



## Modelling in-season pulses of recruitment and hyperstability-hyperdepletion in the *Loligo gahi* fishery around the Falkland Islands with generalized depletion models

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The time-series of daily catch, fishing effort, and mean body mass of the summer fishing seasons of the squid, *Loligo gahi*, in the Falkland Islands from 1990 to 2009 are investigated with generalizations of depletion models that account for in-season pulses of recruitment (i.e. open populations) and non-linear relationships between catch as the response variable, and effort and abundance as the predictor variables. Two main results were found. First, stock dynamics are more complex than assumed by Leslie–Davis or De Lury depletion models, because in most years, there are several major in-season recruitment pulses, sometimes even larger than the pre-season pulse, contradicting the basic assumption of a decline in catch rates over the fishing season. Second, the fishery operates under a regime of hyperstability—catch rates decline slower than abundance—at low stock abundance and hyperdepletion—catch rates decline faster than abundance—at intermediate and high stock abundance. The hyperdepleted regime is far more prevalent, a result attributed to the availability of refuges from fishing operations, which may lower the abundance threshold to pass from the low-abundance hyperstable regime to the higher-abundance hyperdepleted regime.

**Keywords:** depletion models, Falkland Islands, hyperstability, hyperdepletion, squid stocks, stock assessment.

### Introduction

Commercially important squid stocks are characterized by fast population dynamics, exploitation of mostly single short-lived cohorts, and spatial dynamics, where the stock recruits into the feeding grounds from nursery areas and leaves after a few months to spawn and die (Boyle and Rodhouse, 2005). Given the fast dynamics, Leslie–Davis or De Lury depletion models have been used for stock assessments of such stocks (Rosenberg *et al.*, 1990; Brodziak and Rosenberg, 1993; Agnew *et al.*, 1998; McAllister *et al.*, 2004; Young *et al.*, 2004; Roa-Ureta and Arkhipkin, 2007; Xinjun *et al.*, 2008). There are three main assumptions underlying these depletion models: (i) the population is closed, (ii) the response of catch to effort and abundance is directly proportional, and (iii) the natural mortality rate over the fishing season is constant. Note that (i) and (ii) imply that the catch per unit effort (cpue) is a decreasing function of time over the fishing season, and that (ii) implies that catchability is constant.

Brodziak and Rosenberg (1993) and McAllister *et al.* (2004) have presented extensions to deal with problems with the first assumption. Brodziak and Rosenberg (1993) allowed for perturbations to a pure depletion process by in-season stock additions—pulses of increased abundance—relying on additional catch and effort data from outside the fishing grounds, and applied this approach to the inshore fishery for *Loligo pealei* in the Northwest Atlantic. Brodziak and Rosenberg's model is a precursor of the approach to be presented here, although their model relies on additional data and still assumes that assumption (ii) above holds. McAllister *et al.* (2004) modelled the *Loligo gahi* stock in the Falklands by assuming that (i) and (ii) actually held, but increasing cpue series are sometimes observed because of sampling variation, i.e. a true depletion hidden by sampling variability. Roa-Ureta and Arkhipkin (2007) recognized the limitations of the closed-population assumption by separately modelling multiple depletion episodes within the same fishing season of the *L. gahi* fishery, but they relied on dividing the season into periods when the closed-

population assumption held. In this work, I show generalized depletion models that do not depend on assumptions (i) and (ii), but instead allow for open populations and a nonlinear relationship between catch as the response, and effort and abundance as the predictors. This was necessary to successfully model the range of dynamic behaviour observed over the twenty summer fishing seasons (1990–2009) of the *L. gahi* stock examined.

The meta-analysis by Harley *et al.* (2001) of commercial cpue series and scientific survey abundance estimates showed that the hypothesis of proportionality between cpue and stock abundance is untenable. These authors found that most fleet-stock systems chosen for their compilation are hyperstable, whereby cpue declines slower than abundance when abundance declines, although a sizable minority also exhibited hyperdepletion, with cpue declining faster than abundance when abundance declines. The existence of this non-linear relationship between cpue and abundance has been assumed for some time (Hilborn and Walters, 1992). The emphasis of previous work has been on one of the aspects of this alleged non-linearity, namely hyperstability, because ignoring it when it is present leads to over-optimistic assessment of stocks. The cod (*Gadus morhua*) off Newfoundland is a classic example (Walters and Maguire, 1996) and new cases continue to arise (Erismann *et al.*, 2011). Hyperstability is one of three possible regimes that also include proportionality and hyperdepletion. Thus, another purpose of this paper is to explore the prevalence of all three regimes and the conditions of stock abundance under which they are present.

## Material and methods

### Stock assessment model

Table 1 describes all mathematical symbols used in this work. Let  $C$  be the true catch in numbers of a single stock and fishing operation in a given year. The catch rate is assumed to be the result of two causes, nominal fishing effort  $E$  (hereafter “effort”) and stock abundance  $N$ ,  $dC/dt = f(E, N)$ . In this hypothesis, the fishing operation enters directly through the effort metric. It is further assumed that effort is an *observed* predictor of catch, whose values are known exactly, whereas abundance  $N$  is a *latent* predictor of catch. It is possible to expand the latent predictor  $N(t)$  to represent it as the result of estimable parameters and observed variables. A power relation was assumed for both predictors, abundance and effort. Under these assumptions and switching to discrete time-steps, the Supplementary material shows that a solution to the catch rate equation above is,

$$C_t = kE_t^\alpha N_t^\beta e^{-\frac{Mt}{2}}$$

$$= kE_t^\alpha \left( N_0 e^{-Mt} + \sum_{i=1}^t P_i e^{-M(t-i)} - e^{-\frac{Mt}{2}} \sum_{i=1}^{t-1} C_i e^{-M(t-i-1)} \right)^\beta e^{-\frac{Mt}{2}} \tag{1}$$

where  $t > 0$ ,  $C_t \geq 0$ ,  $E_t \geq 0$ ,  $k > 0$ ,  $N_0 > 0$ ,  $\alpha > 0$ ,  $\beta > 0$ ,  $M > 0$ , and  $-N_0 e^{-M} \leq P_i \leq +\infty$ . This model is a generalized depletion model — (i) relaxing the closed-population assumption via in-season perturbations  $P_i$  and (ii) relaxing the proportionality assumption on both predictors of catch via  $\alpha$  and  $\beta$  — which has been used as the standard model for formal stock assessment of the *L. gahi* stock in the Falkland Islands since 2009. It has been implemented in the R language (R Development Core Team,

**Table 1.** List of symbols used in mathematical notation.

Description	Symbol
Expected catch (billions)	$C$
Nominal effort (number of vessels)	$E$
Abundance (billions)	$N$
Time-step (days)	$t, i$
Scaling (1/number of vessels)	$k$
Abundance response	$\alpha$
Effort response	$\beta$
Natural mortality (1/day)	$M$
Initial abundance (billions)	$N_0$
Total initial abundance (billions)	$A_0$
Abundance perturbations (billions)	$P_1, P_2, P_3, P_4$
Index of perturbation	$j$
Number of time-steps from start of season to perturbation	$s$
Catchability (1/number of vessels)	$q$
Observed catch (billions)	$X$
Variance of observed catch (billions <sup>2</sup> )	$\sigma^2$
Adjusted profile likelihood	$l$
Relative spread of estimates	$Q$
Index of model fitted	$m, n$

2012), package CatDyn, available through the CRAN repository (see [www.r-project.org](http://www.r-project.org)). The model has free parameters  $\theta = [k \alpha \beta N_0 M \{P_i\}]$ . These parameters belong in two groups. The first group are the fishing operational parameters,  $k$ ,  $\alpha$ , and  $\beta$ . Parameter  $k$  scales down the determination of catch, so it is termed “scaling”, and is related to catchability by  $q(N) = kN^{1-\beta}$ . Parameter  $\alpha$  modulates the output of catch from a certain amount of effort, so it is termed “effort response”. Its value reflects the presence of three regimes: effort saturability ( $\alpha < 1$ , the fishing gear catches proportionally less with every additional unit of effort), effort synergy ( $\alpha > 1$ , every additional unit of effort yields a disproportionate increase in catch), and effort proportionality ( $\alpha \approx 1$ ) (Bannerot and Austin, 1983; Quinn and Deriso, 1999). Parameter  $\beta$  is the “abundance response” parameter, reflecting how fishers perceive fish abundance (hyperstability:  $\beta < 1$ ; hyperdepletion:  $\beta > 1$ ).

