

# Hyperstability and Hyperdepletion Regimes in the *Loligo gahi* Fishery of the Falkland Islands

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## Abstract

Models of the daily fishing operations of *Loligo gahi* fishing seasons in the Falkland Islands over the period 1990 to 2009 revealed a regime of hyperstability at low stock abundance and hyperdepletion at intermediate and high stock abundance. The hyperdepleted regime was far more prevalent. The availability of natural protected areas where the stock can find refuge from fishing operations is proposed as the cause of the prevalence of hyperdepletion.

## Introduction

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 nonlinear relationship between CPUE and abundance has been suspected for some time (Hilborn and Walters, 1992). The emphasis of previous work has been on the prevalence of one of the aspects of this suspected non-linearity, namely hyperstability, because ignoring it when it is present leads to over-optimistic assessment of stocks. The cod of Newfoundland being a classic example (Hutchings and Myers, 1994; Walters and Maguire 1996; Hilborn and Walters, 1992). Hyperstability is one outcome of a three-regime phenomenon that also includes proportionality and hyperdepletion. The main purpose of this paper is to explore the prevalence of all three regimes and under which conditions they are present, for a specific instance of application.

## Materials and Methods

### Stock Assessment Model

Let  $C$  be the true catch in numbers of a single stock and fishing operation in a given fishing season.

The catch rate is assumed to be the result of two causes, nominal fishing effort  $E$  (hereafter 'effort') and stock abundance  $N$ ,

$$(1) \quad \frac{dC}{dt} = f(E, N) \quad .$$

In this hypothesis the fishing process enters directly through a measure of human work and capital, such as the number of vessels operating at a given time. I further assume 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  $N(t)$  to represent it as the result of estimable parameters and observed variables. Harley et al.'s (2001) adopted a power relation between CPUE and stock abundance predictor. I assume a power relation for both predictors, stock abundance and effort. Under these assumptions and expressing the model in discrete time steps I show in the Appendix that a solution to the catch rate equation above is,

$$(2) \quad C_t = k E_t^\alpha N_t^\beta e^{-M/2} = k E_t^\alpha \left( N_0 e^{-Mt} + \sum_{i=1}^t P_i e^{-M(t-i)} - e^{-M/2} \sum_{i=1}^{t-1} C_i e^{-M(t-i-1)} \right)^\beta e^{-M/2}, \quad .$$
$$t > 0, C_t \geq 0, E_t \geq 0, k > 0, N_0 > 0, \alpha > 0, \beta > 0, M > 0, -N_0 e^{-M} \leq P_i \leq +\infty$$

This model is used as the standard model for formal stock assessment of the *L. gahi* stock in the Falkland Islands since 2009. The model has free parameters  $\theta = [k \ \alpha \ \beta \ N_0 \ M \ \{P_i\}]$ . From a process point of view these parameters belong in two distinct groups. The first group are the fishing operational parameters,  $k$ ,  $\alpha$  and  $\beta$ . Parameter  $k$  scales down the determination of catch by effort so it is called here the '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. Its value determines the presence of three regimes of effort response: effort saturability ( $\alpha < 1$ ), effort synergy ( $\alpha > 1$ ), and effort proportionality ( $\alpha \approx 1$ ) (Bannerot and Austin, 1983; Quinn and Deriso, 1999, p. 28). Parameter  $\beta$  is the abundance response parameter, controlling how fishermen perceive fish

47 abundance. Hyperstability ( $\beta < 1$ ) occurs when a decrease in abundance results in a lesser incremental  
 48 decrease of catch, whereas hyperdepletion ( $\beta > 1$ ) happens when a decrease in abundance results in a  
 49 greater incremental decrease of catch.

