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ARTICLE

Catchability of snow crab (*Chionoecetes opilio*) by the eastern Bering Sea bottom trawl survey estimated using a catch comparison experiment

David A. Somerton, Kenneth L. Weinberg, and Scott E. Goodman

Abstract: Catchability of the eastern Bering Sea (EBS) bottom trawl survey for snow crab (*Chionoecetes opilio*) was estimated from experimental data to provide a constraint on the survey catchability parameters in the stock assessment model. The experiment utilized a second fishing vessel to conduct side-by-side trawling with each of two survey vessels at 92 stations using an experimental trawl assumed to capture all crabs in its path. Trawl efficiency, or the captured proportion of crabs in the trawl path, was estimated for the 83-112 Eastern otter trawl from experimental data using a nonparametric smooth function of carapace width, sediment size, and depth. Survey catchability was then estimated as the catch-weighted average of the predicted trawl efficiency at all 275 survey stations where snow crabs were captured. The fitted model indicated that trawl selectivity was greater in sand than mud and greater in shallow water than deep. At a carapace widths >95 mm, the minimum commercial size limit, the estimated survey catchability of males is considerably less than previously reported.

Résumé : Le potentiel de capture des relevés au chalut de fond du crabe des neiges (*Chionoecetes opilio*) dans la mer de Behring orientale (EBS) a été estimé à partir de données expérimentales pour éclairer la détermination des paramètres relatifs au potentiel de capture des relevés dans le modèle d'évaluation des stocks. Pour ce faire, un deuxième navire de pêche a été utilisé afin d'effectuer deux relevés au chalut côte-à-côte avec deux navires à 92 stations, à l'aide d'un chalut expérimental dont il était présumé qu'il capturerait tous les crabes sur son passage. L'efficacité du chalut, soit la proportion capturée de crabes sur le passage du chalut, a été estimée à partir des données expérimentales pour un chalut à panneau de type 83-112 Eastern, en utilisant une fonction non paramétrique continue de la largeur de la carapace, de la granulométrie des sédiments et de la profondeur. Le potentiel de capture des relevés a ensuite été estimé en calculant la moyenne pondérée en fonction des prises de l'efficacité prévue du chalut aux 275 stations où des crabes des neiges ont été capturés. Le modèle ajusté indique que la sélectivité du chalut était plus grande sur du sable que sur de la boue et en eau peu profonde qu'en eau profonde. Pour des largeurs de carapace >95 mm, soit la limite minimum des prises commerciales, le potentiel de capture des relevés estimé pour les mâles est considérablement plus faible que ce qui avait été signalé par le passé. [Traduit par la Rédaction]

Introduction

Bottom trawl surveys are often conducted to provide fisheries-independent indices of relative abundance that can be utilized in fishery stock assessment models, along with other types of data, to estimate stock abundance. Stock assessment models typically consider these indices as proportionally related to the true population abundance with a functional relationship that is constant with time and generally increasing with body size (Bence et al. 1993). This function, which we refer to here as the survey catchability, has a shape determined by parameters that are typically estimated along with other model parameters when the model is fitted to data (Turnock and Rugolo 2010). In some cases, however, it may be possible to conduct field experiments that allow the direct estimation of survey catchability independent of the model. Because model parameters associated with growth, natural mortality, and survey catchability are inherently correlated (He et al. 2011; Thompson 1994), such externally derived estimates could be used to specify or constrain survey catchability parameters and thereby reduce model indeterminacy caused by parameter correlation. Constraining survey catchability in this manner is especially important in situations where either growth or natural mortality is poorly known or where the survey time series is short or fragmented by changes in gear or survey design (Somerton et al. 1999).

For bottom trawl surveys, catchability is largely determined by trawl efficiency or the proportion of the animals in the swept area (whole water column) that is retained. If a survey trawl were completely efficient, and the spatial distribution of the stock were entirely sampled, then swept area estimates of stock abundance (Alverson and Pereyra 1969) would be absolute estimates, rather than relative indices, and survey catchability would be unity. However, trawl efficiency typically varies with body size and can additionally vary with bottom type (Dawe et al. 2010), current speed (Weinberg et al. 2002), water depth (von Szalay and Somerton 2005; Weinberg and Kotwicki 2008), wave height (Stewart et al. 2010), and perhaps other factors that can vary over the survey area. Thus, while survey catchability pertains to the scale of an entire survey area, trawl efficiency pertains to the scale of an individual trawl tow.

In this study we estimate the survey catchability of the annual eastern Bering Sea (EBS) bottom trawl survey (Stauffer 2004) for

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snow crab (*Chionoecetes opilio*), one of the most valuable commercial species in Alaska. This was accomplished, in part, by conducting a field experiment to estimate the efficiency of the trawl used on this survey, that is, the 83-112 Eastern bottom trawl (Stauffer 2004). Trawl efficiency is usually considered to be a function of the various components of the trawl catching process, including avoidance, vertical and horizontal herding, and footrope and mesh escapement (Dickson 1993*a*), and experiments designed to collect data on trawl efficiency typically focus on these individual processes (Engås and Godø 1989*a*, 1989*b*). Such experimental data are then combined using a mathematical model of the whole trawl catching process (Dickson 1993*b*; Somerton et al. 2007). For snow crab, however, this is simplified because video observations (K. Weinberg, unpublished data) have indicated that they are not herded by the trawl bridles, and therefore the primary determinant of trawl efficiency is escapement under the footrope.

Based on this knowledge, an experiment to estimate the efficiency of the 83-112 Eastern trawl for snow crab was conducted in which the crabs escaping under the footrope were captured using an auxiliary net attached under the trawl net (Somerton and Otto 1999). Estimates of trawl efficiency, calculated as the trawl proportion of the combined trawl and auxiliary net catches, were initially considered sufficiently constant spatially to be used to calculate Bayesian priors for survey catchability parameters in the snow crab stock assessment model (Turnock 2010). However, subsequent research (Weinberg and Kotwicki 2008) indicated that the distance between the footrope and bottom on the 83-112 Eastern trawl was dependent upon depth and sediment size, both of which varied considerably over the EBS survey area. Since the escapement of snow crab under the footrope was clearly related to this distance, and the original experiment occurred in a relatively small geographic area at the extreme southern portion of the snow crab distribution in the EBS, the assumption of spatial constancy was put into question, and thus so too was the validity of the snow crab survey catchability estimates.

One potential solution to this problem would have been to repeat the auxiliary net experiment over a sufficiently broad area of the EBS to ensure that the spatial variation in trawl efficiency was adequately sampled. However, there were concerns that the auxiliary net footrope, which was heavily weighted to ensure a high capture rate of escaping crabs, caused sufficient drag to distort the geometry of the trawl and affect its fishing performance. This led to the choice of a different experimental design, one based on side-by-side trawling (Wileman et al. 1996). With this experimental design, the need for increased bottom contact could be separated from its potential effect on the performance of the survey trawl by having an additional vessel accompany the survey vessels during their normal survey operations and take simultaneous, nearby hauls using a specially designed and heavily weighted bottom trawl assumed to catch all crabs in its path.

