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Length-selective retention of walleye pollock, *Theragra chalcogramma*, by midwater trawls

Kresimir Williams [1,2]*, André E. Punt [2], Christopher D. Wilson [1], and John K. Horne [2]

[1] *National Marine Fisheries Service, Alaska Fisheries Science Center, Resource Assessment and Conservation Engineering Division, 7600 Sand Point Way NE, Seattle WA 98115, USA*

[2] *School of Fisheries and Aquatic Sciences, University of Washington, 1122 NE Boat Street, Seattle, WA 98105, USA*

**Corresponding Author: tel: +1 206 526 4133; fax: +1 206 526 6723; e-mail: kresimir.williams@noaa.gov.*

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Midwater trawls are commonly used during acoustic surveys of fish abundance to determine species and length compositions of acoustically sampled fish aggregations. As trawls are selective samplers, catches can be unrepresentative of sampled populations and lead to biased abundance estimates. Length-dependent retention of walleye pollock was estimated using small recapture nets, so-called pocket nets, attached to the outside of the trawl. Experimental haul sets comprising eight hauls each were conducted in the Gulf of Alaska in 2007 and 2008 and in the eastern Bering Sea (EBS) in 2007. Pocket-net catches were then modelled by fitting parameters for selectivity and escapement location along the trawl. Within- and between-haul variability was jointly estimated using hierarchical Bayesian methods. There was significant undersampling of juvenile (<25 cm) pollock, with the length-at-50%-retention (L_{50}) estimated between 13.5 and 26.1 cm among haul sets. In the EBS set, L_{50} values were correlated with light level, escapement being greater at night. Trawl selectivity may be a significant source of error in acoustic-survey estimates of the abundance of pollock.

Keywords: acoustic surveys, trawl selectivity, walleye pollock.

Introduction

Walleye pollock (*Theragra chalcogramma*; pollock hereafter) stocks in waters off Alaska sustain the world's second-largest, single-species fishery by catch weight (FAO, 2009). Management of the fishery depends on regular fishery-independent acoustic surveys to estimate age-specific abundance (Karp and Walters, 1994). During these surveys, midwater trawls are used to identify the species and length compositions of the fish aggregations detected acoustically. Catch data are then used to scale measurements of acoustic backscatter into abundance (Honkalehto *et al.*, 2009).

It is assumed that catch compositions in trawls accurately represent the source of the backscattering measured by a vessel's acoustic instrumentation. However, all trawl gears are size selective to some degree (Wileman *et al.*, 1996), so smaller individuals are typically not represented proportionally. This bias may become significant in situations where the insonified population contains a range of sizes. Pollock trawl catches commonly contain a broad range of fish lengths (9–70 cm), so trawl-gear selectivity is potentially an important source of error in survey abundance estimates.

Trawl selectivity has different functions in commercial and research settings. For commercial fishing operations, it is desirable to minimize bycatch (non-targeted species or undersized target fish) by designing gear that is selective for market-sized individuals of the target species (MacLennan, 1992). Research on trawl selectivity of commercial gear has focused on estimating the escapement of unwanted fish from codends. In contrast, trawls used for stock assessment aim to minimize selectivity to ensure representative sampling of fish populations (Dremiere *et al.*, 1999). Establishing the selectivity of research trawl gear requires estimates of escapement from the entire trawl gear, i.e. the trawl body and the codend. Codend escapement can be measured directly by recapturing all the escaping fish in a codend cover (Wileman *et al.*, 1996). Estimating trawl-body escapement poses technical challenges, especially for midwater trawls where the surface area of the trawl is very large. For example, a bottom trawl used in the Alaskan trawl surveys has a surface area of ~550 m^2 compared with the ~6500 m^2 area of a midwater trawl.

The escapement of pollock from a midwater trawl was investigated by attaching small recapture bags on the outside of the trawl surface. Previous experiments with such so-called pocket nets have shown that the fish caught in them are smaller than those caught in the codend (Nakashima, 1990; Suuronen *et al.*, 1997). To estimate the total escapement from the trawl body, pocket-net catches have to be expanded to represent the entire trawl surface (Polet, 2000). Extrapolation of pocket-net catches does not explicitly incorporate error from the random effects of sampling a small portion of the trawl area. Owing to concerns regarding the potential errors in scaling, Dremiere *et al.* (1999) used a more conservative approach by not expanding recapture net catches to the entire trawl surface, but rather to partitions of the trawl for which the recapture net could be considered as representative, so underestimating total escapement. In this study, trawl selectivity was estimated using a modelling approach to incorporate additional uncertainty stemming from the partial sampling of escapement. The model used a hierarchical Bayesian approach (HBA) to incorporate additional uncertainty in selectivity resulting from haul-to-haul variability in selectivity.

We also introduce a new analytical approach for estimating selectivity and apply this methodology to evaluating the pollock acoustic-survey trawl gear. Our aim was to outline not only the methodological developments for research groups using similar trawl gear in a scientific setting, but also to provide insight on potential trawl-based error specific to the pollock-management process.

Material and methods

Characteristics of midwater trawls

Pollock acoustic surveys conducted by the Alaskan Fisheries Science Center of the National Marine Fisheries Service use a four-seam Aleutian wing trawl (AWT) with a headrope of ~90 m, a smaller version of the commercial trawl commonly used in the commercial fishery for pollock. The AWT has an opening of ~25 m in the vertical and 35 m in the horizontal while fishing. The trawl diameter at the codend is ~1.5 m. Trawl length is ~140 m from the aft-most point of the headrope to the end of the codend. The mesh sizes of the trawl range from 3.25 m (stretch measurement) at the opening to 100 mm in front of the codend. Meshes >100 mm are constructed of white nylon twine, and the final section of 100 mm meshes forward of the codend is constructed of orange polyethylene twine. The codend in the research trawl is constructed of 100 mm mesh constructed of twine of 4 mm thickness and double-bar polyethylene, and it contains a 12-mm nylon mesh liner for the full length of the codend. With the liner in place, the codend is assumed to retain most pollock >8 cm long.

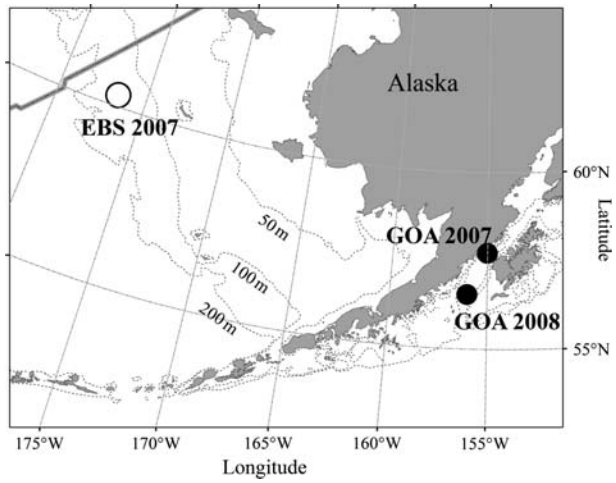

Figure 1. The locations of the selectivity trials. The two GOA experimental sets were conducted during the Shelikof Strait acoustic pollock spawning survey during March, and the EBS set during the EBS pollock summer survey during July.

