Capture efficiency and size selectivity of hydraulic clam dredges used in fishing for ocean quahogs (*Arctica islandica*): simultaneous estimation in the SELECT model

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Estimates of capture efficiency and size selectivity for commercial dredges are important in estimating stock biomass and setting catch limits for the ocean quahog off Iceland and the United States. Ocean quahogs are long-lived, slow-growing, and sensitive to overharvest resulting from poor estimates of capture efficiency and stock biomass. Capture efficiency and size selectivity were estimated simultaneously in mixed-effect SELECT models using diver and commercial dredge experiment data from the shallow-water habitats off Iceland. Estimated capture efficiency for the commercial dredge $E = 92\%$ ($CV = 8\%$) was high for large [107.5 mm shell length (SL)] ocean quahogs. Size selectivity followed an ascending logistic curve, with $L_{50} = 70.5$ mm SL (CV 4%), a selectivity range of 17.6 mm SL, and substantial variability among experimental dredge tows. Estimated capture efficiency was higher than that for ocean quahogs in US waters, possibly because of the deep habitats off the United States or uncertainty about dredge position during US depletion experiments. Scaling maximum selectivity from the SELECT model to one reduces correlations between size-selectivity and capture-efficiency parameters and may enhance the utility of selectivity estimates in stock assessment modelling. Our experimental and modelling approach may be useful for studies with other non-mobile benthic species.

Keywords: *Arctica islandica*, hydraulic dredge capture efficiency, ocean quahog, SELECT model, size selectivity.

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Introduction

The ocean quahog (*Arctica islandica*) is a bivalve mollusc found on continental shelves mainly in sand and silt where temperatures are relatively low (<12°C for the Icelandic stock). The species is regionally abundant and broadly distributed around the North Atlantic between Cape Hatteras in the United States and the Bay of Cadíz, Spain (Merrill and Ropes, 1969). The most northern stock is found off the coast of Iceland, where their densities are highest at depths of 5–50 m and the fishery operates mainly at depths of 20–40 m (Eiríksson, 1988; Thorarinsdóttir and Einarsson, 1996). In contrast, densities off the United States are highest at depths of 50–100 m (NEFSC, 2000) and the fishery operates mainly at depths of 73–110 m (Serchuk and Murawski, 1997). The shallow-water habitat off Iceland facilitates diver sampling, which is assumed to be unaffected by size selectivity and capture efficiency. In contrast, diver sampling is difficult in deep-water habitats off the United States.

Ocean quahogs are long-lived, grow slowly and are relatively unproductive on a per-individual basis. Estimates of maximum age exceed 200 years (Jones, 1983; Steingrimsson and Thorarinsdóttir, 1995; Kilada *et al.*, 2007; Wanamaker *et al.*, 2008). Off Iceland, ocean quahogs approach maximum size at about age 60 (Steingrimsson and Thorarinsdóttir, 1995) and may reach 118 mm SL (shell length, the longest anterior–posterior distance across an intact shell; Thorarinsdóttir and Einarsson, 1996). Off the United States, ocean quahogs reach 90% of average maximum size (∼100 mm SL) at age 40–80 years, depending on region (Cargnelli *et al.*, 1999; Lewis *et al.*, 2001).

Seasonal patterns in ocean quahog life-history characteristics influence the capture efficiency and size selectivity of the commercial fishing gear used to target them. In particular, quahogs off Iceland (GGT, unpublished data) and the United States (Cargnelli *et al.*, 1999) are found relatively deep in sediments during winter when phytoplankton abundance and water temperatures are low. At that time, they may cease feeding and respire anaerobically (Theede *et al.*, 1969).

The fishery for ocean quahogs off Iceland is small, under development, and currently consists of a single vessel. In US waters, ocean quahogs support a valuable fishery, with average annual ex-vessel revenues of about $US 20 million and landings of

~15 000 t of meat during the period 2005–2008. US landings are used in commercial soup, chowder, and sauce, and the fishery consists of some 80 vessels with permits managed under an Individual Transferable Quota system (Weinberg *et al.*, 1997).

Ocean quahogs are harvested in Icelandic and US fisheries with the same type of commercial hydraulic clam dredge (hereafter referred to as a commercial dredge; Murawski and Serchuk, 1989a; Thorarinsdóttir and Einarsson, 1996). Water jets placed in front of the dredge blade (orientated obliquely forward and down) dislodge the buried clams. Dislodged clams are swept over the blade and into the dredge as it moves along the bottom. The water jets and dredge dig a track ~10 cm deep as the dredge is pulled across quahog habitat.

Here, the probability of capture for ocean quahogs of any size in the path of a dredge is defined as the product of size selectivity and capture efficiency. Size selectivity is the probability (0–1) of capture for ocean quahogs of various sizes relative to the probability of capture for large, fully selected animals. Size selectivity increases asymptotically with SL for ocean quahogs in commercial dredges (Thorarinsdóttir and Jacobson, 2005) because the dredges are designed to select large ocean quahogs with the highest meat weight and to minimize the capture of small ocean quahogs, along with other unwanted invertebrates, fish and trash (Murawski and Serchuk, 1989a). Therefore, SL distributions for the catch and the population differ because small ocean quahogs are underrepresented in the catch.

Estimates of size selectivity are key parameters in many analytical techniques used to provide scientific information about ocean quahog and other fisheries (Hilborn and Walters, 1992; Quinn and Deriso, 1999). In particular, the estimates are used to estimate maximum sustainable yield and to calculate the per-recruit reference points (e.g. $F_{0.1}$ and F_{MAX}) used to recommend catch limits and fishing effort levels and to define healthy or overfished stock conditions for ocean quahogs (Thorarinsdóttir and Jacobson, 2005) and other stocks (Hilborn and Walters, 1992).