The second group are the stock abundance parameters,  $N_0$ ,  $M$ , and  $\{P_i\}$ .  $N_0$  is the abundance of the stock at the time-step immediately before the first step of the fishing period. The  $\exp(-M)$  term quantifies the natural change as the probability of individual survival during one time step,  $N_t/N_{t-1}$ .  $\{P_i\}$  is the set of in-season perturbations of the depletion process. These are pulses of abundance that, when positive, reset the depletion process to a higher catch rate. If  $\{P_i\}$  is the empty set, the model in equation (1) is a pure depletion model, and the stock is a closed population; when  $\{P_i\}$  is not empty, the model accounts for episodic pulses of abundance, and the stock is an open population. In this paper, only positive perturbations are considered. These can be waves of immigration into the fishing grounds or spatial expansions of the fleet’s operation that make new parts of the stock available to fishing.

The model in equation (1) is a catch model, but under the assumption that effort is observed exactly, it is easily transformed into a cpue model by dividing both sides by effort, leading to  $CPUE_t = kE_t^{\alpha-1} N_t^\beta e^{-\frac{Mt}{2}}$ ,

without any statistical consequences except for offsetting the effort-response parameter by -1. The advantage of formulating the model for catch is conceptual: in this form, catch is the random-response variable, and effort and abundance are the fixed-

predictor variables in a standard non-linear recursive regression model.

Two probability models are considered for the catch observations, additive and multiplicative:

$$\begin{aligned}\chi_t &= C_t + \varepsilon_t, \varepsilon_t \sim \text{Normal}(0, \sigma^2) \\ \chi_t &= C_t e^{\varepsilon_t}, \varepsilon_t \sim \text{Normal}(0, \sigma^2)\end{aligned}\quad (2)$$

where  $\chi$  is the observed catch. For each year of data, both normal and lognormal models were fitted and it was decided on a case-by-case basis which was better, using several statistical criteria (see below). The assumption is that the catch process occurs along a continuum from additive to multiplicative, so that each year's data can be realized closer to one or the other extreme. Although it might be interesting to estimate the variance parameter in the distribution of  $\chi$ , here it is considered a nuisance, eliminated by adopting a modified profile-support function as an approximation to the exact support function (Pawitan, 2001)

$$\begin{aligned}l_p(\theta; \{\chi_t, E_t\}) &= \frac{T-2}{2} \log \left( \sum_{i=1}^T (\chi_i - C_i)^2 \right), \text{Normal model} \\ l_p(\theta; \{\chi_t, E_t\}) &= \frac{T-2}{2} \log \left( \sum_{i=1}^T (\log(\chi_i) - \log(C_i))^2 \right), \\ &\text{Lognormal model}\end{aligned}\quad (3)$$

where  $C_t$  is equation (1), the true catch under the process model.

## Data and implementation

The best model for each year was identified by estimating the free parameters  $\theta = [k \ \alpha \ \beta \ N_0 \ M \ \{P_i\}]$  from data consisting of the daily catch and effort of the fleet fishing for *L. gahi* in the summer fishing seasons of 1990–2009 using the CatDyn R package. A detailed description of the stock's spatial dynamics and its fishery can be found in Arkhipkin *et al.* (2004a, 2008). The effort data are particularly clean (see Table S1, Supplementary material) and can be considered accurate and exhaustive (Arkhipkin *et al.*, 2008). It was available in two measures: trawling time per day by the fleet and number of vessels fishing per day. For statistical adequacy, it is better to use the measure of effort that has the least chance of having any statistical error in it, which is the number of vessels. In addition, for a number of years, the number of vessels shows a tighter relation between catch and effort (see Figure S1, Supplementary material). Thus, the number of vessels fishing per day was the measure of nominal effort.

To avoid complications that were considered non-essential, the whole series was treated as if it were produced by a homogeneous fleet. This simplification is justified on two grounds: all vessels in the series are large factory trawlers, with a clear predominance of Spanish/Falklands vessels, and the measure of effort chosen is less affected by differences in fishing power. Regarding the first justification, previous authors (Agnew *et al.*, 1998; McAllister *et al.*, 2004) working with older and shorter time-series (1987–1996 and 1987–2000, respectively) distinguished fleets with different catchability based on nationality and size of the vessels. Agnew *et al.* (1998) defined seven fleets, while McAllister *et al.* (2004) simply modelled the Spanish/Falklands fleet in the mid-size category and ignored the other vessels. The present analysis examined the longest and most updated time-series (1990–2009), in which

the Spanish/Falklands factory trawlers are vastly predominant. Regarding the second justification, both Agnew *et al.* (1998) and McAllister *et al.* (2004) used hours of trawling as the measure of effort. The effect of any structure of the fleet, in terms of fishing power, would be stronger for hours of trawling than for number of vessels, because the former first requires summation within vessels and then summation across the fleet. To be correct, the second summation has to be carried out over homogeneous hours of trawling; for that reason, there is a need to define fleets based on some proxy of fishing power. The single summation over the number of vessels is still affected by different fishing power, but less so than hours of trawling. This is, incidentally, further reason to adopt the number of vessels as the preferred measure of effort.

To transform catch recorded in biomass to catch in numbers, daily length frequency data and a previously fit length–body mass power model (Roa-Ureta and Arkhipkin, 2007) were used to estimate daily mean body mass. The length frequency data were a sample from 1–3 observers in a fleet that reached a maximum of 30 vessels operating on a given day, but that now amounts to only 16 vessels.

In the summer fishing season, the fleet harvests the autumn spawning cohort (ASC) (Arkhipkin *et al.*, 2008). In principle, it could be possible to model the entire daily series from 1990 to 2009 simultaneously, assessing all ASCs over the multiannual period, using a spawning stock–recruitment relationship to connect years. The study by Agnew *et al.* (2000) suggests the existence of a Ricker-type spawning stock–recruitment relationship in the ASC, but the relationship found was weak, at best. Furthermore, these authors did not find a useful environmental correlate of recruitment. Therefore, to assess the stock without introducing assumptions about interannual population dynamics, model parameters were estimated separately for each year.

The stock is managed by threshold policies (Quinn *et al.*, 1990; Mendoza-Meza and da Silveira-Costa, 2011). The management objective is to leave an escapement biomass of at least 10 000 t at the end of each fishing season, which can be cut short if the real-time assessment shows that the stock will cross the threshold (Arkhipkin *et al.*, 2008). Thus, in this application, it is of interest to estimate biomass at the end of the season. Biomass was estimated by averaging the mean body mass in the last 7 days of the season and multiplying this average by the model-predicted numbers in the stock on the last day of the season. In addition, total initial abundance was estimated as

$$\hat{A}_0 = \hat{N}_0 + \sum_j \hat{P}_j e^{s_j \hat{M}}, \quad (4)$$

where  $j$  counts over the perturbations (if any) and  $s_j$  is the number of time-steps from the start of the season to the time-step of perturbation  $j$ . Total initial biomass was estimated as the product of  $\hat{A}_0$  and the mean body mass in the first 7 days of the season.

Within each probability model, model selection was first done using the Akaike Information Criterion, AIC. This was considered conclusive when the difference between the best and the second-best models was  $\geq 3$  (more conservative than the value of 2 suggested by Sakamoto *et al.*, 1999). When the models for a year's data did not yield a conclusive AIC difference, one model was selected by inspecting optimization diagnostics, such as gradients, standard deviation estimates, correlations between estimates,

and by consistency of the escapement biomass estimate with previous years. This model-selection procedure still selected the two best models, one from each distribution. The better of these two was chosen by again considering the optimization diagnostics listed above, and the consistency of the escapement biomass estimate. Any model where any of the parameter estimates was on a gradient greater than 1 was discarded.

Considering two distributions and five model processes, up to 10 different versions can be fitted to any given year's data, which amounts to potentially 45 paired comparisons of models. To evaluate the spread of estimates for parameters common to pure depletion and perturbation models, namely  $M$ ,  $N_0$ ,  $k$ ,  $\alpha$ ,  $\beta$ , and the derived parameter-escapement biomass, a non-parametric measure of relative spread of parameter estimates was calculated as

$$Q = \left( \frac{\max\{\hat{\theta}_m - \hat{\theta}_n\}}{\text{med}(\{\hat{\theta}_m\})} \right) \quad (5)$$

where  $m \neq n$  are indices that run through the number of models fitted on a given year, the numerator is the set of all paired differences between parameter estimates for a specific common parameter, and the denominator is the median of the set of parameter estimates for the same specific parameter.

## Results

Considering all models fitted, including those clearly inadequate, the  $Q$  measure of relative spread shows that the estimate of escapement biomass is usually fairly insensitive to model specification, although in a few cases (5 out of 40), the estimates spread substantially, with a  $Q$  measure reaching as high as 88 (Table 2). Among the five parameters that are common to all perturbation models, the widest spread occurs with natural mortality and scaling, and the narrowest spread with effort response and abundance response; the effort-response parameter, in particular, is almost insensitive to model choice (Table 2).