50 The second group of parameters are the fish abundance parameters,  $N_0$ ,  $M$  and  $\{P_i\}$ . Parameter  $N_0$   
 51 is the abundance of fish at the time step exactly before the first step of the fishing period. The  $\exp(-M)$   
 52 term quantifies the natural change as the probability of individual survival during one time step,  $N_t/N_{t-1}$ .  
 53  $\{P_i\}$  is the set of perturbation abundance parameters. If  $\{P_i\}$  is the empty set the model in eq. (2) is a pure  
 54 depletion model and the stock is a closed population whereas when  $\{P_i\}$  is not empty the model accounts  
 55 for episodic pulses of abundance and the stock is an open population. In this paper only positive  
 56 perturbations are considered. These can be waves of immigration into the fishing grounds, or expansions  
 57 of the fleet spatial distribution that make new parts of the stock available to fishing. The catch term  
 58 includes fish from  $N_0$  and from the  $\{P_i\}$ .

59 The model in eq. (2) is a catch model but under the assumption that effort is observed exactly it is  
 60 easily transformed into a CPUE model by dividing both sides by effort, leading to  
 61  $CPUE_t = k E_t^{\alpha-1} N_t^\beta e^{-M/2}$ , without any statistical consequences except for offsetting the effort response  
 62 parameter by -1. The advantage of formulating the model for catch instead of for CPUE is conceptual: in  
 63 the catch form the catch is the random response variable and effort and abundance are the fixed predictor  
 64 variables in a standard nonlinear recursive regression model.

65 Two probability models are considered for the catch observations, additive (normal) and  
 66 multiplicative (lognormal):

$$67 \quad (3) \quad \begin{aligned} \chi_t &= C_t + \varepsilon_t, & \varepsilon_t &\sim \text{Normal}(0, \sigma^2) \\ \chi_t &= C_t e^{\varepsilon_t}, & \varepsilon_t &\sim \text{Normal}(0, \sigma^2) \end{aligned}$$

68 where  $\chi$  is the observed catch. A justification for the additive hypothesis is given in Roa-Ureta and  
 69 Arkhipkin (2007). A more pragmatic approach is employed here, fitting all seasons to both the normal and

lognormal models and deciding on which is better case by case, using several statistical criteria (see below). The assumption behind this pragmatic choice is that the catch process occurs along a continuum from additive to multiplicative, so that each season'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  $\chi$  in eq. (3), in these implementations it was considered a nuisance, eliminated from the inference by adopting a modified profile support function as an approximation to the exact support function (Pawitan 2001, section 10.6)

$$(4) \quad \begin{aligned} l_p(\theta; \{\chi_t, E_t\}) &= -\frac{T-2}{2} \log \left( \sum_{t=1}^T (\chi_t - C_t)^2 \right), & \text{Normal model} \\ l_p(\theta; \{\chi_t, E_t\}) &= -\frac{T-2}{2} \log \left( \sum_{t=1}^T (\log(\chi_t) - \log(C_t))^2 \right), & \text{Lognormal model} \end{aligned}$$

where  $C_t$  is eq. 2, the true catch under the process model. The class of stock assessment model described here has been implemented in the R package *CatDyn*, available through the CRAN repository (see [www.r-project.org](http://www.r-project.org)).

## 80 Data and Implementation

The models defined above were applied to the daily catch and effort data of the factory trawling fleet fishing in the summer seasons of the squid *Loligo gahi* in the Beauchene fishing grounds of the Falkland Islands, from 1990 to 2009. A more detailed description of the fishery can be found in Roa-Ureta and Arkhipkin (2007). The catch and effort data is particularly clean and can be considered accurate and exhaustive. The effort data was available in two measures: total number of hours and minutes of trawling 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: the number of vessels. In addition, for a number of seasons the number of vessels shows a tighter relation between catch and effort (Fig. 1). Thus the number of vessels fishing per day was the measure of nominal effort.

To transform catch recorded in biomass to catch in numbers daily length frequency data and a previously fit length-body mass power model to estimate daily mean body mass. The length frequency data

was a sample from one to three observers in a fleet that reached a maximum of 30 vessels operating on a given day but that now amounts to 17 vessels. In the summer season the fleet harvests the Autumn Spawning Cohort (ASC). In principle, it could be possible to model the whole daily series from 1990 up 2009 simultaneously. However, since there is no data relevant to the model in the off-season part of the year, a simultaneous estimation would be meaningful by adding assumptions about how to connect abundance in a previous season with abundance in the current season, a spawning stock and recruitment model. In order to assess the stock without introducing assumptions about population dynamics, model parameters were estimated to each season separately.

