal.

Reference

Moran, P.A.P. 1969. Statistical inference with bivariate gamma distributions. Biometrika, **56**(3): 627–634. doi:10.1093/biomet/56.3.627.