Table 3 shows the AIC values used to identify a best perturbation model for each of the two distribution models. For both distributions, in 12 out of 20 cases, the AIC was conclusive. In the 8 remaining cases, optimization diagnostics usually pointed to the model with fewer perturbations. Table 3 also shows the best model when comparing the best normal and the best lognormal model using optimization diagnostics and serial consistency of escapement biomass. Half of the best models were normal and half were lognormal. All model processes, from pure depletion to up to 4 perturbations, are selected in at least two years. There remained four years, for each distribution, when the model selection was still inconclusive because of AIC ties (1990, 1992, 1998, and 2009). Further consideration of additional numerical diagnostics, especially the ability to estimate standard errors and reduce correlations between estimates, identified the best model for those years. Table S2 in the Supplementary material shows the relative spread of the four years whose models did not yield conclusive AIC differences. Table S3 in the Supplementary material shows quartiles of the correlations between parameter estimates for each best model. This shows that the degree of parameter aliasing is low, with most pairwise correlations achieving values that cover both positive and negative domains, indicating no systematic trend. Some exceptions are the correlations for neighboring perturbations (P1 with P2, P2 with P3, and P3 with P4), which, as expected, are negative. Since one of the purposes of

this work was to study hyperstability and hyperdepletion, it is interesting to inspect the degree of correlation of the abundance-response parameter  $\beta$  with all other parameters to examine whether the regimes of hyperdepletion and hyperstability could be artifacts of model misspecification. Table S2 shows that  $\beta$  correlates weakly with other parameters in the model, and that most of its pairwise correlations cover both positive and negative domains.

Graphical display of stock assessment results is presented for summer fishing seasons of 2000, 2004, and 2008, as examples. The best model for 2000 was a 4-perturbation (4P) model combined with a normal-distribution model, whereas the best model for 2008 was a pure depletion model (0P) combined with a lognormal-distribution model (Table 3). The 2004 fishing season was selected because it was an unusual year with a stepwise increase in observed catch, far away from a single depletion process. Figures 1–3 are standard prediction plots produced by the CatDyn R package. They are used to select good initial parameter values and to visually examine estimation results.

In 2000 (Figure 1), there were several spikes in catch that could not be explained by spikes in effort. Positive perturbations were put at days 38, 68, 111, and 142. Simpler models with fewer perturbations were attempted, and the AIC clearly showed that the 4P model was best for both observation models: normal and lognormal (Table 3). The 4P-normal-observation model was preferred over the 4P-lognormal model because the former showed better numerical optimization diagnostics, namely smaller gradients and smaller standard errors of estimates. Setting positive perturbations at days 38 and 68 did not completely explain the catch spikes in those days. Conversely, setting perturbations at days 111 and 142 completely brought the predictions in line with the observations. On the day after the first spike, day 39, the catch was much lower than predicted, creating a large negative residual. Currently, the model cannot deal with large negative residuals, so they are assumed to be extreme values. The distribution of residuals overall is symmetric, and the residual scatterplot shows a random scatter with homogeneous variance. The Q-Q plot shows good agreement with the normality hypothesis, except for the large negative residual.

The 2004 fishing season was the most unusual year of the series (Figure 2). The AIC was conclusive in favour of the 4P model for the lognormal-distribution model, whereas optimization diagnostics in the four models attempted (Table 3) were equally poor, including all models failing to produce a correlation matrix due to a non-positive-definite Hessian matrix. The estimated initial abundance was the lowest of the series, but there were four perturbations of increasing abundance, until the fourth, 40 days after the start of the fishing season, that was 22 times higher than initial abundance. It is clear that, in this year, the Leslie–Davis or De Lury depletion models cannot possibly account for the observations. Residual plots of the 4P model show some departures from distributional assumptions, mostly by the model being unable to deal with two very low catch days.

In 2008 (Figure 3), there was an overall declining catch over the fishing season, suggesting 0P process. However, two catch spikes can be observed at days 62 and 92 in the residual scatterplot. The AIC of the normal model showed that a 2P model was best, but the AIC of the lognormal model did not support this model and pointed to a 0P model (Table 3). When examining the detailed optimization results, it was noted that the 2P-normal model was unable to produce a standard error of any parameter estimate, so the 0P-lognormal model was finally determined to be the best.

**Table 2.** Parameter estimates relative spread for all models attempted for all summer seasons of the *Loligo gahi* fishery in the Falkland Islands.

Distribution	Year	Relative spread							
		Minimum AIC difference	Maximum AIC difference	Escapement biomass	Natural mortality (M)	Initial abundance ( $N_0$ )	Scaling (k)	Effort response ( $\alpha$ )	Abundance response ( $\beta$ )
Normal	1990	0.03	17.59	2.1	1.77	2.29	26.77	0.10	1.93
	1991	0.41	42.86	0.68	2.92	0.78	2.01	0.36	0.43
	1992	0	37.43	11.34	> 104	12.83	11.90	0.27	1.39
	1993	0.79	144.01	88.05	2.72	90.25	> 104	0.53	1.21
	1994	1.27	16.89	0.38	> 104	1.71	> 104	0.24	1.24
	1995	0.41	4.14	1.02	41.28	15.70	0.03	0.03	0.73
	1996	1.14	126.56	3.37	2.59	2.89	2.14	0.90	8.93
	1997	3.24	13.03	0.15	1.60	0.16	0.75	0.10	0.10
	1998	0.51	10.54	7.2	4.17	1.90	1.49	0.08	2.68
	1999	0.06	25.23	0.9	> 104	1.32	6.05	0.16	2.69
	2000	2.01	90.65	1.27	1.49	1.54	29.62	0.15	0.24
	2001	9.13	9.13	0.14	0.28	0.54	1.03	0.29	0.31
	2002	0.12	43.82	0.37	3.59	0.34	9.32	0.74	0.32
	2003	7.97	374.83	1.96	> 104	9.84	> 104	0.95	0.77
	2004	0.08	0.08	1.14	0.20	0.01	0.18	0.02	0.22
	2005	4.86	39.11	14.75	1.15	14.81	7.63	0.50	1.74
	2006	0.9	12.54	1.62	1.14	0.78	7.59	0.20	1.79
	2007	1.87	1.87	0.1	1.30	0.08	0.18	0.00	0.07
	2008	3.94	19.19	1.29	1.93	0.64	0.29	0.03	0.67
	2009	0.06	19.1	0.35	6.87	0.38	1.82	0.07	0.42
Lognormal	1990	0.81	13.67	1.02	17.88	2.97	6.19	0.01	1.21
	1991	0.53	31.73	0.7	> 104	0.77	> 104	0.16	1.34
	1992	0.43	29.91	1.33	2.81	1.11	> 104	0.10	1.09
	1993	6.42	80.79	31.13	9.77	35.39	> 104	0.08	1.29
	1994	0.79	20.98	0.78	1.42	0.74	11.37	0.08	0.71
	1995	2.08	2.08	0.01	0.22	0.01	0.00	0.00	0.01
	1996	1.19	59	52.89	14.10	7.12	3.78	0.21	14.38
	1997	1.98	37.85	3.7	2.15	2.10	1.09	0.06	1.35
	1998	0.39	11.93	0.81	1.33	0.89	0.41	0.03	0.53
	1999	2	18.86	0.83	0.96	0.72	6.96	0.06	1.95
	2000	2.02	89.4	0.97	1.54	1.05	16.39	0.08	0.42
	2001	0.85	2.86	0.91	0.72	4.17	0.42	0.05	2.84
	2002	2.6	39.19	0.12	1.10	0.11	2.59	0.09	0.27
	2003	0	0	0	0	0	0	0	0
	2004	3.22	3.22	1.45	0.52	0.04	0.22	0.31	0.42
	2005	13.78	13.78	1.59	1.89	1.67	0.17	0.12	1.96
	2006	3.74	3.74	1.79	1.55	1.45	1.90	0.04	1.04
	2007	0	0	0	0.00	0.00	0.00	0.00	0.00
	2008	1.84	3.72	0.57	1.05	0.34	0.79	0.01	0.67
	2009	0.31	4.19	0.34	3.48	0.35	1.72	0.05	0.59

Table 4 shows the maximum likelihood estimates of squid abundance parameters. Estimated natural mortality rates are much lower than the fixed value assumed until now (Roa-Ureta and Arkhipkin, 2007). However, there are very large standard errors associated with the estimates. Table 3 also shows that initial abundance  $N_0$  and the perturbations can be estimated with fairly high precision. This shows that fishing operational catch-and-effort data alone contain substantial information about stock abundance. The perturbations constitute an important part of a year's abundance, 26% on average; a range of 0% in years without perturbations to 96% in the unusual 2004 fishing season.