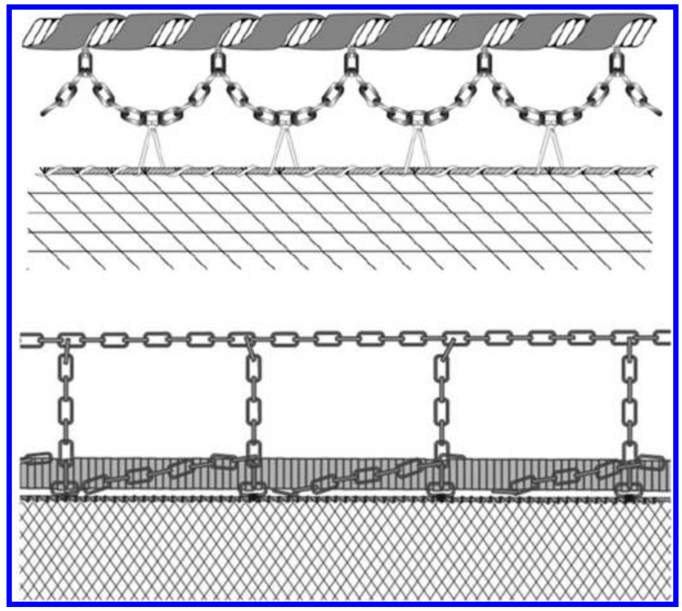
In addition to a different sampling design, we use a different analytical approach to estimate trawl efficiency by extending the catch comparison methodology of Fryer et al. (2003) and Holst and Revill (2009) to model efficiency as smooth functions of body size and environmental covariates.

Methods

Description of the trawls

The 83-112 Eastern trawl is a two-seam flatfish trawl with a 25.5 m headrope and a 34.1 m footrope. Over the EBS survey area, the net spread, between wing tips, ranges between 15 and 19 m, and the headrope height, at its center, ranges between 1.8 and 2.2 m. The net is constructed of 10.2 cm (stretched measure) nylon mesh in the body, 8.9 cm mesh in the intermediate and cod end, and 3.2 cm mesh in the cod-end liner. The footrope is constructed of 1.6 cm diameter fiber core wire rope wrapped with 1.3 cm polypropylene rope. The edge of the net mesh is connected to the footrope with loops of 0.8 cm chain (Fig. 1; a complete description with construction plans is provided in Stauffer (2004)).

Fig. 1. Comparison of the footrope and net attachments of the 83-112 Eastern trawl (upper) and the *Nephrops* trawl (lower). Compared with its initial design, described in Conan et al (1994), the *Nephrops* trawl was modified by wrapping chain around the footrope to increase its mass and adding a tickler chain to lift crabs off the bottom before they encountered the footrope. Both modifications were intended to increase the snow crab capture efficiency of the *Nephrops* trawl.

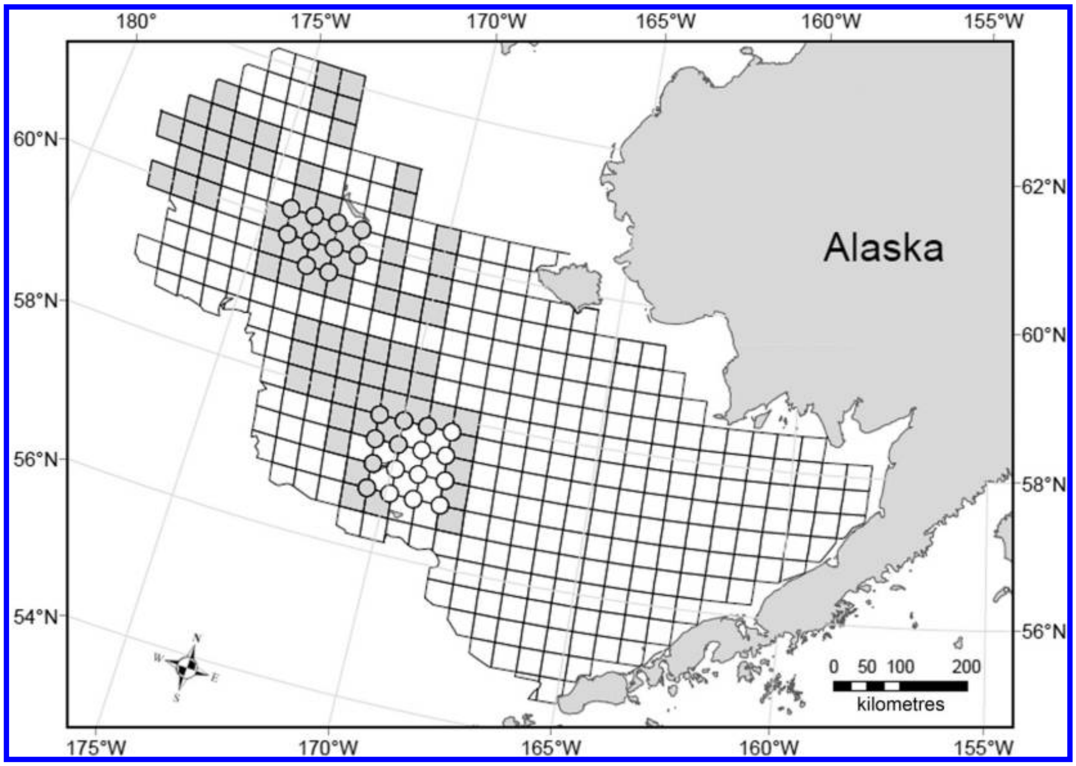


The *Nephrops* trawl, which was used in the side-by-side towing experiment to estimate the absolute density of snow crab, is also designed to be used on a smooth bottom, but is somewhat smaller with a 20 m headrope and a 27 m footrope. Over the area of the EBS inhabited by snow crab, the trawl net has a spread ranging from 10 to 14 m between the wing tips and a headrope height ranging from 0.9 to 1.1 m. The trawl net is constructed of 8.0 cm web in the body, 6.0 cm web in intermediate, and 5.0 cm web in the cod end. The footrope is constructed of 15 mm diameter wire rope covered with 6 cm diameter rubber disks (complete description with construction plans is provided in Conan et al. 1994). To increase the catch of snow crab, the footrope was modified by wrapping it with 8 mm galvanized chain to increase its bottom contact and attaching a 8 mm tickler chain to help lift crabs off the bottom before they encountered the footrope (Fig. 1). Video observations (S. Goodman, unpublished data) showed that that footrope contact was quite good, and no crabs were seen to escape beneath the footrope or to be herded into the trawl path.

Side-by-side experiment

The standard EBS bottom trawl survey has a systematic sampling design consisting of 375 stations positioned mostly on a 20 nautical mile (nmi) (1 nmi = 1.852 km) grid (Fig. 2). The survey grid is sampled from east to west using two vessels that are coordinated to sample clusters of stations in a pattern that minimizes travel time. The side-by-side experiment was designed to have a third vessel join the two survey vessels when they reached the area inhabited by snow crab and to conduct side-by-side trawling with these vessels at 92 of the 275 stations that had a catch of at least one snow crab during the 2009 survey. Since the third vessel had to synchronize its operation with the two survey vessels, the sampling stations were not chosen randomly, but rather were selected to minimize travel time between stations and satisfy other logistic considerations (Fig. 2). However, the general areas of

Fig. 2. The standard eastern Bering Sea (EBS) survey consists of sampling sites that are located at the centers of a 20 nmi × 20 nmi grid (1 nmi = 1.852 km) and, additionally in some locations, at the corners of the grid elements (circles). Of the 375 standard sampling sites, 92 (shaded) were chosen to conduct the 2010 side-by-side trawling experiment.



sampling were chosen to be representative of the carapace width distribution of both sexes of snow crab and to capture the spatial variability in depth, sediment size, and net width that occurs over the survey area (Figs. 3, 4).

