

Is catch-per-unit-effort proportional to abundance?

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Abstract: We compiled 297 series of catch-per-unit-effort (CPUE) and independent abundance data (as estimated by research trawl surveys) and used observation error and random effects models to test the hypothesis that CPUE is proportional to true abundance. We used a power curve, for which we were interested in the shape parameter (β). There was little difference among species, ages, or gear types in the distributions of the raw estimates of β for each CPUE series. We examined three groups: cod, flatfish, and gadiformes, finding strong evidence that CPUE was most likely to remain high while abundance declines (i.e., hyperstability, where $\beta < 1$). The range in the mean of the random effects distribution for β was quite small, 0.64–0.75. Cod showed the least hyperstability, but still, 76% of the mass of the random effects distribution was below 1. Based on simulations, our estimates of β are positively biased by approximately 10%; this should be considered in the application of our findings here. We also considered the precision of CPUE indices through a meta-analysis of observation error variances. The most precise indices were those from flatfish (median coefficient of variation of ≈ 0.42).

Résumé : La compilation de 297 séries de données de capture par unité d'effort (CPUE) et des données indépendantes d'abondance (estimées par des inventaires scientifiques au chalut) ainsi que l'utilisation de modèles d'erreur d'observation et d'effets aléatoires nous ont permis de vérifier l'hypothèse que la CPUE est proportionnelle à l'abondance réelle. Nous avons utilisé une courbe exponentielle, dont nous étions intéressés au paramètre de forme (β). Il y a peu de différence entre les espèces, les âges ou les engins de pêche en ce qui concerne la distribution des estimations brutes de β pour chaque série de CPUE. Chez les trois groupes examinés, les morues, les poissons plats et les gadiformes, il y a de fortes indications que la CPUE a une grande probabilité de rester élevée alors que l'abondance décline (i.e., une hyperstabilité, lorsque $\beta < 1$). L'étendue de la moyenne de la distribution des effets aléatoires pour β est très faible, 0,64–0,75. Ce sont les morues qui montrent le moins d'hyperstabilité; néanmoins, 76% de la masse de la distribution des effets aléatoires est inférieure à 1. D'après nos simulations, les estimations de β sont surestimées d'environ 10%, ce qui doit être pris en compte dans l'application de nos résultats. Nous avons aussi examiné la précision des indices de CPUE à l'aide d'une méta-analyse des variances des erreurs d'observation. Les indices les plus précis sont ceux des poissons plats (coefficient médian de variation de $\approx 0,42$).

[Traduit par la Rédaction]

Introduction

Despite its well-documented shortcomings, the catch-per-unit-effort (CPUE) from many commercial and recreational fisheries is used in the assessment of fish populations, with strict proportionality between CPUE and abundance frequently assumed. It has long been recognized that CPUE may not accurately reflect changes in abundance (Beverton and Holt 1957).

Paloheimo and Dickie (1964) reviewed the early use of CPUE data in fisheries and argued the importance of understanding both the spatial distribution of fish and the allocation of fishing effort to interpret CPUE data. Possibly the first use of CPUE data in a fisheries setting is attributed to Baranov (1918) who incorporated catch data in the analysis of herring (Seber 1982). Reasons why CPUE might not be proportional to abundance have been investigated by simulation (Sampson 1990; Swain and Sinclair 1994; Gillis and Peterman 1998) and through examination of empirical data (Peterman and Steer 1981; Crecco and Overholtz 1990; Rose and Leggett 1991). The most common form of nonproportionality involves CPUE remaining high while abundance declines. This is known as "hyperstability" (Hilborn and Walters 1992) and can lead to overestimation of biomass and underestimation of fishing mortality (Crecco and Overholtz 1990).

The model of proportionality between CPUE U and abundance N at time t is

$$(1) \quad U_t = qN_t$$

where q is the catchability coefficient. A number of nonlinear models have been proposed, the simplest being the power curve

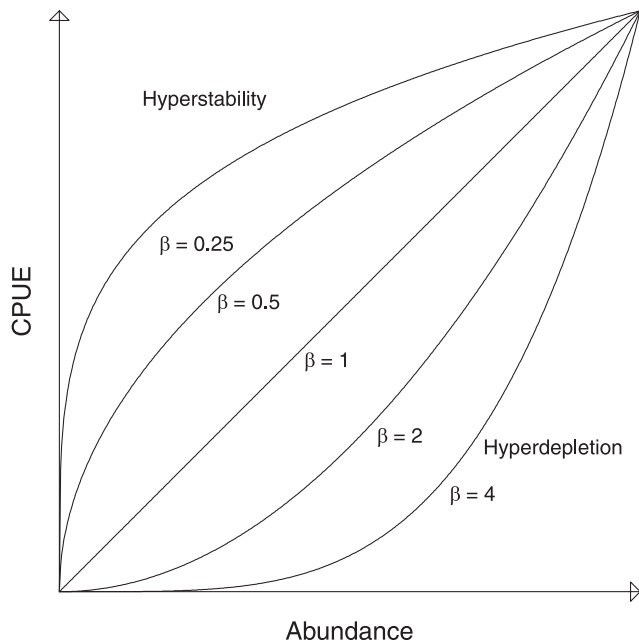
$$(2) \quad U_t = qN_t^\beta$$

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Fig. 1. Relationship between CPUE and abundance based on different values of the shape parameter β .



where if $\beta = 1$ the model reduces to eq. 1 and if $\beta \neq 1$, then catchability changes with abundance (Fig. 1). When $\beta > 1$, U declines faster than N in a situation known as “hyperdepletion”; conversely, if $\beta < 1$, U declines slower than N , which results in hyperstability. This model does have the property that when $\beta \neq 1$, catchability is no longer given by q , but rather a function of q and β (catchability = $qN^{\beta-1}$). Other nonlinear models have been proposed; Bannerot and Austin (1983) allowed nonlinearity in both effort and abundance, while Richards and Schnute (1986) proposed a very general and flexible range of three-parameter models.

Our interest here is in the relationship between CPUE and abundance and we consider the traditional catchability parameter, q , as a nuisance parameter. We consider the shape parameter of the power curve, β . We prefer to use the power curve, as it requires the estimation of only one additional parameter. In doing so, we admit that we are limiting the forms of the relationship.

While many studies have focused on CPUE for a single stock or fish community, there have been few attempts to compile data across fisheries and examine the problem in a broader context. This type of synthesis or “meta-analysis” has proved useful in many fisheries contexts. A meta-analytical approach has provided insights into the maximum reproductive rate of fish (Myers et al. 1999).

Dunn et al. (2000) examined the relationship between CPUE and abundance for all available New Zealand data sets as well as a number from Atlantic Canada. In general, it was found that the small numbers of paired CPUE/survey observations lead to considerable difficulties in estimating β . They also compared CPUE indices with model estimates of abundance (that had not used CPUE data), as this led to longer time series. Simulations showed that with few paired observations (four to eight), a very large (>50%) reduction in

biomass was required to accurately estimate β . When $\beta = 1$, a reduction of up to 75% was required to distinguish between proportional, hyperstable, and hyperdepleted relationships. When the reduction in abundance was low (12.5–25%), $\hat{\beta}$ tended to 1, regardless of the true β .

Here, we compile a large number of CPUE and survey abundance indices from International Council for the Exploration of the Sea (ICES) stock assessment reports. We use commonly accepted observation error models to obtain individual estimates of β and the estimation error variance, which we then combine using basic meta-analytical techniques for the combination of treatment effects.

