Disentangling the effects of capture efficiency and population abundance on catch data using random effects models

Verena M. Trenkel and Hans J. Skaug

We propose a random effects model for disentangling population abundance and capture efficiency effects on bottom-trawl catches. The spatial distribution of individual fish is assumed random leading to a Poisson distribution for the number of individuals in the trawl path (no schooling). Capture efficiency, i.e. the proportion of individuals in the trawl path being retained by the gear, is modelled as a random variable. We propose model extensions that include the effects of body size on haul efficiency. We applied the models to several species from the Celtic Sea groundfish community based on small-scale repetitive hauls. The resulting abundance estimates allowed us to study population abundance ratios; the estimated capture efficiencies were comparable between species and showed that generally gear efficiency increases for larger species with the exception of haddock (*Melanogrammus aeglefinus*), which had low estimated gear efficiency despite its large body size. Model identifiability was studied using simulations and an independent trawl data set from the same area.

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Introduction

Abundance of fish stocks is often inferred from catch information from commercial fisheries or scientific trawl surveys. Selecting the correct probability distribution of catches is important for choosing the correct estimator for survey-derived population abundance indices (Pennington, 1983; Myers and Pepin, 1990; Terceiro, 2003) or the correct error distribution in a stock assessment model. The distribution of catch numbers per trawl haul is commonly characterized by many zeros and some extreme values, resulting in a rather skewed distribution. This shape is not unique to trawl catch data and occurs in many studies of animal distribution. Welsh *et al.* (1996) summarized the different model classes that have been employed to deal with data that feature "extra zeros". In two stage models, the probability of obtaining a non-zero observation is modelled separately from the distribution of the number of animals observed or caught conditional on it being non-zero. The distribution of non-zero observations might be truncated Poisson (Terceiro, 2003), truncated negative

binomial (O'Neill and Faddy, 2003), or even gamma (Stefánsson, 1996). This class of models is known as conditional models or more commonly in the fisheries literature as the delta approach (Stefánsson, 1996). The probability of non-zero catches as well as the mean catch per haul is then modelled using generalized linear models with explanatory variables such as area or depth (Stefánsson, 1996). A slight modification of this leads to considering the observations to follow a mixture distribution of a Poisson or negative binomial distribution and a Bernoulli draw (finding/observing animals or not) (Welsh *et al.*, 1996). Applied to catch data, the first component of this model can be interpreted as the spatial distribution of fish abundance and the second as the probability of the gear catching a particular fish.

Two biological processes underlie trawl catches: the abundance and spatial distribution of fish populations and capture (trawl) efficiency. The first component determines the number of fish in the trawl path (swept area) and the second describes how many of these will end up in the codend. Capture efficiency is primarily influenced by fish

reactions such as herding, escapement, and net selectivity (see Wardle, 1993; Engås, 1994 for reviews). Traditionally in stock assessment models, capture efficiency, or more generally catchability, has been described by a parameter that might vary among ages or from year to year but which is generally regarded as constant (e.g. XSA, Shepherd, 1999). Dickson (1993a) proposed a deterministic model for trawl efficiency that takes account of the effects of sweeps, otterboards, and the trawlnet. Harley and Myers (2001) used selectivity curves with the parameters for a particular species coming from a common distribution. Recently, Fryer *et al.* (2003) extended this approach and introduced the concept of random selectivity curves, which vary among hauls. Using this idea, we regard haul catchability as a random process.

In this paper we propose an approach for estimating population abundance separately from trawl catchability based on catch numbers per haul. We assume that fish capture is a random process that causes catchability to vary from haul to haul. We develop a model for catch numbers per haul including species catchability as a random effect. In fisheries science, the concept of random effects is best known from generalized linear mixed models (Venables and Dichmont, 2004). The model is tested using a data set of repetitive bottom-trawl hauls carried out in a single statistical rectangle within the Celtic Sea taken over a short time interval. We then deal with the identifiability of such a model. The crucial question is whether it is actually possible to disentangle the catch process, and the local population abundance and estimate all parameters reliably. Parameter identifiability is addressed using simulations and an independent data set from the same area but a different year. Finally, some model extensions are considered that take into account explanatory variables for both the capture process and the abundance distribution.

Catch process

Model development (model 1)

We model the distribution of catch data as a mixture of population abundance and random capture efficiency. If individual fish were randomly distributed in space, considering the two-dimensional fish distribution once fish from a certain water layer were projected onto the sea floor, then the number of individuals encountered in a given area would follow a Poisson distribution. Consequently, the distance between (projected) individuals along a transect line would be described by an exponential distribution. Few studies have looked at the spatial distribution of fish at the scale of a fishing haul. Some information comes from a study on Greenland halibut: using videos from a system mounted on the trawl headline, Albert *et al.* (2003) found that the distance between individuals followed an exponential distribution. Data derived from video observations obtained with an ROV suggest that a number of deep-sea

species are randomly distributed on a small scale (Trenkel, unpublished data). Hence, it might be reasonable to assume that demersal and benthic fish species are randomly distributed in an area with homogeneous substrate and depth conditions. This assumption implies that individuals do not form (big) schools, though a few individuals might occur together without violating the assumption. The effect of schooling will be further considered in the discussion.

Let us turn now to the capture process which we view as a random process. For each species, a given fishing haul has a particular capture efficiency, and all capture efficiencies are described by a common parametric distribution. Differences in efficiency among hauls might be due to gear properties, environmental, or biological factors. If we take the swept area over a wide enough scale, capture efficiency can be interpreted as the proportion of animals caught which takes values between zero and one.

In summary, the model assumptions are that (i) individual fish are randomly distributed in space (ignoring the vertical component) and do not form large schools; (ii) capture efficiency is a random variable in the range (0,1); (iii) the width of the swept area is the same for all hauls, but trawled distance can vary. We can now write down this simple capture model.

For the ith haul, denote by n_i the number of individuals present in the trawl path of which a certain proportion q_i was caught, where $i = 1, \ldots, m$, and the capture efficiencies q_i are independent random variables. Modelling the number of individuals in the trawl path by a Poisson distribution, we have

$$n_i \sim \text{Poisson}(\lambda), \quad n_i = 1, 2, \ldots \tag{1}$$

The capture efficiencies q_i are modelled through normally distributed random variables p_i, which a logistic transformation puts into the appropriate range $q_i \in (0, 1)$.

$$p_i \sim N(\mu, \sigma^2) \tag{2}$$

$$q_i = \exp(p_i)/(1 + \exp(p_i)) \tag{3}$$

The probability density of q_i is shown in Figure 1a for different combinations of the parameters μ and σ. It is seen that the two-parameter family of densities is flexible, and can accommodate the same shapes as the beta-distribution.