The stock is managed by threshold policies (Quinn et al. 1990, Mendoza-Meza and Da Silveira-Costa, 2011). An unrestricted catch is taken by a licensed group of factory vessels during a given period of time. The management objective is to leave an escapement biomass of at least 10 thousand tons at the end of each season. The season can be cut short if the real-time assessment shows that the stock will cross the 10 thousand tons threshold before the end of the season. Thus in this application it is of interest to estimate the biomass at the end of the season. This escapement biomass was estimated by averaging the mean body mass in the last seven days of the season and multiplying this average by the model predicted numbers in the stock at the last day of the season. In addition, total initial abundance, including perturbation, was estimated as

$$(5) \quad \hat{A}_0 = \hat{N}_0 + \sum_j \hat{P}_j e^{s_j \hat{M}},$$

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 further estimated as the product of total initial abundance and the mean body mass in the first 7 days of the season. The estimation variance of total initial biomass was calculated using Taylor series approximations (the Delta method).

Within each probability model, normal and lognormal, model selection among the candidate processes was first done using the AIC. The AIC was considered to be conclusive when the difference

116 between the best model and the second best model was 3 or higher (more conservative than the value of 2  
117 suggested by Sakamoto et al., 1999). This means that there might be cases when a pair of models has an  
118 AIC difference higher than 3 but just the same the complete set of models is considered as tied, because  
119 the best model is not clearly superior to the second best model.

120 When the models for a season's data were tied, I selected one model by (i) inspecting optimization  
121 diagnostics such as gradients, standard deviation estimates, and correlations between estimates, and (ii) by  
122 consistency of the escapement biomass estimate with previous years. For example in 2004 the normal  
123 model with three perturbations obtained the same AIC as the normal model with four perturbations. The  
124 latter however predicted an escapement biomass so high as to be inconsistent with the biomass predicted  
125 by the five previous years where the AIC pointed to a unique model. The model with three perturbations  
126 did predict a biomass consistent with the five previous estimates. This model selection procedure still  
127 produced two selected models, one from each distribution. The best between these two was chosen by  
128 considering again the optimization diagnostics listed above and the consistency of the escapement biomass  
129 estimate. Any model where any of the parameter estimates was laying on a gradient greater than one, was  
130 discarded.

131 In seasons that generally showed a decline in catch through the season, modeling started by  
132 estimating a pure depletion model. The time step of the largest positive residual of this pure depletion  
133 model, or one time step before, was then tried as the time step of the perturbation in a 1-perturbation  
134 model. This process was carried on to models with more perturbations until the 4-perturbations model, or  
135 until models did not converge, or until there was no large positive residual to assign a perturbation to. In  
136 seasons that showed an overall increase in daily catch through the season, the pure depletion model and  
137 some lower order perturbation models could not possibly account for the catch data and thus model fit  
138 and selection started with higher order perturbation models.

139 Considering two distributions and five types of models, up to ten different version can be fit to any

given season'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 was calculated as

$$(6) \quad Q = \left| \frac{\max \{ \hat{\theta}_m - \hat{\theta}_n \}}{\text{med}(\{ \hat{\theta}_m \})} \right|$$

where  $m \neq n$  are indexes that run through the number of models fit on a given season, 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 fit, including those clearly inadequate, with a higher AIC, the  $Q$  measure of relative spread shows that the estimate of escapement biomass usually is fairly invariant to model specification, although in a few cases (5 out of 40 in our case) the estimates from different models can be spread wildly, with a  $Q$  measure over 10 or reaching as high as 88 (Table 1). Among the five parameters directly estimated by the model, 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 invariant to model choice (Table 1).