Capture efficiency is defined as the absolute probability of capture for a large fully selected ocean quahog in the path of the dredge. Not all large fully selected ocean quahogs may be caught because the water jets from the hydraulic dredge displace some outside the track of the dredge and because some pass under the blade (Murawski and Serchuk, 1989b). Although they can burrow slowly, ocean quahogs are sessile and unable to move purposefully out of the path of a dredge as it approaches.

Capture-efficiency estimates have substantial effects on the biomass estimates used by managers to specify target catch levels, particularly in the United States. In particular, $I = qB = (a/A) \times EB$, where q is a scaling parameter (catchability coefficient) that relates commercial catch rate or survey index data I to stock biomass B (already adjusted for size selectivity in this example), a the area swept by a one unit of fishing effort (one dredge tow), A the area covered by the stock, and E the capture efficiency (Paloheimo and Dickie, 1963). Rearranging the terms gives $B = (A/aE) \times I$, so the estimates of biomass are inversely proportional to the estimated capture efficiency. For example, halving E doubles the biomass, and vice versa.

The capture efficiency and the size selectivity of ocean quahogs in a hydraulic dredge are influenced by dredge design, operational characteristics (towing speed, the ratio of warp length vs. water depth, duration of the tow, the pressure of the water jets, etc.), and environmental factors (depth, current speed, and bottom type). In addition, capture efficiency may be affected by seasonal and site-specific differences in the depth of ocean quahogs within the sediments (Taylor, 1976).

Capture efficiency for dredges has been estimated for a number of bottom-dwelling commercial bivalves, primarily scallops (Mason *et al.*, 1979; Fifas and Berthou, 1999; Rudders *et al.*, 2000; Beukers-Stewart *et al.*, 2001). Direct estimates of capture efficiency and size selectivity for the dredges used to harvest infaunal bivalves can be obtained by comparing representative samples of the population from undisturbed sediments with catches in the same area using the same dredges (Caddy, 1968; Mason *et al.*, 1979; Fifas, 1991; Powell *et al.*, 2007). For ocean quahogs, we compare samples from divers using suction equipment with samples taken by dredges. Model-based estimates from depletion studies conducted off the United States indicate that the commercial capture efficiency for ocean quahogs averages ~60% in relatively deep water (27–60 m; NEFSC, 2007a) and ~70% for the larger Atlantic surfclam (*Spisula solidissima*) in shallower water (21–41 m; NEFSC, 2007b). The dredges used for Atlantic surfclams are configured to retain larger animals than the dredges used to catch ocean quahogs off the United States because Atlantic surfclams grow larger and are more efficient to process.

The fishery off Iceland is managed with annual quotas, which are set at 2.5% of the surveyed stock biomass (Anon., 2005). Fishable biomass estimates in Icelandic waters are based on resource surveys conducted using a commercial vessel and a clam dredge. The biomass estimates are made assuming that the dredges capture all ocean quahogs in their path (i.e. the capture efficiency is assumed to be 1; see below). For example, Anon. (2005) expanded survey-density estimates for ocean quahogs in Icelandic waters (kg m^{-2}; total catch weight divided by the area swept in the survey using commercial fishing gear) to compute the biomass for the stock. This approach underestimates the actual biomass of the stock because hydraulic dredges tend to select larger ocean quahogs (the survey biomass is less than the total biomass because of size selectivity). Moreover, it will underestimate the fishable stock to the extent that capture efficiency is <1.

The procedures used to estimate the biomass of ocean quahogs in US waters are more complex, but the capture efficiency of the commercial dredge plays a key role (NEFSC, 2007a). Biomass and mortality estimates for the US fishery are from a biomass-dynamics stock assessment model fitted to commercial catch data and triennial research clam survey data. Capture efficiency for the survey dredge is lower and more variable than that for modern commercial dredges. Therefore, information about the absolute density and abundance of ocean quahogs from field studies is used to develop auxiliary estimates of survey dredge capture efficiency and ocean quahog density for use in the stock assessment model.

The auxiliary information about survey-dredge capture efficiency in US waters is from survey-specific depletion studies undertaken by commercial vessels using commercial dredges. The depletion studies are conducted at field sites previously sampled by survey gear (NEFSC, 2007a). The spatial model of Rago *et al.* (2006) is used to estimate the density D of ocean quahogs in absolute terms, and the commercial capture efficiency E from the depletion study data. Survey-dredge capture efficiency is estimated as $E = S/D$, where S is the density of ocean quahogs as measured by the survey dredge.

The primary goal of this study was to estimate the capture efficiency for ocean quahogs in dredges operating off Iceland, to

Table 1. Summary of dredge and diver data collected off Iceland and used to estimate size selectivity and capture efficiency for ocean quahogs in a commercial hydraulic clam dredge.

Experiment	Date	Tow	Temperature (°C)	Area swept (m^2)	Dredge catch (kg)	Number of quahogs in dredge sample	Mean weight of quahogs in dredge sample (kg quahog^{-1})	Weight of dredge sample (kg)	Dredge subsample fraction (f)	Dredge catch number	Boxcore samples/area sampled (a, m^2)/number quahogs in samples
1	July 2002	1	8	2 148	3 167	70	0.112 (assumed)	7.8	0.00248	28 277	24/6/408
		2		2 035	2 325	60		6.7	0.00289	20 759	
		3		1 967	3 581	100		11.2	0.00313	31 973	
		4		2 639	4 931	140		15.7	0.00318	44 027	
2	September 2002	1	8	2 204	3 003	106	0.089	9.4	0.00313	33 864	12/3/582
		2		2 057	2 416	119	0.088	10.5	0.00435	27 381	
3	April 2003	1	2	1 475	2 000	51	0.125	6.4	0.00320	15 938	24/6/507
		2		1 684	2 706	64	0.113	7.2	0.00266	24 053	
		3		1 622	2 513	61	0.120	7.3	0.00290	20 999	

refine estimates of commercial size selectivity, and to characterize the variability in size selectivity among experimental tows. Thorarinsdóttir and Jacobson (2005) estimated size selectivity based on the same data used here, but they did not estimate dredge efficiency or variability in size selectivity.