Methods

CPUE and abundance data

For this study, we require estimates of fishery CPUE and fishery-independent estimates of true abundance. We use research survey abundance estimates as the fishery-independent estimate of abundance. It could also be possible to use biomass estimates from a stock assessment model that did not use CPUE data, but we have not considered this potential data source. With the procedures used here (described in sections below), we require a CPUE time series for a population where there is also available either (i) one research survey time series with a reliable estimate of its sampling error, (ii) multiple research surveys, or (iii) a single “reliable” survey series and multiple CPUE series. We restricted ourselves to data of the second and third types, as this did not require assumptions about the observation error of the survey series.

ICES stock assessment reports offer a standard format and data from a number of fisheries. The larger number of trawl surveys conducted in the ICES region and the length of these series made it possible to obtain a large number of data sets for a range of species (Table 1). The CPUE and survey indices were obtained from the data input files for the stock assessments conducted in 1999. In each case, the CPUE indices were chosen by the experts in each ICES assessment committee as a series representative of the stock status. In some cases the CPUE indices were corrected for fishing power, e.g., horsepower, and sometimes the assessment biologist did not believe that it was necessary. The ICES CPUE indices represent data that are typical of those used by experienced assessment biologists. Details are given in each of the assessment reports available from ICES. The data files can be obtained directly from ICES (<http://www.ices.dk/committe/acfm/acfm.htm>) or from the corresponding author.

ICES data are usually presented in an age-disaggregated form leading to the large number of data sets available. One limitation of using published data is that in many cases, data were not presented for all ages, e.g., survey data for ages 1–6 and CPUE data for ages 4–9. In such cases, we were only able to use the ages where there was overlap. Also, there were instances where there was no overlap, when survey data were used for the younger ages and CPUE for the older ages. Thus, to a certain extent, we were limited by which data were readily available. We restricted ourselves to data sets where there were at least nine paired observations of CPUE and survey abundance because shorter series are unlikely to produce reliable estimates (Myers and Cadigan 1993; Dunn et al. 2000). This did not result in the exclusion of many data sets.

The CPUE series represented a range of different gear types or fleets (Table 2). For the majority of the trawl data, the specific trawl type was not given. Most gears involve a single vessel towing a net of some type. The Danish seine gear is the only gear that is not towed, but rather, it is set and then hauled, and the pair trawl gear represents a net jointly towed by two vessels.

Table 1. CPUE data used in the meta-analysis.

Species/stock	CPUE series	Ages	Years	Multiple RV surveys
Blue whiting (<i>Micromesistius poutassou</i>)				
Northeast Atlantic	1	1–5	12	Yes
Atlantic cod (<i>Gadus morhua</i>)				
ICES IV and IIIa (North Sea and Skaggeak)	5	1–5	16	Yes
ICES VIIe–k (Western Channel)	3	1–5	10	No
ICES (Kattegat)	3	2–5	12	No
Four spot megrim (<i>Lepidorhombus boscii</i>)				
ICES VIIIc and IXa (West Iberian Shelf)	2	1–7	11	No
Haddock (<i>Melanogrammus aeglefinus</i>)				
ICES IV (North Sea)	2	0–5	10	Yes
ICES VIb (Rockall Bank)	3	2–7	10	No
Hake (<i>Merluccius merluccius</i>)				
ICES IIIa, IV, VI, VII, and VIIIab (North)	4	2–5	12	No
Megrim (<i>Lepidorhombus whiffiagonis</i>)				
ICES VII and VIIIab (Bay of Biscay)	1	2–9	9	Yes
ICES VIIIc and IXa (West Iberian Shelf)	2	1–7	10	No
Plaice (<i>Pleuronectes platessa</i>)				
ICES VIIe (Western Channel)	3	3–5	10	No
ICES VIIfg (Celtic Sea)	3	2–5	9	No
ICES VIIa (Irish Sea)	2	2–4	10	No
ICES VIId (English Channel)	3	2–5	9–10	Yes
Pollock (<i>Pollachius virens</i>)				
ICES IV and IIIa (North Sea and Skaggeak)	3	3–7	9	No
Sole (<i>Solea vulgaris</i>)				
ICES VIIa (Irish Sea)	2	3–9	10–11	No
ICES VIId (English Channel)	2	2–4	11	No
ICES IV (North Sea)	2	2–4	13	Yes
ICES VIIfg (Celtic Sea)	2	2–5	11	No
ICES VIIIab (Bay of Biscay)	2	1–8	11	No
ICES VIIe (Western Channel)	2	3–6	15	No
Whiting (<i>Merlangius merlangus</i>)				
ICES IV (North Sea)	3	2–5	16	Yes
ICES VIa (West of Scotland)	3	2–6	11	No
ICES VIIe–k (Celtic Sea)	2	1–6	12	No

Note: RV, research vessel.

Observation error models

PROC CALIS (Covariance Analysis and Linear Structural equations) estimates parameters of linear structural equations using covariance structure analysis (SAS Institute Inc. 1990). This is a general framework that can include observation error models as a special case. To obtain individual population estimates of β , we use the power curve

$$U_t = q N_t^\beta e^{\epsilon_t}$$

Model notation is summarized in Table 3.

We take the logarithm of the different components such that $n_t = \log(N_t)$ and $u_t = \log(U_t)$. An important assumption that we will use is normality of the independent variable, so we have $n_t \sim N(\mu, \phi)$, which states that the true abundances, N_t , are independently lognormally distributed.

As we do not actually observe the true abundances, rather estimates from research trawl surveys, the observation error in n_t can be incorporated into the model by

$$o_t = n_t + \zeta_t$$

$$o_t \sim N(\mu, \phi + \sigma_\zeta^2)$$

where o_t is the observed value of n_t from the survey and the observation error is assumed to be normal, i.e., $\zeta_t \sim N(0, \sigma_\zeta^2)$. For CPUE, we can write

$$u_t = \log(q) + \beta n_t + \epsilon_t$$

$$u_t \sim N(\log(q) + \beta\mu, \beta^2\phi + \sigma^2)$$

where β is the slope of the relationship between the logarithm of CPUE and the logarithm of the abundance and σ^2 is the estimation error variance. From these assumptions, the theoretical variance–covariance matrix (Σ) of the joint distribution of the CPUE series (u_t) and the observed survey series (o_t) is

$$(3) \quad \Sigma = \begin{bmatrix} \phi + \sigma_\zeta^2 & \beta\phi \\ \beta\phi & \beta^2\phi + \sigma^2 \end{bmatrix}$$

where the parameters to estimate are β , ϕ , σ_ζ^2 , and σ^2 . This problem is not identified, i.e., unique solutions do not exist, unless one of the four parameters can be estimated independently. This is because there are four unknown parameters but only three elements of Σ . This example represents a standard structural regression problem.

The identification problem is overcome if we have multiple surveys or multiple CPUE series. If we have two surveys, and with the same assumptions as before, the survey estimates are

$$o_{t,1} = n_t + \zeta_{t,1}, \text{ where } \zeta_{t,1} \sim N(0, \sigma_{\zeta_1}^2) \\ o_{t,2} = n_t + \zeta_{t,2}, \text{ where } \zeta_{t,2} \sim N(0, \sigma_{\zeta_2}^2)$$

and the theoretical variance-covariance matrix of the CPUE and two survey series is

$$\Sigma = \begin{bmatrix} \phi + \sigma_{\zeta_1}^2 & \phi & \beta\phi \\ \phi & \phi + \sigma_{\zeta_2}^2 & \beta\phi \\ \beta\phi & \beta\phi & \beta^2\phi + \sigma^2 \end{bmatrix}$$

where the parameters to be estimated are $\sigma_{\zeta_1}^2$, $\sigma_{\zeta_2}^2$, σ^2 , β , and ϕ . As there are more free parameters than unique elements of the observed variance-covariance matrix, the model is identified. It is simple to extend Σ for the case of more than two surveys and the case of multiple CPUE series and a single survey series. The case of two CPUE series and one survey series is exactly identified. We used all trawl surveys that were available (and used in the stock assessment) for a stock (two to four) (Table 1).