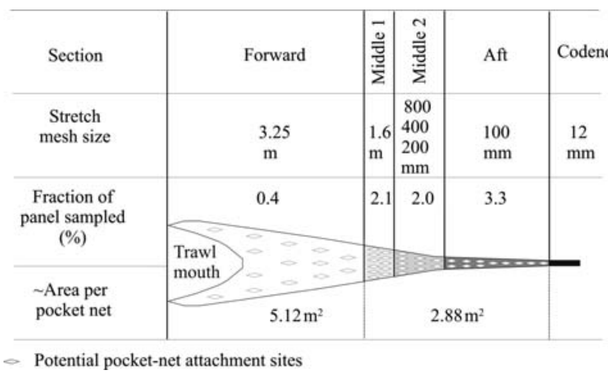

Figure 2. The experimental design used in the selectivity trials. The figure represents one of four trawl panels (top, bottom, port, and starboard sides). A single pocket net was attached to one position selected randomly on each section. The sampling fraction is the ratio of the number of meshes covered by the pocket net to the total number of meshes in each section/panel.

Fishing operations

Catch and related observations were collected from three sets of eight hauls, each taken within a 24–36-h period during the standard stock-assessment surveys. Two sets were taken in Shelikof Strait and in the Gulf of Alaska (GOA) by the NOAA ship "Miller Freeman" in March 2007 (GOA07) and the NOAA ship "Oscar Dyson" in March 2008 (GOA08). A third set was collected in the eastern Bering Sea (EBS) by the "Oscar Dyson" in July 2007 (EBS07; Figure 1). A technical comparison of these vessels can be found in De Robertis and Wilson (2010). Locations for each set were selected to sample a wide range of pollock lengths. Acoustic netsondes attached at the headrope were used to confirm the effective opening of the trawl while fishing. All sets were sampled using the same net with a target trawling speed of 3.5 knots. For each trawl, a Seabird SBE-39 depth and temperature logger and a Wildlife Computers MK-9 light-level logger were attached to the trawl headrope. Measurements from the logger were converted to light intensity (μE m^{-2} s^{-1}) using the calibration equation from Kotwicki *et al.* (2009).

For each haul, 12 pocket nets were attached to the outside trawl-mesh surface during deployment and removed after retrieval. A stratified random design was used to determine attachment locations for the pocket nets to control for placement effect. The trawl was subdivided from trawl wings to codend into four parts, referred to as the forward, middle 1, middle 2, and aft sections (Figure 2). Each section was further subdivided into a bottom, top, port, and starboard panels. Within each trawl partition, defined by a section and panel (e.g. forward bottom), 9–14 locations were uniformly distributed and marked for the attachment of pocket nets. Pocket-net placement was determined by randomly choosing an attachment point on a trawl partition. A single pocket net was attached to the top, bottom, and one of the side panels, resulting in three nets being placed in each section. They were attached to the trawl along trawl-netting bars, forming a diamond-shaped opening. Two sizes of pocket net were used, nine with an opening of ~2.88 m^2 were placed on the back three sections, and three with an opening of ~5.12 m^2 were used on the larger meshes of the forward section (Figure 2). Pocket nets were constructed of ~19 mm stretch-mesh monofilament netting and were ~5 m long.

The primary concern in the design of the pocket nets was to reduce potential methodological biases in sampling the escaping fish. Monofilament netting was chosen because of its low visibility and lesser drag, resulting in reduced obstruction of flow over the covered meshes. Preceding the experimental trails in the GOA 2006 survey, pocket nets were attached to the trawl and observed *in situ* using a Dual-Frequency Identification Sonar (DIDSON, Sound Metrics Inc.). Analysis of the DIDSON data revealed that the pocket nets did not adversely affect fish movements relative to the surrounding uncovered meshes. Fish were observed entering the pocket nets and did not actively avoid the attachment location within the trawl.

Codend catch and the contents of each pocket net were identified to species and weighed. Some 300 pollock were measured to the nearest centimetre from a sample taken from the codend catch. All fish caught in the pocket nets were identified to species and measured, except for those from a single large catch, for which a random sample of 50 pollock was measured and scaled up to the entire catch using the weight fraction of the sample.

Pocket-net model

Midwater-trawl selectivity was estimated by modelling the pocket net and codend catches. A fish of length i entering the mouth of the net has a length-dependent probability S_i of being retained in the codend, modelled as a logistic selection curve parametrized in terms of the length-at-50%-retention (L_{50}) and the selection range (SR; length in cm between 25 and 75% retention):

$$S_i = (1 + e^{(k(L_{50}-i)/SR)})^{-1}, \qquad (1)$$

where $k = 2\log(3)$ (Millar, 1993). The complementary probability of escapement from the trawl before the codend is $1 - S_i$. Escaping fish could exit the trawl out of any of the four sections, expressed as a multinomial probability variable P_j, where j indicates the section. A fish exiting a given section j can escape out of the top, side, or bottom panels of a section, resulting in an additional multinomial probability conditional of leaving section j, $R_{j,k}$, where k is the panel conditional on P_j. The total probability of a fish of length i being caught in the pocket net in section j and panel k is

$$H_{i,j,k} = (1 - S_i)P_j R_{j,k} Q_{j,k}, \qquad (2)$$

where $Q_{j,k}$ is the sampling fraction for the pocket nets located in section j and panel k, calculated as the ratio of the number of meshes covered by the pocket net to the total number of meshes in that trawl partition.

The escapement-location parameters P and R were multinomial-logit-transformed for computational ease:

$$P_j = \begin{cases} \dfrac{e^{\pi_j}}{1 + e^{\pi_1} + e^{\pi_2} + e^{\pi_3}} & \text{for } j = 1 \text{ to } 3 \\ 1 - (P_1 + P_2 + P_3) & \text{for } j = 4 \end{cases}, \qquad (3)$$

$$R_{j,k} = \begin{cases} \dfrac{e^{\rho_{j,k}}}{1 + e^{\rho_{j,1}} + e^{\rho_{j,2}}} & \text{for } k = 1, 2 \\ (1 - [R_{j,1} + R_{j,2}])0.5 & \text{for } k = 3 \end{cases}. \qquad (4)$$

The estimated proportion of fish exiting from the side, $R_{j,3}$, is multiplied by 0.5 because the pocket net was placed on one of the two side panels of the net. The probability of being captured in the codend and measured is

$$h_i = S_i U, \qquad (5)$$

where U is the subsample fraction (sample weight/total catch weight) of the codend catch. Although length data from catch samples are often extrapolated to the entire catch via the sampling fraction, use of unscaled measurement results is a more appropriate representation of the overall uncertainty in the model (Millar, 1994). For notational convenience, H and h are combined into a single matrix $F_{i,m}$ with columns $m = 1$ to 12 for each pocket net and column 13 for the codend-retention probability for fish of length i.