This formulation corresponds to a random effects model for catchability. The resulting model of catch numbers is

$$C_i \sim \text{Poisson}(q_i \lambda D_i/2), \quad i = 1, \ldots m, \tag{4}$$

where D_i is the distance trawled by haul i, such that $D_i/2$ is a factor for standardizing to the nominal trawl distance of 2 nm in the Celtic Sea study. Figure 1b shows the probability distributions of C_i corresponding to the random effects distributions in Figure 1a when $\lambda = 70$. Given the
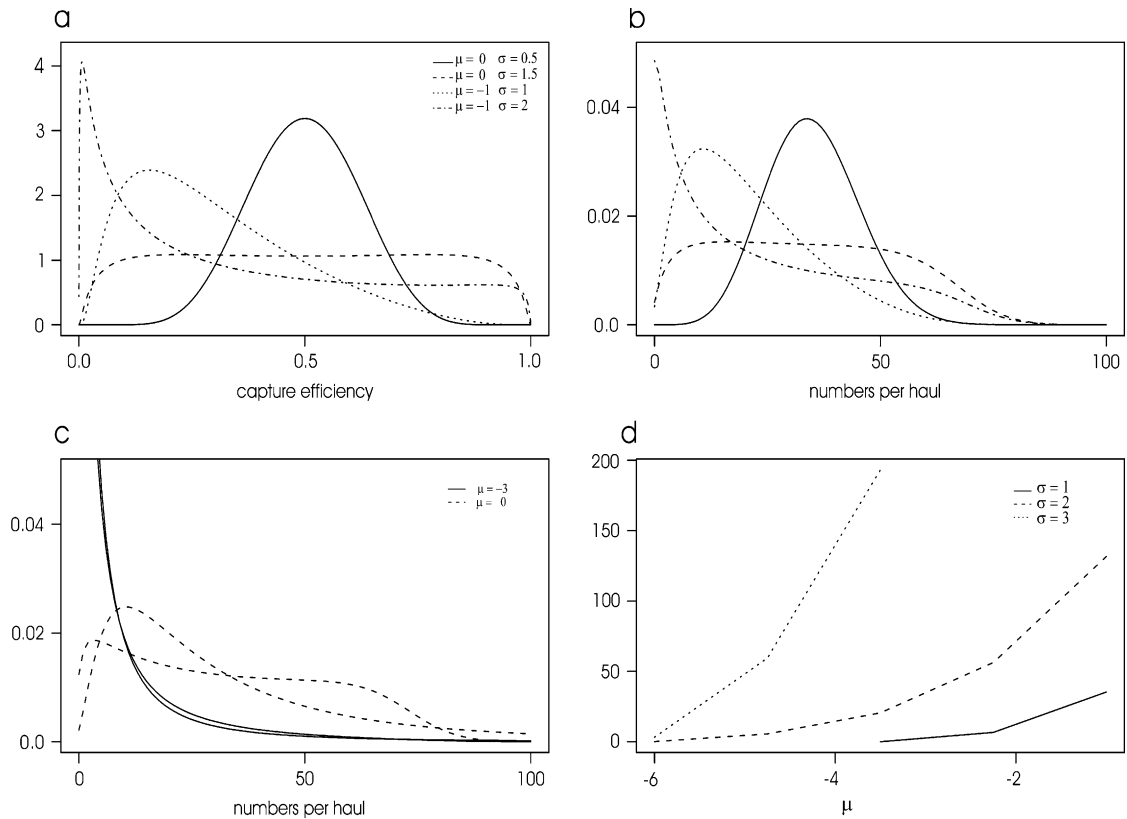
Figure 1. Illustration of the different distributional shapes that can be accommodated by capture model 1. (a) Probability density of the capture efficiency q for different parameter values; (b) corresponding probability functions for catch numbers C ($\lambda = 70$); (c) comparison of the two- and three-parameter families of probability densities for two values of μ ($\sigma = 2$); (d) likelihood ratio between the two- and three-parameter families as a function of μ for different values of σ.

flexibility of the distribution, its shape can resemble that of a negative binomial distribution.

Parameter estimation

We estimate the three model parameters λ, μ, σ by maximum likelihood. To this end, we need to calculate the marginal probability distribution for the catch C_i of haul i:

$$f(C_i|\lambda, \mu, \sigma) = \int_{-\infty}^{\infty} f_P(C_i|q(p_i), \lambda)\phi(p_i; \mu, \sigma)dp_i, \qquad (5)$$

where f_P is the probability function corresponding to Equation (4), $q(p_i)$ is given by Equation (3), and $\phi(p_i; \mu, \sigma)$ is the Gaussian probability density distribution. The log-likelihood function is then given as

$$l(\lambda, \mu, \sigma) = \sum_{i=1}^{m} \log\{f(C_i|\lambda, \mu, \sigma)\} \qquad (6)$$

The likelihood function is maximized using the random effects module of the software package AD Model Builder (Fournier, 2005), which uses the Laplace approximation to evaluate the integral in Equation (5) (Skaug and Fournier,

http://bemata.imr.no/laplace.pdf). AD Model Builder automatically calculates uncertainty estimates based on the observed Fisher information matrix. It should be noted that the Laplace approximation provides only an approximation of the integral (5), which may lead to biased estimates of parameters in some situations (Breslow and Lin, 1995). One should therefore always attempt to assess the accuracy of the Laplace approximation. We carry out a simulation study to investigate the finite sample properties of the approximate maximum likelihood estimates.

Model properties

The proposed model has three parameters: λ, μ, σ, and the only information available for estimating these is the empirical distribution of C_i, i = 1, …, m. Depending on the shape of the distribution, the parameters will be confounded to a varying degree, and as an extreme it may be impossible to estimate all three parameters simultaneously. What happens then is that the model collapses during the estimation process to a two-parameter family: $\lambda \exp(\mu)/(1 + \exp(\mu)) \to \alpha$ as $\lambda \to \infty$ and $\mu \to -\infty$. Here, α is a single parameter replacing the two parameters λ and μ.

The resulting two-parameter model is a Poisson−lognormal mixture distribution for catches C_i, i.e. a Poisson distribution where the mean follows a lognormal distribution.

In practical terms, the phenomenon described above means that the two-parameter family fits the catch numbers C_i equally well as the three-parameter family. To illustrate this point we simulate a large data set (1000 realizations of C_i) and fit both the two-parameter and three-parameter families by maximum likelihood. Technically speaking, we obtain the two-parameter family from the three-par family by fixing μ at the very low value of -7. We generate data for two different parameter settings: $\mu = -3$ and $\mu = 0$. It is seen from Figure 1c that when μ is small ($\mu = -3$) the two probability distributions lie close to each other, and hence will yield approximately the same fit to data. For a given value of μ, the closeness of the two- and three-parameter families depends on the value of σ. So, at which point does the three-parameter family collapse to the two-parameter family? To investigate this, we plot the likelihood ratio between the two models as a function of μ, for three different values of σ (Figure 1d). To eliminate simulation error we use a large sample size (m = 1000). The figure shows that the 'breakdown point' (the value of μ below which the likelihood ratio is zero) depends on σ.