We used maximum likelihood methods to estimate the parameters of Σ (details of the methods can be found in Bollen (1989)). The basic estimation procedure is to fit the observed variance-covariance matrix with the theoretical one. The fitting function that is minimized to find the maximum likelihood estimates is

$$(4) \quad \log|\Sigma| + \text{tr}(\mathbf{S}\Sigma^{-1}) - \log(|\mathbf{S}|) - d$$

where “tr” is the matrix trace and d is the dimension of \mathbf{S} (Bollen 1989). Maximum likelihood does not always produce sensible results, i.e., the parameters describing the variance can be estimated to be <0 if they are not constrained. This often happens with short time series in which the sample variance is not an adequate approximation to the true variance. Any model in which at least one of the estimates of the variance parameters had to be constrained to be >0 or whose estimates were very small (<0.06) was rejected. We will return to the robustness of and alternative approaches to this problem later. Standard errors are estimated using the inverse of the Hessian matrix.

We use a structural as opposed to a functional regression approach for estimation in the presence of measurement errors (Fuller 1987). In the structural approach, we make the assumption that the independent variable, i.e., the true abundance, is a random variable that has a common distribution. The functional approach, which we did not use, assumes that the independent variables are fixed, and each must be estimated. The functional approach has the advantage that changes over time can be easily modeled but has the considerable disadvantage that a separate unknown abundance would have to be estimated for each year. This leads to an estimator that is not guaranteed to be consistent because more parameters are estimated as more data are added (Fuller 1987).

Meta-analysis of individual parameter estimates

A range of techniques exist for combining effect sizes or a parameter of interest across studies or populations (Cooper and Hedges 1994). Here, we will combine estimates of β and the estimation error variance (σ^2) for each data set within a Gaussian “random effects” framework. We assume that there is an underlying distribution for the parameter of interest. If we consider the shape parameter β , we assume that each of the true unobserved β_i s are normally distributed, i.e., $\beta_i \sim N(\mu_\beta, \sigma_\beta^2)$. We also assume that each of the true values for β_i is estimated with error. We assume

normal observation error, $\hat{\beta}_i \sim N(\beta_i, v_i)$, where v_i is the estimation variance, $(\text{SE}(\hat{\beta}_i))^2$. Finally, the variability observed in $\hat{\beta}_i$ (i.e., all of the individual estimates) can be written as a sum of two variances:

$$\text{var}(\hat{\beta}_i) = \sigma_\beta^2 + v_i$$

We followed the maximum likelihood approach of Hardy and Thompson (1996) for combining the estimates of β_i . This approach allows the estimation of both the underlying distribution from which the β_i s are drawn and the profile log likelihood, which can be used to calculate confidence limits. The form of the joint log likelihood in terms of μ_β and σ_β^2 is

$$(5) \quad l(\mu_\beta, \sigma_\beta^2) = -\sum_{i=1}^k \frac{1}{2} \log 2\pi(\sigma_\beta^2 + v_i) - \sum_{i=1}^k \frac{(\hat{\beta}_i - \mu_\beta)^2}{2(\sigma_\beta^2 + v_i)}$$

We repeated the analysis for the estimation error variance of the relationship between CPUE and abundance (σ_i^2). To meet the assumption of normality, we assumed that $\log \sigma_i$ was a normal random variable (i.e., $\log \sigma_i \sim N(\mu_{\log \sigma}, \sigma_{\log \sigma}^2)$). We also assumed that the errors were normal so that $\log \sigma_i \sim N(\log \sigma_i, \omega_i)$. We derived approximate estimates of ω_i using the delta method. An advantage of using $\log \sigma$ is that σ is approximately equal to the coefficient of variation (CV) of the series under reasonable conditions. For this reason, we will discuss our results in terms of σ .

The random effects distribution could also be seen as a “prior” distribution that we would expect individual values of a parameter to be from. As we used maximum likelihood estimation (MLE), the random effects distribution can be referred to as the MLE prior (Efron 1996), i.e., the maximum likelihood estimate of the prior distribution. In this case the MLE prior distribution reflects the distribution from which the true individual values of a parameter are drawn. We prefer this term here, as it better reflects how these distributions might be used in practice.

Results

Large fluctuations in the CPUE and survey indices were observed. The median relative range (maximum/minimum CPUE index) in CPUE was approximately 12-fold, and the 95th percentile was 0.69. This suggests that there is enough contrast in the data to estimate β . It was also found that the lowest point in a CPUE series was just as likely to be the first or last year, although overall the median decline in log CPUE was 5% per year.

While it is not possible to display all data used in the analysis, nine randomly selected data sets from the 297 considered in the analysis (using a random number table) are presented in Fig. 2. Seven of the nine series had estimates of $\beta < 1$ from our maximum likelihood structural models. The series in Fig. 2d exhibited hyperdepletion, and the series in Fig. 2g did not provide feasible results (i.e., negative variance estimates described below). From an examination of the data, there is no evidence for more complex models.

Of the 297 data sets that were analyzed, 209 were retained for the subsequent meta-analysis. That is, data sets were excluded if the maximum likelihood estimates for σ^2 were negative or if the estimates for ϕ were either negative or very small (<0.06). In the case where ϕ was very small, there was very little estimated variation in true abundance, and thus, it was not possible to obtain accurate estimates of how CPUE

Table 2. Gear types of CPUE series.

Code	Gear type	Data sets
BeTrawl	Beam trawl	55
DSeine	Danish seine	32
LTrawl	Light trawl	32
NTrawl	Shrimp trawls	20
OTrawl	Otter trawl	12
PTrawl	Pair trawl	5
Trawl	Unspecified trawl	142

changed with abundance (i.e., regression with estimates of the dependent variable at only a single value of the independent variable). Sensitivity to this cutoff criterion is discussed at the end of the results section and was investigated by the simulations of Myers and Cadigan (1993).

We compared the data series where estimates of β were obtained and those that were excluded. No differences were found in the length of series or contrast in the CPUE or survey indices. It was found, however, that the presence of multiple surveys was different between the two groups. For data sets where multiple surveys were available, 87% of the series gave acceptable results (positive variances) versus 67% for those without. This finding was not surprising, and we then compared the results of those data sets that gave acceptable results on the basis of whether there were multiple surveys or not. There was evidence (not statistically significant by an analysis of medians) that the individual estimates of β were greater for those series without multiple surveys (median of 0.84 versus 0.67). However, the standard errors were also higher, indicating that these estimates were less precise. Overall, the variance estimates were lower and less variable for the series with multiple surveys.

Except perhaps for data from the one hake stock, the distribution of the shape parameter β did not differ significantly across the species (Fig. 3), and most of the $\hat{\beta}_i$ s were <1 . Estimates for hake were mostly >1 and considerably different from those for other species that were examined. Possible problems with these data will be discussed later. For species other than hake, in most cases the upper quartile of the distribution of β was <1 and the upper 95% confidence limit for the median was <1 . Data for the youngest (0) and oldest ages (8 and 9) were variable, but there were few observations for these ages. There is some evidence that the upper quartile increases with age, but any trend in median $\hat{\beta}$ at age is unclear (Fig. 3). None of the gear types appear to be significantly different from one another. Aside from the median $\hat{\beta}$ for the otter trawl, which is close to 1, the median for all of the other gear types is approximately the same (≈ 0.7). The 95% confidence limits for the medians for both beam trawl and trawl are below 1. Only one obvious outlier was present among the estimates of $\hat{\beta}_i$; this was an estimate of -3.23 for age-1 whiting in ICES area VIIek for a nephrops trawl. This estimate had a high standard error (2.31) and had very little influence on the subsequent random effects meta-analysis.