Catches of fish by length, conditional on pocket-net location, were assumed to be Poisson distributed, because this distribution has been used routinely to model length-dependent fish escapement in selectivity studies (Millar, 1992) and is appropriate for discrete count data. The likelihood function for a single haul is:

$$L(x|\theta, \mu) = \prod_i \prod_m \frac{(\mu_i F_{i,m})^{x_{i,m}} e^{-\mu_i F_{i,m}}}{x_{i,m}!}, \qquad (6)$$

where θ is the individual haul parameter vector $\theta = \{L_{50}, \mathrm{SR}, \pi, \rho\}$, $x_{i,m}$ the number of fish of length i measured in each pocket ($m = 1$ to 12) and the codend ($m = 13$), and μ_i the number of fish of length i entering the mouth of the trawl. This variable constitutes a "nuisance" parameter, not being of direct interest, when estimating selectivity, and was handled by marginalization, assuming uniform priors for the μ_i (Appendix A). The negative logarithm of the resulting integral is

$$-\log \hat{L}(x|\theta) \propto \sum_i \left(\sum_m [-x_{i,m} \log\{F_{i,m}\}] + \log\left[\sum_m F_{i,m}\right]\left[\sum_m x_{i,m} + 1\right]\right). \qquad (7)$$

Between-haul variation

Variation between hauls in a set was modelled using the HBA in which individual haul parameters and additional parameters describing the entire set are estimated simultaneously. Hierarchical Bayesian models specify prior distributions from which parameters for individual sampling units are drawn. Priors were applied to hauls within each set. Between-set variation was not modelled; each set was analysed separately. Priors assigned to haul-specific parameters include

(i) $L_{50} \sim N(\mu_{L_{50}}, \tau_{L_{50}})$

(ii) $SR \sim N(\mu_{SR}, \tau_{SR})$,

(iii) $P \sim \mathrm{Dirichlet}(D)$, and

(iv) $R \sim \mathrm{Dirichlet}(G)$.

L_{50} and SR were assumed to be normally distributed, based on independent haul analyses where samples of posterior parameter distributions approximated a normal distribution. Codend selectivity methods for estimating between-haul variation commonly assume normality for selectivity parameters (Fryer, 1991; Wileman *et al*., 1996). Variables D and G represent the Dirichlet distribution parameters that describe escapement proportions in sections (D) and among panels within each section j (G_j) across all hauls in a set. One prior was applied to escapement among sections P, and four priors for escapement among panels in each section, i.e. $G_{1,1}$, is the Dirichlet distribution parameter associated with the proportion of fish escaping out of the top panel in the forward section across all hauls in a set.

Uniform hyperpriors were placed on the selectivity parameters $\mu_{L_{50}}$, $\tau_{L_{50}}$, *and* μ_{SR}, and the Dirichlet-escapement-location parameters D and G, and a weakly informative, scaled inverse-Chi distributed hyperprior was placed on prior τ_{SR}:

$$-\log P(\tau_{SR}|\nu_{\tau_{SR}}, \sigma_{\tau_{SR}}) = \frac{\nu_{\tau_{SR}}\sigma^2_{\tau_{SR}}}{2\tau_{SR}} + \left(1+\frac{\nu_{\tau_{SR}}}{2}\right)\log\tau_{SR}. \quad (8)$$

This hyperprior avoids degenerate solutions in which the maximum posterior density estimate is zero for all variance parameters. Values of the hyperpriors were set at $\nu_{\tau_{SR}} = 2$ and $\sigma_{\tau_{SR}} = 3$. Alternative hyperprior values were explored, but they did not appear to influence posterior selectivity parameter distributions at values $\nu_{\tau_{SR}} > 1$ and $\sigma_{\tau_{SR}} > 1$.

The logarithm of the posterior distribution is proportional to

$$\log P(\phi, \theta|\text{data}) \propto \sum_{h=1}^{n}\log L(\text{data}_h|\theta_h) + \log P(\theta|\phi) + \log P(\phi), \quad (9)$$

where ϕ is the parameter vector for the priors $\phi = \{\mu_{L_{50}}, \tau_{L_{50}}\mu_{SR}, \tau_{SR}, D, G\}$ and n the haul number within a set. An overview of model components is given in Table 1.

Light effect

The HBA assumes that parameter estimates from individual hauls have a common distribution (Gelman *et al.*, 2003) and that individual haul observations are exchangeable. Exchangeability implies that the specific location or the order in which hauls were taken does not affect the outcome. This assumption may be inappropriate when factors contributing additional explanatory power to between-haul variance are known. Substantially more fish were caught in pocket nets during the four night-time tows in the EBS07 set, indicating that hauls within the set may not be exchangeable because of the possibility of a light-level effect on selectivity. To account for the potential effect of light on selectivity, an expanded model was fitted with an additional parameter to allow L_{50} to depend on light intensity. Individual haul estimates of L_{50} were expressed as a log-linear function:

$$L_{50n} = Z_n + \lambda\log(L_n), \quad (10)$$

where Z_n is the haul-specific intercept, λ a slope parameter, and L_n the light intensity ($\mu E\ m^{-2}\ s^{-1}$) for each haul n. In the HBA structure, $\mu_{L_{50}}$ *and* $\tau_{L_{50}}$ were replaced by μ_Z and τ_Z. A uniform prior was assumed for λ. The base model (124 parameters; Table 1) was compared with the expanded light-level model (125 parameters) using the deviance information criterion (DIC; Appendix B) to evaluate whether the inclusion of ambient light levels in the model was appropriate.

Analysis

Posterior distributions for model parameters were estimated using the MCMC (Markov chain Monte Carlo) algorithm implemented in the package Automatic Differentiation Model Builder (Fournier, 2001). For each haul set, 10 million cycles were sampled, with every 2000th sample retained to reduce the autocorrelation in the MCMC samples. The first 2500 parameter vectors were then discarded as a burn-in period, allowing the MCMC sampling algorithm to stabilize. Convergence of the MCMC

Table 1. A description of the variables and parameters of the midwater-trawl, selectivity-estimation model based on pocket net and codend catches.