At each of the stations, a standard EBS survey trawl tow was conducted by either the *Alaska Knight* (44 m stern trawler; 77 stations) or the *Aldebaran* (40 m stern trawler; 15 stations), both of which are chartered commercial fishing vessels. These tows were made at 3 knots (1 knot = 1.852 km·h^{-1}) for 30 min using a 83-112 Eastern trawl and standard survey operating protocols (Stauffer 2004). Additionally, at each station, the *American Eagle* (39 m stern trawler), chartered by the Bering Sea Fisheries Research Foundation (BSFRF), made a tow at 2 knots for 5 min with a *Nephrops* trawl by one of the survey vessels. These tows has a simultaneous start as the Alaska Fisheries Science Center (AFSC) tows and a parallel course but were separated by a distance of roughly 0.1–0.2 nmi. The reduced speed and duration of the BSFRF tow resulted in a much smaller swept area than the National Marine Fisheries Service (NMFS) tow, but the reduction was considered necessary because the *Nephrops* trawl had such high catches of benthic invertebrates and debris that the weight and drag of the catch jeopardized good trawl performance for longer tows. All vessels continuously measured net width, from wingtip to wingtip, using a Netmind acoustic trawl mensuration system and measured tow duration, from first to last bottom contact, using a bottom contact sensor that was custom-made at the AFSC (Somerton and Weinberg 2001) and mounted at the center of the footrope. Tow length in metres was estimated as the straight line distance between the GPS positions measured at the start and end of bottom contact. Swept area of each tow was estimated as the mean net width multiplied by the tow length.

Catch processing on both vessels proceeded identically. Snow crab catches were separated by sex, then subsampled by mass, if the catches were larger than 300 individuals, before measurement of carapace width in millimetres with digital calipers. Since AFSC trawl tows had a greater swept area (approximately seven times) than BSFRF tows, the catches of snow crab were much larger, and therefore the subsampling proportions (i.e., subsample mass/total catch mass) were typically lower.

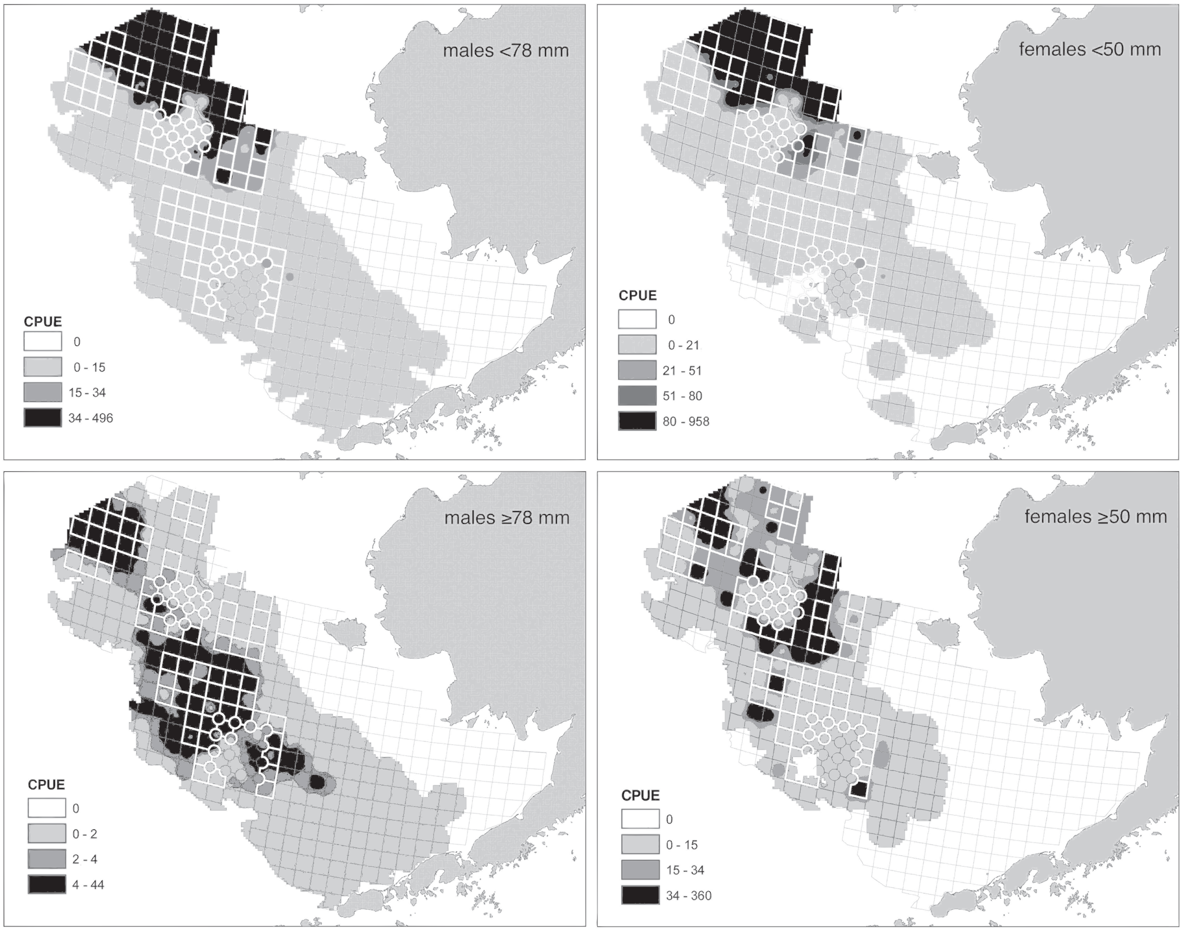
Trawl performance variables

At the experimental stations as well as at all other AFSC survey stations where snow crabs were caught, data on several variables suspected of influencing trawl efficiency were either collected or predicted. Depth in metres was estimated as the sum of the trawl depth, measured with a Seabird pressure sensor attached to the trawl headrope, and the distance between the headrope and the bottom, measured with a Netmind acoustic sensor. Net width was measured as described previously. Sediment size, expressed in units of phi (–log of grain diameter inmillimetres), was estimated using data from an EBS sediment database maintained at the AFSC (Smith and McConnaughey 1999). The locations of the sediment samples were not always at the stations, so the sediment sizes were estimated from the 2587 samples in the database using a GIS interpolation function (kriging). The spatial density of the sediment samples was distinctly higher closer to shore. Consequently, the interpolated sediment size estimates could be located as much as 30 km from an actual sediment sampling location in some offshore areas, although the spatial gradients of sediment size in these areas were weak (Fig. 4).