Table 2 shows the Akaike Information Criterion (AIC) values to select the best predictive model for each of the two choices of distribution models. For both distributions, in twelve out of twenty cases the AIC was conclusive. In the eight remaining cases for each distribution optimization diagnostics usually pointed to the model with less perturbations. Table 2 also shows the model finally selected when comparing the best normal and the best lognormal model using optimization diagnostics and serial consistency of the escapement biomass estimate. Half the selected models were normal and half lognormal. All model processes, pure depletion to up to four positive perturbations, are selected in at least

163 two seasons. When intersecting model selection by the AIC within a distribution and model selection by  
164 numerical diagnostics and escapement biomass consistency between distributions, there remained four  
165 years when the model selection was still inconclusive because of AIC ties (1990, 1992, 1998, 2009). Table 3  
166 shows that the spread of common parameters of model for those seasons is very limited. Further  
167 consideration of numerical diagnostics, especially the ability to estimate standard errors and reduce  
168 correlations between estimates, allowed to discern the model to keep for those seasons.

169         Statistics of the empirical distribution of Pearson correlation coefficients between parameter  
170 estimates of the models selected are shown in Table 4. The degree of parameter aliasing is low, with most  
171 pairwise correlations achieving values that cover both positive and negative domains, indicating no  
172 systematic trend. Some exceptions are the correlations for neighboring perturbations (P1 with P2, P2 with  
173 P3, and P3 with P4), which as expected fall in negative correlation domain. Since the main purpose of this  
174 work is study hyperstability and hyperdepletion, it is interesting to inspect the degree of correlation of the  
175 abundance response parameter  $\beta$  with all other parameters, to examine whether the regimes of  
176 hyperdepletion and hyperstability could be artifacts of model miss-specification. Table 4 shows that  $\beta$   
177 correlates weakly with other parameters in the model and that most of its pairwise correlations cover both  
178 positive and negative domain.

179         Graphical display of stock assessment results are presented for summer seasons of 2000, 2004 and  
180 2008 as examples. The model selected for the 2000 season was a 4-perturbations model combined with a  
181 normal distribution model whereas the model selected for the 2008 season was a pure depletion model  
182 combined with a lognormal distribution model (Table 2). The 2004 season was selected because it is an  
183 unusual season with a stepwise increase in observed catch, far away from a single depletion process. Figs. 2  
184 to 4 are standard prediction plots produced by the *CatDyn* R package. They are used to select good initial  
185 parameter values and to visually examine estimation results. In the 2000 summer season (Fig. 2) there were  
186 several spikes of catch that could not be explained by spikes in effort, so positive perturbations were put at



187 days 38, 68, 111, and 142 of the season. Simpler models with less perturbations were tried and the AIC  
188 clearly showed that the 4-perturbations (4P) model was the best for both observation models, normal and  
189 lognormal (Table 2). The 4P normal observation model was preferred over the 4P lognormal model  
190 because the former showed better numerical optimization diagnostics, namely smaller gradients and smaller  
191 standard errors of estimates. It is observed that setting positive perturbations at days 38 and 68 did not  
192 completely explain the spike of catch in those days. Conversely, setting perturbations at days 111 and 142  
193 completely brought the predictions in line with the observations. The day after the first spike, day 39, the  
194 catch was much lower than predicted creating a large negative residual. Currently the model cannot deal  
195 with large negative residuals so they are assumed to be extreme values. The distribution of residuals overall  
196 is symmetrical and the residual scatter-plot shows a random scatter with homogeneous variance. The Q-Q  
197 plot shows a good agreement with the normality hypothesis except for the large negative residual.

198         The 2004 season was the most unusual season of the series (Fig. 2). The AIC was conclusive in  
199 favor of the 4-Perturbation model for the lognormal distribution models whereas optimization diagnostics  
200 in the four models tried (Table 2) were equally poor, including all models failing to produce a correlation  
201 matrix due to a non positive-definite Hessian matrix. The estimated initial abundance was the lowest of the  
202 series but there were four perturbations of increasing abundance, until the fourth pulse, forty days after the  
203 start of the season, that was 22 higher than initial abundance. It is clear that in this season a pure depletion  
204 model cannot possibly account for the observed catch series. Residual plots of the 4-perturbations model  
205 show some departures from distributional assumptions, mostly by the model being unable to deal with two  
206 very low catch days. In this season the AIC was conclusive in favor of the 4-Perturbation model for the  
207 lognormal distribution models whereas optimization diagnostics .