Group	Name	Number	Description
Data	x		Observed catches in 12 pocket nets and sampled from the codend
Variables	μ		Number of fish at length entering the trawl mouth
	H		Proportion of μ escaping through each pocket net
	h		Proportion of μ sampled in the codend
	Q		Panel-sampling fraction (pocket-net area/panel area)
	U		Codend subsampling fraction (weight of subsample/total species weight in the haul)
	S		Selectivity, i.e. the proportion of μ that is retained in the codend
Parameters (θ) fitted	L_{50}	8	Length at 50% retention (one parameter per haul in set)
	SR	8	SR, difference between the 25 and 75% length-at-retention (in cm)
	π	3 × 8	Parameters used to derive the multinomial variable P (n sections (4) − 1)
	ρ	8 × 8	Parameters used to derive the multinomial variable R
Parameters (θ) calculated	P	4 × 8	Four-way proportional distribution of escapement by section
	R	(3 × 4) × 8	Three-way proportional distribution of escapement by panel, one per section
Hyperparameters (ϕ) fitted	$\mu_{L_{50}}$, $\tau_{L_{50}}$	2	Two parameters describing the underlying normal distribution to which individual trawl L_{50} belong
	μ_{SR}, τ_{SR}	2	As above for SR
	D	4	Four-way Dirichlet distribution parameter for escapement by section
	G	3 × 4	Four separate three-way Dirichlet distributions for escapement by panel, one for each section
Prior distribution parameters specified	$\nu_{\tau_{SR}}$, $\sigma_{\tau_{SR}}$	1+1	Scaled inverse-Chi-squared prior distribution for τ_{SR} set at $\nu_{\tau_{SR}} = 2$, $\sigma_{\tau_{SR}} = 3$
Total parameters			104 fitted base parameters (for set of eight hauls), 20 hyperparameters, 4 priors

algorithm was checked by inspecting trace plots (the value of parameter plotted against the ordered sample number) visually for each parameter and the objective function value [Equation (10)], by computing the Gelman–Rubin statistic from multiple MCMC chains initiated from different starting parameter values (Gelman and Rubin, 1992). The performance of the model was also verified with simulated data of known selectivity.

Posterior predictive distributions for the selectivity parameters L_{50} and SR were constructed by taking a random sample from a normal distribution defined by the hyperparameters $\mu_{L_{50}}, \tau_{L_{50}}, \mu_{SR}, and\, \tau_{SR}$. This process was repeated for all MCMC posterior samples, yielding 2500 values for L_{50} and SR for an "unknown haul" at each set location and year. For the model including light level, predictive distributions for L_{50} were additionally dependent on the light level. These were constructed by repeating the procedure described above for Z in Equation (10), then using the posterior sample of λ to generate L_{50} values. Predictive distributions were similarly constructed for the escapement location along the trawl using the posterior distributions of the Dirichlet distribution parameters to generate realizations of escapement-location parameters.

Results

Haul collections

For inter-haul consistency, an attempt was made to keep the fishing duration and gear depth as constant as possible (Table 2). However, these had to be varied if fish density dropped as observed on the ship's echosounder or if fish aggregations changed depth. Fishing conditions were most constant during set GOA07, with little change in fishing duration and depth. Tow durations were longest and most variable in set EBS07 as a result of variable fish density, typical of pollock aggregations in the EBS. The GOA08 set varied both in duration and fishing depth, because towing location and direction were altered to avoid commercial-fishing traffic.

In set EBS07, light intensity at fishing depths ranged from $1.4 \times 10^{-6}\,\mu\text{E m}^{-2}\,\text{s}^{-1}$ at night to $4.8 \times 10^{-2}\,\mu\text{E m}^{-2}\,\text{s}^{-1}$ by day. In contrast, average light intensity in the GOA sets was lower than the night levels in the EBS ($4.0 \times 10^{-7}\,\mu\text{E m}^{-2}\,\text{s}^{-1}$) and was less variable between hauls ($CV = 0.45$) compared with the EBS set ($CV = 1.28$). Lower light in the GOA sets was expected given the reduced sunlight in winter and the greater fishing depths.

Pollock dominated the catch in set EBS07, contributing an average of 98.9% by weight. In the GOA sets, catches averaged 57.7 and 67.5% pollock by weight in 2007 and 2008, respectively, with an average 95% of the remaining catch made up of eulachon (*Thaleichthys pacificus*), a 10–20-cm semi-pelagic smelt abundant in Shelikof Strait.

Pocket-net catch

Catches of pollock in the pocket nets ranged from 0 to 283 fish. The proportion of nets in each haul with no catch varied between 25 and 92%. The species present in the pocket-net catches were primarily pollock in the EBS (97.4% by weight), but in the GOA, there was on average pf 81.3 and 60.9% eulachon by weight in 2007 and 2008, respectively. The length frequency of pollock caught in the pocket nets differed markedly from that in the codend (Figure 3), being predominantly age 1 (9–18 cm) and 2 (19–28 cm) fish; age classification was based on otolith samples taken from earlier surveys. The mean lengths of pollock caught in pocket nets and the codend were significantly different (two-way ANOVA by haul, $p < 0.001$ across all sets). Substantial numbers of pollock aged 2 were caught in pocket nets in set GOA07, whereas the codend contained proportionally fewer fish aged 1 than the other sets. Pollock were captured in all four sections of the trawl in the GOA sets. In contrast, in set EBS07, there was no escapement from the two forward sections, and just one pollock was caught in the third section. Mean pollock lengths from the pocket nets placed on different sections of the trawl in the GOA sets were not significantly different (Table 3), despite large differences in mesh size among the trawl sections.

Modelling results

The fit of the model to the observed catches was explored by plotting mean differences between predicted and actual catches in the pocket net and codend (Figure 4). Model predictions were based on samples from the posterior distributions for the parameters (Appendix C). As expected, residual values were largest near the modes of the length frequencies from the pocket-net catches (Figure 3) and showed greater spread for codend catches as a consequence of the larger number of fish caught. The model predictions differed most from observations in the GOA07 catches of fish aged two years. Mean residuals for that age class were negative for pocket nets, implying that the model predicted more fish in the nets than were observed. The reverse was observed in the model fitted to the codend catch, with predicted numbers being fewer than in the observed catch. Model fits for the other two haul sets did not show strong length-dependent patterns, meaning that the logistic selectivity functional form used in the model captured length-dependent behaviour reasonably well.

Selectivity parameters

Posterior predictive distributions for the selectivity parameters L_{50} and SR derived using the HBA represent the expectation of selectivity for an "unknown" haul, combining within- and between-haul uncertainty from the experimental sets. As between-set variation was not included in the model, a comparison of set-level estimates of selectivity is qualitative. The posterior distributions of L_{50} varied between sets in both modal position and estimation

Table 2. Haul conditions and catches during three haul sets taken to estimate the midwater-trawl selectivity of walleye pollock in the GOA and EBS.

Set	Gear depth (m)	Haul duration (min)	Gear temperature (°C)	Light level (μE m^{-2} s^{-1})	Codend catch range (numbers)	Combined pocket-net catch range (numbers)
GOA07	262 ± 4	9.7 ± 0.7	2.5 ± 0.2	$(4.3 \pm 2.0) \times 10^{-7}$	1 605–3 728	12–88
EBS07	126 ± 4	26.9 ± 12.5	1.3 ± 0	$(1.6 \pm 2.1) \times 10^{-2}$	1 596–5 072	12–325
GOA08	235 ± 12	18.9 ± 7.8	4.5 ± 0	$(3.7 \pm 1.7) \times 10^{-7}$	1 639–7 929	4–133

Columns 2–5 show means and standard deviations of eight hauls taken in each set, and columns 6 and 7 show the catch ranges.