Estimating trawl efficiency

Trawl efficiency was estimated for each sex and 5 mm interval of carapace width using a modified version of the SELECT method developed by Millar (1992, 1994) and Wileman et al. (1996) for analyzing catch comparison data from side-by-side trawling experiments. This method was initially developed to estimate the size selectivity of one cod-end mesh (test trawl) relative to that of another (control trawl). Our situation differed from the SELECT method in two respects. First, we assumed that the control trawl,

Fig. 3. Distribution of large and small width groups of both sexes of snow crab and the sampling stations chosen for the 2010 side-by-side experiment (edged in white). Note that these are primarily located in the area occupied by large males and females. Also note that both sexes display a southeasterly shift in the spatial distribution between small and large individuals.



in our case the BSFRF trawl, captured all crabs in its swept area, and consequently our estimates of selectivity are intended to be estimates absolute selectivity for the whole trawl gear (Dickson 1993*a*), that is, trawl efficiency. Second, while the logistic form of the selection function used in the SELECT method is adequate for describing relative mesh selection, it has been found to be overly rigid for describing whole trawl selectivity (Skalski and Perez-Comas 1993; Lauth et al. 2004). Therefore we followed the approach of Fryer et al (2003) and Holst and Revill (2009) and utilized a more flexible selection function.

Based on these previous studies, an estimator for the efficiency of the 83-112 Eastern trawl is developed as follows. If C_a and C_b are the numbers of crabs in each width interval measured from the catches of the AFSC and BSFRF trawls in each paired comparison tow (for simplicity, subscripts denoting width interval and tow number are omitted), then the measured catch in the AFSC trawl, given the combined measured catch in the two trawls, can be modeled as a binomially distributed random variable with a probability of success equal to ϕ, that is, the expected proportion of the combined measured catch in the AFSC trawl. This proportion can be expressed in terms of the unknown trawl efficiency (r_a) of the AFSC trawl:

$$(1) \qquad \phi = \frac{S_a p r_a}{S_a p r_a + S_b(1 - p)}$$

where S_a and S_b are the catch sampling proportions in each tow of each trawl and p is the split parameter, or the probability that a crab within the combined swept area of the two trawls enters the AFSC trawl. Assuming that there is no preferential avoidance or attraction of snow crab to either trawl, p can be estimated as the proportion of the combined area that is swept by the AFSC trawl, that is,

$$(2) \qquad p = \frac{A_a}{A_a + A_b}$$

where A_a and A_b are the measured swept area of the two trawls.

Letting $R_A = A_b/A_a$ and $R_S = S_b/S_a$, eq. 1 can be simplified to

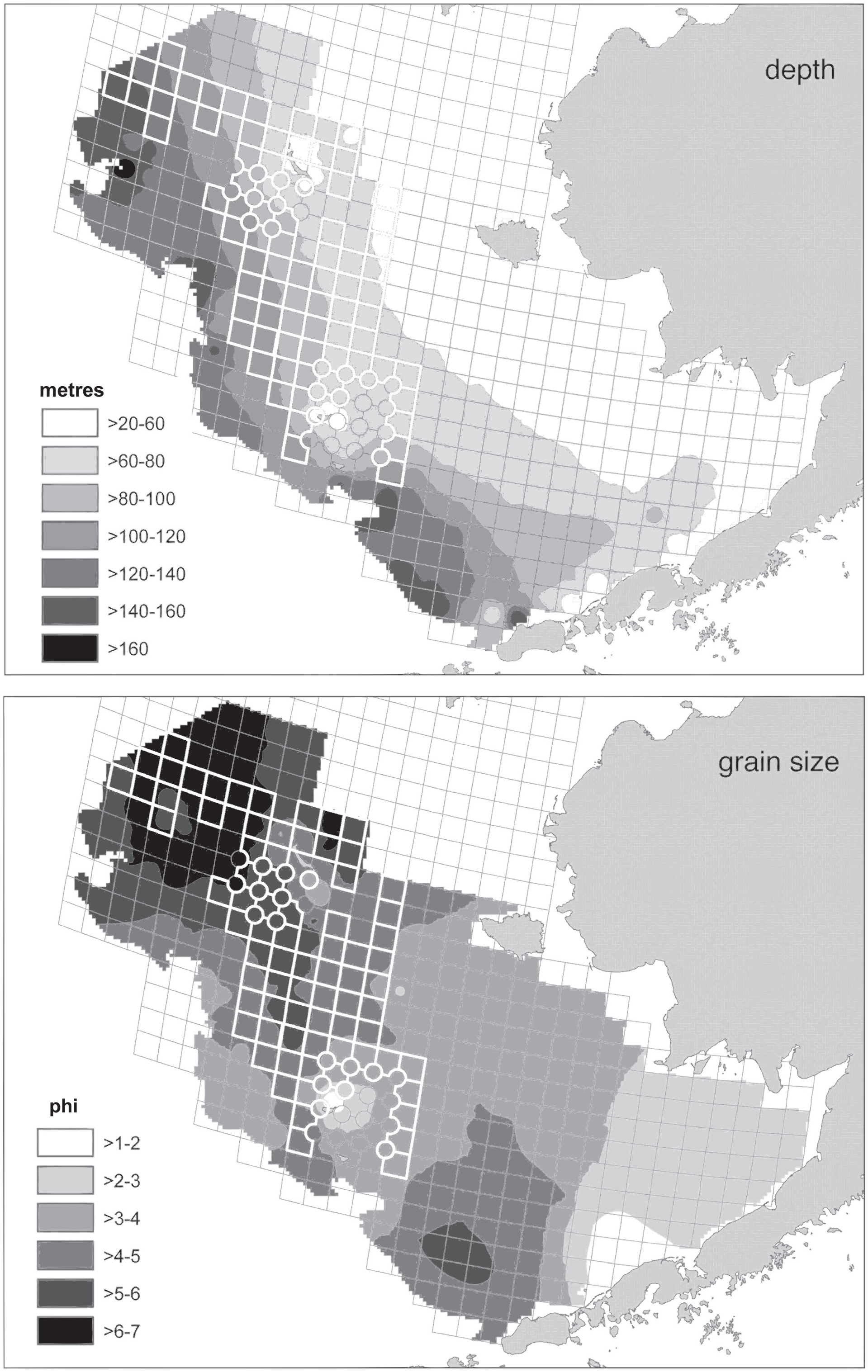
$$(3) \qquad \phi = \frac{r_a}{r_a + R_A R_S}$$

which, after transformation to a logit scale, is expressed as

$$(4) \qquad \text{logit}(\phi) = \log(r_a) - \log(R_A R_S)$$

Following the approach of Fryer et al. (2003), we modeled logit(ϕ) as a sex-specific smooth function of carapace width and one or more variables from a set of spatial covariates consisting of net

Fig. 4. Spatial distributions of depth in metres and sediment grain size expressed in phi units (–log(diameter, in mm)) and the locations of the side-by-side sampling stations (edged in white).



width, depth, and sediment size. This was done by approximating logit(ϕ) with logit[C_a/(C_a + C_b)] and fitting the following model using generalized additive modeling (GAM; R Development Core Team 2008), weighting by the combined catch in each paired tow and considering the error as binomially distributed. The model formulation is

$$\text{logit}\left(\frac{C_a}{C_a + C_b}\right) = \Omega_1(W) + \Omega_2(X) \quad (5)$$

where Ω_i represents nonparametric smooth functions, W is carapace width (in mm), and X is one or more of the spatial covariates.

The covariates depth, sediment size, and net width were added individually or jointly (thin plate splines) until the model with the lowest value of the Akaike information criterion (AIC; Burnham and Anderson 1998) was determined.