Following Millar *et al.* (2004), we used fixed- and mixed-effects statistical approaches and modified existing selectivity models (Fryer, 1991; Millar, 1992) to estimate capture efficiency and size selectivity simultaneously, using diver and dredge samples collected during the experiments. The main advantage in estimating capture-efficiency and size-selectivity parameters in the same model is to make them consistent and to make capture-efficiency estimates independent of the size structure of the underlying population. The model simultaneously estimated capture efficiency, in effect, after making adjustments for size selectivity and the size structure of the underlying population. This approach may be useful in other situations where capture efficiency is of particular interest.

Mixed-effects models were useful in the analysis because (i) data were limited and the number of model parameters was reduced, (ii) differences in size selectivity among experiments and tows were random rather than attributable to experimental treatments, and (iii) the variances for random effects on size selectivity were of interest. Moreover, in estimating the underlying population means for size-selectivity and capture-efficiency parameters, it was important to understand the precision of the estimates apart from the variability of parameters for different experiments (Pinheiro and Bates, 2000).

An important motivation for our collaborative analysis was its potential applicability to commercial fishing operations in US waters. The accuracy of depletion experiments and the relative complexity of the Rago *et al.* (2006) spatial depletion model used to estimate capture efficiency off the United States have not been fully evaluated. The accuracy of model estimates may be influenced by the uncertainty in dredge position data. Uncertainty about dredge position increases with depth because the ship's GPS location is used as a proxy for dredge location during depletion studies (NEFSC, 2007a, b). The relationship between the positions of the ship and the dredge may be variable at the depths where ocean quahogs are found in US waters. The model of Rago *et al.* (2006) is applied to data for large ocean quahogs only (83+ mm SL), which are believed, based on preliminary size-selectivity estimates in Thorarinsdóttir and Jacobson (2005), to have size selectivities of at least 0.85 (NEFSC, 2007a). The spatial model has not been extended to estimate size-selectivity parameters simultaneously, which would permit the use of ocean quahogs of all sizes taken in depletion experiments. Exclusion of data on smaller animals reduces the sample size considerably and increases the variance of estimates from the spatial model. Therefore, direct field-based estimates of capture efficiency using other methodologies that account for size selectivity are of interest. It is also possible that our statistical approach to simultaneously estimating capture-efficiency and size-selectivity parameters might be applicable to depletion-study analysis.

Material and methods

Three experimental fishing trips were carried out in Thistilfjordur off the northeast coast of Iceland during July and September 2002 and April 2003, using the fishing vessel ÞH-362 Fossá, the only vessel currently targeting ocean quahogs in Iceland waters. A different experimental site in the Thistilfjordur area was utilized during each experimental fishing trip. The seabed at all sites was smooth, tightly packed sand, typical ocean quahog habitat (Cargnelli *et al.*, 1999). Sampling depths ranged from 9 to 11 m, and water temperatures at 6-m depth ranged from 2 to 8°C (Table 1). Ocean quahogs can have a patchy spatial distribution with catches sometimes characterized using a negative binomial distribution (NEFSC, 2007a). However, experimental sites were selected to have relatively high densities of ocean quahogs, with a relatively even spatial distribution.

Commercial dredge sampling

The hydraulic dredge used in the study was based on the design of dredges used in the United States (735 cm long, 150 cm high, 365 cm wide). The cutting blade was 305 cm wide and extended 8 cm below the dredge. During all tows in each experiment, tow speeds ($\sim$4.4 km h^{-1}), tow duration ($\sim$5 min), the ratio of warp length to water depth, and water pressure at the water pump on deck (7.5 bars) were similar to those in commercial operations. Water pressures are similar in dredges used for ocean quahogs off the United States (6.9–8.3 bars at pumps on deck; D. Wallace, Wallace and Associates Ltd, Cambridge, MD, USA, pers. comm.).

Four dredge tows were taken at the first experimental site during July 2002, two at the second site during September 2002, and three at the third site during April 2003 (Table 1). Divers marked the start and endpoints of the intended dredge path for each tow with buoys, and GPS coordinates of these locations were recorded aboard the ship. In shallow water, the ship's position is a good proxy for dredge position because the distance and relative positions of the dredge and vessel are relatively constant. Dredge tows were parallel and close together so that one set of diver samples could be used to measure the underlying population length composition and density of ocean quahogs in each experiment (Table 1).

After each tow, the total catch weight and tow path length (based on ship positions) were recorded. An approximately random sample (~15 kg) of ocean quahogs was taken from each tow after the dredge was emptied and before any sorting took place. Individual quahogs >10 mm SL in the sample were counted and measured with callipers to the nearest 0.1 mm. Dredge samples from tows during September and April were weighed in aggregate, but samples during July were not. Based on results from a variety of studies (GGT, unpublished data), the weight of subsamples from the July dredge catches was calculated assuming a mean ocean quahog body weight of 112 g. This assumption increases the uncertainty in estimates of capture efficiency made from the experiments conducted during July, but it has only a small effect on the overall capture-efficiency estimate from this study (see Discussion).