208         In the summer season of 2008 (Fig. 2) there was an overall declining catch over the season  
209 suggesting a pure depletion process. However two spikes of catch can be observed at day 62 and 92 in the  
210 residual scatter-plot. The AIC of the normal model showed that a 2-perturbation (2P) model was best but

the AIC of the lognormal model did not support this model and pointed to a pure depletion process (0P) (Table 2). When comparing the detailed optimization results it was noted that the 2P-normal model was not able to produce standard error of any parameter estimates so the 0P-lognormal model was finally selected.

Table 5 shows the maximum likelihood estimates of squid abundance parameters. Estimated natural mortality rates  $M$  are much lower than the fixed value assumed up to the present (Roa-Ureta and Arkhipkin, 2007). However, this finding is in general not solid due to large standard errors associated to the estimates. Table 5 also shows that initial abundance  $N_0$  and the positive perturbations can be estimated with fairly high precision. This shows that fishing operational catch and effort data alone may contain substantial information about stock abundance. Note that the positive perturbations make an important part of a season's abundance, 26% on average; a range of 0% in seasons without perturbations to 96% in the unusual 2004 season. Table 6 shows the timing of events during each season. Notice how the season was shortened in 2003 allowing for a longer time for cohorts to recruit into the fishing grounds, and as an immediate consequence seasons with pure depletion started to be common.

Table 7 shows the maximum likelihood estimates of fishing operational parameters, scaling ( $k$ ), effort response ( $\alpha$ ) and abundance response ( $\beta$ ). Except for a few exceptions, these parameters are estimated with high precision. The scaling parameter is extremely variable inter-seasons, encompassing five orders of magnitude. This parameter is not the same as catchability. In these models catchability is a function of scaling  $k$ , abundance  $N$ , and the abundance response parameter  $\beta$ . The control of catch by effort is more linear than the control of catch by abundance. This is shown by the effort response parameter estimate ranging from roughly 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 Fig. 1 of Harley et al. 2001). There were 2 year-seasons with proportionality between catch and effort, 9 year-seasons with

235 saturability ( $\alpha < 1$ ), and 9 seasons with synergy ( $\alpha > 1$ ). Seventeen seasons showed hyperdepletion, and the  
236 3 remaining seasons, the seasons with the lowest escapement biomass in the series, showed hyperstability.

237 Fig. 3 shows the *post-boc* reconstruction of the serial information for stock abundance. Both  
238 numbers of squids and biomass show an earlier short period (3 years) of higher abundance, at close to 100  
239 thousand tonnes left after the seasons, or 5 to 6 billion squids recruiting at season's start and during the  
240 season. This period is followed by a lower abundance period lasting to the present, centered at about 40000  
241 tonnes of escapement biomass or about 2 billion squids recruiting. In this longer period of 17 seasons  
242 with lower abundance there were two seasons when the escapement biomass hit the management target of  
243 a minimum of 10 thousand tonnes.

244 Fig. 4 shows the observed relation between four measures of stock biomass and the abundance  
245 response parameter. For all four measures hyperdepletion is only present at the highest biomass.  
246 Conversely, for three measures hyperstability is only present at the lowest biomass. The plots also suggest a  
247 functional relation whose rate of change is steep at low biomass and that levels off at intermediate  
248 biomass. The shape of the relation also shows that the regime of proportionality will be rarely experienced.

## 249 Discussion

250 The *Loligo gahi* fishery of the Falkland Islands is hyperdepleted at high and intermediate  
251 abundance levels and is hyperstable at low abundance levels. Hyperstability has been thought to be caused  
252 by fleets targeting highly aggregated fish such as spawning aggregations (Hanchet et al. 2005, Erisman et al.  
253 2011). The degree of stock aggregation may certainly be dependent on the abundance level, as argued by  
254 Hanchet et al. (2005). These authors found little evidence of hyperstability in the relation between CPUE  
255 and abundance in the southern blue whiting fishery of New Zealand, in spite of two fleets targeting  
256 spawning aggregations; they actually found that CPUE was proportional to abundance. However they note  
257 a subtle departure from proportionality when examining an earlier period of low stock abundance and a  
258 later period of high stock abundance caused by a strong year class becoming available to the fleets in 1994.