Catch comparison experiments such as the one considered here often find sufficient site-to-site variation in trawl efficiency to cause overdispersion or more residual error than would be expected for the assumed binomial distribution. If not taken into consideration, such overdispersion can lead to invalid statistical tests and confidence intervals (Fryer et al. 2003; Crawley 2007). To determine whether the covariates that were added into the model accounted for this between-site variation or whether sufficient variation remained to invalidate the assumption of binomial error, we fit the GAM model as described above but with the assumption of quasibinomial error, which can account for this extra variability (Crawley 2007), then compared the goodness-of-fit with that of the previous model. Because the method of fitting the quasibinomial model is an approximation and not a true likelihood, AIC cannot be used for the model comparison; instead the comparison was based on the generalized cross-validation (GCV) score (Crawley 2007). Like the AIC, the more appropriate model is indicated by a lower value of GCV.

Once the best-fitting model was determined, logit(ϕ) was predicted for each sex and carapace width interval at each of the 92 stations using the station-specific values of the spatial covariates. These values were then transformed to trawl efficiency estimates as follows:

$$r_a = \exp[\text{logit}(\phi) + \log(R_a R_s)] \quad (6)$$

Survey catchability

In stock assessment models, survey catchability is applied to estimates of relative stock size provided by a survey. For EBS snow crab, these estimates are obtained from the trawl survey data using swept area techniques (Alverson and Pereyra 1969). To obtain estimates of survey catchability appropriate for describing how the survey samples the entire stock, survey catchability was calculated as a catch-averaged mean of the trawl efficiency estimates. For each sex and width interval, this averaging can be expressed as

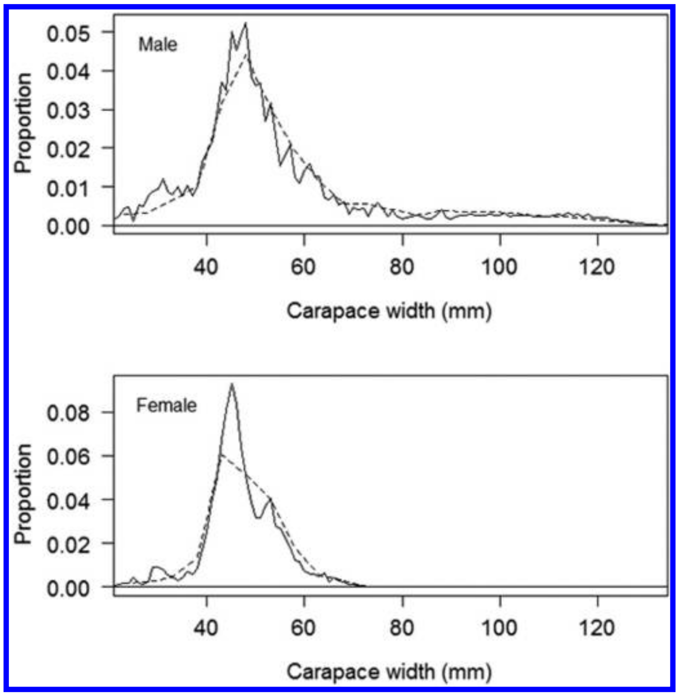
$$\bar{r}_a = \frac{\sum n_i r_{a,i}}{\sum n_i} \quad (7)$$

where n is catch in numbers and i is station number.

However, owing to the nonrandom selection of the sampling stations, we suspected that this estimate might be biased. To produce an alternate estimate likely to be less biased, mean trawl efficiency was also calculated by predicting trawl efficiency at all of the 275 positive snow crab stations not sampled by the third vessel, using the station-specific carapace widths and environmental variables, then calculating a catch-weighted average of the trawl efficiency estimates over all 275 stations. To distinguish the two estimates, the former is called sampled survey catchability and the latter expanded survey catchability.

Precision of the estimates of the expanded survey catchability was estimated using bootstrapping (Efron and Tibshirani 1993; Fryer et al. 2003). The bootstrap samples were chosen in two stages. First, the experimental data were resampled by choosing 92 of the original 92 experimental stations with replacement. Second, for each of the chosen stations, the width frequency distributions from the NMFS and BSFRF tows were each sampled with replacement, choosing samples equal in size to the originals (an example of this form of within-station bootstrapping is provided in Millar (1993), but for a covered cod-end experiment). The analysis of each bootstrap sample to estimate expanded survey catchability proceeded as described above; however, the model form and the specific covariates chosen for the original model were always maintained. Bootstrap resampling and data analysis were repeated 1000 times, and the approximate empirical 95% confidence intervals were determined for each size interval as the 25th and the 975th elements of the sorted array.

Fig. 5. Carapace width frequency distribution, expressed as a proportion of the total, by sex, of the snow crabs caught by the AFSC vessel summed over the 92 stations sampled in the side-by-side trawling experiment (dashed line) and summed over the entire eastern Bering Sea survey area (solid line).



Results

Side-by-side experiment

The side-by-side trawling experiment sampled 92 stations at which 10 216 male and 7385 female snow crabs were measured on the NMFS vessels, and 9472 male and 12 503 females crabs were measured on the BSFRF vessel. The carapace width distribution of the crabs from the 92 experimental stations were very similar to those from all 275 positive snow crab survey stations (Fig. 5), although there was a slight undersampling at the smallest carapace widths. This is likely due to the nonrandom choice of the sampling stations that apparently undersampled areas inhabited by small snow crabs (Fig. 3).

Trawl efficiency estimation

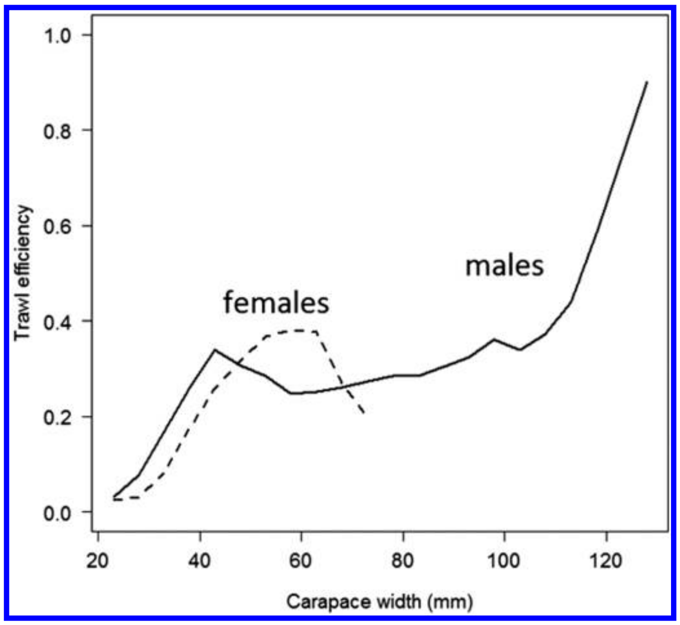
The trawl efficiency model for each sex producing the best fit (lowest value of AIC) included a smooth function of carapace width and a smooth bivariate function of sediment size and depth (Table 1). When the spatial covariates were left out of the function, R^2 and percent explained deviance were both substantially reduced and AIC was substantially increased (Table 1), indicating that these variables were informative for explaining the spatial variation in trawl efficiency over the experimental area. The models assuming binomial error had a lower value of GCV (1.20 for males) than the model assuming quasibinomial error (2.26) and had a slightly higher value of explained deviance (45.4% compared with 45.2%), indicating that the residual errors were not significantly overdispersed and that the assumption of binomial error

Table 1. Diagnostics of the fit of trawl efficiency generalized additive models to the side-by-side experimental data for each sex.