Table 5 shows the maximum likelihood estimates of fishing operational parameters, scaling ( $k$ ), effort response ( $\alpha$ ), and abundance response ( $\beta$ ). Excluding a few exceptions, these parameters are estimated with high precision. The scaling parameter

is extremely variable between years, encompassing five orders of magnitude. The control of catch by effort is more linear than the control of catch by abundance, because the effort-response parameter estimate ranged from 0.4 to 1.9, whereas the abundance-response parameter estimate varied from 0.34 to 10.3. Mean (and median)  $\alpha$  estimate ( $\bar{\alpha} = 1.1$ ) was almost exactly proportional, while mean (and median)  $\beta$  estimate ( $\bar{\beta} = 4.7$ ) was well in the hyperdepletion regime (see Figure 1 of Harley *et al.*, 2001). There were two years with proportionality between catch and effort, nine years with saturability, and nine years with synergy. Seventeen years exhibited hyperdepletion, and the three remaining years, those with the lowest escapement biomass in the series, showed hyperstability.

Figure 4 shows the *post hoc* reconstruction of the serial information for stock abundance along with estimates from previous

**Table 3.** AIC of all models attempted for all summer seasons of the *Loligo gahi* fishery in the Falkland Islands, the conclusion from AIC comparisons, and the model finally selected.

Year	Normal					AIC conclusive	Lognormal					AIC conclusive	Best model
	0P	1P	2P	3P	4P		0P	1P	2P	3P	4P		
1990	-728.3	<b>-744.7</b>	<b>-745.9</b>	<b>-745.9</b>	<b>-745.0</b>	No	294.7	<b>281.8</b>	<b>281.0</b>	<b>282.9</b>	<b>284.7</b>	No	Lognormal 1P
1991	-768.6	-771.2	-769.0	-775.0	<b>-811.4</b>	Yes	249.6	254.0	253.4	247.9	<b>222.2</b>	Yes	Lognormal 4P
1992	-755.1	-760.1	-760.1	<b>-792.5</b>	-780.9	Yes	319.4	317.0	319.0	<b>291.4</b>	<b>289.5</b>	No	Lognormal 3P
1993	-867.8	-986.8	<b>-1 011.8</b>	<b>-1 011.0</b>	-985.4	No	506.3	453.3	432.9	<b>425.5</b>	439.4	Yes	Normal 2P
1994	-856.8	-865.6	-863.6	<b>-872.5</b>	<b>-873.7</b>	No	261.2	260.4	262.4	255.4	<b>241.4</b>	Yes	Lognormal 4P
1995	-919.9	-919.5	<b>-915.8</b>	CF	CF	Yes	<b>134.0</b>	<b>136.0</b>	CF	CF	NT	No	Normal 2P
1996	-858.2	-859.3	CF	-965.0	<b>-984.7</b>	Yes	521.6	520.4	472.8	<b>462.6</b>	NT	Yes	Lognormal 3P
1997	NT	NT	-1 073.4	-1 070.2	<b>-1 083.2</b>	Yes	NT	NT	307.6	<b>269.7</b>	<b>271.7</b>	No	Normal 4P
1998	-875.8	<b>-885.9</b>	<b>-884.5</b>	<b>-886.4</b>	CF	No	352.4	<b>340.4</b>	<b>342.4</b>	<b>342.8</b>	<b>344.8</b>	No	Lognormal 1P
1999	-1 069.8	-1 071.9	-1 069.8	<b>-1 095.0</b>	-1 091.8	Yes	307.3	302.6	304.6	<b>291.3</b>	<b>288.5</b>	No	Normal 3P
2000	-610.8	-608.8	-674.1	-669.0	<b>-699.4</b>	Yes	395.8	397.8	-	344.2	<b>308.4</b>	Yes	Normal 4P
2001	NT	NT	CF	-958.0	<b>-967.1</b>	Yes	NT	NT	<b>385.2</b>	<b>387.2</b>	<b>384.3</b>	No	Lognormal 4P
2002	NT	-934.1	-934.0	<b>-977.8</b>	-951.0	Yes	NT	360.3	362.9	<b>323.7</b>	347.8	Yes	Normal 3P
2003	-326.1	-365.9	<b>-373.8</b>	CF	CF	Yes	<b>89.8</b>	CF	CF	NT	NT	Yes	Lognormal 0P
2004	NT	NT	NT	<b>-358.6</b>	<b>-358.7</b>	No	NT	NT	NT	87.9	<b>84.7</b>	Yes	Lognormal 4P
2005	-308.4	-327.6	-342.7	CF	<b>-347.5</b>	Yes	46.2	<b>32.4</b>	CF	CF	NT	Yes	Normal 4P
2006	-345.4	<b>-356.8</b>	<b>-357.9</b>	<b>-355.9</b>	<b>-354.0</b>	No	NT	45.5	<b>41.8</b>	CF	NT	Yes	Normal 1P
2007	NT	NT	NT	<b>-397.3</b>	<b>-395.5</b>	No	NT	NT	NT	CF	<b>96.1</b>	Yes	Normal 3P
2008	-447.7	-462.9	<b>-466.9</b>	CF	CF	Yes	<b>81.5</b>	83.4	85.2	CF	CF	Yes	Lognormal 0P
2009	-418.1	<b>-435.1</b>	<b>-436.0</b>	<b>-437.2</b>	<b>-435.1</b>	No	<b>71.8</b>	<b>70.6</b>	<b>69.1</b>	<b>67.6</b>	<b>67.9</b>	No	Normal 1P

In bold are the AIC of the best models. NT, not tried; CF, convergence failure.

studies for later comparison. Both numbers and biomass of squid show an earlier short period (three years) of higher abundance, at close to 100 000 t of escapement biomass, or 5–6 billion squid recruiting. After that, there is a lower abundance period extending to the present, centered at about 40 000 t of escapement biomass or about 2 billion squid recruiting. In this longer period, there were two years when the escapement biomass hit the management limit of a minimum of 10 000 t.

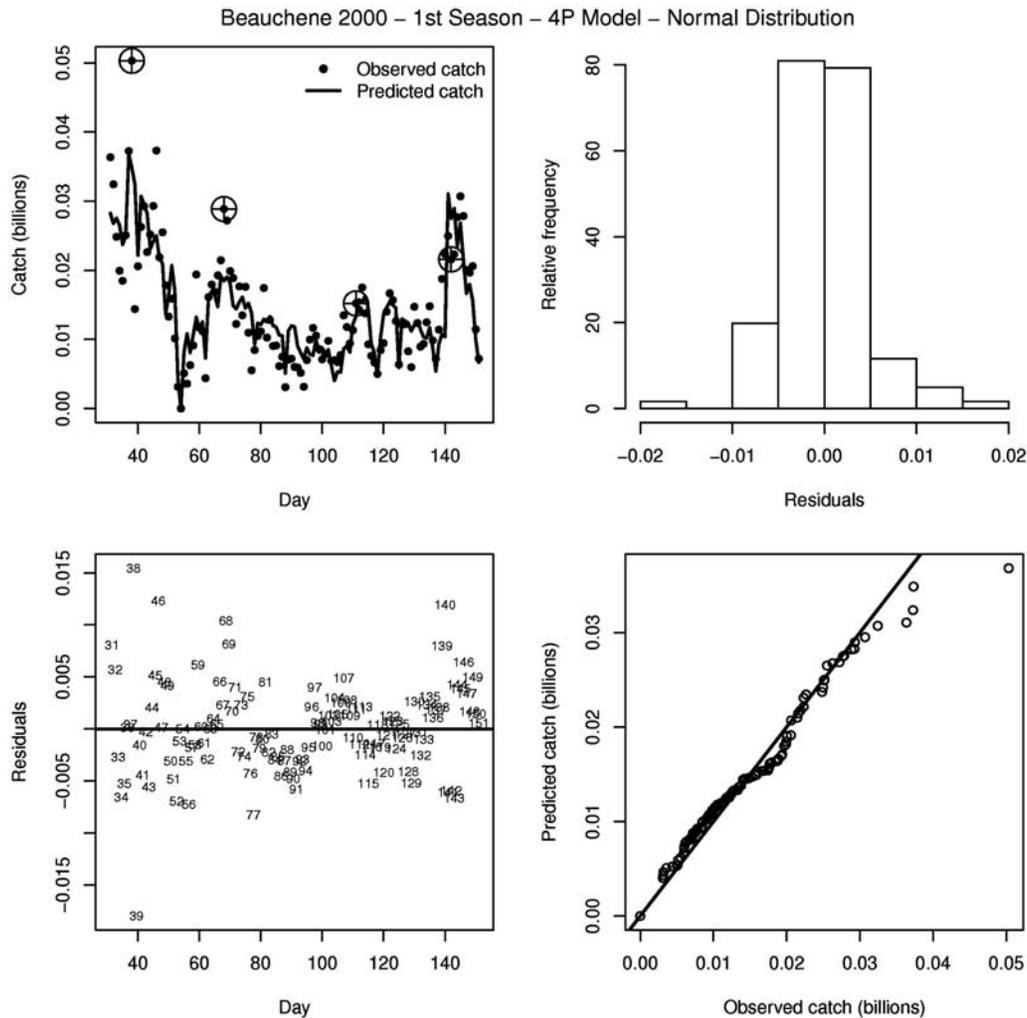
Figure 5 shows the observed relationship between four measures of stock biomass and the abundance-response parameter. For all four measures, hyperdepletion is only present at the highest biomass. Conversely, for three measures, hyperstability is only present at the lowest biomass. The plots also suggest a functional relationship, whose rate of change is steep at low biomass and levels off at intermediate biomass. The shape of the relationship also shows that the regime of proportionality will be rarely experienced.