Sole and whiting had the lowest median $\hat{\sigma}$ (≈ 0.4) (Fig. 4). Estimates for the flatfish species were generally lower (but not significantly different) than those of the gadiformes. The highest estimates of σ were for haddock, with the upper quartile >0 (i.e., $CV > 1$). The youngest ages had the highest

Table 3. Summary of notation used in this paper.

Symbol	Description
U_t	CPUE index in year t
q	Catchability coefficient
N_t	Abundance in year t
β_i	Shape parameter of the power curve for CPUE series i
ϵ_t	True log deviation from the power model in year t
o_t	log of true abundance (unobserved) in year t
σ_{ϵ}^2	Observation error variance of the log-transformed survey
ϕ	Variance in true abundance of the log-transformed time series
μ	Mean true abundance of the log-transformed time series
σ^2	Estimation error variance of the log-transformed CPUE series
$\log \sigma$	log of the square root of the estimation error variance of the CPUE series
v_i	Estimation variance for β_i , $(\widehat{SE}(\beta_i))^2$
ω_i	Estimation variance for $\log \sigma_i$, $(\widehat{SE}(\log \sigma_i))^2$
Σ	Theoretical variance-covariance matrix
S	Observed variance-covariance matrix
μ_{β}	Mean of random effects distribution for β
σ_{β}^2	Variance of random effects distribution for β
$\mu_{\log \sigma}$	Mean of random effects distribution for $\log \sigma$
$\sigma_{\log \sigma}^2$	Variance of random effects distribution for $\log \sigma$

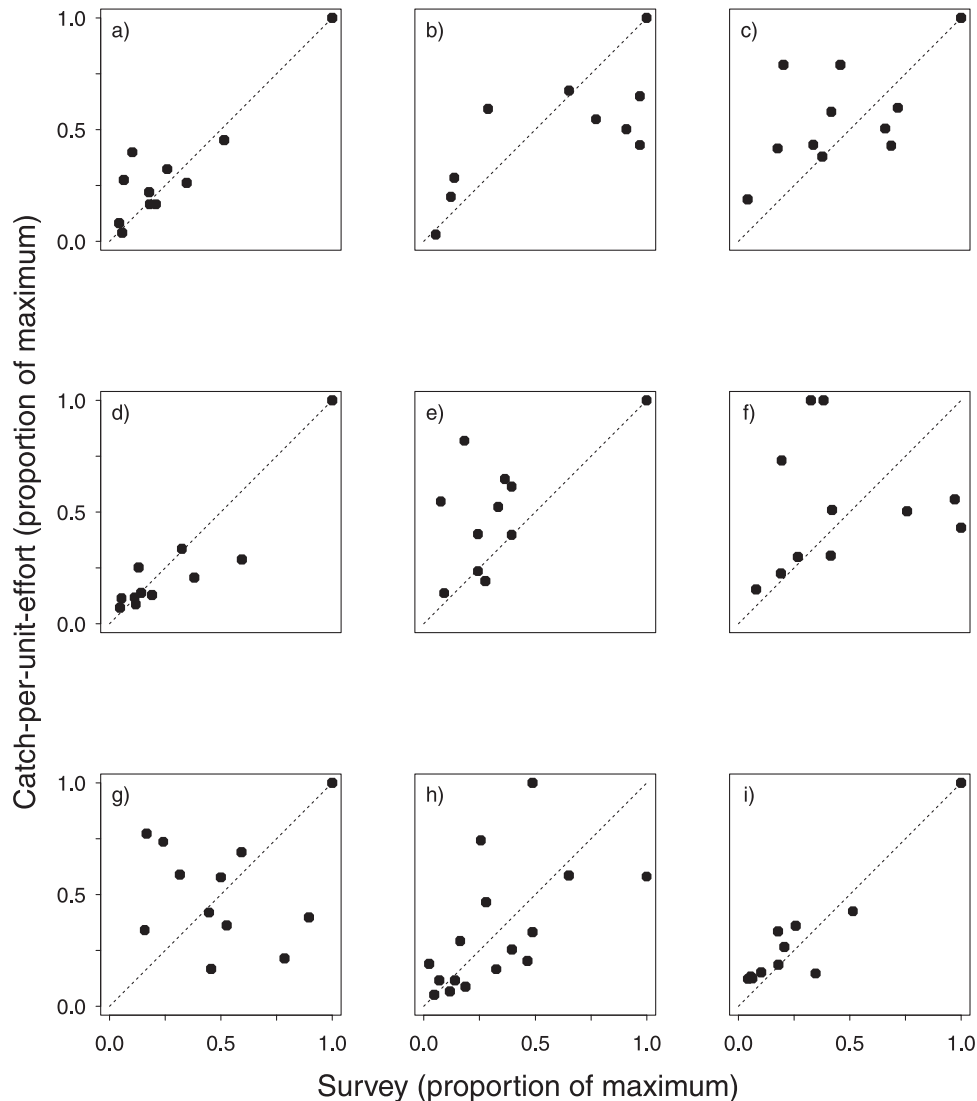
estimates of σ , and the distributions of σ were very similar for the other ages. Beam trawl estimates of σ showed little variation and had the lowest median (but not significant different) of the gear types. Trawl estimates were also tightly distributed.

Estimates of the MLE priors for both β and $\log \sigma$ for cod were the least certain, as indicated by the wide 95% confidence regions (Fig. 5). The random effects variances were also largest for cod, indicating higher inherent variability in the true distributions. However, the sample size for cod was less than for the other groups. The confidence region for the gadiformes was within the cod regions. The variance of the MLE prior for $\log \sigma$ for flatfish was 0. For none of the groups does the 95% confidence joint region include $\beta > 1$.

For all groups, most of the $\hat{\beta}_i$ s were between 0.6 and 0.9 (Fig. 6). The mean of the MLE prior for both cod and gadiformes was similar (0.75 and 0.73, respectively) and higher than that for flatfish (0.64). The variances of the MLE priors were similar for all groups. The mean of the MLE prior for $\log \sigma$ was the same for both cod and the gadiformes (-0.65), which represents a median CV of 0.52 (Fig. 7). This was lower than for flatfish (-0.86 , representing a CV of 0.42). This suggests that flatfish CPUE provides more precise abundance indices (i.e., lower noise) than those of gadiformes.

We repeated the random effects analysis for β using different criteria for inadmissible estimates of variances. The original criteria was $\phi < 0.06$, so cutoffs of 0 and 0.1 were examined for sensitivity. None of the estimates of μ_{β} or σ_{β}^2 varied by more than 5% from the 0.06 case used for the

Fig. 2. Nine randomly chosen series of CPUE and an associated series of trawl survey abundance. Both series are scaled to a maximum of 1. Estimates of $\beta < 1$, implying hyperstability, are associated with data sets, with the majority of points above the 1:1 line (dashed) that is provided for reference. (a) Age-4 sole, Irish Sea, trawl, $\hat{\beta} = 0.73$; (b) age-3 megrim, ICES VIIIc and IX, trawl, $\hat{\beta} = 0.87$; (c) age-4 whiting, ICES VIa, Danish seine, $\hat{\beta} = 0.38$; (d) age-6 sole, Irish Sea, beam trawl, $\hat{\beta} = 1.20$; (e) age-5 sole, ICES VIIId, beam trawl, $\hat{\beta} = 0.66$; (f) age-3 whiting, ICES VIa, Danish seine, $\hat{\beta} = 0.80$; (g) age-4 blue whiting, Northeast Atlantic, pair trawl, $\hat{\beta} = -21.70$; (h) age-3 plaice, ICES VIIId, beam trawl, $\hat{\beta} = 0.53$; (i) age-4 sole, Irish Sea, beam trawl, $\hat{\beta} = 0.62$.



analysis. Similar results were obtained for different cutoffs of the estimation error variances.