Diver sampling

Two divers collected core samples randomly (each core covered 0.25 m^2 of seabed) from undisturbed areas along and at least 5 m away from each dredge track (Table 1). In all, 24 cores (6 m^2) were collected during July 2002 and April 2003, and 12 (3 m^2) during September 2002. The corers were pushed 25 cm past the surface of the substratum. Ocean quahogs have not been observed >15 cm below the surface of the substratum off Iceland during winter, when burrowing behaviour is pronounced (GGT, unpublished data). Sediments were extracted from corers with an underwater suction sampler, and sieved through a mesh of 1 mm. All ocean quahogs >1 mm SL in the diver samples were measured, those >10 mm with callipers to the nearest 0.1 mm, and smaller ones under a stereoscope.

In Experiment 3 during April 2003, 24 core samples were also taken at random locations within each of the three dredge tracks after the dredge had been towed, using the same equipment and approach used in adjacent undredged areas. The total area sampled by divers in the dredge tracks was the same as the total area of undredged substratum sampled in Experiment 3 (Table 1).

The primary data from the dredge were counts of ocean quahogs ($C_{x,t,L}$) in each experiment (x), tow (t), and SL category (L) for samples from the catch. The primary diver data were counts of ocean quahogs ($D_{x,L}$) collected in cores by the divers for each experiment and SL category.

A model to estimate size selectivity and capture efficiency

A modified version of Millar's (1992) SELECT model was used to estimate the capture efficiency and the size selectivity for the experimental dredge simultaneously. Following Thorarinsdóttir and Jacobson (2005) and NEFSC (2007a), size selectivity (s_L) for ocean quahogs was assumed to increase with size:

$$s_L = \frac{(1/1 + e^{\alpha - \beta L})^{1/\delta}}{K}, \tag{1}$$

and

$$K = \left(\frac{1}{1 + e^{\alpha - \beta L_{\mathrm{MAX}}}}\right)^{1/\delta}, \tag{2}$$

where L is SL, L_{MAX} (107.5 mm SL) the maximum SL in the data used to fit the selectivity curves (and near the maximum size for ocean quahogs off Iceland), $\beta = e^{B}$, $\delta = e^{\Delta}$, and α, B and Δ are parameters. K is the unscaled selectivity at L_{MAX}. When $\delta = 1$ ($\Delta = 0$), Equation (1) describes the traditional logistic selectivity curve, which is symmetrical. When $\delta \neq 1$ ($\Delta \neq 0$), Equation (1) describes an asymmetric "Richards" curve (Millar and Fryer, 1999). In particular, the left side of the curve is elongated when $\delta > 1$ ($\Delta > 0$) and the right side is elongated when $0 < \delta < 1$. The log scale parameters B and Δ ensure that the terms β and δ are positive and facilitate parameter estimation.

The SL at which the selectivity in Equation (1) reaches a specified percentage π ($0 < \pi < 1$) is

$$L_p = \frac{\alpha - \ln[(K\pi)^{-\delta} - 1]}{\beta}. \tag{3}$$

The SL at 50% selectivity ($L_{50\%}$) was used to describe the position of the selectivity curve with respect to size (Millar and Fryer, 1999). Similarly, the selectivity range ($\mathrm{SR} = L_{75} - L_{50}$) was used to describe the steepness of the curve (Millar and Fryer, 1999).

Ignoring the subscripts and considering large fully selected quahogs, the expected count of ocean quahogs collected by divers is $d = a\Lambda$, where d is the expected value of the observed counts D, a the area sampled by the core sampling, and Λ the density of ocean quahogs (numbers m^{-2}) in the study area. The expected count of quahogs subsampled from the dredge catch and measured is $c = AEf\Lambda$, where c is the expected value of the observed counts C, A the area swept by the dredge (the product of blade width and tow distance, m^2), E the dredge capture efficiency, and f the fraction subsampled (weight of a random subsample divided by weight of total catch). Capture efficiency was calculated from $E = 1/(1 + e^{\eta})$, where η is an estimated parameter. This formulation enhances model stability and ensures that efficiency estimates were between 0 and 1.

The proportion of total catch taken in the dredge was used as the dependent variable in fitting selectivity curves by the SELECT method. The expected proportion of the total catch for large, fully selected ocean quahogs taken by the dredge is

$$p = \frac{c}{c + d} = \frac{AEf\Lambda}{AEf\Lambda + a\Lambda} = \frac{AEf}{AEf + a}. \tag{4}$$

Millar (1992) described p as the "relative fishing intensity", but in practice it is often called the "split parameter".

Size selectivity reduces the catch of small ocean quahogs in the dredge. The expected proportion of the total catch taken by the dredge for one SL group (Millar, 1992) is

$$\phi_L = \frac{ps_L}{ps_L + 1 - p}. \quad (5)$$

Note that Equation (5) reduces to Equation (4) for fully selected individuals with selectivity $s_L = 1$. Equation (5) is perhaps easiest to understand with $s_L = 1$ (no loss of dredge catch through size selectivity) because it reduces to $\phi = p = c/(c + d)$ from Equation (4). With size selectivity $s_L \leq 1$, the proportion taken in the dredge (p) in the denominator of Equation (5) must be reduced to account for losses through size selectivity. Given the selectivity model Equation (1) and conditioning on the observed total catch, $N_L = C_L + D_L$, the expected count of ocean quahogs taken by the dredge, subsampled and measured, is $c_L = \phi_L N_L$.

During commercial operations, catches are sorted mechanically to remove small objects (including small ocean quahogs that did not fall out between the bars in the dredge) then by hand to remove larger unwanted objects. The samples in our experiments were taken directly from the dredge, before mechanical sorting. The effects of sorting and any resulting differences between catch and landings were not included in our analysis.