259 Their Figure 2 shows that in the earlier period of low abundance the CPUE was hyperstable, in their words  
260 it 'resisted to decrease' even though the stock was decreasing. Conversely, in the later period of high  
261 abundance the CPUE was hyperdepleted, lagging behind the increase in abundance. At the risk of over  
262 interpreting their results their Figure 2 shows a further period of decreasing abundance, starting in 1999,  
263 where the CPUE becomes once again hyperstable. Their analysis can only produce an annually averaged  
264 estimate of the abundance response parameter  $\beta$  so regime shift from hyperdepletion to hyperstability and  
265 viceversa cannot be studied. However, in the light of my results we can hypothesize that Hanchet et al.  
266 have found proportionality because they averaged over regimes and what we are actually seeing in their  
267 Figure 2 is a situation similar to what I found in the *L. gahi* fishery of the Falkland Islands: regime shift  
268 from hyperstability to hyperdepletion and back, caused by corresponding changes in stock abundance from  
269 low to high and back and the response of fishermen to these variations in stock abundance.

270         Although the relation between stock abundance and the presence of hyperdepletion or  
271 hyperstability could be a general characteristic of fisheries, the precise abundance level at which a  
272 hyperstable fishery may become a hyperdepleted one could be highly specific of the conditions under  
273 which a fishery operates. In the case of the *L. gahi* fishery of the Falkland Islands the hyperdepleted regime  
274 is far more prevalent and the abundance level at which the fishery shifts to hyperstability is quite low. From  
275 direct information from skippers and from our observations at sea we know that the seabed at the  
276 Beauchene fishing grounds is covered to a large degree by rocky bottoms that trawling gear are unable to  
277 sweep. We show a map of these rocky seabed areas in Figure 2 of Roa-Ureta and Arkhipkin (2007). From  
278 anecdotal reports received by this author skippers believe that squids often 'hide' in these areas and that  
279 this is a fundamental aspect of the stock's sustainability. Hilborn and Walters (1992) have hypothesized that  
280 a possible mechanism for hyperdepletion is the existence of cryptic habitat where the stock makes itself  
281 unavailable. Thus the *L. gahi* fishery may have a low abundance threshold to switch from the low-  
282 abundance hyperstable regime to the intermediate- and high-abundance hyperdepleted regime because of

283 the presence of cryptic habitat. In this interpretation these rocky untrawable bottoms in the Beauchene  
284 fishing grounds act like natural marine protected areas (MPAs). A corollary is that if the current interest in  
285 MPAs materializes into fishery management practice then the stocks for which those MPAs are effective  
286 will be characterized by a low-abundance threshold to switch from hyperstability to hyperdepletion.

287         Eighteen selected models out of 20 *Loligo gahi* seasons studied in this work showed perturbations  
288 to a pure depletion process by additions or pulses of increased abundance. In general this can be  
289 interpreted in two ways: there were waves of immigration into the fishing grounds or the fleet expanded its  
290 area of operation making new parts of the stock available. For the particular application considered in this  
291 paper only the first explanation is plausible because all the assessments carried out concern a very specific  
292 area in the southern part of the Falklands continental shelf (see Fig. 2 in Roa-Ureta and Arkhipkin, 2007).  
293 In fact it is typical that this fleet fishes exclusively in the Beauchene area during the summer season,  
294 whereas during the winter season (not studied in this work) it covers a wider area, expanding into the  
295 north-eastern part of the Falklands continental shelf. Therefore my results indicate that a squid cohort is  
296 normally composed of a group of waves of squids leaving the nursery grounds at different times during  
297 the same season. Having said that, it is also true that in 15 out of the 18 seasons with perturbations, initial  
298 abundance  $N_0$  was higher than the sum of all in-season positive perturbations, indicating that generally the  
299 season is well timed to harvest squid that have already left the inshore nursery grounds and had come *en*  
300 *masse* to the feeding and fishing grounds, especially after 2003 when the season start was delayed by one  
301 month.