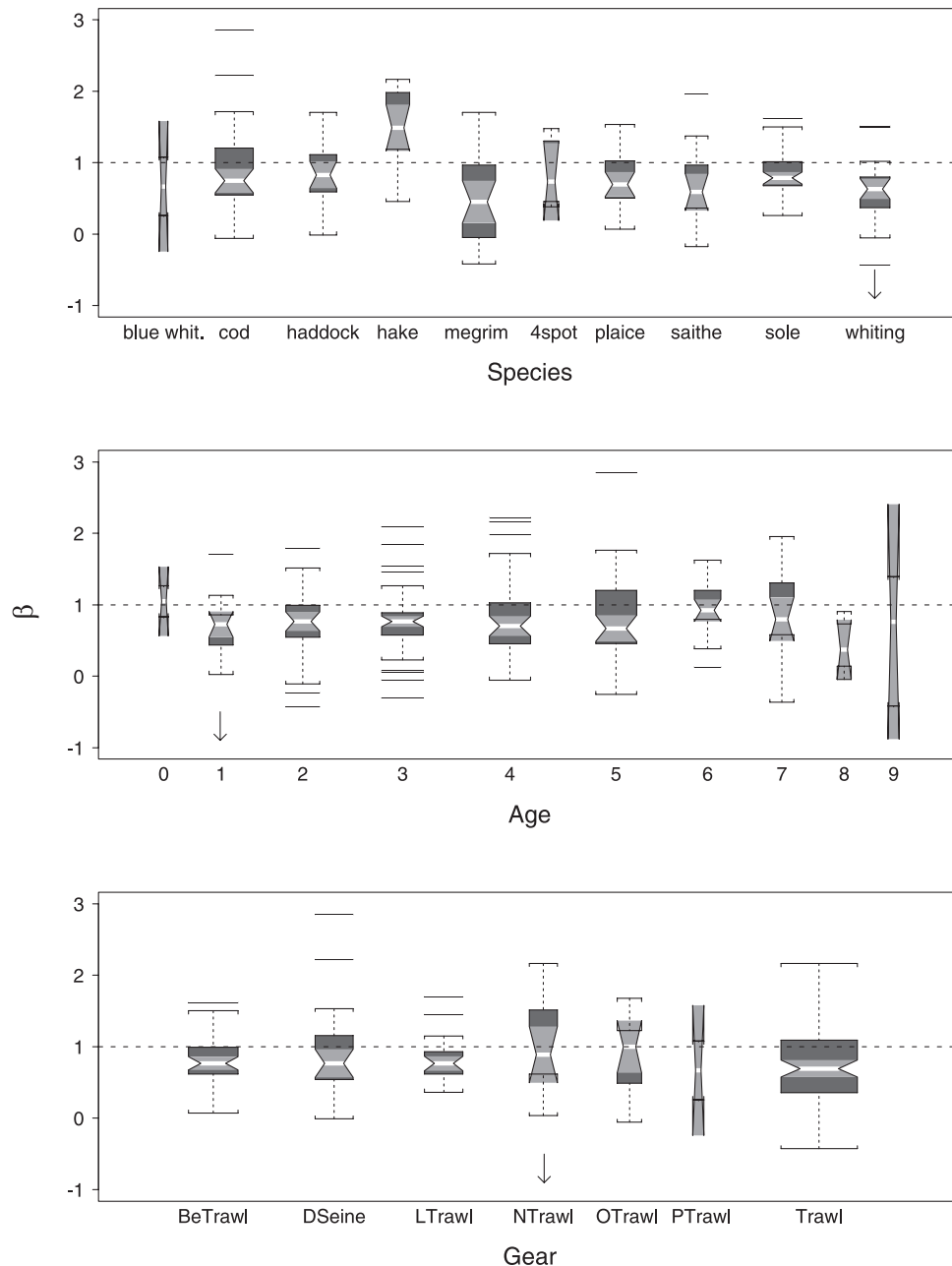
Discussion

While the validity of CPUE as proportional index of abundance has long been questioned, our analysis provides the first large-scale attempt to test the assumption of proportionality. Our findings here, while based on data from a single area, must lead to concern among those who model CPUE data assuming proportionality. Focusing on data from the ICES region, we obtained 297 data sets of which we were able to obtain estimates of β for 209. We have taken data from ICES assessments because it was possible to get large amounts of data in a standard format.

It was found that the availability of multiple survey series was related to the ability to obtain reasonable estimates of β . Of the series where estimates of β were possible, only 62 (30%) were >1 . It is not surprising that most of the estimates were <1 ; in fact, many researchers have found evidence of hyperstability in the relationship between CPUE and abundance (e.g., Peterman and Steer 1981; Crecco and Overholtz 1990; Swain and Sinclair 1994). We believe now that it is time to move on and incorporate this new information into stock assessment models.

The MLE prior for β had most of its weight well below 1 for all three groups. For cod, 76% of the mass was below 1, and this was lower than that for flatfish (86%) and gadiformes (81%). This represents the first large-scale examination of the relationship between CPUE and abundance, and as such provides the strongest evidence against the as-

Fig. 3. Summary of shape parameter β by species, age, and gear type. The boxplots show the limits of the middle half of the data (the line inside the box represents the median). The amount of data is shown as the width of the boxes that are proportional to the square root of the number of data points. The notches are the approximate 95% confidence intervals of the median. If the notches on two boxes do not overlap, this indicates a difference at a rough 5% significance level. The upper quartile and lower quartile provide the outline of the box. Whiskers are drawn to the nearest value not beyond 1.5(interquartile range) from the quartiles; points beyond are drawn individually as outliers. The arrows indicate the outlier with $\hat{\beta} = -3.23$ (details given in text). Details of the species and gear types are given in Tables 1 and 2, respectively.