Parameter estimation

All models assumed that the dredge catches in each size group were sampled from a binomial distribution, with probability of success $\phi_{x,t,L}$ and sample size $N_{x,t,L}$ that might vary between experiments (x), tows (t), and shell height bins (L). Diver and dredge catch data were aggregated by 5-mm shell height groups. The midpoints of shell height bins were used in calculations (e.g. 22.5 mm was used in calculations for ocean quahogs in the 20–24.9 mm SL group). SLs were centred on the mean SL in our data during parameter estimation to reduce spurious correlations in parameter estimates that might affect modelling decisions (Pinheiro and Bates, 2000). Modelling results are, however, reported in terms of the original SL measurements.

Following Millar *et al.* (2004), size-selectivity and capture-efficiency parameters were estimated by maximum likelihood in fixed- and mixed-effects statistical models, using the SAS program NLMIXED (Littell *et al.*, 2006). Fixed-effects models were used primarily to make decisions about the final mixed-effects model structure (Pinheiro and Bates, 2000). Fixed-effects models are the original approach to fitting the SELECT models (Millar, 1992), and they assume no random variability in model parameters among experiments or tows. Random variability in selectivity parameters is possible in many circumstances (Fryer, 1991), and it can be accommodated using non-linear mixed-effects models and maximum likelihood, as demonstrated by Millar *et al.* (2004). In particular, mixed-effects models in this analysis assumed that random effects on parameters (E, α, B, and Δ) were independently and normally distributed, with mean zero and variances estimated in the model. For example, random effects on the α parameter would be modelled as $\alpha_{x,t} = \alpha + \omega_{x,t}$, where α is the mean parameter value for the population, and $\omega_{x,t} \sim N\ (0,\sigma_\omega^2)$ are normally distributed random effects with estimated variance σ_ω^2.

The selectivity model applied to our data in Equation (5) has four main parameters that potentially require estimation (η for capture efficiency and α, B, and Δ for size selectivity). Mixed-effects models also require estimation of variance and covariance parameters for any random effects included in the model (Pinheiro and Bates, 2000). If selectivity follows a symmetric logistical pattern ($\Delta = 0$), then the number of parameters to estimate is reduced by at least one (two, including the potential random effects).

Akaike's Information Criterion (AIC) and Bayesian Information Criterion (BIC) statistics were used to evaluate the goodness-of-fit in choosing the "best" model for our data. Models with smaller AIC and BIC statistics are better on statistical grounds than models with larger AIC and BIC statistics. AIC and BIC are similar except that BIC is based on the number of observations, as well as the likelihood and the number of parameters (Pinheiro and Bates, 2000). Deviance residuals and observed and predicted values of p were plotted to evaluate the goodness-of-fit (Millar, 1992).

Results

Based on the diver samples collected in 2002 and 2003 (Table 1), ocean quahogs of 20–30 and 50–60 mm SL were most common (Figure 1) in the population at Thistilfjordur. SL data from the hydraulic dredge and diver samples indicated that the dredge was highly selective towards large ocean quahogs because ocean quahogs <50 mm SL were scarce in the dredge samples (5% of total catch number), but common in diver samples (47% of total number; Figure 1). All the ocean quahogs recovered from samples within the tracks after dredging in Experiment 3 were relatively small (<65 mm SL), indicating that the dredge was selective towards large ocean quahogs.

Ocean quahog density was higher at experimental sites off Iceland than at US depletion study sites. Based on diver samples, the density of ocean quahogs 90+ mm SL was 4.1 per m^2 off

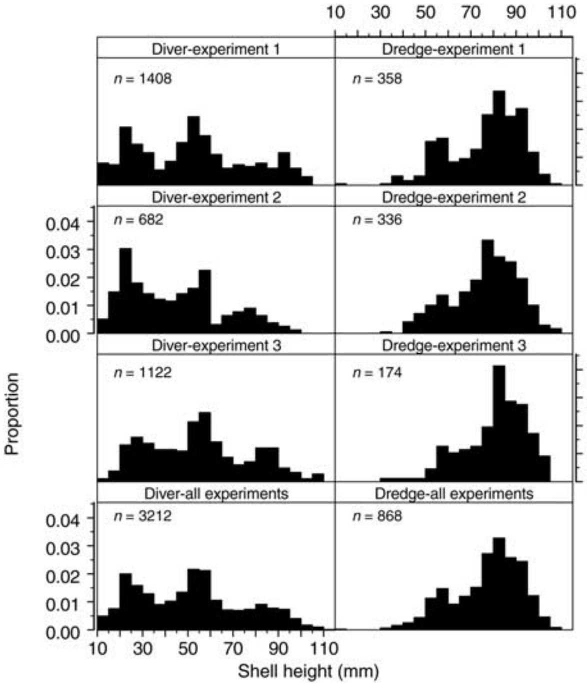

Figure 1. Size composition data for ocean quahogs in diver and dredge samples for each experimental fishing trip, and all trips combined.

Iceland compared with a median value of 0.88 per m^2 at US depletion study sites.

Fixed-effects models

The set of all possible fixed-effects models with either one (for all tows) or nine (one for each tow) sets of α, β, Δ, and η parameters were fitted, and the AIC and BIC statistics were compared. The set included models with asymmetrical selectivity curves (1 or 9 Δ parameters), and symmetrical selectivity curves with $\Delta = 0$. The simplest model had a single set of α, B, and E parameters, and $\Delta = 0$ (three estimated parameters). The most complicated or "full" model successfully fitted had nine α, β, and η parameters, and a single asymmetry parameter Δ (28 estimated parameters). Intermediate models had all possible combinations of one and nine α, β, and η parameters (e.g. one β, and nine α and η parameters). Fixed-effects models with multiple asymmetry parameters did not converge.