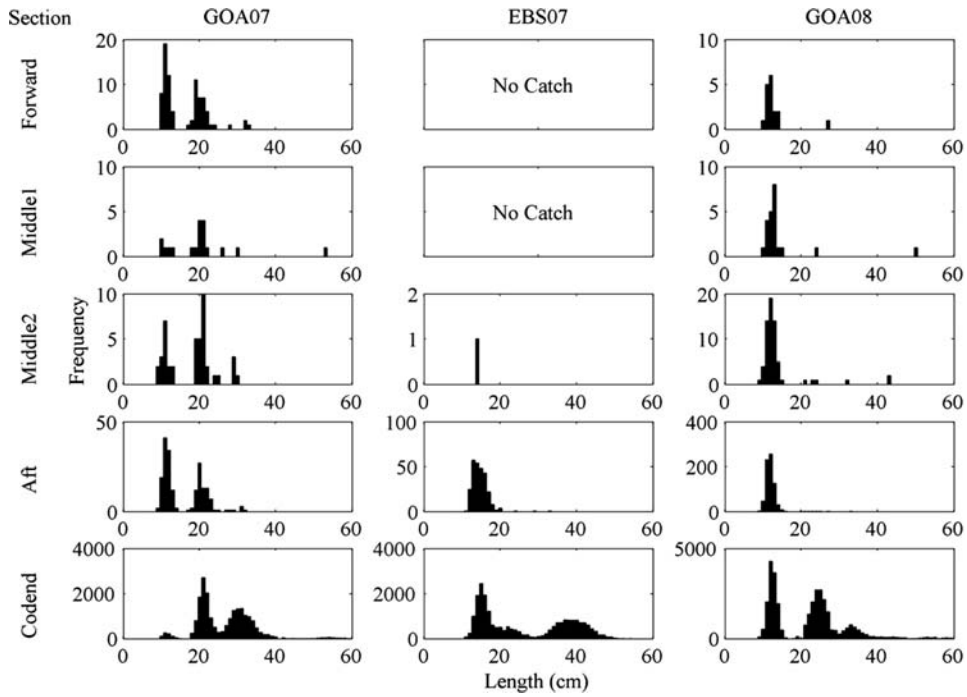

Figure 3. The length frequency of walleye pollock from the three experimental sets. Catches in the pocket nets in each section and in the codend were pooled across eight hauls in each set.

uncertainty (Figure 5). The EBS set had the most uncertainty in L_{50} and SR estimates resulting from the greater spread in the modes of the marginal posterior distributions of selectivity parameters for individual hauls. Less between-haul variation was observed within the GOA sets, although the maximum *a posteriori* estimates of L_{50} were different between the two sets (26.4 and 15.2 cm for 2007 and 2008, respectively). Posterior distributions for SR were similar between the two GOA sets, with GOA07 being more variable. Individual haul marginal distributions of L_{50} and SR show the effect of being "pulled" towards the global mean, as seen by the skew in the distributions farthest from the means of the predictive distributions.

Light effect

The inclusion of light as a covariate in the model for set EBS07 resulted in a lower value of DIC relative to the base model ($\Delta =$ 10 log-likelihood units), suggesting that light levels influenced the rates of trawl escapement in that experimental set. Estimates of L_{50} were lower for daytime hauls, indicating that smaller fish were more likely to be retained when the netting was more visible (Figure 6). Mean L_{50} estimates ranged from 10.8 to 20.7 cm between the highest and the lowest light intensities encountered during the set.

Escapement distribution

Differences in the escapement rate between trawl partitions were analysed using the posterior predictive distributions (Figure 7) derived from hyperparameters *D* and *G*. Panel-escapement distributions were weighted by section escapement and averaged, so that panels in sections where there was little escapement did not influence directional trends disproportionately. The posterior predictive distributions followed patterns in the catch data (Figure 3), providing additional information on variability among hauls in a set. Fish escaped mainly from the forward section in set GOA07 (84.9% maximum *a posteriori* estimate), and primarily out of the aft section in the other two sets (96.5% in EBS07 and 68.2% in GOA08). The EBS set was unique in that fish escaped almost exclusively out of the aft section. Moderately narrow posterior predictive distributions show that the patterns of escapement by section were consistent among hauls within sets. Most fish were lost though the bottom panels in the GOA sets, and the direction of fish escapement was more variable in the EBS set, evenly divided among the top, side, and bottom panels.

Table 3. Two-way analysis of variance of the mean lengths of walleye pollock caught in pocket nets placed in four different sections of a midwater trawl, hauls collected in the GOA in 2007 and in 2008 being analysed separately.

Set	Source	Sum of squares	d.f.	Mean square	*F*-value	Prob>*F*
GOA07	Sections (4)	85.2	3	28.4	1.71	0.209
	Hauls (8)	335.4	7	47.9	2.88	0.041
	Error	249.8	15	16.7		
	Total	709.6	25			
GOA08	Sections (4)	12.8	3	4.3	0.96	0.432
	Hauls (8)	28.2	7	4.0	0.91	0.520
	Error	84.1	19	4.4		
	Total	124.7	29			

Selection curves

Selection curves from the posterior distributions for L_{50} and SR are shown in Figure 8. Estimates of trawl selectivity were highly uncertain. Uncertainty was greatest in set GOA07, where the posterior predictive distribution for the retention probability of a fish 26 cm long was 0.03 (5th percentile) and 0.96 (95th percentile).

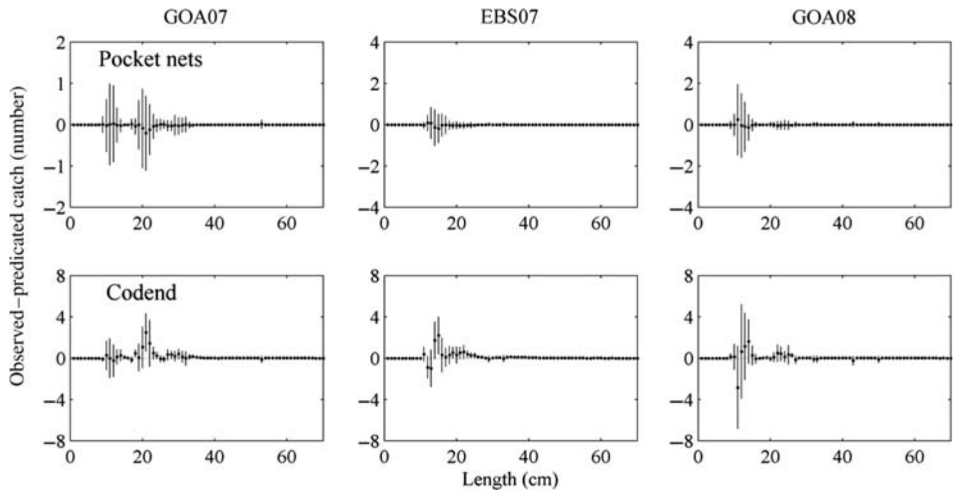

Figure 4. Model fits for pocket-net catches. Points represent mean residuals between the data and the model-predicted catches computed by sampling the posterior distributions of the parameters. The lines represent the standard deviation of the residuals at each length averaged across all hauls and pocket nets.