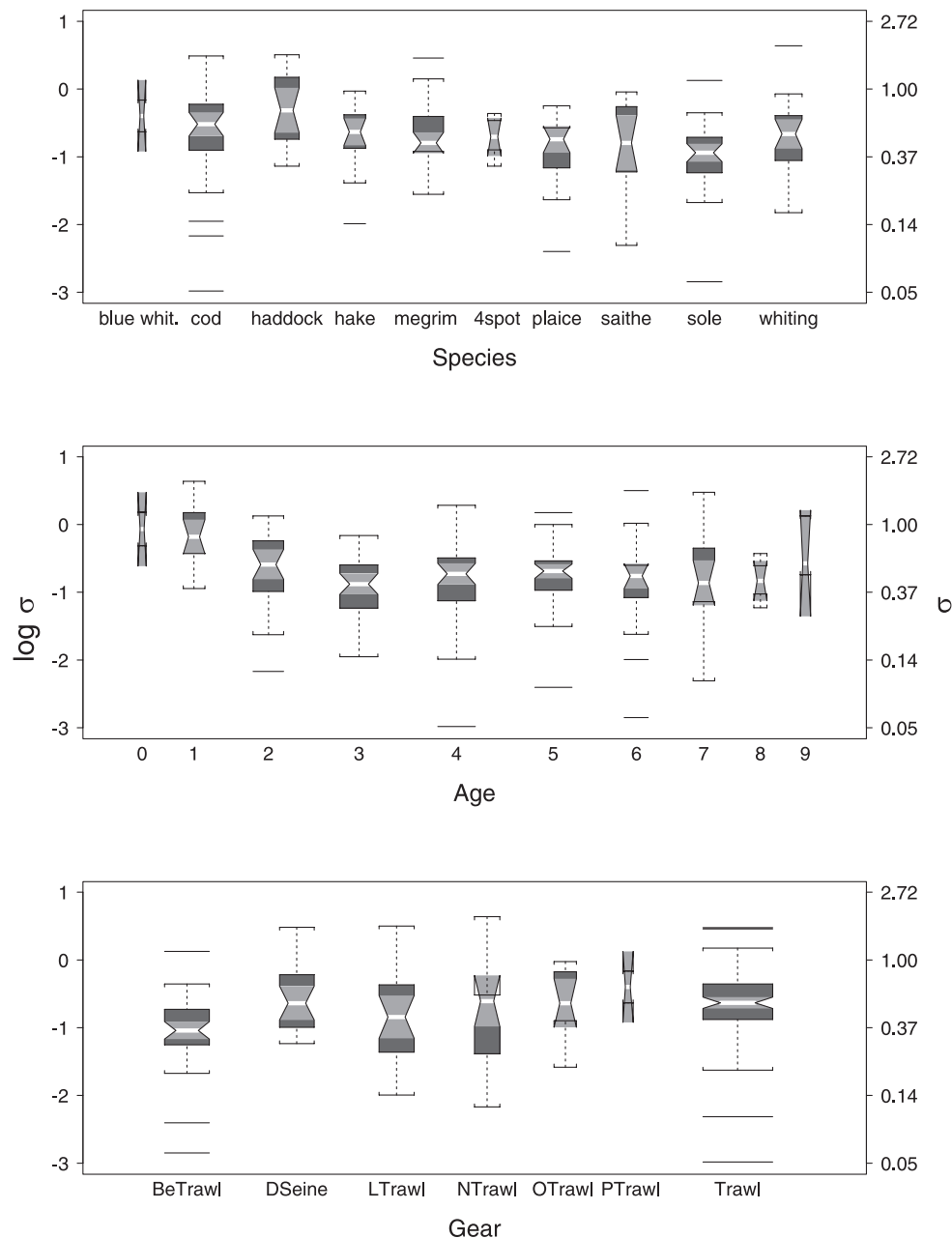
sumption of proportionality. However, here, we have only examined a limited number of gear types, mainly trawl-type gears. For example, we have not examined any CPUE series from purse-seine fleets, although the fishing process of these types of vessels has been studied previously, with evidence of hyperstability (Clark and Mangel 1979; Allen and Punsly 1984).

There do exist stock assessment procedures that consider nonlinearity in the relationship between CPUE and abun-

dance (e.g., Darby and Flatman 1994). However, this assessment package does not currently have the ability to incorporate information on β , such as that provided by the MLE priors presented here. Furthermore, in many ICES assessments the power curve is most commonly used for only the youngest ages-classes. Here, we show that the power curve is the appropriate model at all ages.

Bayesian assessment methods allow the incorporation of additional information in the form of prior distributions

Fig. 4. Summary of the log of the estimation error standard deviation ($\log \sigma$) by species, age, and gear type. See Fig. 3 for a description of the boxplot.



(Walters and Ludwig 1994; Punt and Hilborn 1997; Meyer and Millar 1999). In Bayesian analysis, the prior distributions are combined with the likelihood components for the data to give posterior probability distributions that are used for inference. It would also be possible to use the MLE priors as penalty factors or as an additional component of the total likelihood in a non-Bayesian analysis.

We have also obtained estimates of the observation error variance of a CPUE series, $\log \sigma$. As σ represents the square root of the observation error variance of a CPUE series, if the distribution of the ϵ_i s is approximately lognormal, then σ is an approximation of the CV of the CPUE data source. This gives an indication of the precision of CPUE indices and is extremely important for situations where alternative

data types (e.g., CPUE and trawl survey) are available for a stock assessment. In such cases the weighting of the different data sources can be important (Quinn and Deriso 1999). This distribution for $\log \sigma$ will also be useful for simulation studies. We found that $\log \sigma$ was generally lower for flatfish than for the gadiformes. This implies that CPUE data from flatfish will be more useful for “tuning” stock assessment models.

Here, we have provided estimates of the MLE prior for β as well as confidence regions based on the log likelihood profiles. The MLE prior represents the distribution from which we can expect the true values of β_i to be drawn. The variance of this distribution may be an underestimate of the true variance, as it does not consider the uncertainty in the

estimation of β and σ_β^2 (Efron 1996). For this reason, it may be important to “increase” the variance by some factor before using these distributions as Bayesian priors or as additional likelihood components.

In some fisheries, research survey abundance indices may not be available or the survey series may be quite recent and not provide information on historical stock sizes. If CPUE data exist, it may be possible to get some indication of historical stock sizes using the priors for β that we have derived here.

Robustness and alternative methods

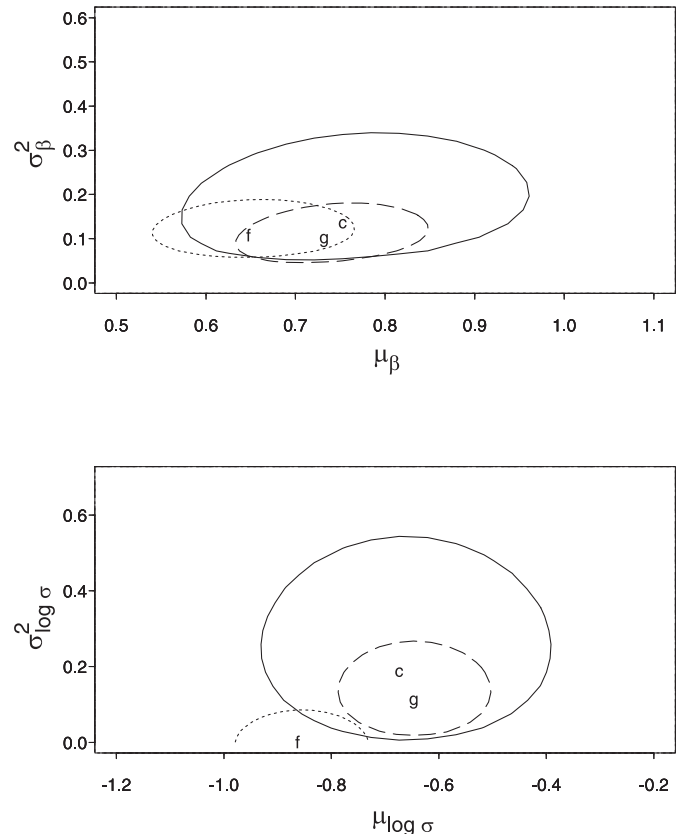
The analysis presented here is completely reliant on the assumption that research surveys indices are proportional to true abundance. If the surveys were carried out within some random sampling framework, then one would hope that this assumption would hold. However, in some cases the surveys may not cover the whole stock. In such circumstances, proportionality may still hold, but nonproportionality is also possible. By using the data used by the assessment scientists, we are making the same assumptions that they have made. Given this, we are more confident in estimates for stocks where multiple surveys were available or the surveys provided good coverage of the stock area.

The model used to estimate density-dependent catchability was used in a slightly different formulation to estimate density-dependent mortality by Myers and Cadigan (1993). Cadigan (1993) and Myers and Cadigan (1993) carried out extensive simulations to determine the effect of small sample size and violations of the model assumptions on bias of the parameter mathematically equivalent to our β . Both studies found that reasonable violations of the model assumptions (alternative distributions for the error distributions, autocorrelation, and time trends in the series) had relatively little effect on bias but that small sample size generally led to overestimation of the parameter mathematically equivalent to our β parameter by $\approx 10\%$ and underestimation of the estimation error variance by $\approx 10\%$. Cadigan (1993) developed two methods to correct for bias in the individual estimates but found that they did not work well in practice. We recommend that the estimates of β presented here be reduced by 10% to account for the general trends in bias observed in these simulation studies.