## Discussion

Modelling the daily catch dynamics of 20 years of summer fishing for *Loligo gahi* in the Falklands showed that perturbations—in-season pulses of abundance—to a pure depletion process occur often (in 18 of those years). This can be interpreted in two ways: there were waves of immigration into the fishing grounds or the fleet expanded its area of operation, making new parts of the stock available. In these applications, only the first explanation is plausible because all the assessments carried out concern a specific area in the southern part of the Falklands continental shelf (see Figure 2 in Roa-Ureta and Arkhipkin, 2007). Therefore, the present results indicate that a squid cohort is normally composed of several successive waves of squid [Boyle and Rodhouse (2005) termed these “microcohorts”], entering the fishing grounds at different times during the fishing season. This

is a much more complex situation than assumed by simple depletion models. For example, in 2004 (Figure 2), the daily catch dynamics clearly are the result of multiple pulses in abundance, causing a real in-season, stepwise increase in catch rate. Having said this, it is also true that, in 15 of the 18 years with perturbations, initial abundance  $N_0$  was higher than the sum of all in-season positive perturbations, indicating that the fishing season was well timed to harvest squid that had already left the inshore nursery grounds and had come *en masse* to the fishing grounds.

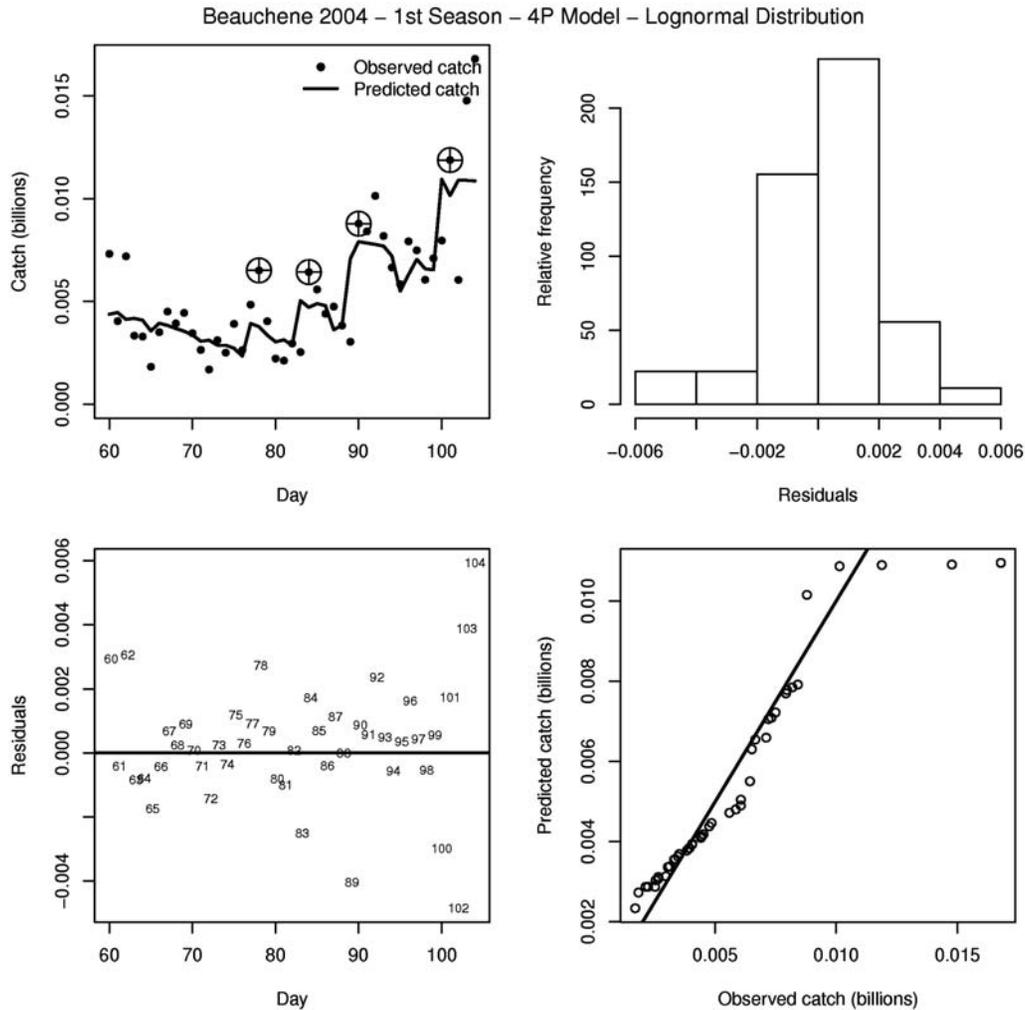
Results of the generalized depletion models can be compared with results from three previous studies on the same fishery that employed simple depletion models. Agnew *et al.* (1998), covering 1987–1996, observed that catch rates in some years did not decline as expected under the assumption of a closed population. To provide timely in-season advice for management in those troubling years, they introduced an *ad hoc* procedure by which catchability estimates from previous years could be used as fixed values in the troubling years to estimate initial abundance (Arkhipkin *et al.*, 2008). McAllister *et al.* (2004), covering 1987–2000, in a follow-up paper, argued that a real decreasing trend in catch rates can be masked by spikes in catch rates due to sampling error, making it appear as if the population is open when, in fact, the population is closed. They developed a Bayesian hierarchical model to deal with these masked decreasing trends by using catchability information from previous years. All three assumptions of the classical depletion model were assumed to hold: closed population, catch rate proportional to abundance (i.e. constant in-season mean catchability), and fixed natural mortality rate, whose value is known exactly. Generalized depletion models improve the assessment by allowing for the more dynamical situation of an open population, via the concept of perturbations to a depletion process, in the form of parameters that can be



**Figure 1.** Fishing operational results and model fit diagnostics for the 2000 summer season of the *Loligo gahi* fishery in the Falkland Islands. Top-left panel: predicted and observed catch and the timing of perturbations (target symbols). Top-right panel: distribution of residuals. Bottom-left panel: residual scatterplot. Bottom-right panel: Q-Q residual plot.

estimated from the same data as a simple depletion model. Here, these perturbations are in-season waves of immigration to the fishing grounds. This is more realistic because intracohort differences in the timing of spawning or hatching (Shaw *et al.*, 2004) or shifts in critical environmental variables (Arkhipkin *et al.*, 2004b) may produce differences in the timing of recruitment, leading to the formation of microcohorts (Boyle and Rodhouse, 2005) and ultimately an open population. Roa-Ureta and Arkhipkin (2007) recognized the existence of in-season increases in abundance in the 2005 fishing summer season, but they accounted for it by modelling separate depletion processes. Generalized depletion models allow for a simultaneous modelling of the entire season in the presence of increasing trends in abundance. A second advancement of the generalizations is that constant catchability is not assumed. This has been highlighted as an important component of more realistic stock assessment models by Harley *et al.* (2001). The effect is mostly observed in the assessment results of the earlier years (see Figure 4), where our estimates tend to be much higher than those of Agnew *et al.* (1998) and McAllister *et al.* (2004) due to the existence of

hyperdepletion at higher stock abundance. A third improvement is that generalized depletion models use all the available data from a fishing season, whereas simple depletion models discard data from time-steps outside a main declining cpue period, which is defined by the modeller (e.g. McAllister *et al.*, 2004). A fourth and less crucial improvement of the generalized models is that natural mortality is a free parameter estimated from the data. Our estimate is, on average, two orders of magnitude lower than the fixed value used in previous studies (Rosenberg *et al.*, 1990; Agnew *et al.*, 1998; McAllister *et al.*, 2004; Roa-Ureta and Arkhipkin, 2007), although standard errors are very large. This result is less crucial because it does not have a strong effect on stock assessment. In fact, a shift in the order of magnitude from  $10^{-3}$  to  $10^{-5}$  means that, instead of 99.1% daily survival, the stock has a 99.9% daily survival. However, the lower estimates make more biological sense when the semelparity of the squid reproductive strategy is considered. A rate in the order of  $10^{-3}$  daily is consistent with a rate averaged over the lifespan, using Hewitt and Hoening's (2005) empirical formula (Roa-Ureta and Arkhipkin, 2007), whereas the daily rate estimated here is the