Sex	Spatial covariates	R^2	% Deviance explained	*N*	AIC
Male	*s* (depth, sediment)	0.49	45	1445	5837
	s (depth) + *s* (sediment)	0.47	43		5936
	s (depth)	0.43	40		6134
	s (sediment)	0.38	35		6406
	None	0.25	23		7093
Female	*s* (depth, sediment)	0.55	54	699	4312
	s (depth) + *s* (sediment)	0.50	48		4628
	s (depth)	0.43	41		5032
	s (sediment)	0.33	31		5675
	None	0.15	15		6667

Note: Models all contain a smooth term (denoted by "*s*()") for carapace width and additionally for various combinations of sediment size and depth. Goodness-of-fit is expressed as R^2, percentage of the deviance explained by the model, and the Akaike information criterion (AIC). Sample size (*N*) represents the number of carapace width intervals containing at least one crab. For each sex, the models are ranked by ascending value of AIC; the model with the lowest values of AIC was chosen as the best.

Fig. 6. Mean trawl efficiency (unweighted average over the 92 sampling stations) of male (solid line) and female (dashed line) snow crab expressed as a function of carapace width.

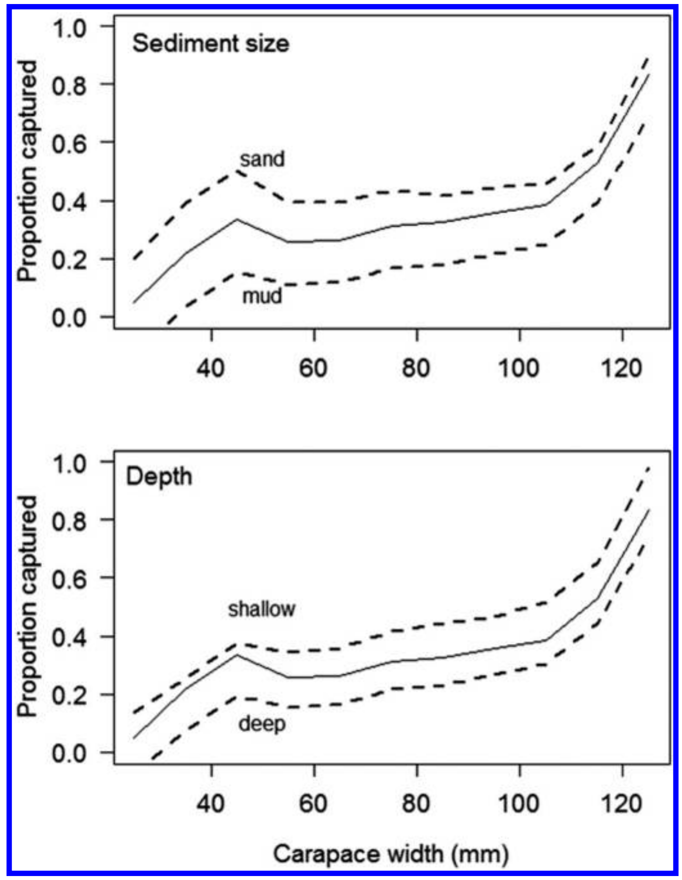


was appropriate (Crawley 2007). When averaged by width interval, trawl efficiency of both sexes does not increase monotonically with carapace width but instead has either a local maximum (males) or a global maximum (females) at a carapace width less than the maximum width (Fig. 6). These patterns are clearly different from those that would have been predicted by a logistic equation and indicate that the use of a nonparametric smooth representation rather than a parametric logistic function was appropriate for these data. Over the size range 45–70 mm, trawl efficiency was greater for females than for males (Fig. 6). When evaluated at the range extremes of sediment size, male trawl efficiency was higher in sand (low phi) and lower in mud (high phi; Fig. 7). Likewise, when similarly evaluated for depth, male trawl efficiency was higher in shallow water and lower in deeper water.

Survey catchability

Estimates of the expanded survey catchability (averaged across 275 stations) for both sexes varies with carapace width in a pattern similar to that of the sampled survey catchability (averaged across

Fig. 7. Trawl efficiency function for male snow crab evaluated at the extremes of sediment grain size and depth over the 92 stations in the side-by-side trawling experiment and smoothed to increased clarity as a function of carapace width. This shows that the selectivity was less in mud than in sand and less in deep water than in shallow.



92 stations; Fig. 8), but for males the magnitude is distinctly lower at smaller carapace widths. This sexual difference is due in part to the difference in the spatial distribution of sexes (Fig. 3) and the undersampling of smaller males and females in our experimental design. By including habitat variables in the estimator for trawl efficiency and calculating the expanded survey catchability as a weighted spatial average over the entire snow crab distribution, the effects of nonrandom sampling in our experimental design were corrected.

The uncertainty of the expanded survey catchability estimates increased with carapace width as the abundance of each sex, and the number of nonzero samples, declined. For females, spread of the 95% confidence intervals at widths above ~50 mm was greater than for similar sized males (Fig. 9). This greater uncertainty is likely due to a sexual difference in adult spatial patchiness of snow crab in the EBS. For example, over the 92 sampling stations, the variance in the catches of 53 mm wide females was more than seven times greater than that of the same size males.

Discussion

One important finding of this study is that the snow crab survey catchability function we estimated is clearly not a logistic function of carapace width as is currently assumed in the snow crab stock assessment model (Turnock and Rugolo 2010). The more complex shape was due to the spatial variation in the sampling efficiency of the 83-112 Eastern trawl for snow crab as well as the spatial pattern in the distribution of snow crab in the EBS.

Fig. 8. The survey catchability (solid line) evaluated over the 275 positive snow crab stations and the trawl efficiency (dashed line), both expressed as proportion captured, evaluated over the 92 stations where the side-by-side trawling was conducted.