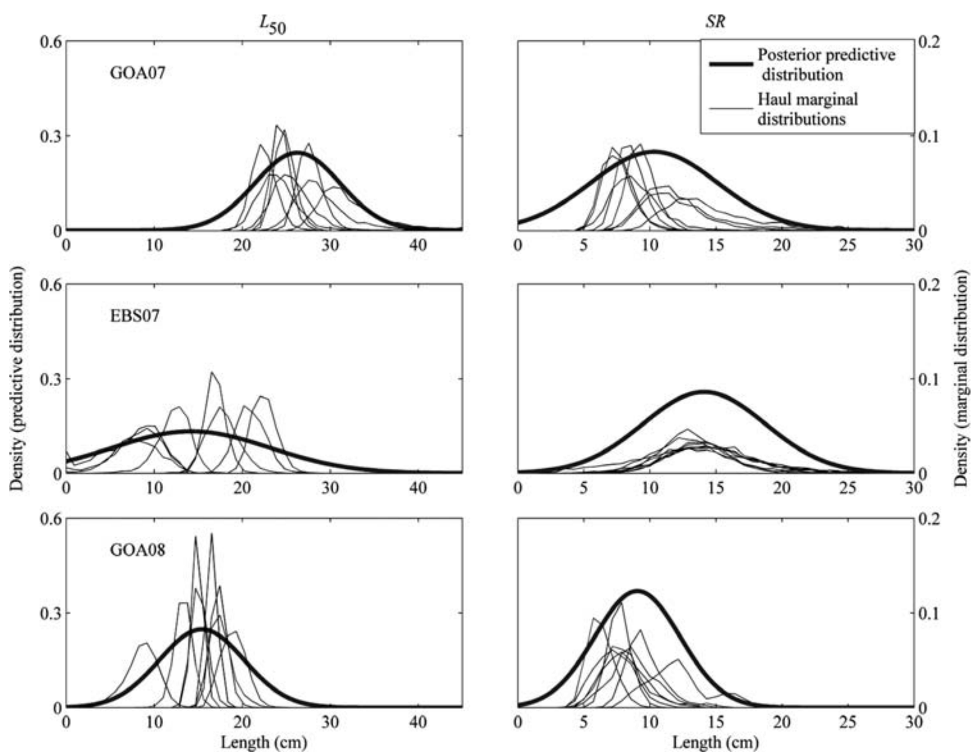

Figure 5. Posterior distributions of selectivity parameters. Three datasets were analysed separately (shown in plot rows). Posterior distributions of L_{50} and SR for each individual haul in a set ($n = 8$) are shown as thin lines, and the posterior predictive distribution of L_{50} that incorporates within- and between-haul variation in each parameter as the heavy black line.

Selectivity observed in EBS07 night catches represents an intermediate level between the two GOA sets. Set GOA07 was distinct from the other two sets in that full retention (>0.95%, median curve) was not achieved until a length of 46 cm, compared with 36 cm in EBS07 night samples and 28 cm in GOA08 samples.

Discussion

Our results indicate substantial undersampling of juvenile (<25 cm) pollock by the survey trawl used in pollock acoustic surveys. Length-dependent escapement varied substantially among the three sets, demonstrating that retention was influenced by factors not directly related to the trawl-gear design. Differences in selectivity between surveys (EBS and GOA) were not unexpected because the environmental conditions varied. Differences between the GOA sets were greater than the differences among hauls within each set (Figure 5), showing that selectivity can differ markedly from year to year within each survey. Higher estimates of L_{50} in GOA07 corresponded to fewer fish aged 1 in the codend and a bigger catch of pollock aged 2 in the pocket nets relative to GOA08, with most escapement out of the front section of the trawl in GOA07 as opposed to the aft section in GOA08. The lower numbers of pollock aged 1 in the codend in set GOA07 likely indicate a lesser abundance of that age class in the population in 2007, because the pocket-net catches of pollock aged 1 were comparable in both years of the GOA sets.

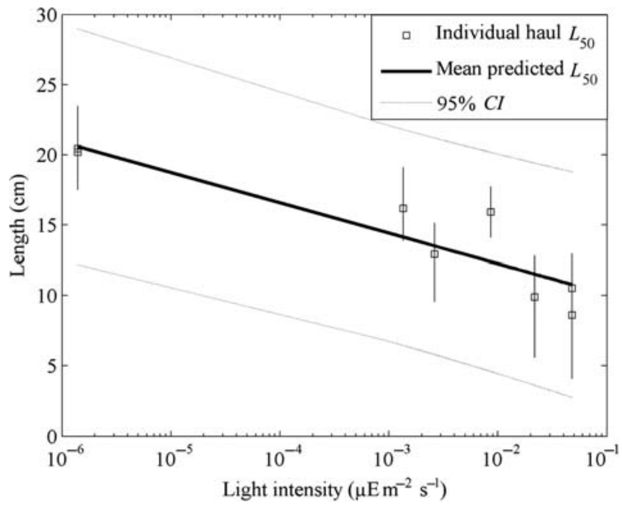

Figure 6. Haul estimates of L_{50} plotted as a function of ambient light levels. Points represent the median of the posterior distribution with the 10th and 90th posterior intervals indicated by error bars. The lines represent the mean and variance of the posterior predictive distribution of L_{50} at the given light level.

A closer look at the data suggests several potential causal mechanisms that could explain the differences observed in selectivity between the GOA datasets. For example, pollock aged 2 were larger (25.7 cm) in 2008 than in 2007 (22.2 cm), and they averaged 7.7% more in terms of mean weight per length. These differences indicate that pollock aged 2 in 2008 had undergone more rapid growth and may have been in better condition, which may have positively affected their ability to be herded by the trawl. In addition, a 2°C higher gear-depth temperature was observed in 2008. Temperature impacts swimming ability in pollock (Arimoto *et al*., 1991), with an estimated 80% increase in maximum swimming speed of a fish 20 cm long with a temperature increase of 2–5°C, comparable with the respective temperature levels recorded in the two GOA sets (Table 2). Arimoto *et al*. (1991) suggested that changes in maximum swimming speed could increase the ability of pollock to avoid entering a trawl. Swimming ability could also influence selectivity once fish enter a trawl. The results of this study show that higher temperatures were correlated with greater retention of juveniles, suggesting that faster swimming may increase retention in midwater trawls by facilitating herding.