**Figure 2.** Fishing operational results and model fit diagnostics for the 2004 summer season of the *Loligo gahi* fishery in the Falkland Islands. Top-left panel: predicted and observed catch and the timing of perturbations (target symbols). Top-right panel: distribution of residuals. Bottom-left panel: residual scatterplot. Bottom-right panel: Q-Q residual plot.

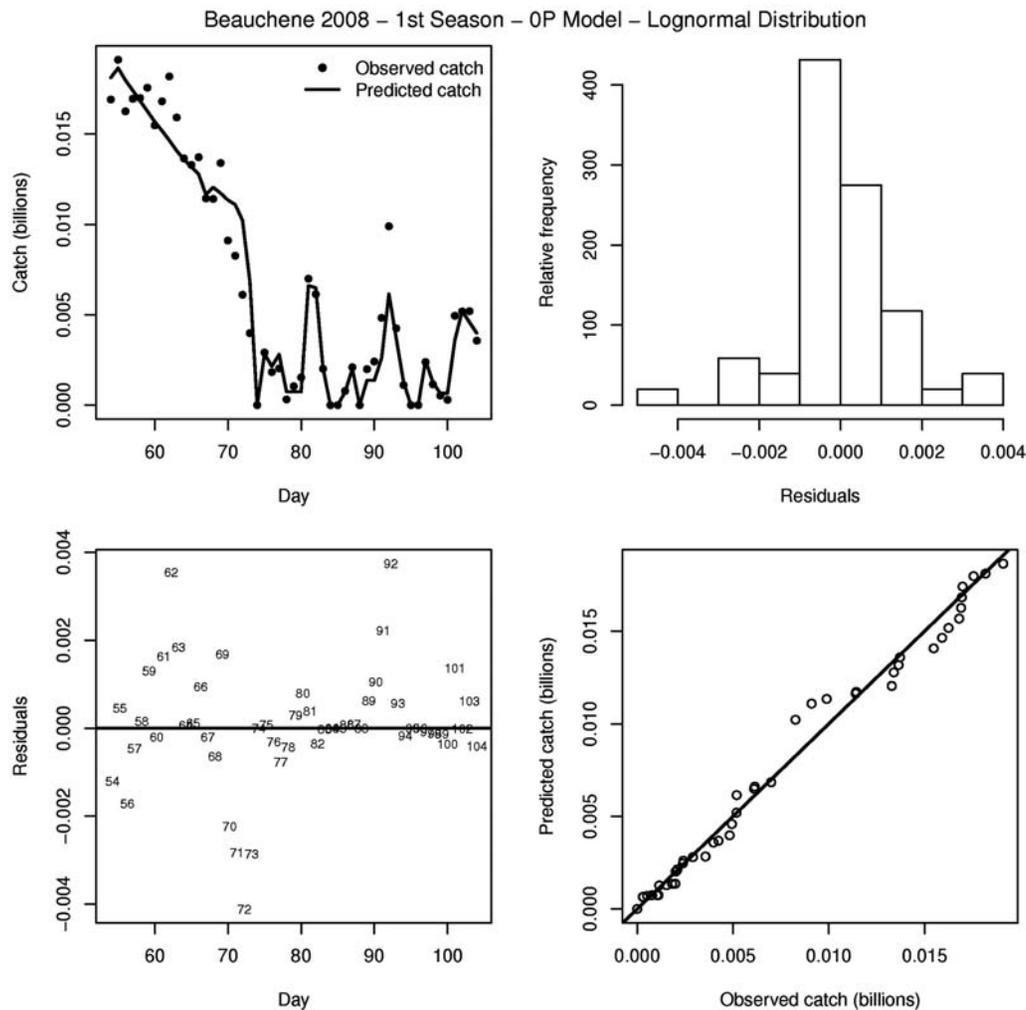
rate experienced exclusively during the fishing season. After the season, the squid eventually migrate inshore, spawn on the kelp beds, and die *en masse*. Thus, most natural mortality is concentrated in the last part of the lifespan. It should be expected that the natural mortality rate during the fishing season would be much lower than the rate averaged over the lifespan, because the latter includes the catastrophic rate experienced after spawning.

Generalized depletion models are new stock assessment models that can be used for squid stocks and probably other stocks. However, several components of the model need to be improved by further research in order to make it a more effective general tool. First, the model requires exhaustive catch-and-effort data and a measure of effort that is free of statistical error. In many actual situations, total catch and effort are estimated from observations of a sample of fishing trips, so both effort and catch shall be considered random variables. This requires further development of the statistical model. Second, the openness of the population is modelled by up to four positive perturbations that happen at exactly one time-step each, whereas actual immigration pulses each probably occur over a number of time-steps. Third, losses other than those caused by natural mortality and catch are not counted. Emigration events may also take place, but modelling

them as negative perturbations incurs the risk of counting the emigrated animals twice when estimating escapement biomass. This is because, once an emigration pulse is defined by a large negative residual, the emigrated animals have to be kept in a separate accounting to calculate their natural decline, but then (part of) these may return to the fishing grounds in a later pulse of abundance, and they would be counted twice when evaluating escapement biomass. Note that minor immigration and emigration events are accounted for in the random variability of catch. Fourth, a simplifying assumption applied to the *L. gahi* fishery that may require careful attention in other applications is that the fleet was assumed to be homogeneous in terms of fishing power. If the fleet is heterogeneous, then the model needs to be generalized to a multiple-fleet model. In those cases, the model is of the form

$$C_t = \sum_f k_f E_{t,f}^{\alpha_f} N_t^{\beta_f} \tag{6}$$

where  $f$  is the fleet index. Note also that when expanding the latent predictor  $N_t$ , it might be necessary to make the perturbation parameters fleet-dependent. In these more complicated cases, the parameters that would be common to all fleets and would, thus, justify



**Figure 3.** Fishing operational results and model fit diagnostics for the 2008 summer season of the *Loligo gahi* fishery in the Falkland Islands. Top-left panel: predicted and observed catch. Top-right panel: distribution of residuals. Bottom-left panel: residual scatterplot. Bottom-right panel: Q-Q residual plot.

the simultaneous estimation would be initial abundance  $N_0$  and natural mortality  $M$ .

Inspection of the estimated and limit escapement biomass (Figure 4) shows that once the catch stabilized at around 40 000 t (1997–2009) from a previous higher level around 70 000 t (1990–1996), the limit-escapement biomass became adequate and the exploitation rate became stable on average; thus, management intervention to cut the season short has not been necessary. Nevertheless, the annual changes in estimated escapement biomass have not been modest, reaching as much as threefold during the more stable period starting in 1999. These oscillations may well be within natural limits, but they may also result from or be amplified by excessive fishing pressure in good years. A study of the productive capacity of the stock to complement the working limit-escapement biomass might be useful. Provided a sound method to estimate productive capacity is defined and the estimate is re-evaluated with new data every year, it can be used to set a higher catch limit in good years, so that the exploitation rate moves within narrower bounds set by the limit-escapement biomass and a maximum catch.

Agnew *et al.* (2000) presented evidence for density-dependence in both cohorts of the *L. gahi* stock of the Falkland Islands using spawning stock and recruitment estimates from the De Lury depletion models of Agnew *et al.* (1998). It is interesting to re-examine their findings using the estimates of spawning biomass and recruitment presented in this study, both because the number of observations is higher and because the current estimates come from improved stock assessment models. The relationship between escapement biomass and recruitment from this study is shown in Figure S2 of the Supplementary material. We do not observe evidence of density-dependence. The relationship appears linear, with more escapement biomass leading to more recruitment, with high variance. Thus, it seems that the suggestion of density-dependence by Agnew *et al.* (2000) is not robust to departures from the assumptions of simple depletion models, at least for the case of the ASC.