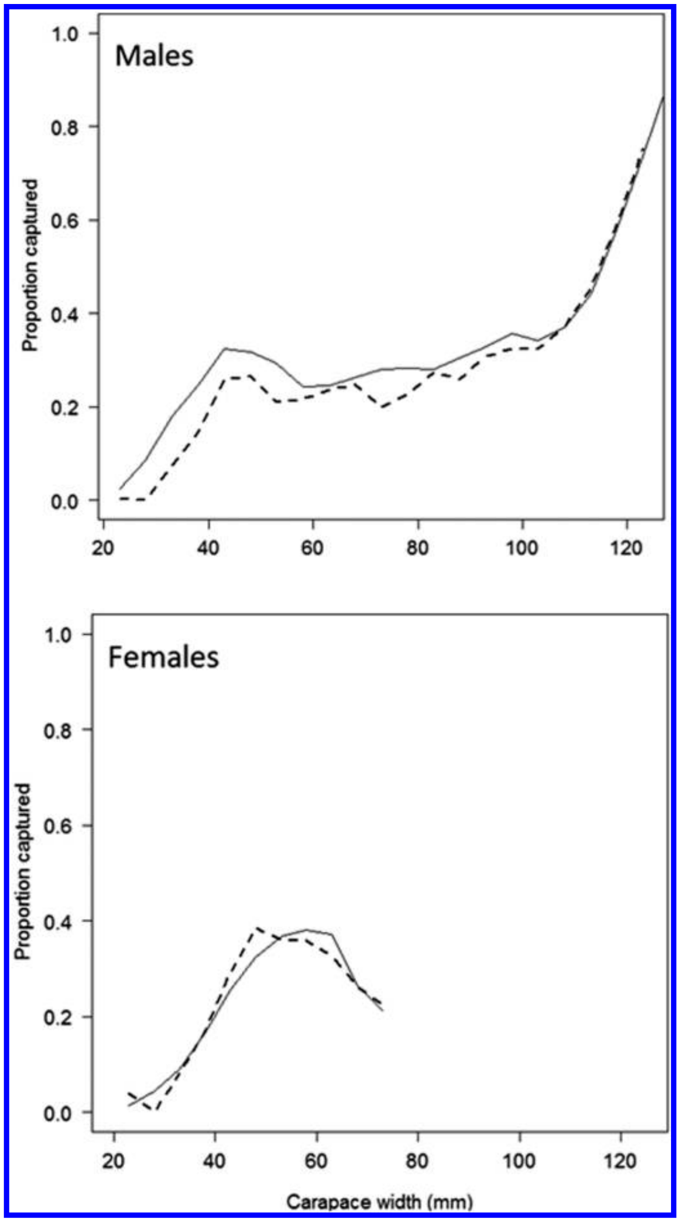
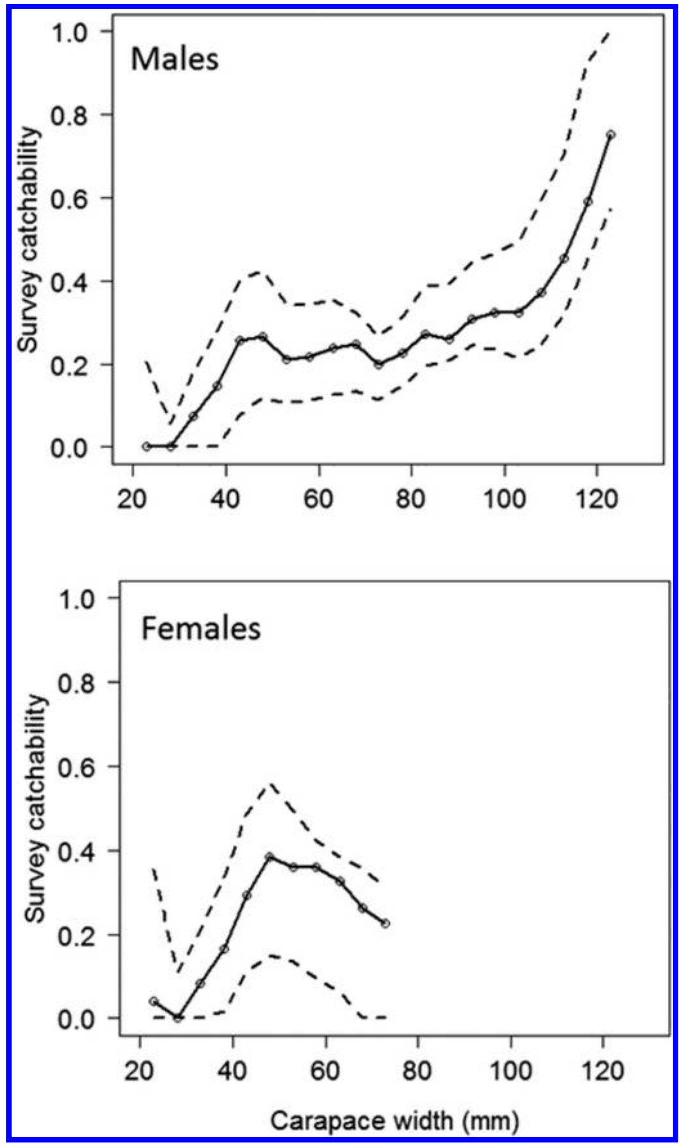


Fig. 9. Expanded estimates of survey catchability, by sex, as a function of carapace width. Empirical 95% confidence limits are shown with dashed lines.



Trawl efficiency varied spatially primarily because of the influence that depth and sediment size have on the distance separating the trawl footrope and seabed. This was documented for the 83-112 Eastern trawl by Weinberg and Kotwicki (2008), who showed that off-bottom distance, measured with bottom contact sensors, increased with increasing depth and decreasing sediment size. Because snow crabs escape capture primarily by passing beneath the footrope, trawl efficiency is expected to show the reverse trend to these variables, and this is exactly the pattern displayed by our experimentally derived estimates of trawl efficiency (Fig. 7); that is, efficiency decreases with increasing depth and decreasing sediment size. Furthermore, because depth and sediment size have distinct spatial patterns over snow crab distribution (Fig. 4), the linkage between trawl performance and these two environmental variables leads to distinct spatial patterns in trawl efficiency. Our findings of decreased efficiency of the 83-112 Eastern trawl in mud contrast those of Dawe et al. (2010) for the efficiency of the Campelen trawl for snow crab in Newfoundland. Although differences in the sediment compaction may play a role in this difference, we have found that footrope off-bottom distance is strongly correlated to net spread, perhaps through changes in footrope tension, and net spread has been shown to increase with both increasing depth and decreasing sediment size (Weinberg and Kotwicki 2008). For the 83-112 Eastern trawl, this effect may be more pronounced than any tendency for the trawl to settle into softer sediment.

Another contributing factor to the nonlogistic shape of the estimated survey catchability function was the spatial distribution of snow crab. Ernst et al. (2005) demonstrated that snow crab in the EBS undergo an ontogenetic migration in which they progressively move southward and into deeper water as they grow (Fig. 3), which, for males, leads from a shallower, muddy habitat when they are small to a deeper, sandy habitat when they reach maturity (Fig. 10).

Taken together, the spatial variation in both trawl efficiency and crab size and the correlation of both factors with depth and sediment size leads to the complicated shape of the survey catchability function. There are essentially three interrelated

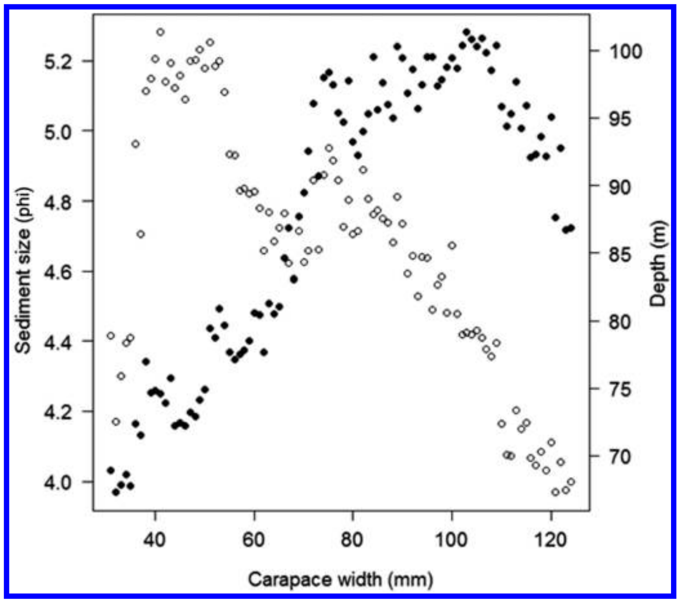


Fig. 10. Mean depth in metres (solid circles) and sediment size in phi units (–log grain size, in mm; open circles) for male snow crab as a function of carapace width. Means include data from 275 stations that were positive for snow crab in the 2010 EBS survey.