Let us now consider the case where the model (Equations 1−4) is fitted separately for several species. One of the model assumptions is that the width of the area swept by a haul is the same for all hauls but not the trawled distance. This width is also the same for all species and as a consequence the values for the capture efficiencies are directly comparable between species. Similarly, the population abundances can be compared. Of course this is only the case if model assumptions are true, in particular that individuals are randomly distributed in space. However, estimates would not be comparable for two species if one of them responded to the trawl by herding behaviour, which in our model would imply a larger swept area (due to assuming capture efficiency <1) compared with a species that would disperse or scatter at the approach of the trawl and for which the implied swept area would be smaller.

Case study

In October 1994, the Mirec study consisting of small scale bottom trawling was carried out in the Celtic Sea using the standard survey gear (36/47 GOV) equipped with rubber bobbins. Within 6 days (daytime only), 31 hauls of 30-min duration at 4 knots were performed in an area 1° wide and half a degree high centred on 48° 45′N and 8° 30′W. All hauls but two were carried out at depths 140−160 m; the two other hauls were located around 120 m. Overall 25 species were caught, counted, and their length measured. Nine species were caught in sufficient numbers and in enough hauls to attempt fitting the capture model (model 1).

Figure 2 shows the distributions of observed numbers per haul that all have long right hand tails. Empirical dispersion factors (variance/mean of catch numbers) ranging from 6.2 for megrim (LEPIWHI) to over 3000 for horse mackerel (TRACTRA) confirmed the strong overdispersion for all species. The expected distributions (obtained by parametric bootstrapping from the fitted model 1) are plotted as continuous lines for all but two species. Based on visual inspection the model seemed to provide a good description of the shape of the catch data. The two species for which no estimates were obtained were red gurnard (CHELCUC) and megrim (LEPIWHI). The estimation procedure did not converge for these two species as the estimated values for the capture efficiency most likely were below the critical value for which the three-parameter model becomes a two-parameter model (see section on Model properties), so the model was not identifiable. For the remaining species population abundances (λ) were estimated with variable precision (Table 1, model 1); the estimate for haddock (MELAAEG) was particularly unreliable but also the smallest value. The ratios of estimated population abundance and mean observed catch (standardized to 2-nm haul length) varied between around 3.3 for poor cod (TRISMIN) and 20 for haddock.

The estimates of the mean μ of the random capture variables were all in the range -5.21 to -1.55 (Table 2, model 1). The smaller the value, the smaller the capture efficiency q (Equation 3). However, this effect can be counterbalanced by large variances σ, estimates of $\ln(\sigma)$ are given in Table 2. Note that the estimates of $\ln(\sigma)$ were rather imprecise for small values. Haddock had the smallest average capture efficiency $\bar{q}$ of 0.05, poor cod the largest of 0.28 (Table 2). The full distributions for the capture efficiency q are shown in Figure 3. Note how the distributions for blue whiting (MICMPOU) and poor cod have larger values for q close to 1 compared with the other species. This explains the large average capture efficiency for poor cod and the relatively large value for blue whiting although their respective distributions had most of the mass close to zero.

In order to check the appropriateness of the normal distribution for the random effect p_i, the histograms of estimated random effects were plotted (results not shown). These histograms looked rather symmetric and a comparison with the assumed normal distributions confirmed this impression. However, there were two cases, silvery cod (GADIARG) and haddock, which showed a somewhat heavy right hand tail. Thus, there might be some factor with respect to which the estimated random effects exhibit a relationship and which could explain the non-normal distribution of the random effects. An obvious candidate would be fish length. To investigate this further, the estimated random effects were plotted against the mean length of the species in the catch (Figure 4). These figures suggested that indeed mean fish length in the catch might be an important factor in determining the capture efficiency of a given haul. We will come back to this later when we consider possible model extensions but we will first consider the issue of model validation for this simple model.
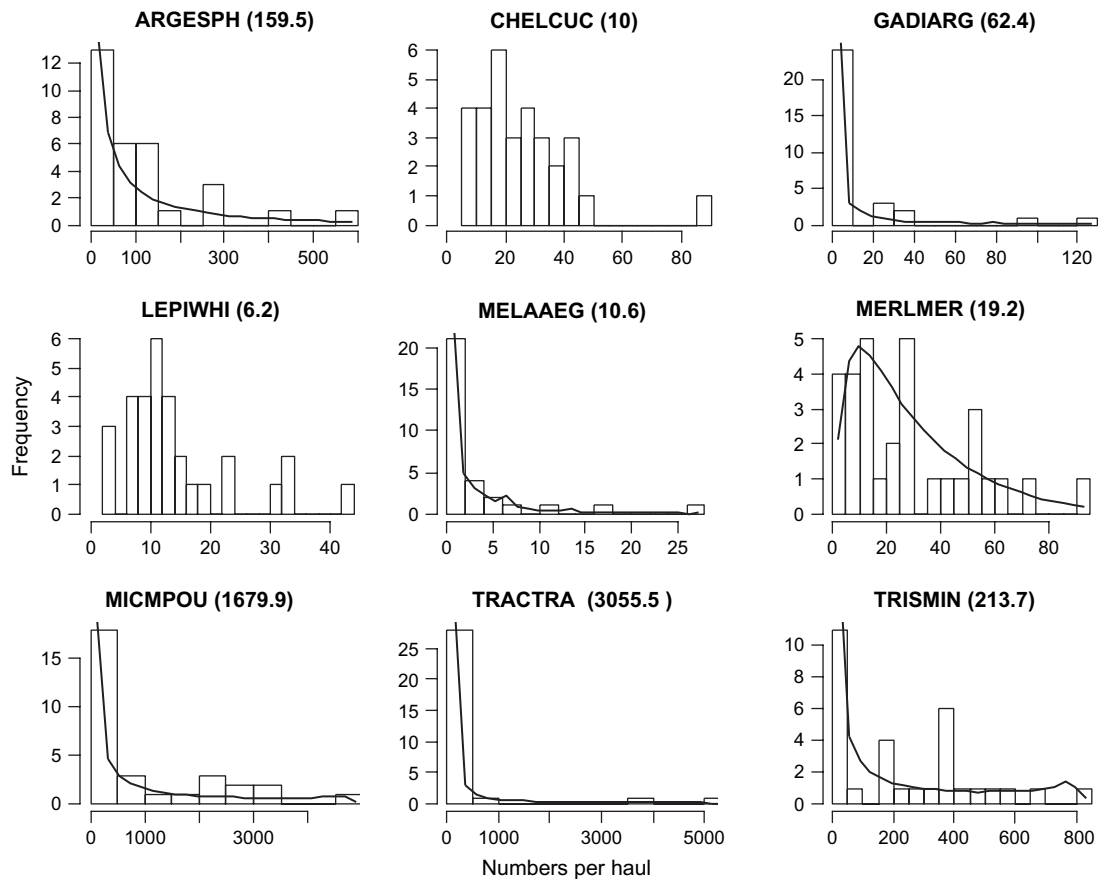
Figure 2. Histograms of numbers per haul, numbers in parenthesis are dispersion indices (var/mean) for the Mirec case study. Continuous lines are expected histograms obtained by parametric bootstrap from fitted model 1.