The *L. gahi* fishery of the Falkland Islands is hyperdepleted at high and intermediate abundance levels and is hyperstable at low abundance levels. Hyperstability has been thought to be caused by fleets targeting highly aggregated fish, such as spawning

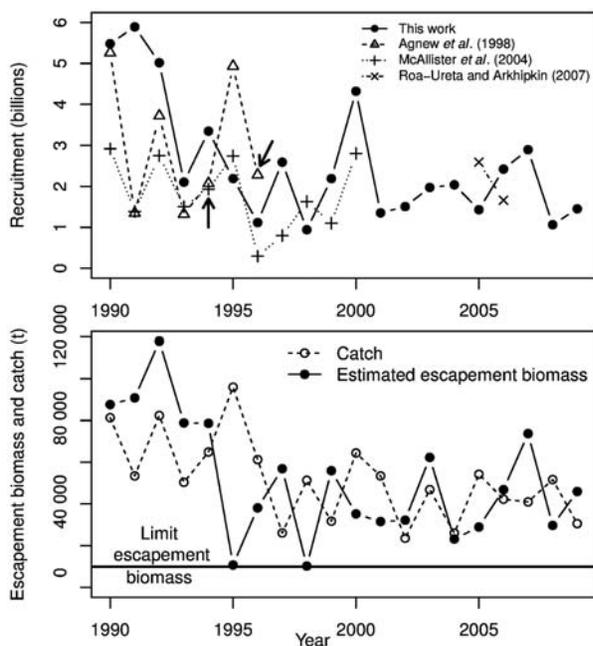
**Table 4.** Abundance parameter estimates of selected models, their standard errors (in parentheses), and the timing of events in Julian days (right-hand integer number) for the autumn spawning cohorts (summer seasons) of the *Loligo gahi* stock in the Falkland Islands, 1990–2009.

Year	Model	Distribution	$10^{-5}M$ ( $day^{-1}$ )	$N_0$ (billions)	P1 (billions)	P2 (billions)	P3 (billions)	P4 (billions)	$B_{esc}$ (t)
1990	1P	Lognormal	8.49 (36.14)	4.832 (0.180) 31	0.650 (0.117) 71	–	–	–	87 646 150
1991	4P	Lognormal	1.42 (9.63)	4.619 (NA) 31	0.295 (0.108) 37	0.222 (0.059) 56	0.460 (0.052) 95	0.297 (0.054) 120	90 850 150
1992	3P	Lognormal	1.38 (10.13)	3.731 (0.027) 31	0.547 (0.072) 37	0.300 (0.062) 62	0.439 (0.053) 116	–	117 909 151
1993	2P	Normal	4.99 (14.46)	1.664 (0.008) 31	0.120 (0.021) 51	0.319 (0.020) 92	–	–	78 840 150
1994	4P	Lognormal	1.11 (8.85)	2.614 (0.029) 31	0.306 (0.044) 44	0.0005 (0.004) 58	0.223 (0.032) 86	0.204 (0.034) 123	78 663 150
1995	2P	Normal	56.12 (733.08)	2.176 (0.709) 31	0.010 (0.068) 32	0.003 (0.015) 121	–	–	10 772 150
1996	3P	Lognormal	0.23 (2.69)	0.694 (0.439) 31	0.164 (0.019) 45	0.172 (0.020) 121	0.086 (0.021) 140	–	38 114 151
1997	4P	Normal	2.18 (9.77)	1.915 (0.031) 31	0.244 (0.050) 64	0.007 (0.033) 74	0.066 (0.035) 89	0.359 (0.024) 118	56 911 150
1998	1P	Lognormal	5.11 (88.35)	0.467 (0.262) 31	0.474 (0.086) 45	–	–	–	10 248 150
1999	3P	Normal	0.82 (6.02)	1.850 (0.011) 31	0.129 (0.038) 51	0.065 (0.017) 73	0.144 (0.014) 121	–	55 952 150
2000	4P	Normal	4.69 (27.47)	2.714 (0.065) 31	0.283 (0.051) 38	0.173 (0.050) 68	0.436 (0.055) 111	0.717 (0.062) 142	35 259 151
2001	4P	Lognormal	0.20 (2.24)	0.670 (0.189) 31	0.259 (0.064) 39	0.029 (0.039) 49	0.277 (0.063) 129	0.116 (0.042) 143	31 569 150
2002	3P	Normal	0.07 (1.69)	1.213 (0.033) 31	0.036 (0.018) 90	0.143 (0.020) 122	0.112 (0.011) 144	–	32 238 150
2003	0P	Lognormal	1.01 (16.09)	1.972 (0.196) 59	–	–	–	–	62 294 103
2004	4P	Lognormal	9.88 (NA)	0.072 (NA) 60	0.036 (NA) 78	0.087 (NA) 84	0.269 (NA) 90	1.573 (NA) 101	23 224 104
2005	4P	Normal	33.56 (215.36)	0.787 (NA) 59	0.290 (0.039) 67	0.065 (0.027) 76	0.182 (0.035) 81	0.105 (0.029) 92	28 984 103
2006	1P	Normal	31.93 (90.03)	2.150 (0.082) 54	0.268 (0.047) 64	–	–	–	46 874 103
2007	3P	Normal	20.20 (90.15)	2.044 (0.059) 54	0.336 (0.071) 75	0.245 (0.051) 87	0.270 (0.046) 94	–	73 721 103
2008	0P	Lognormal	3.06 (30.02)	1.063 (0.209) 54	–	–	–	–	29 711 104
2009	1P	Normal	3.62 (19.95)	1.369 (0.014) 54	0.082 (0.010) 69	–	–	–	45 995 103

$B_{esc}$  is biomass at the end of season;  $M$  is the natural mortality rate; 0P, 1P, ... refer to the number of perturbations in the process model; P1, P2, ... refer to the magnitude of positive abundance perturbations, if any.

**Table 5.** Fishing operational parameter estimates of selected models and their standard errors (in parentheses) for the autumn spawning cohorts of *Loligo gahi* stock in the Falkland Islands, 1990–2009.