Based on goodness-of-fit statistics (AIC = 554.7, BIC = 590.6), the best fixed-effects model was symmetrical ($\Delta = 0$), with different α parameters for each tow, and single β and capture-efficiency parameters ($E = 0.92$, s.e. 0.076), for a total of 11 estimated parameters. For comparison, selectivity estimates from the full fixed-effects model with 28 estimated parameters were AIC = 569.5 and BIC = 687.2, and the capture efficiencies were 0.65, 0.74, 0.79, 0.90, 1.00, 0.61, 0.61, 0.68, and 0.79 (order the same as in Table 1), with an average value of $E = 0.74$ (s.e. = 0.13).

Mixed-effects models

The preferred mixed-effects model was symmetrical ($\Delta = 0$), with random effects on α ($\sigma^2_\omega = 0.53$, s.e. = 0.30) only (Table 2). Estimated capture efficiency was $E = 0.92$ (s.e. = 0.076) for ocean quahogs of 107.5 mm SL, $L_{50} = 70$ mm (s.e. = 2.7) mm, and SR = 18 (s.e. = 1.1) mm. There were substantial correlations with absolute value >0.5 among estimates of the capture-efficiency parameter (η) and size-selectivity (α, B) parameters (Table 3). However, the correlation between final estimates of size selectivity and capture efficiency were minimized because maximum selectivity was rescaled to 1 in Equation (1). Diagnostic plots showed a generally good model fit, although there was a cluster of positive residuals for ocean quahogs 60+ mm SL in the fit to data from Tow 1 in Experiment 2.

For the preferred model, AIC = 568.5 and BIC = 569.3, compared with AIC = 554.7 and BIC = 590.6 for the best fixed-effects model. Therefore, the best fixed-effects model was better based on AIC, whereas the preferred mixed-effects model was better based on BIC. The mixed-effects modelling approach was preferred overall because it provided an estimate of the mean underlying population size-selectivity curve and a formal estimate of the variability in size selectivity among tows (Table 4, Figure 2). We did not use AIC and BIC models to choose between the fixed- and mixed-effects modelling approaches. Our strategy was to choose the best among all possible fixed-effects models based on AIC, then to identify a preferred mixed-effects model that was nearly equivalent in structure (Pinheiro and Bates, 2000). The best fixed-effects and preferred mixed-effects models gave identical estimates of average capture efficiency ($E = 0.92$), although the standard error was much smaller for the preferred mixed-effects model (0.076; Table 2) than for the best fixed-effects model (0.13).

Table 2. Parameter estimates for the preferred mixed-effects model for ocean quahogs collected off Iceland.

Parameter	Estimate	s.e.	CV (%)
α	8.7005	0.5190	6
σ^2_ω	0.5397	0.2996	56
B	−2.0945	0.0712	3
$\beta = e^B$	0.1231	0.0088	7
η	−2.4462	1.0302	42
$E = 1/(1 + e^\eta)$	0.9203	0.0757	8
L_{50}	70.4871	2.6740	4
SR	17.6187	1.1446	6

Variances were calculated using the delta method.

Table 3. Estimated correlation matrix (delta method) for capture-efficiency and size-selectivity parameter estimates in the preferred mixed-effects model.

Parameter	α	$B = \ln(\beta)$	η	σ^2_ω
α	1			
B	−0.65	1		
η	−0.58	0.50	1	
σ^2_ω	−0.10	0.20	0.091	1

Table 4. Population selectivity curve based on the preferred mixed-effects size-selectivity model fitted to experimental data for ocean quahogs off Iceland.

SL	Selectivity	s.e.	CV (%)
2.5	0.0002	0.0001	50
7.5	0.0004	0.0002	47
12.5	0.0008	0.0003	43
17.5	0.0014	0.0006	40
22.5	0.0027	0.0010	37
27.5	0.0049	0.0017	34
32.5	0.0091	0.0029	32
37.5	0.0168	0.0050	30
42.5	0.0306	0.0086	28
47.5	0.0552	0.0148	27
52.5	0.0976	0.0249	26
57.5	0.1669	0.0403	24
62.5	0.2709	0.0597	22
67.5	0.4083	0.0773	19
72.5	0.5624	0.0842	15
77.5	0.7064	0.0761	11
82.5	0.8199	0.0581	7
87.5	0.8978	0.0386	4
92.5	0.9464	0.0227	2
97.5	0.9749	0.0116	1
102.5	0.9911	0.0044	0
107.5	1.0000	n.a.	n.a.

Variances were calculated by the delta method and measure variation in size selectivity among tows in the experiment. SLs in the table are the middle of 5-mm SL intervals. n.a., not applicable.

Discussion

As expected based on other studies, the commercial hydraulic clam dredge used in this study was highly selective towards large ocean quahogs. In dredge catches, 18% of all ocean quahogs were <60 mm SL (Figure 1). In comparison, 68% of ocean quahogs were <60 mm SL in diver samples. Length composition data for

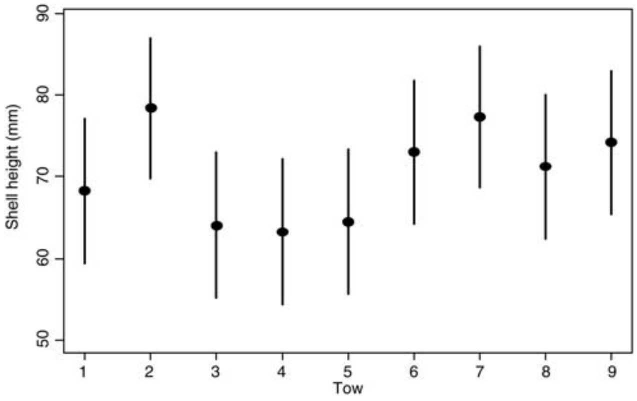

Figure 2. Estimated $L_{50\%}$ (dots) and selectivity range (SR, vertical lines) for selectivity curves from the preferred mixed-effects model. Tows 1–4 are Experiment 1, Tows 5 and 6 are Experiment 2, and Tows 7–9 are Experiment 3 (the same order as Table 1).

ocean quahogs from commercial dredges in US studies are similar, with animals <60 mm SL rarely caught (NEFSC, 2007a).