Model validation

Simulation study

We carried out a simulation study in order to assess the identifiability of our capture model for the Mirec catch data. The two yardsticks we used were bias and precision of parameter estimates. The questions are: can we on average

get correct estimates for all model parameters for all species, and are precision estimates provided by AD Model Builder of the right size?

The estimated parameter values (Tables 1 and 2) and the model (Equations 1–4) were used in a parametric Monte Carlo approach to simulate catch data (200 data sets). The data simulations were carried out separately for all species.

Table 1. Estimates of average population abundance (λ) and ratio population abundance/mean catch per haul ($\lambda/\overline{C}$) for capture models 1 and 2 (capture efficiency is a function of body length) for the Mirec case study. Standard deviations are in parenthesis.

			Model 1		Model 2
Code	English name	Species	λ	$\lambda/\overline{C}$	λ
ARGESPH	Argentine	*Argentina sphyraena*	655.4 (112.8)	6.0 (1.3)	657.4 (114.2)
GADIARG	Silvery cod	*Gadiculus argenteus*	134.1 (21.6)	10.4 (4.1)	133.2 (20.5)
MELAAEG	Haddock	*Melanogrammus aeglefinus*	66.5 (109.4)	20.0 (7.6)	67.1 (112.1)
MERLMER	Hake	*Merluccius merluccius*	129.7 (56.3)	4.4 (0.7)	125.6 (49.0)
MICMPOU	Blue whiting	*Micromesistius poutassou*	4829.7 (155.4)	4.6 (1.0)	4884.5 (214.1)
TRACTRA	Horse mackerel	*Trachurus trachurus*	5137.3 (236.7)	13.6 (7.4)	5170.8 (298.5)
TRISMIN	Poor cod	*Trisopterus minutus*	806.2 (35.0)	3.3 (0.5)	808.7 (36.42)

Table 2. Comparison of estimates of the mean (μ), log-transformed standard deviation ($\log(\sigma)$) of the random capture variable and mean capture efficiencies for capture model 1 and model 2 (population abundance is a function of age) for the Mirec case study. Standard deviations are in parenthesis.

Code	Model 1			Model 3		
	μ	$\log(\sigma)$	$\bar{q}$	μ	$\log(\sigma)$	$\bar{q}$
ARGESPH	−2.41 (0.41)	0.60 (0.16)	0.17	−2.37 (0.41)	0.57 (0.16)	0.17
GADIARG	−5.10 (0.81)	1.20 (0.23)	0.09	−4.29 (0.88)	1.27 (0.24)	0.14
MELAAEG	−4.04 (1.68)	0.51 (0.29)	0.05	−4.0 (1.64)	0.51 (0.29)	0.05
MERLMER	−1.55 (0.62)	0.08 (0.21)	0.22	−0.45 (0.51)	0.25 (0.23)	0.42
MICMPOU	−2.59 (0.52)	1.03 (0.14)	0.22	−1.64 (0.47)	0.91 (0.15)	0.29
TRACTRA	−5.21 (0.63)	1.21 (0.16)	0.08	−4.6 (0.62)	1.12 (0.18)	0.10
TRISMIN	−2.06 (0.57)	1.11 (0.16)	0.28	−1.97 (0.57)	1.12 (0.16)	0.29

The capture model was then fitted to each simulated catch data set. For all three model parameters, true parameter values lay within the 10 and 90 percentiles of the distribution of simulated estimates (Figure 5). The average relative bias over all seven species (mean of estimates from simulated data minus true value divided by true value) was 1% (range −20 to 40%) for population abundance estimates (λ), 6% (range −9 to 38%) for the mean μ of the random capture variable, and −4% (range −38 to 9%) for its standard deviation ($\ln(\sigma)$). Thus, the parameter estimates in Tables 1 and 2 were not likely to be severely biased. In order to assess whether the estimates of precision of parameter estimates were correct, we compared the sample standard deviations of the parameter estimates obtained from the simulated data with the original standard deviation estimates from the Mirec data set. The sample standard deviations for population abundance estimates were larger than the Mirec values for all species (λ: average 226%,

range 26−484%). For the parameters of the random capture variable, the difference was less striking (μ: average 47%, range −8 to 119%; $\ln(\sigma)$: average 6%, range −9 to 48%). This indicates that the variance of all population abundance estimates for the Mirec case study might have been severely underestimated, as would the other two parameters, but to a lesser degree. It seems likely that the quadratic approximation to the maximized likelihood function used by AD Model Builder to obtain standard deviations for parameter estimates was not completely satisfactory for this model. We will have to bear this in mind when comparing parameter estimates in the next section.

Test data set

Another way of validating the model estimates and the appropriateness of the capture model more generally comes from using an alternative data set. In 1996, an intercalibration study was carried out between the old research vessel "Thalassa 1" and the new one "Thalassa 2" (see Pelletier, 1998, for a description of the study). One of the sites selected for this intercalibration study was the same as for the Mirec study. Thirty parallel hauls were carried out leading to two data sets: Intercal 1 ("Thalassa 1") and Intercal 2 ("Thalassa 2"). These data sets provide the opportunity to compare capture efficiency estimates for two data sets (Mirec vs. Intercal 1) obtained using exactly the same gear and the same vessel but coming from different years (1994 vs. 1996). This leads to the null hypothesis $H0_q$: q(Mirec) = q(Intercal 1). It was also possible to compare abundance estimates for the same time (1996) and area obtained using the same gear but different vessels (Intercal 1 vs. Intercal 2). The null hypothesis for this comparison is $H0_\lambda$: λ(Intercal 1) = λ(Intercal 2).