We only considered one model for the relationship between CPUE and abundance (eq. 2). This power curve is the simplest model allowing nonlinearity between CPUE and abundance. There was no evidence that more complicated models would provide more parsimonious fits to the data. In fact, even with a large number of data sets, it was difficult to obtain reliable estimates of the shape parameter of the power curve.

We used maximum likelihood to estimate the parameters of the random effects distributions, but other approaches are possible. A moment estimator for the mean of the random effects distribution was provided by DerSimonian and Laird (1986). This approach required that the variance of the random effects distribution (σ_β^2) was known, and thus, no estimate of its uncertainty is possible. The likelihood approach presented by Hardy and Thompson (1996) enables the analyst to obtain profile-based confidence limits for both the mean and the variance of the random effects distribution. It

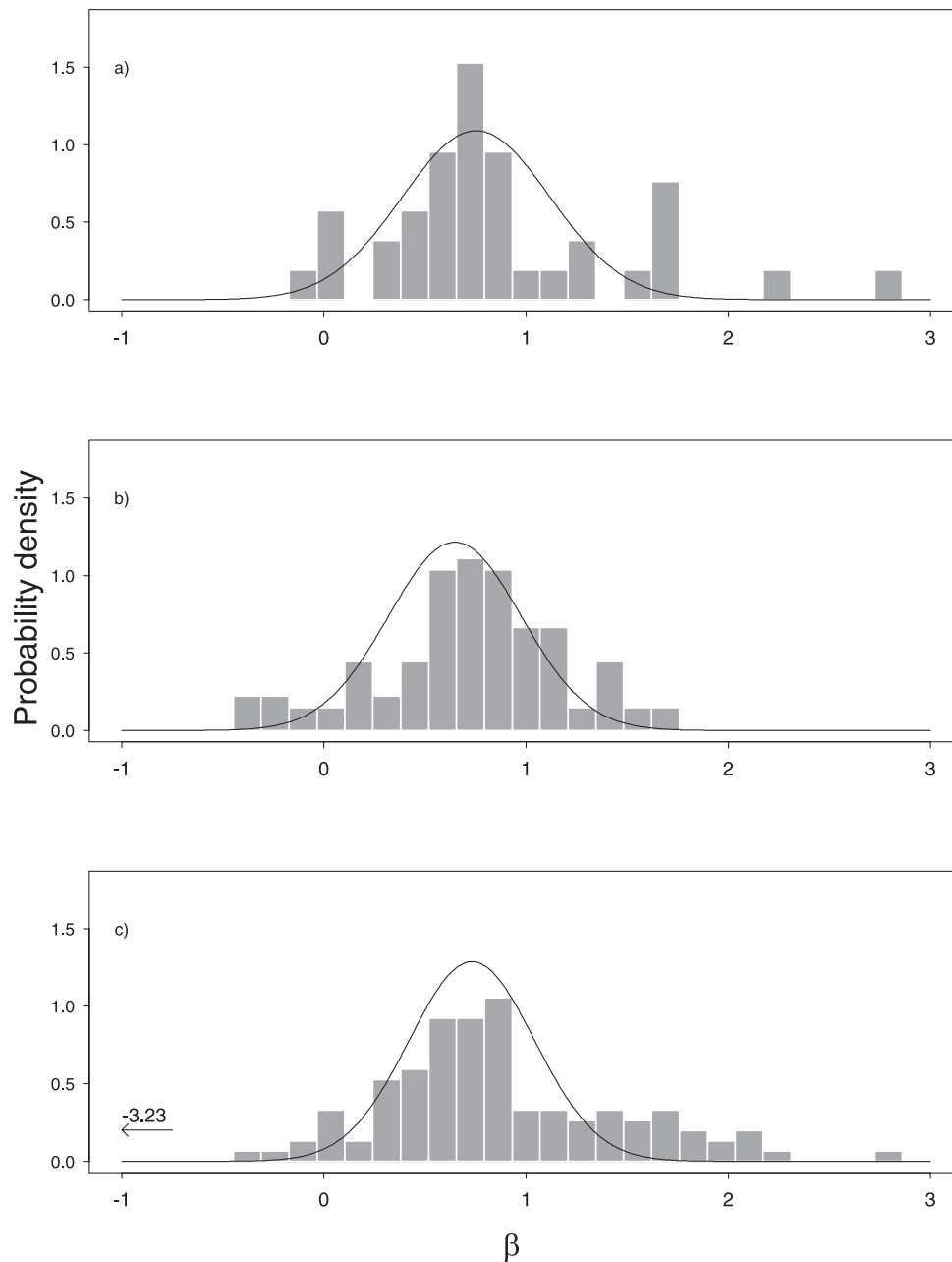
Fig. 5. Log likelihood contours for μ_β and σ_β^2 (top) and $\mu_{\log \sigma}$ and $\sigma_{\log \sigma}^2$ (bottom) for cod (solid line), flatfish (dotted line), and gadiformes (dashed line). The contours represent the approximate 95% joint confidence region ($\chi_{0.05,2}^2 / 2 \approx 2.991$). The maximum likelihood estimates for each group are indicated by lowercase letters, i.e., c for cod, f for flatfish, and g for gadiformes.



would also be possible to use hierarchical Bayesian methods to estimate the random effects distribution (Carlin and Louis 1996; Liermann and Hilborn 1997). When using Bayesian methods, it is necessary to specify prior distributions for the mean and variance of the random effects distribution. In instances where the maximum likelihood estimates for the variance are significantly different from 0, it is unlikely that the prior specification for variance in a Bayesian model would lead to estimates different from those from the likelihood approach. However, in cases where the data are poor, it is common for the maximum likelihood estimate of random effects variance to be 0 (Searle et al. 1992). In such circumstances, the choice of prior for the Bayesian analysis is likely to be important.

It is also possible to do a fully Bayesian analysis of these data. The individual modeling of the relationship between CPUE and abundance for each series could be performed simultaneously, where the β s are estimated, while considering the information provided by other data sets. In such a case, we would estimate the prior distribution within the analysis rather than separately as we have done here. This type of approach has been used in the estimation of the maximum reproductive rate from spawner–recruitment data (Myers et al. 1999). While this approach is theoretically possible, it would be computationally intensive but will be the focus of future

Fig. 6. Histogram of individual estimates of β_i with overlaid MLEs of the prior. The histogram has been scaled to sum to 1 so that it is directly comparable with the prior density function. (a) Cod: based on 38 data sets; the MLE prior for β was $\beta \sim N(0.75, 0.13)$; (b) flatfish: based on 98 data sets, $\beta \sim N(0.65, 0.11)$; (c) gadiformes: based on 111 data sets, $\beta \sim N(0.73, 0.10)$. The arrow indicates the outlier described in the text.



research. It is possible that this approach would help overcome some of the problems encountered estimating the variance components.