Differences in the two GOA sets could also potentially be attributed to a vessel effect, because different vessels were used. The two vessels had standardized trawl rigging, used the same trawl, and were operated under the standard survey protocols for trawl

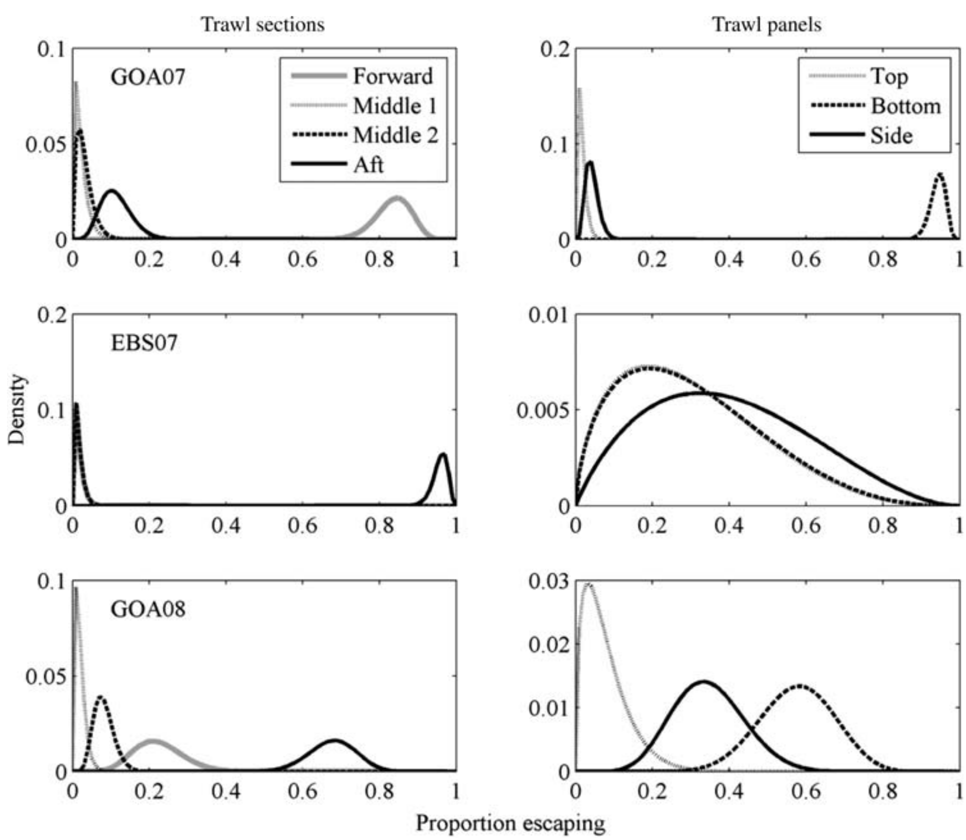

Figure 7. Posterior distributions for the proportion of the total escapement of walleye pollock from different areas of the trawl. The results are based on beta distribution fits to samples from the posterior distributions.

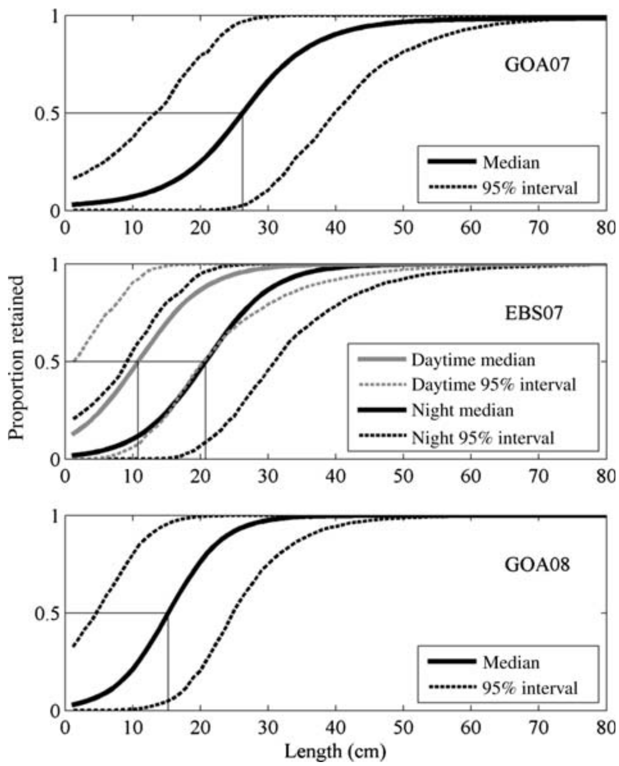

Figure 8. Selectivity estimates (i.e. the proportion of fish entering the net that are being caught in the codend) for the three haul sets. The EBS set reflects estimates of selectivity at the minimum (night) and the maximum (day) levels of light observed during data collection. Credibility intervals are based on samples from the posterior distributions for the selectivity parameters.

deployment and trawling speed. The main difference between the vessels was the level of underwater-radiated noise. Ambient noise can impact fish behaviour (Popper, 2003), and vessel noise does impact pollock behaviour in some situations (De Robertis and Wilson, 2010). During the latter study, a stronger pollock diving response was observed in acoustic measurements from the older, noisier vessel ("Miller Freeman"), used to sample set GOA07. Escapement out of the front, bottom portion of the trawl is consistent with rapid downward movement of fish following the passage of a vessel.

Escapement in other sets conducted with the noise-reduced vessel ("Oscar Dyson") increased with proximity to the codend. This pattern was also observed in midwater-trawls fishing capelin (Nakashima, 1990) and in bottom trawls fishing pollock (Matsushita *et al*., 1993). Increased escapement is thought to be linked to increasing fish density within the trawl near the codend. Little or no escapement out of the large forward meshes implies that juvenile fish were effectively herded by the front sections of the trawl, even in low light during set GOA08 or night tows during the EBS set. It also suggests that escapement is an active process, because the expectation under passive escapement would be equal escapement over the entire trawl surface, possibly depending on the angle of attack of the mesh.

Fish capture by trawls involves a balance of visual and auditory stimuli (Glass and Wardle, 1989; Engås and Ona, 1990), although vision is thought to be the dominant modality once fish are in the trawl (Wardle, 1993). The effect of light on pollock escapement observed in the EBS further supports the significance of vision during trawl capture. Retention of juvenile pollock by the trawl was positively correlated with ambient light, suggesting that fish escape in part because of a failure to detect the trawlnetting. Suuronen *et al*. (1997) reported that herring (*Clupea harengus*) did not escape though trawl-body netting during daylight, perhaps because of stronger herding effects.

Increased total escapement in low light is consistent with several studies on pollock visual behaviour. Ryer and Olla (2000) found that juvenile pollock in the laboratory tended to swim closer to and make contact with net panels more frequently at lower levels of light. Similarly, Olla *et al*. (1997) reported that the light levels required for 50% of juvenile pollock to swim actively within a simulated net were 2×10^{-3} μE m^{-2} s^{-1}, a level that separates night tows from those taken made by day and at dusk in the EBS set (night-time mean = 1.4×10^{-6} μE m^{-2} s^{-1}, day/transitional mean = 2.2×10^{-2} μE m^{-2} s^{-1}).