The comparison of model estimates was possible for five species. For three out of the five species, the shapes of the distributions of capture efficiency (q in Equation 3) were nearly identical for all three data sets (figure not shown). For the other two species, silvery cod and poor cod, the distributions were more similar for the same year (Intercal
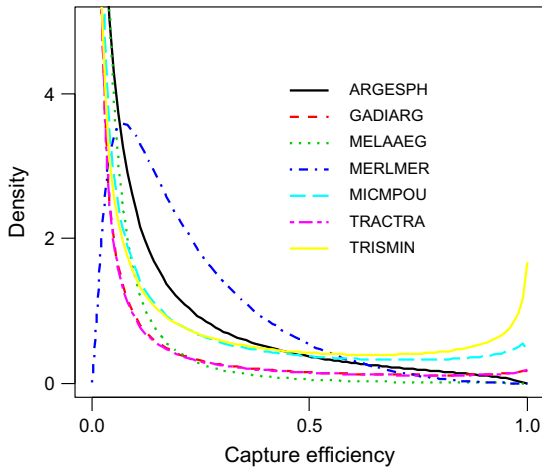
Figure 3. Comparison of the estimated probability density distributions of capture efficiency (model 1) for different species for the Mirec case study.
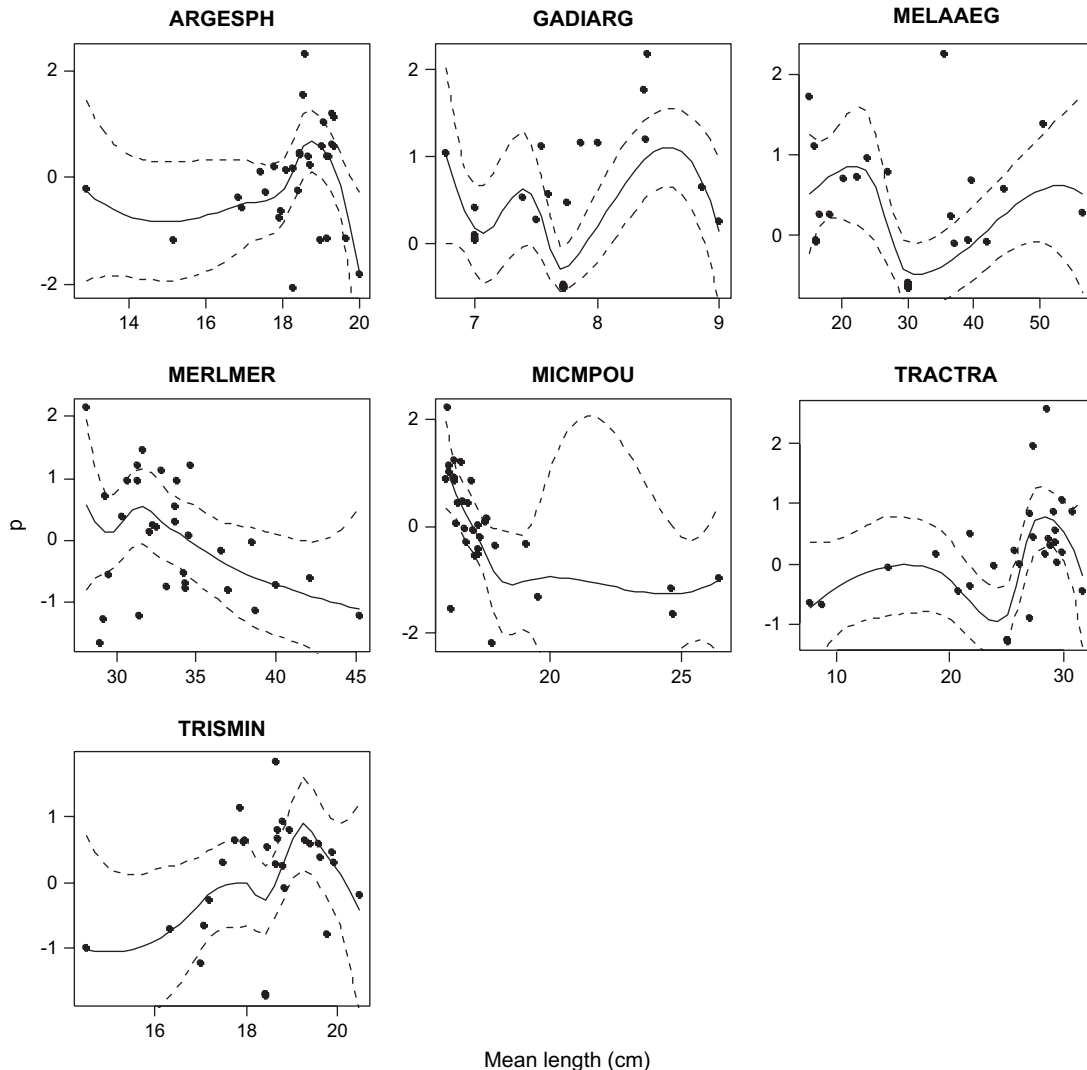
Figure 4. Estimated random effects (model 1) plotted against mean length in the catch for the Mirec case study. Continuous lines are smoothed nonparametric estimates (with 95% confidence bands).

1 vs. 2) than for different years (Intercal vs. Mirec). The comparison of model estimates, however, showed that the values of the mean (μ) of the random capture variables were not significantly different for silvery cod and poor cod due to low estimation precision (Figure 6). Significant differences were found for argentine and horse mackerel for which the shapes of the capture efficiency distributions were similar. Thus, $H0_q$ is rejected for two out of five species.

Comparing the two population abundances estimates (λ) for 1996 (Intercal 1 vs. 2), significant differences were found for silvery cod and poor cod leading to rejecting $H0_\lambda$ for two out of the five species tested. It might be hypothesized that the precision of population abundance estimates was underestimated, which in turn would have led to significant differences, though there were none in

reality. Although the simulation study found that the precision of abundance estimates of these two species was underestimated by 74% and 27%, respectively, increasing the standard deviations by these amounts still yields significant differences in population estimates.