The potential effects of assuming that the mean weight of ocean quahogs in dredge samples during Experiment 1 was 112 g (Table 1) are relatively small. The mean weight is used to compute the sampling fraction $f = Nw/C$ in Equation (4), where N is the number of ocean quahogs sampled from the dredge catch, $w = 0.112$ kg the mean weight, and C the total dredge catch in kilogrammes. The sampling fraction influences capture efficiency but not estimates of size selectivity. Substituting Nw/C for the sampling fraction f in Equation (4) and solving for capture efficiency gives $E = paC/ANw(1-p) = K/w$, where K is a constant calculated with the data from Experiment 1. This means that a 1% underestimate of mean weight would result in a ∼1% overestimate of capture efficiency in Experiment 1, and vice versa. Effects on the best estimate of capture efficiency from all three experiments would be smaller.

There was substantial variability among tows in the α selectivity parameter ($\sigma_{\omega}^2 = 0.540$; Table 2) not apparent to Thorarinsdóttir and Jacobson (2005). The variance in α caused substantial variability in L_{50} among tows (Figure 2). Based on our preferred mixed-effects model (Figure 3), $L_{50} = 70$ mm and SR = 18 (Table 2). In comparison, Thorarinsdóttir and Jacobson (2005) estimated $L_{50} = 72$ mm and SR = 21 mm by combining all datasets and using a simple fixed-effects SELECT approach.

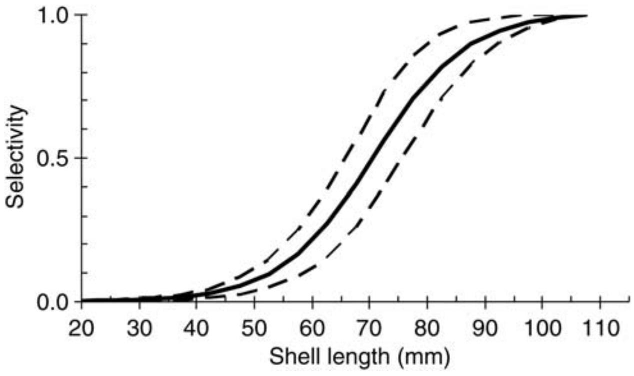

Figure 3. Estimated population size-selectivity curve for the ocean quahog off Iceland in a commercial clam dredge, with approximate 95% confidence intervals shown.

The estimates ($E = 0.92$, s.e. = 0.076) from our preferred model indicate that capture efficiency was close to 1.0 for ocean quahogs taken by the commercial dredge in our experiments. The 95% confidence interval for $\eta = -2.45$ (s.e. = 1.03) from the NLMIXED program is (−4.83, −0.0671). Ignoring non-linear effects, an approximate 95% confidence interval for $E = 1/(1 + e^{\eta})$ is (0.517, 0.992). Capture-efficiency estimates from depletion studies in US waters for Atlantic surfclam (at depths of 21–41 m; NEFSC, 2007b) and ocean quahogs (35–65 m; NEFSC, 2007a) indicate that capture efficiency is <1 for commercial clam dredges. Large ocean quahogs displaced by the dredge or observed in the dredge track would be the strongest direct evidence that capture efficiency is <1. No ocean quahogs >65 mm SL were found in core samples in the dredge tracks in Experiment 3. However, the number of samples (six cores) was relatively small, and the probability of detecting a large quahog after fishing with a highly efficient ($E = 0.92$) commercial clam dredge may be low. In contrast, Murawski and Serchuk (1989b) reported ocean quahogs remaining in and displaced laterally up to 5 m away from the dredge track. It seems likely that there is displacement in shallower waters off Iceland too.

The preferred mixed-effects estimate for capture efficiency ($E = 0.92$, s.e. = 0.076) was substantially higher than the mean commercial capture-efficiency estimates for ocean quahog off the United States, i.e. $E = 0.66$ (s.e. = 0.065) from the spatial model of Rago *et al.* (2006) and 17 commercial depletion experiments in US waters (see Table A12 of NEFSC, 2007a). However, the 95% confidence interval for capture efficiency in our experiments (0.517, 0.992) contains the mean $E = 0.66$ and lies within the range of individual estimates ($E = 0.15$–1.0) for ocean quahogs in US waters, demonstrating that statistical difference cannot be shown.

Differences in SL do not explain the difference between capture-efficiency estimates from our study and from depletion experiments in US waters. As described above, NEFSC's (2007a) estimate of $E = 0.60$ (Table A12 of NEFSC, 2007a) is for ocean quahogs ≥90 mm SL that were assumed to have size selectivity ≥0.85. Animals included with shell heights near the cut-off have selectivity near 0.85 and cause negative bias in NEFSC's (2007a) estimates of capture efficiency. Using the product of capture efficiency (Table 2) and size selectivity (Table 4) to adjust for shell height differences, the capture efficiency for ocean quahogs ≥90 mm SL off Iceland is ≥0.75, still higher than the corresponding estimate for US waters.

We were not able to evaluate fully the hypothesis that season, habitat, and substratum type explained the differences in capture-efficiency estimates for the United States and Iceland. It is possible, for example, that ocean quahogs in depletion experiments were relatively deep in sediments and hard to sample because of season effects. However, US depletion experiments were conducted from April to September at depths of 35–65 m, where catch rates are normally high (Table A11 of NEFSC, 2007a). Rocks and habitat structure may reduce capture efficiency, but US depletion experiment sites were in sandy habitats where ocean quahogs were abundant, catch rates relatively high, commercial dredges operate efficiently, and where rocks would not be expected to interfere with the depletion experiment.