Larger fish did not appear in pocket nets irrespective of the levels of ambient light. Although no data are available on length-dependent visual thresholds of pollock, estimates of pollock length-dependent resolving ability based on eye morphology (Zhang and Arimoto, 1993) show that adult pollock (40 cm) have relatively better distance sight than juveniles (15 cm). Adults were able to resolve a target of 2 cm diameter at a distance of 8 m compared with 4 m for juveniles under adequate lighting. It is also possible that non-visual herding may be more important in adults than in juveniles, resulting in effective herding irrespective of ambient light levels. Field observations of adult pollock behaviour in trawls by Olla *et al*. (2000) showed that orientation was much more variable under low light (6×10^{-4} μE m^{-2} s^{-1}) and that swimming appeared to be reduced, suggesting that fish may be more likely to strike the net (Glass and Wardle, 1989). Fish reactions after striking a net may result in either retention or escapement, and if the distribution of these reactions is length-dependent with larger fish having a higher probability of being retained, it would provide a non-visual mechanism to explain the selectivity patterns observed. Resolving whether escapement through meshes of the midwater-trawl body results from a passive failure to herd or by active directed movement through the meshes will require direct observations of the escapement process using acoustic or optical instruments.

The results of this study have provided insight into appropriate sampling efforts for determining between-haul variance. Results from the EBS set revealed greater between-haul variability relative to the GOA sets as a result of changing light conditions. In the EBS case, increasing the number of hauls sampled might have further reduced uncertainty when covariates such as light were added to the model. In the GOA sets, haul-to-haul variation was substantially less, suggesting that uncertainty may not be improved greatly by increasing the number of hauls. Our study sought to validate the pocket-net method in determining trawl selectivity, as well as providing specific estimates of selectivity for pollock surveys. To evaluate the method, we had to collect hauls under as similar conditions as possible, so facilitating assessment of the variability inherent in pocket-net sampling of escapement. A more-dispersed sampling effort with fewer hauls in more locations would broaden inferences that can be made regarding the entire survey area and would likely result in much higher variance.

The HBA provided a straightforward method of assessing uncertainty in selectivity estimates across multiple haul samples. HBA achieves a balance between pooling data within sets and making independent estimates for each haul (Gelman *et al*., 2003). Bayesian methods, and specifically HBA, have been successfully applied in fishery stock-assessment modelling and meta-analyses (e.g. Harley and Myers, 2001). Although the need to incorporate variance across multiple sampling units is commonly encountered in gear research for fisheries, few applications exist in the literature (Askey *et al.*, 2007). The HBA methodology provides a straightforward framework for many problems in gear research. MCMC-based analyses can be computationally demanding, but improvements in computer processing power and the availability of software have expanded the applicability of these methods to a wider research community.

The impact of biased trawl catches on the accuracy of acoustic-abundance estimates is greatest where adult and juvenile fish commonly co-occur in trawl catches, because catch-derived, length frequency estimates are less representative of the sampled population than cases where the sampled fish aggregate by size and catches are more uniform in terms of fish length. Even with substantial under-retention of juvenile fish, acoustic-based estimates of abundance are strongly affected because they depend on the strength of the acoustic returns rather than on catch per unit effort. In populations of mixed size, the expected effect of selectivity-induced error on abundance-at-age estimates will underestimate juvenile abundance and, to a lesser degree, overestimate adult abundance, because some of the backscatter from juveniles would be erroneously attributed to adult fish.

This study has presented a new method of estimating the selectivity of midwater trawls and its uncertainty. A greater difference was observed between sets than within sets, suggesting that fish retention by the trawl depended on environmental factors at the locations and times where the samples were collected, or perhaps features of the fish populations themselves. Despite relatively great uncertainty in selectivity estimates, there was significant undersampling of juveniles, potentially leading to biased survey estimates of abundance.

Acknowledgements

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Appendix A

Deriving the integral for μ

The Poisson likelihood of observing a fish of a given length class in each pocket net ($m = 1$–12) and in the codend sample ($m = 13$) is

$$L(x|\mu, F) = \prod_m \frac{(\mu F_m)^{x_m} e^{-\mu F_m}}{x_m!},$$

where x are the observed data, F the probability of retention by the pocket nets and codend, and μ the number of fish at a given length entering the net. This equation can be simplified to yield

$$L(x|\mu, F) = \left(\prod_m \left[\frac{F_m^{x_m}}{x_m!}\right]\right) \mu^{\sum_m x_m} e^{-\mu \sum_m F_m}.$$

The next step is to integrate this equation with respect to μ:

$$\widehat{L}(x|F) = \int_0^\infty \left(\prod_m \left[\frac{F_m^{x_m}}{x_m!}\right]\right) \mu^{\sum_m x_m} e^{-\mu \sum_m F_m}\, d\mu,$$

which yields

$$\widehat{L}(x|F) = \left(\prod_m \left[\frac{F_m^{x_m}}{x_m!}\right]\right) \frac{\Gamma\left(\sum_m x_m + 1\right)}{\left(\sum_m F_m\right)^{\left(\sum_m x_m + 1\right)}},$$

where Γ is the gamma function and $\widehat{L}$ is the integral of the likelihood function. The negative logarithm of $\widehat{L}$ used in the analysis is proportional to

$$-\log \widehat{L}(x|\theta) \propto -\sum_m (x_m \log[F_m]) + \log\left(\sum_m F_m\right)\left(\sum_m x_m + 1\right),$$

after removal of the additive constant terms dependent only on the data. This equation summed over all length classes results in Equation (7).

Appendix B

Deviance information criterion (Spiegelhalter *et al.*, 2002)

The DIC is defined as $DIC = p_D + \bar{D}$, where p_D is the effective number of parameters, and $\bar{D}$ is the mean of the deviance, defined as $D = -2\log(l)$, where l is the likelihood function [Equation (9)]. The effective number of parameters is computed as $p_D = \bar{D} - D(\bar{\theta})$, where $D(\bar{\theta})$ is the deviance evaluated at the means of the posterior MCMC samples of the model parameters.

Appendix C

Computation of residuals

The residuals for a given haul were computed as the distance between the model predictions of the pocket net and codend catches, and the observed values where the expected catch in a pocket net, y, are $y_{i,j,k} = H_{i,j,k}\mu$ for a fish of length i in the pocket net located in section j and panel k. The expected codend sample w is $w_i = h_i\mu$.

To calculate these quantities, the maximum likelihood estimate for μ was computed as

$$\mu_i = \frac{\sum_j \sum_k x_{i,j,k} + c_i}{\sum_j \sum_k H_{i,j,k} + h},$$

where x and c were the observed catches in the pocket net and codend, respectively (Kirkwood and Walker, 1986). H and h were calculated from samples of the posterior distributions of the parameters (L_{50}, SR, π, ρ). This process was repeated for all hauls in a set.