Model extensions

Selecting explanatory variables

The catch process model (model 1) can be extended by including the effects of explanatory variables. An obvious candidate is body length, which affects net selectivity and fish reactions directly. If individuals occur together by length or age, population abundance present in the path of
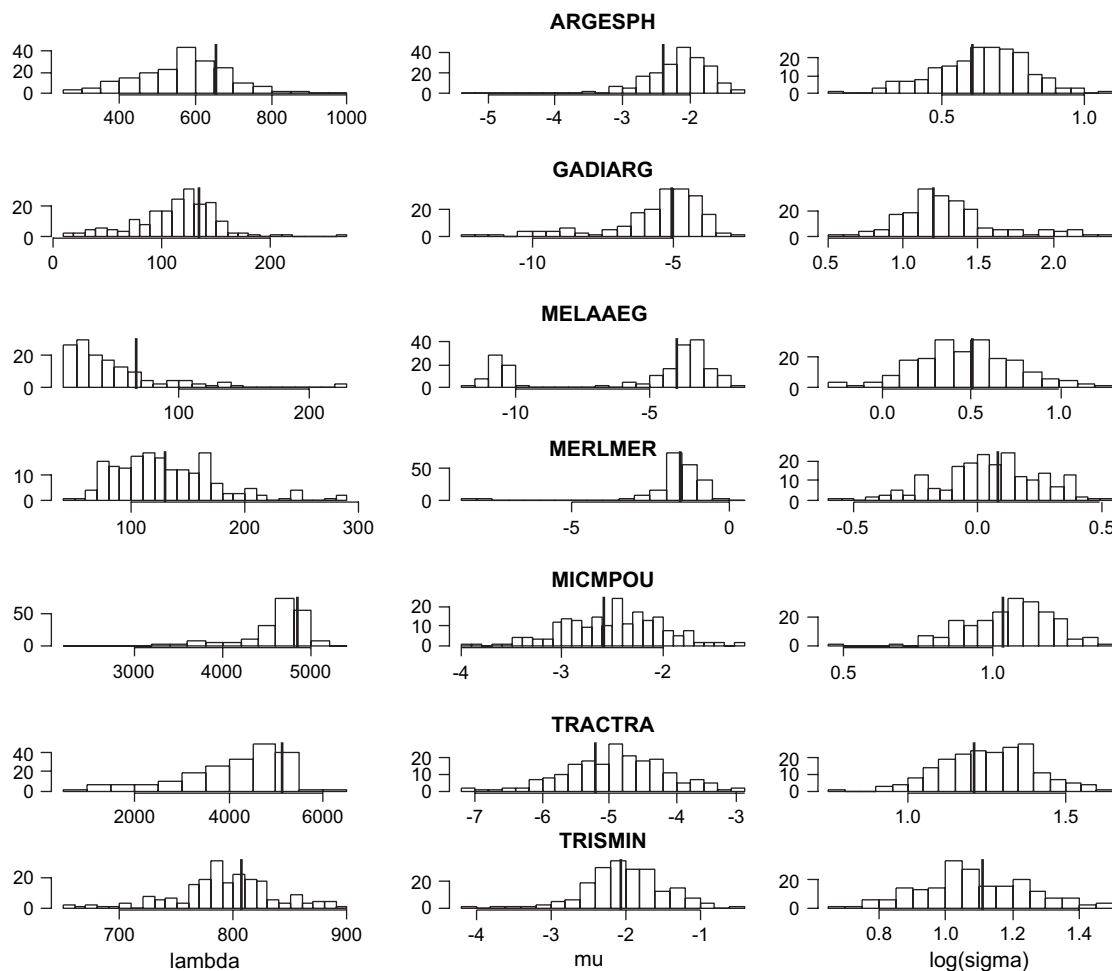
Figure 5. Histograms of estimated parameter values of capture model 1 from simulations. The catch data were simulated from model 1 fitted to the Mirec case study. True parameter values are given by vertical lines.

a given trawl haul might be "explained" by body length indirectly. Thus, body length can either be used as an explanatory variable for the capture efficiency (Equation 2) or the population abundance (Equation 1).

In order to study the impact of body length on capture efficiencies, the mean estimated capture efficiency $\bar{q}$ (model 1) was plotted against the average body length in the catch (Figure 7a). The relationship was a clearly increasing function with two exceptions, haddock and horse mackerel. Both had low average capture efficiency despite having large average body size.

Capture efficiency as a function of body size (model 2a and b)

Modelling the mean of the random capture variable as a linear function of the average body length (l_i) in haul i, we get

$$\mu_i = a + bl_i \tag{7}$$

$$p_i \sim N(\mu_i, \sigma^2) \tag{2a}$$

This means that the capture efficiency q_i (Equation 3) is a logistic function of body length, which corresponds to a classical selectivity model. The model for population abundance remained as before (Equation 1). We used average body length in a haul to represent the length effects of a given species. Hauls with no observations (zero hauls) pose a problem, as no mean length is available. The question is whether this is a case of randomly or non-randomly missing information. To put it differently, is the fact that no individuals were observed in a given haul caused by small local abundance, in which case the information would be randomly missing, or is it caused by the individuals present being too small to be retained in the net, which would mean
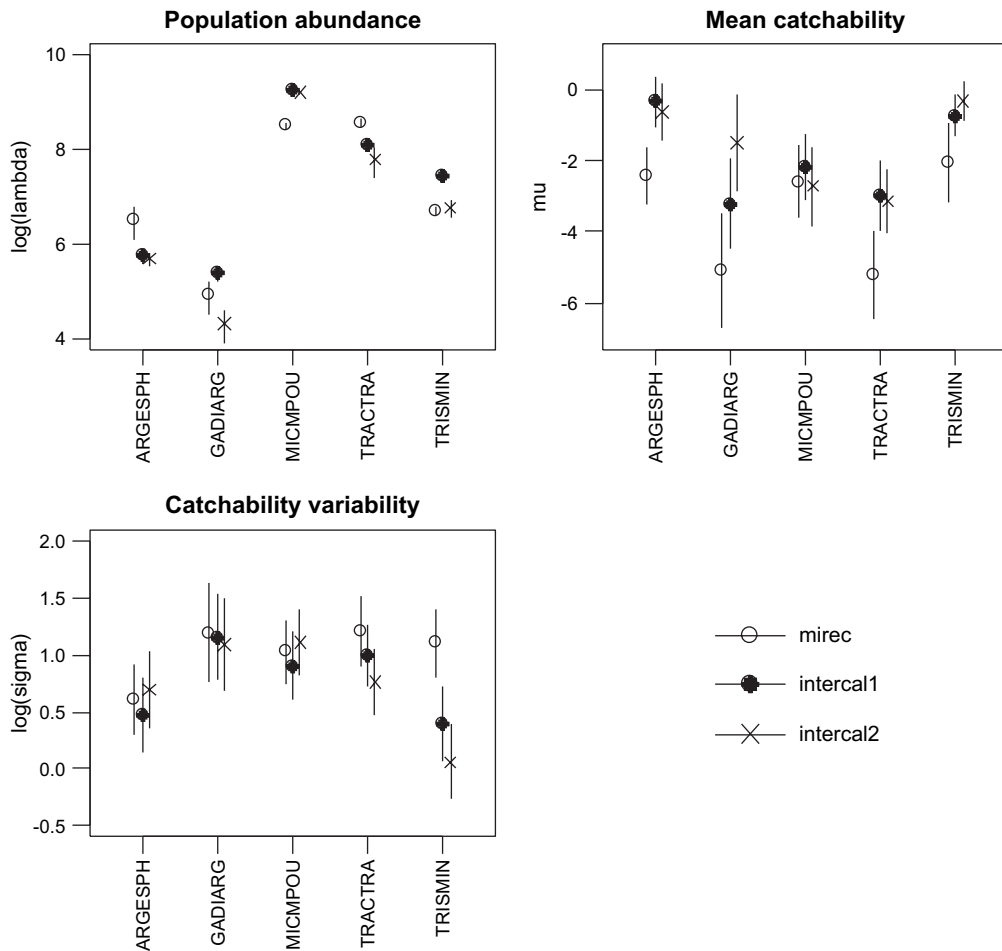
Figure 6. Comparison of estimated parameter values (model 1) for the Mirec and Intercal 1 and 2 case studies. Mirec study in 1994 with "Thalassa 1". Intercal 1 in 1996 with "Thalassa 1" and Intercal 2 in 1996 with "Thalassa 2". Vertical lines indicate 95% confidence intervals.

non-randomly missing information? It might also be a mixture of both. But given the rather large body size of the species in the Mirec study, in most cases zero hauls were more likely to be due to low local abundance. Support for this hypothesis comes from the observation that, for all species, zero hauls were surrounded by small hauls. Thus, we decided to estimate the covariate for zero hauls by the mean of the average haul length from all non-zero hauls.