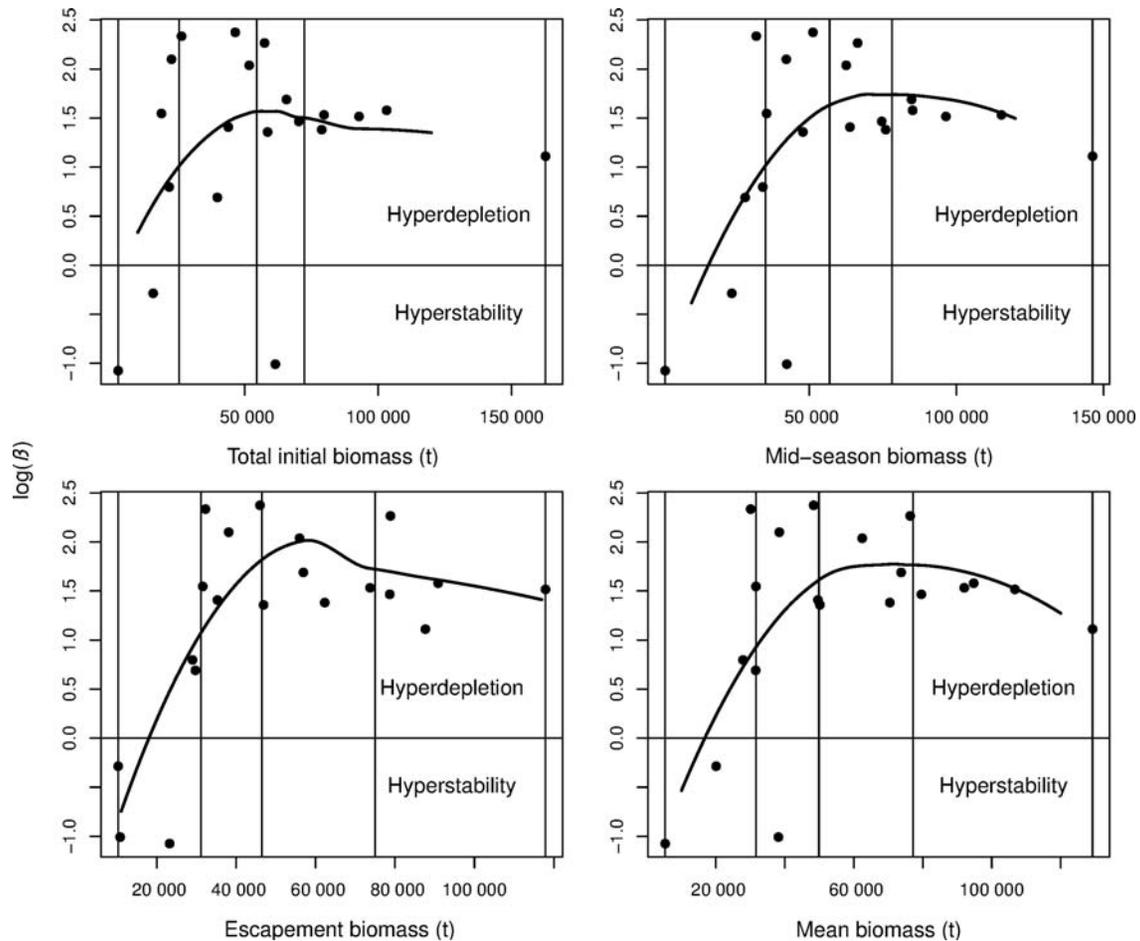
Year	Model	Distribution	$10^{-7}k$ (1/number of vessels)	$\alpha$	$\beta$
1990	1P	Lognormal	8.0 (0.4)	1.796 (0.058)	3.037 (0.097)
1991	4P	Lognormal	14.9 (0.2)	0.793 (0.030)	4.851 (0.003)
1992	3P	Lognormal	17.7 (0.3)	1.168 (0.024)	4.556 (0.017)
1993	2P	Normal	4.4 (0.1)	1.461 (NA)	9.632 (0.043)
1994	4P	Lognormal	79.6 (1.2)	1.091 (NA)	4.332 (0.036)
1995	2P	Normal	5 647.1 (170.6)	1.244 (0.060)	0.365 (0.274)
1996	3P	Lognormal	48 333.3 (164 119.8)	0.840 (0.098)	8.161 (5.102)
1997	4P	Normal	75.1 (1.2)	0.854 (NA)	5.416 (0.035)
1998	1P	Lognormal	6 424.9 (1 494.0)	1.129 (0.093)	0.751 (0.412)
1999	3P	Normal	38.0 (0.7)	0.820 (0.047)	7.674 (0.036)
2000	4P	Normal	227.0 (5.2)	1.154 (NA)	4.089 (0.088)
2001	4P	Lognormal	11 871.8 (9 328.8)	0.791 (0.075)	4.697 (1.794)
2002	3P	Normal	7 520.8 (1 378.5)	0.443 (0.136)	10.326 (0.597)
2003	0P	Lognormal	450.6 (111.9)	1.097 (0.095)	3.982 (0.766)
2004	4P	Lognormal	10 707.2 (NA)	0.851 (NA)	0.341 (NA)
2005	4P	Normal	13 199.1 (NA)	1.108 (NA)	2.220 (NA)
2006	1P	Normal	69.3 (3.0)	1.857 (0.054)	3.890 (0.174)
2007	3P	Normal	349.1 (8.6)	0.626 (NA)	4.630 (0.052)
2008	0P	Lognormal	12 228.2 (4 656.7)	0.951 (0.057)	1.995 (0.822)
2009	1P	Normal	371.9 (11.2)	0.897 (NA)	10.739 (0.200)

**Figure 4.** Estimated history of abundance of the *Loligo gahi* stock in the Falkland Islands, 1990–2009. The arrows in the top panel indicate the years when Agnew *et al.* (1998) fixed the catchability estimate because the simple depletion model failed to estimate both catchability and initial abundance.

aggregations (Hanchet *et al.*, 2005; Erisman *et al.*, 2011). The degree of stock aggregation may certainly be dependent on the abundance level, as argued by Hanchet *et al.* (2005). These authors noted departures from proportionality when examining an early period (1986–1992) of low stock abundance and a late period (1996–2002) of high stock abundance caused by a strong year class becoming available to the fleets in 1994. Their Figure 2 shows that in the earlier period of low abundance, cpue was hyperstable; in their words it “resisted to decrease” even

though the stock was decreasing. Conversely, in the later period of high abundance, cpue was hyperdepleted, lagging behind the increase in abundance. It is plausible then, in light of our results, to hypothesize that Hanchet *et al.* (2005) have found regime shift from hyperstability to hyperdepletion, caused by corresponding changes in stock abundance from low to high, similar to our findings in the *L. gahi* fishery of the Falkland Islands.

Although the relationship between stock abundance and the presence of hyperdepletion or hyperstability could be a general characteristic of fisheries, the precise abundance level at which a hyperstable fishery may become hyperdepleted could be specific of the conditions under which a fishery operates. In the case of the *L. gahi* fishery, the hyperdepleted regime is far more prevalent, and the abundance level at which the fishery shifts to hyperstability is low. The seabed at the Beauchene fishing grounds is covered, to a large degree, by rocky bottoms where trawling gear cannot operate (see Figure 2 of Roa-Ureta and Arkhipkin, 2007). From anecdotal reports received by this author, fishing vessel captains believe that squid often “hide” in these areas, and that this is a fundamental aspect of the stock’s sustainability. Hilborn and Walters (1992) have hypothesized that a possible mechanism for hyperdepletion is the existence of cryptic habitat where the stock makes itself unavailable. Our results show that this hypothesis is incomplete because the main determinant of the existence of hyperstability or hyperdepletion is stock abundance, while the presence of cryptic habitat plays the role of increasing the chance of observing hyperdepletion by lowering the abundance threshold when a fishery shifts from the low-abundance hyperstable regime to the high-abundance hyperdepleted regime. That the regime of abundance response depends on stock abundance in the *L. gahi* fishery raises the question whether a regime shift may occur within a fishing season, given the rapid in-season changes in abundance observed in some years (see Figure 3). This could certainly happen, and it would imply that by fixing  $\beta$  at a constant level during the fishing season, initial abundance would tend to be underestimated, while escapement biomass would tend to be overestimated, which would be a particularly serious concern for years when initial abundance is close to the above-discussed threshold.



**Figure 5.** Observed relationship between four measures of season biomass and the hyperresponse parameter for the 20 summer seasons of the *Loligo gahi* fishery in the Falkland Islands during the period 1990–2009. The curved line is a local polynomial smoother (R's *loess* function) with smoothing parameter  $\lambda = 1$ . The vertical lines are the 0, 25, 50, 75, and 100% percentiles of the empirical distribution of the biomass measure. The horizontal line is the boundary separating the hyperstability and hyperdepletion regimes.

Harley *et al.* (2001, p. 1765) recommended the incorporation of abundance response into stock assessment models. In models of the rapid-fishing operational dynamics, such as the models presented here, this parameter can be estimated with precision (see standard errors of  $\beta$  in Table 4), in part because the mathematical structure of the model allows for easy numerical calculation of gradients and higher-order derivatives of the support function with respect to  $\beta$ . In the case of population dynamics models, it is usually understood that introducing non-linear abundance response entails introducing  $\beta$  in the relationship between stock abundance and any indexes from cpue standardization that are available (e.g. Walters, 2003; Hanchet *et al.*, 2005). However, abundance response is a general hypothesis for the relationship between catch rates and stock abundance, so it would be coherent to include it in any other catch equation of the stock assessment model. A generalization of the Baranov catch equation allows direct introduction of abundance response into population dynamics stock assessment models. This is shown as follows. In Baranov's hypothesis,  $dC/dt = f(F, N)$ ,  $F$  is the fishing mortality rate. The rate of catch that allows for power abundance response is

$$\frac{dC}{dt} = FN^\beta \quad (7)$$

whose solution is

$$C(t) = \frac{F}{\beta(F+M)} (1 - e^{-(F+M)\beta t}) N_0^\beta \quad (8)$$

This shows that models without this structural change, and that rely on Baranov's hypothesis when the fleet-stock system shows hyperstability ( $\beta < 1$ ), not only artificially inflate the estimation of abundance, but also result in underestimation of the total mortality rate,  $F + M$ . Conversely, when the system exhibits hyperdepletion, total mortality is overestimated. Note also that the abundance response  $\beta$  should be let to vary annually to account for the possible existence of hyperdepletion and hyperstability regimes that depend on stock abundance. In the case of our depletion models, fitted separately to each year, the annual variation in  $\beta$  is implicitly given, whereas in the integrated assessment of multicohort finfish, it should be made explicit by the modeller.

### Supplementary material

Supplementary material is available at the ICESJMS online version of this paper. It includes an appendix with the derivation of the stock assessment model as a generalized Leslie–Davis depletion model, a scatterplot of daily catch vs. daily effort for two measures

of effort, an escapement biomass and recruitment plot, a table with descriptive statistics of effort, and two tables with details of numerical performance by the generalized depletion models.

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