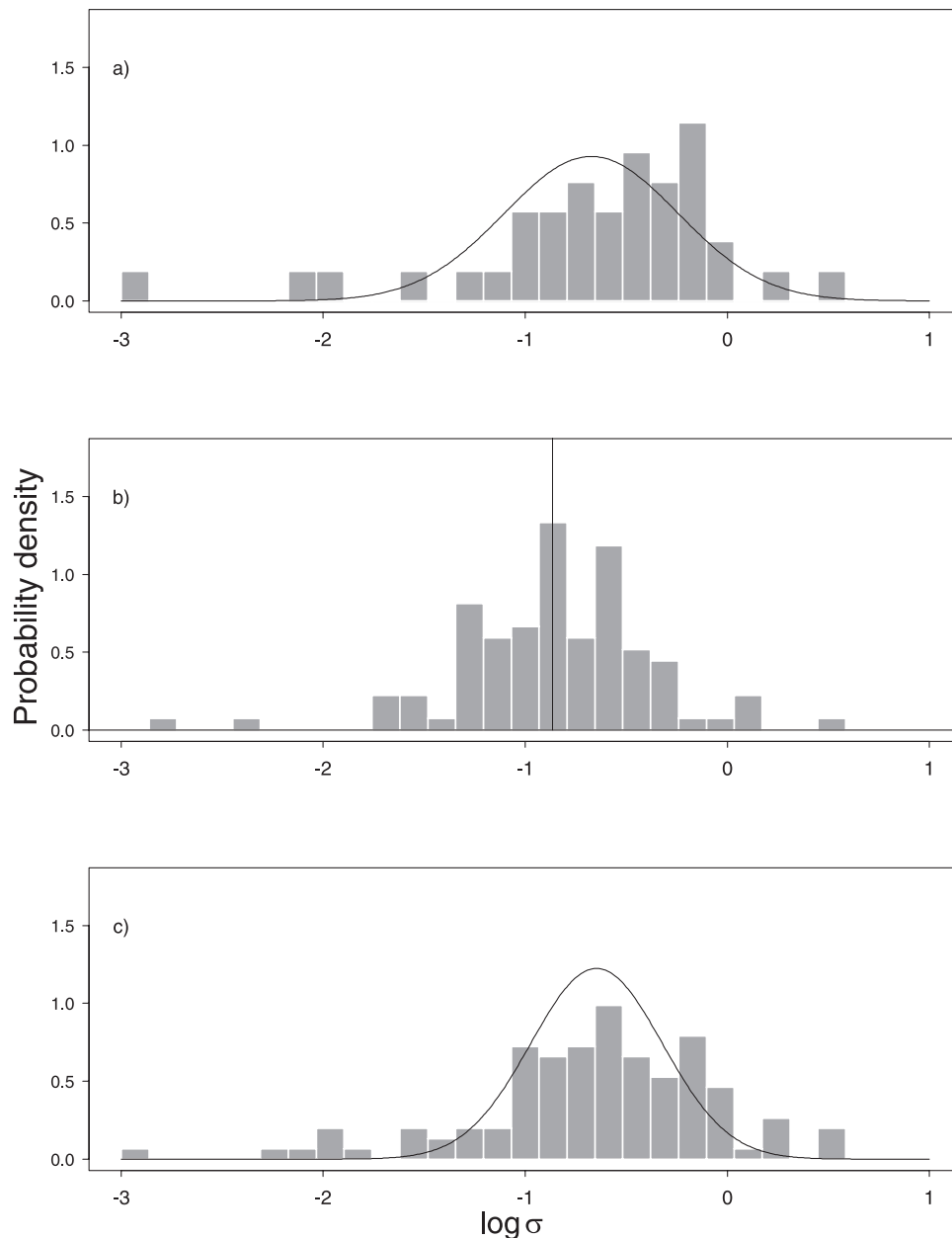
The data used for this analysis were series of age-specific CPUE and research survey abundance indices as used in ICES stock assessments in 1999. As ICES assessment scientists often have access to a number of CPUE and survey series, the data used in the assessment models may be of better quality than those used by assessment scientists with less available data (i.e., they have enough data to consider not using less reliable series). Thus, it is possible that the data used in this analysis are better than those used by assess-

ment scientists elsewhere. Data series that exhibited extreme hyperstability or large observation error may have been excluded by the assessment scientists. If the data that we have included are less noisy (regardless of the value of β), our estimates of the MLE prior for $\log \sigma$ will overestimate the usefulness of CPUE as a predictor of abundance (on the whole).

We have assumed that estimates for the different ages are independent (in the random effects analysis). This may cause us to overestimate the effective number of data sets that we have. This would not bias our results but could cause the confidence regions in Fig. 5 to be underestimated.

Dunn et al. (2000) used both research survey (both acous-

Fig. 7. Histogram of individual estimates of the log of the estimation error standard deviation ($\log \sigma_i$) with overlaid MLEs of the prior. The histogram has been scaled to sum to 1 so that it is directly comparable with the probability density function. (a) Cod: based on 38 data sets; the MLE prior for $\log \sigma$ was $\log \sigma \sim N(-0.67, 0.18)$; (b) flatfish: based on 98 data sets, $\log \sigma \sim N(-0.86, 0.0)$; (c) gadiformes: based on 111 data sets, $\log \sigma \sim N(-0.65, 0.11)$.



tic and trawl) and model-based (e.g., predicted abundance from a statistical catch-at-age model) estimates of abundance in examining the relationship between CPUE and abundance. We have chosen not to use model-based abundance estimates for four reasons, aside from problems that might occur due to biases in the assessment methods. First, there is seldom one single model that is used in any one assessment. A number of structurally different models may be compared and it would require us to choose between models. Second, for the model-based abundance indices to be independent of the CPUE series, we would require that the CPUE data not be included in the model. In many cases, this type of model may not have been considered. Third, it would be difficult to obtain realistic estimates of the observation

error variance for model-based estimates. Finally, the model-based abundance indices are unlikely to be independent from one year to the next as an underlying population dynamics model generates them. This would complicate any analysis, as it would require the incorporation of autocorrelation in the estimation procedure. Thus, while model-based abundance indices have the advantage that they synthesize a range of information on abundance, we felt that the disadvantages of model-based indices outweigh this.

We have used age-disaggregated abundance indices as opposed to the aggregated indices used by Dunn et al. (2000). While aggregated indices may be less noisy (due to averaging of error over a number of ages), any differences in the age-specific selection of the survey and fishing gears will

lead to biases in the estimation of β . It is also easier to get good contrast with age-structured indices due to variability in recruitment. Any ageing error would most likely act to reduce the interannual variability in abundance of the older age-classes. The median relative range (maximum/minimum CPUE index) in CPUE for a series was 12-fold. Based on the simulations performed by Dunn et al. (2000), the variability observed here is sufficient to allow accurate estimation of β .

We have used age-specific estimates of density-dependent catchability, β , as opposed to the more common practice of estimating a single parameter by combining data across all ages. The relationship between age-aggregated CPUE and abundance is likely to be different, so we do not suggest that our results be applied directly in this situation. The relationship between CPUE and abundance is probably a function of total abundance rather than the abundance of individual cohorts. We carried out simulations where we fixed a single β for the entire population and then estimated a separate β for each age-class. We found that the estimates were always closer to 1, suggesting that our age-based estimates may overestimate the extent to which CPUE is proportional.

Changes in catchability, i.e., efficiency of the fishing fleet over time, have the potential to cause biases in the estimates of β if there are trends over time in abundance. For our CPUE data, the lowest value in a series was just as likely to be the first or last year, but the median time trend was a 5% decline per year. We therefore do not believe that this will have a substantial effect on the mean of our estimates of β .

This investigation leads itself to obvious extensions. A meta-analysis of $\log \sigma_{\epsilon}$ (the square root of the estimation error variance from the research surveys) will provide information on the general reliability of research survey data. When combined with the analysis presented here, this will lead to more accurate weighting of alternative data sources.

It is also important to determine the generality of the findings here. It will be important to examine other data, especially from other gear types, to determine if hyperstability is a property of other fishing methods (e.g., longlining and recreational hook and line fisheries).

It will also be important to determine the extent to which β can be predicted for a given CPUE series and population. It is clear that both fish and fisher behavior can lead to hyperstability. Myers and Cadigan (1995) found that northern cod exhibited a substantial contraction in range during the period up to the closure of the fishery, and Hutchings (1996) showed that the areas of high cod density remained constant throughout this time. Density-dependent habitat selection theory (Fretwell and Lucas 1970; MacCall 1990) suggests that range expansion and contraction could occur with changes in abundance. To better understand the relationship between CPUE and abundance, it will be important to determine the extent to which fishers' ability to locate the areas of greatest fish abundance interacts with habitat selection in fish.

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