Assuming the same relationship between the capture variable (species independent b in Equation 7 but separate intercepts a; referred to as model 2a), we obtained mean capture efficiencies which decrease with average body length (Figure 7b). If we assumed however that the relationships differed (species-specific b in addition to a, model 2b), we obtained three classes of species (Figure 7c). Mean capture efficiency clearly increased with body size for argentine, silvery cod, poor cod, and horse mackerel, decreased for hake and blue whiting, and remained constant for haddock. Table 3 summarizes the signs of these

relationships. Thus, the form of the length-specific selectivity function differed between species.

Population abundance as a function of age (model 3)

Modelling population abundance as a decreasing function of age, we obtain

$$\lambda_i = d \exp(-c \, age) \tag{8}$$

$$n_i \sim \text{Poisson}(\lambda_i) \tag{1a}$$

This model corresponds to a classical population dynamics model where c is total mortality and d is average recruitment. The random effects catchability model remained as in model 1 (Equations 2 and 3). Age can be estimated from body length assuming a growth function. Using the inverted von Bertalanffy growth model, we
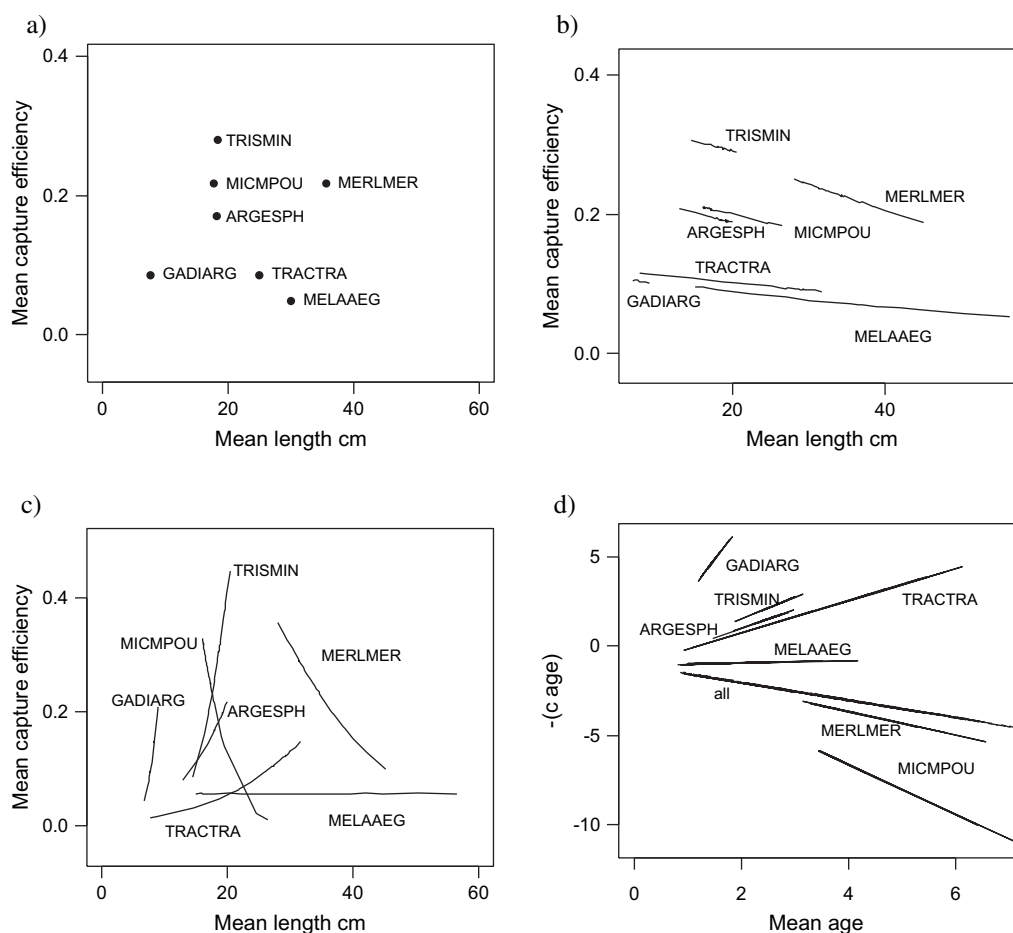
Figure 7. Mirec case study. (a) Mean estimated capture efficiency (model 1) vs. mean length in catch; (b) mean estimated capture efficiency vs. mean length in the catch with common relationships for each species (model 2a); (c) mean estimated capture efficiency vs. mean length in the catch with separate relationships for all species (model 2b), (d) mean estimated abundance vs. mean age in the catch (model 3).

estimated mean age in a haul by first estimating the age of all individuals using growth parameters as in the Appendix of Trenkel and Rochet (2003). For the species not present in that study, we derived values from FishBase (http://www.fishbase.org; GADIARG k = 0.5, Linf = 15; MEL-AAEG k = 0.2, Linf = 100).

Estimating separate mortalities c for all species, only two species (blue whiting and hake) had positive mortalities (negative slopes in Figure 7d and Table 3). These were the same species that had decreasing capture efficiencies with body length (negative slopes for model 2). Thus, only for blue whiting and hake was there evidence that population dynamic effects might have been more important in determining catch numbers per haul than gear efficiency effects.

Model comparison

We have now fitted three different capture models to the Mirec catch data. We used Akaike's information criteria

(AIC) to compare the goodness-of-fit of the different model (Table 4). The simple model (model 1) had the smallest AIC for argentine and haddock, while the model with capture efficiency as a positive function of length (model 2b) was best for poor cod. For hake and blue whiting, the model with abundance as a negative function of age (model 3) had the smallest AIC. For horse mackerel, both models 2b and 3 had identical fits and were better than the simple model. The best fitting model for silvery cod was model 3 with population abundance increasing with age, which does not make much sense biologically unless older individuals immigrated into the survey area.