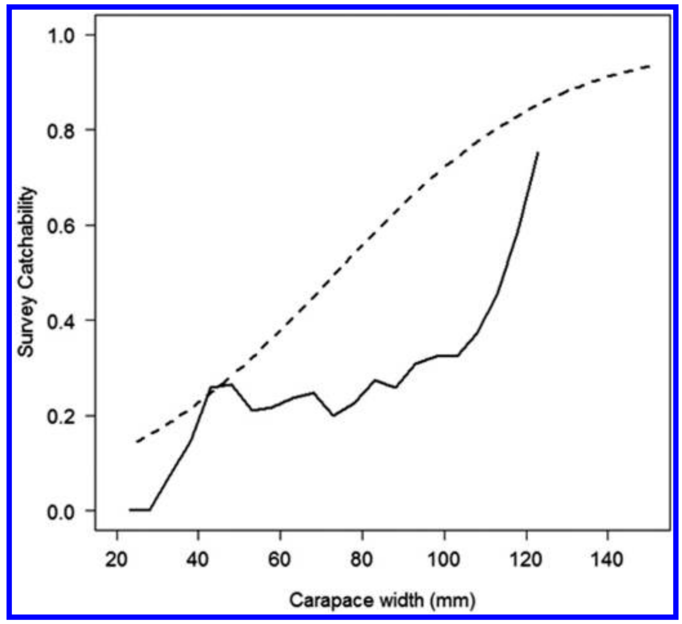


Fig. 11. Comparison of the male expanded survey catchability function estimated in this study (solid line) and the male trawl efficiency function estimated in Somerton and Otto (1999) (dashed line), which was used as a proxy for the survey catchability function in the snow crab stock assessment model (Turnock and Rugolo 2010).

components determining this shape: (*i*) the width-dependent escapement of crabs under a footrope with a fixed distance off-bottom, which is analogous to cod-end mesh escapement, and if acting alone, would result in a logistic shape to the catchability function as in Somerton and Otto (1999); (*ii*) the spatially varying footrope off-bottom distance, which results in the need for spatial averaging but still produces a logistic shape to the catchability function if crabs are randomly distributed by size; and (*iii*) the dependency of both crab size and footrope clearance on depth and sediment size. This last factor can result in the situation where small crabs could experience higher catchability than larger crabs because they prefer a habitat in which the footrope off-bottom distance is smaller. In general, it is likely that the effects of ontogenetic migrations and habitat-specific trawl performance are widespread among marine fish and invertebrates and must be considered when designing experiments to estimate survey catchability.

The inclusion of the covariates depth and sediment size in our model of trawl selectivity was important in our study for two distinct reasons. First, side-by-side trawling experiments typically show considerable between-haul variation in trawl efficiency, possibly leading to overdispersion of the residuals and biased estimates of model error (Fryer 1991; Millar et al. 2004). One approach to dealing with this issue is to consider haul as a random effect along with fixed effects in a mixed model (Fryer et al. 2003; Holst and Revill 2009). However, in our study depth and sediment size were so influential on trawl efficiency that overdispersion was reduced to insignificant levels and the use of a mixed-effect model was not needed. Second, conducting side-by-side trawling at all 275 positive snow crab stations was prohibitively expensive, and conducting it at a random sample of these stations was logistically infeasible. However, the inclusion of depth and sediment size from the 92 experimental stations in the model allowed prediction of trawl efficiency at the survey stations where the experiments were not conducted, which, in turn, allowed catch-weighted averaging of trawl efficiency over all survey stations to produce an estimate of survey catchability that was less likely to be biased by the nonrandom selection of sampling stations.

Our estimates of trawl efficiency are based on the assumption that the BSFRF trawl captured all crabs in its swept area. This will always be a problematic issue for sampling in efficiency experiments such as this, because there is likely no feasible way to ensure complete efficiency of any sampling device. However, we have taken the approach of other researchers studying footrope escapement (Engås and Godø 1989*b*) and chose a trawl footrope with a very hard bottom contact that, hopefully, reduced crab escapement under the footrope to negligible levels. The hard bottom contact can cause increased drag, trawl distortion, and changes in performance, factors that may have been an issue in the earlier study of Somerton and Otto (1999), because the attached underbag could potentially transfer these effects to the survey trawl itself. However, by using the side-by-side experimental design, any effects on the *Nephrops* trawl were isolated from the 83-112 Eastern trawl.

Our estimates of survey catchability are also based on the assumption that the survey covers the entire stock of snow crab in the EBS, an assumption that is considered to be true in the stock assessment model (Turnock and Rugolo 2010). In situations when this is not true (e.g., if some part of the stock was not sampled by the survey), an additional parameter, known as availability, can be included in stock assessment models to scale survey catchability by the surveyed proportion of the stock. However, unless it is possible to obtain a good independent estimate of availability in such cases, we feel that experimental effort to estimate survey catchability will not be informative for stock assessment modeling.

The first estimate of trawl efficiency for EBS snow crab (Somerton and Otto 1999) was questioned for use as a proxy for survey catchability in the snow crab stock assessment model because the experimental trawling procedures differed from those used on the bottom trawl survey (Stauffer 2004) and the habitat characteristics at the experimental site may not have been representative of area inhabited by the EBS snow crab population. Both issues were addressed in this study, and the results indicate that the earlier estimate of snow crab trawl efficiency was indeed inappropriate for use as a survey catchability function because it overestimated the survey catchability of males over much of their size range (Fig. 11). The primary reason for this overestimation is that the original study only sampled snow crab at the extreme southern part of their geographic range in the EBS, an area which is generally shallower and sandier than their typical habitat. In addition, because the sampling area was relatively small, there was little contrast in depth and sediment size, and consequently trawl efficiency was primarily a function of carapace width and conformed quite well to a logistic function (Somerton and Otto 1999). In contrast, the new survey catchability function is spatially averaged over the entire range of snow crab in the EBS and accounts for the variability in the habitat variables most influential on trawl performance. As a consequence, the survey catchability function provided here better represents the entire snow crab stock.

Use of a smooth function rather than a logistic function to describe the size dependency of trawl efficiency is not new, because the studies of Lauth et al. (2004), Skalski and Perez-Comas (1993), Millar (1993), and Maunder and Harley (2011) also found that nonparametric functions described the data better than a logistic function. This is not surprising considering the greater complexity of the fish capture processes leading to whole-trawl efficiency than those leading to cod-end mesh escapement and the use of a logistic function (Wileman et al. 1996). However, use of a smooth function to describe survey catchability leads to complications when employing it to constrain the values of survey catchability in a stock assessment model, because survey catchability is typically specified as some form of the logistic equation (Thompson 1994). If our survey catchability function had been reasonably approximated by a logistic function, then the estimated parameters of this function could have been used to set Bayesian priors on the parameters of the survey catchability in the stock assessment model. We anticipate that our estimate of snow crab survey catchability can still be used to provide such a constraint, but to do so the specification of survey catchability in the stock assessment model needs to have a more complex, but more realistic, shape than provided by the logistic function.

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