Estimates of capture efficiency might differ between Iceland and the United States if commercial dredges operate more efficiently in shallow water. Mean capture efficiency was higher for Atlantic surfclams ($E = 0.70$) in 19 commercial depletion experiments at relatively shallow depths of 21–41 m (NEFSC, 2007b), but Atlantic surfclams do not burrow as deeply as ocean quahogs, are larger, and are likely easier to capture. No clear relationship between depth and commercial capture efficiency was observed in 17 ocean quahog depletion experiments at 35–65 m (NEFSC, 2007a) or in 19 Atlantic surfclam depletion experiments at 24–41 m (NEFSC, 2007b). Inclinometer data collected during depletion studies indicates that heavy commercial dredges operate hard on the bottom at the correct angle of attack over a wide range of depths, and under a wide range of ocean conditions.

Differences between the estimates may be due to bias in the spatial model used to estimate capture efficiency from depletion experiments in US waters (NEFSC, 2007a, b), and this is an issue for future research. The ship's GPS position is used during depletion experiments as a proxy for the position of the dredge. Positional uncertainty probably increases with depth and may be substantial in deep-water ocean quahog habitat off the United States.

The main advantages in working off Iceland in shallow water were that information about the underlying true population length composition and density of quahogs was relatively easy to obtain, sampling conditions were ideal, and the position of the dredge relative to core samples was relatively certain. The main disadvantage was that no direct information on capture efficiency in deep water (or under difficult sampling conditions) was obtained. The applicability of estimates of capture efficiency to the US fishery is uncertain, and Icelandic estimates should not be used for the US fishery. Estimates of size selectivity from our study are likely robust, in contrast, and applicable to commercial dredges in US water of the same design and similar bar width.

NEFSC (2007a, b) considered size selectivity in estimating capture efficiency by excluding the data for relatively small animals. Our study shows that methods that simultaneously estimate both parameters are feasible and probably better, because it is not necessary to discard data. Our approach involves a reasonable number of parameters to estimate (four parameters for ocean quahogs in this study), because capture efficiency replaces the split parameter [p in Equation (4)] used in the original SELECT model (Millar, 1992). In comparison, the spatial model of Rago *et al.* (2006) has three or four estimated parameters, but does not estimate size selectivity or include random effects. Using the SELECT model, we were able to estimate correlations among estimates of capture-efficiency and size-selectivity parameters (Table 3). Of course, our SELECT model and experimental methods would be more difficult to apply for ocean quahogs off the United States, in relatively deep water.

The approach used in our study is among the best methods used to estimate capture efficiency for bivalves (Mason *et al.*, 1979). Another method for estimating dredge efficiency involves comparing the number of shellfish left unharvested in the dredge track with the number of animals captured in the dredge (Caddy, 1968; Medcof and Caddy, 1971; Mason *et al.*, 1979). Using this method, Medcof and Caddy (1971) estimated E to be 76% for hydraulic dredges taking ocean quahogs.

We parameterized the SELECT model in terms of capture efficiency E and additional data (A, f, and a), and estimated E rather than p. It may be generally useful to parameterize the SELECT model in this manner because capture efficiency is easy to interpret, has a long history in fisheries (Paloheimo and Dickie, 1963), and has a particular importance in assessment of non-mobile benthic invertebrates such as ocean quahogs. Similar approaches have been used elsewhere. For example, the SAS NLMIXED program given (Appendix A.2 of Millar *et al.*, 2004), which accommodates sampling fractions, and random effects on α and on catchability, could have been used in our analysis with modification and redefinition of terms. The software we used incorporated random effects in capture efficiency and all selectivity parameters, but the only random effects that proved useful were those on α.

We used K in Equation (1) to scale the SELECT model to a maximum value of 1.0 at 107.5 mm SL. This technique makes selectivity estimates directly useful in size-structured stock assessment models, where maximum selectivity is 1 by definition. Selectivity is scaled to a maximum of 1 in stock assessment models so that fishing mortality (F) and selectivity estimates are unique and not confounded in the product Fs_L (Deriso *et al.*, 1985). Without rescaling, efficiency estimates would be for a hypothetical ocean quahog of infinite size, rather than a realistically large animal. Non-linear models (such as growth curves; Schnute, 1981) can be easier to fit, and estimates may have better statistical characteristics when parameters measure properties in the range of the data. Mixed-effect models, in particular, can be difficult to fit because the number of parameters increases with marginal likelihoods being computed. If L_{MAX} is relatively large, as in our study, the scaling factor K probably has little effect on the estimated selectivity curves beyond potential benefits in characterizing fishing mortality and reducing statistical correlations between estimates of size selectivity and capture efficiency.

Conclusion

Estimates of capture efficiency are important in managing fisheries off the United States and Iceland. Ocean quahogs are relatively unproductive and probably sensitive to overharvest that might result from inaccurate estimates of harvest efficiency. Results of our study indicate that capture efficiency is high ($E = 0.92$) for ocean quahogs in commercial dredges off Iceland. The estimate from our work off Iceland was significantly higher than the distribution of estimates from commercial depletion studies in US waters.

There was substantial variability in size selectivity among tows. The estimated population selectivity curve was relatively steep, with $L_{50} = 50.5$ mm and SR $= 17.6$ mm. Confidence intervals indicate that the estimated population selectivity curve is sufficiently precise for use in stock assessment work (Table 4, Figure 3), but statistical precision does not guarantee applicability to a particular situation.

Selectivity estimates from our experiments off Iceland are probably applicable to similar commercial dredges of the same design and with similar bar width in the US fishery. Those who use the selectivity or efficiency parameters from our analysis should confirm, however, that the fishing gear involved is similar to our experimental gear.

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