Discussion

The estimated capture efficiencies for all species in the Mirec study were all rather low, with a mean below 0.3. Poor cod had the highest estimated mean capture efficiency

Table 3. Sign of slopes for capture efficiency as a function of body length (model 2b) and abundance as a function of age (model 3) for the Mirec case study.

Code	Model 2b	Model 3
ARGESPH	+	+
GADIARG	+	+
MELAAEG	0	+
MERLMER	−	−
MICMPOU	−	−
TRACTRA	+	+
TRISMIN	+	+

Table 4. Comparison of model fits (AIC) for the Mirec case study. The best fitting model is shown in bold.

Code	Model 1	Model 2b	Model 3
ARGESPH	**−28 687.60**	−28 687.40	−28 687.40
GADIARG	−2 236.72	−2 236.66	**−2 239.40**
MELAAEG	**−162.80**	−160.91	−160.91
MERLMER	−4 676.70	−4 681.56	**−4 686.12**
MICMPOU	−433 356.00	−433 366.00	**−433 368.00**
TRACTRA	−154 091.60	**−154 093.20**	−154 093.20
TRISMIN	−74 288.00	**−74 290.00**	−74 289.60

(0.28) followed by blue whiting (0.22) and hake (0.22) (model 1 in Table 2). In comparison, haddock had a low mean capture efficiency (0.05) although it is of similar body size to hake. The estimated standard deviation of the capture random variable (Table 2) was larger for haddock than for hake but still only about half the value for the other species. Both haddock and hake live close to the sea floor and hence it seems unlikely that a variable vertical distribution in the water column contributed to the difference in mean capture efficiency. Thus, the difference must be either due to differences in the reaction to the trawl or non-random spatial distributions of one or both species. The effect of vertical avoidance of haddock in front of the approaching vessel can be excluded, as all hauls took place at depths below 100 m, below which only weak and irregular reactions have been observed for this species (Ona and Godø, 1990).

Let us first consider the available evidence on capture efficiency and reaction behaviour. For Barents Sea haddock, overall capture efficiency of a survey trawl equipped with bobbins (as used here) was estimated to be 0.05 for individuals <20 cm and to increase to 0.37 for individuals >50 cm (Dickson, 1993b). Our estimates are somewhat low compared with these. However, Engås and Godø (1989) noted that escape of small haddock under the ground gear depended much on the sweep lengths, with longer sweeps leading to more escapes. Other gear parameters also impact capture (Reeves *et al.*, 1992). Furthermore, Glass and Wardle (1989) found that haddock reactions increase with increasing light level (artificial light). Using population estimates derived from catch-at-age data, Harley and Myers (2001) estimated length specific survey (IBTS) catchability for North Sea haddock. Catchabilities were around 0.6 and 0.2 (25-cm individual) in autumn and winter, respectively. Again, our values for haddock appear low. Closely linked to reaction behaviour is maximum fish swimming speed which actually allows individuals to escape the approaching trawl. A recent laboratory study found that a 42.0-cm haddock could maintain a swimming speed of about 0.92 m s^{-1} for up to 15 min (at 10°C), with larger burst swimming speeds (Breen *et al.*, 2004). No information is available for hake,

so that it is not possible to establish whether haddock might be a better swimmer.

We now turn to the second explanation for the estimated difference in mean capture percentage for haddock and hake. Given that the survey area was rather small, the substrate homogenous, and the depth range small, horizontal abundance gradients seem unlikely. Hence, schooling might have been a factor. Indeed, using videos on the trawl headline, haddock have been observed to form schools occasionally (Aglen *et al.*, 1997). This hypothesis is supported by the observation that estimated horse mackerel capture efficiency was low given its body size. Horse mackerel is known to form schools (Massé *et al.*, 1996). Let us now consider the effects of schooling on our capture model.

If schooling occurs in some species, the proposed capture model no longer holds for those species. Assuming constant school size τ and a random spatial distribution of schools, the distribution of the number of individuals in the trawl path (Equation 1) becomes $n_i \sim \tau \cdot \text{Poisson}(\lambda)$, where λ is now the expected number of schools. Note that the variance of n_i under this model is $\tau^2\lambda$, which is larger than $\tau\lambda$, the variance under the assumption $n_i \sim \text{Poisson}(\tau\lambda)$. In contrast, the expectations of both models are identical ($E[n_i] = \lambda\tau$). As a consequence, if our (wrong) capture model (model 1) is fitted, the population abundance ($=\lambda\tau$) estimated under this model should be an approximately unbiased estimate of the true population abundance, while the distribution of the capture efficiency will be inflated by the extra variance. This situation can be expected to lead to higher values for capture efficiencies close to one. Indeed both blue whiting and poor cod show this feature of upward bending curves on the right hand side, and to a lesser degree also horse mackerel, but not haddock (Figure 3). Thus, in this case average capture efficiencies are overestimated and the median might be a more robust measure for obtaining interpretable capture efficiencies. Therefore, given that schooling is expected to lead to an overestimate rather than an underestimate of the average capture efficiency, the most convincing explanation for the low haddock estimate is its capability to avoid capture.

Having established that point estimates of abundance estimates should be more or less valid even if schooling occurred, we can now discuss the comparison of our

population estimates with the average catch numbers. Given that we do not know the width of the swept area, we can only compare relative abundances and abundance/catch ratios between species. These ratios vary between 3 and 20, with most species below X (see Table 1 col. 5). Thus, if we were to use our model based abundance estimates instead of the average catch per haul to produce a survey abundance index, our perception of the community species composition would be somewhat different. The species with the highest estimated abundance was horse mackerel, while blue whiting was most abundant in the catch. At the other end of the spectrum, haddock was in both cases the least abundant species, but the order of the remaining species differed.

The proposed capture model was shown to be identifiable (simulation study) and to some degree repeatable (test data set) which means that the two stochastic processes capture efficiency and population abundance distribution could be disentangled conditional on all model assumptions being true. While assuming random capture efficiency might appear reasonable, the fundamental assumption of a random spatial fish distribution (Poisson distribution) needs further verification. One approach would be to use a split-beam echosounder, track individual fish and then determine their spatial distribution (Pedersen, 1996). An alternative is to use videos either fixed on the trawl headline (Albert *et al.*, 2003) or on underwater vehicles (Trenkel *et al.*, 2004). The advantage of videos is that species identification is much easier. Further model extensions are also envisageable by including additional environmental explanatory variables or trawl gear parameters. Correlations between species occurrences could also be included.

In conclusion, the proposed capture model offers a method for disentangling the effects of species abundance and catchability on trawl catches. This provides abundance indices that are comparable between species and that give true species capture efficiencies. It furthermore allows comparing capture efficiency for different species.

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