302         Natural mortality estimates obtained in this work are much lower than the previous fixed value  
303 assumed for the stock and obtained from Hewitt & Hoenig's (2005) empirical relation between longevity  
304 and natural mortality. However, after understanding the nature of both estimates we observe that they  
305 might be consistent. This is because Hewitt and Hoenig's life-history estimate provides a natural mortality  
306 rate averaged over the lifespan, whereas the natural mortality rate estimated here is the rate experienced

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

312 Harley et al. (2001, p. 1765) advice us to move on and incorporate abundance response into stock  
313 assessment models. In models of the rapid fishing operational dynamics such as the models presented here  
314 this parameter can be estimated with precision (see standard errors of  $\beta$  in Table 6) in great part because  
315 the mathematical structure of the model allows for easy calculation of gradients of the support function  
316 with respect to  $\beta$ . Thus numerical methods such as finite differences easily find the maximum support  
317 along the  $\beta$  dimension and in the second stage compute the curvature about the maximum. The same  
318 situation occurs with the effort response parameter  $\alpha$ . In the case of population dynamics models it is  
319 usually understood that introducing nonlinear abundance response entails introducing  $\beta$  in the relation  
320 between stock abundance and any indexes from CPUE standardization that are available (e.g. Walters,  
321 2003; Hanchet et al. 2005). However, abundance response is a hypothesis for the relation between catch  
322 rates and stock abundance so it would be coherent to include it in any other catch equation of the stock  
323 assessment model. A generalization of Baranov catch equation allows direct introduction of nonlinear  
324 abundance response into population dynamics stock assessment models. This is shown as follows. Under  
325 the hypothesis for the catch rate of this work (see eq. 1) the rate of catch that allows for nonlinear  
326 abundance response is

327 (7) 
$$\frac{dC}{dt} = q E^{\alpha} N^{\beta}$$

328 It follows that in Baranov's hypothesis -where the fishing process enters via fishing mortality- the rate of  
329 catch that allows for nonlinear (power) abundance response is

330 (8)  $\frac{dC}{dt} = F N^\beta$

331 whose solution is

332 (9)  $C(t) = \frac{F}{\beta(F+M)} (1 - e^{-(F+M)\beta t}) N_0^\beta$  .

333 This shows that not introducing this structural change into stock assessment models that rely on fish  
 334 population dynamics when the fleet-stock system shows hyperstability ( $\beta < 1$ ) not only artificially inflates  
 335 the estimation of abundance but also results in underestimation of total mortality rate,  $F + M$ . Conversely,  
 336 when the system exhibits hyperdepletion total mortality rate is overestimated.

337 Brodziak and Rosenberg (1993) developed a generalization of Leslie-DeLury depletion model  
 338 that accounted for in-season pulses of migration to the inshore stock of *Loligo pealei* in the north-west  
 339 Atlantic Ocean. Their modeling approach relates to the class of models shown here in that both  
 340 approaches are generalizations of depletion models to open populations. In the case of Brodziak and  
 341 Rosenberg's approach the openness of the population is modeled by relying on catch rate observations  
 342 inside and outside the fishing grounds, whereas my models are supported by data exclusively from inside  
 343 the fishing grounds. Moreover, their model is a multiple linear regression model while the models  
 344 presented here account for non-linearities such as effort and abundance nonlinear response. Thus my  
 345 models are less demanding in terms of data and are more general. Nevertheless, Brodziak and Rosenberg's  
 346 model is a precursor of the current approach because these authors approached the construction of  
 347 CPUE models by recognizing the rapid dynamic nature of fluxes into and out of fishing grounds. This  
 348 recognition is important to capture the fishing operational dynamics of fleets interacting with stocks.

349 Most stock assessment models such as statistical catch-at-age, XSA, VPA, length-structured  
 350 models, biomass dynamics models, and delay-difference models, do not concern themselves directly with  
 351 the operational fishing process. Instead, they use data from fisheries to study fish population dynamics.  
 352 Fig. 7 in Quinn (2003, p. 378) summarizes this as “the current philosophy of fisheries modeling”. This is

of course a valid and useful approach but this work shows that there is more to the modeling of fisheries and the assessment of fish stocks than fish population dynamics.

## Appendix

To carry out the expansion of the abundance latent predictor assume for simplicity a closed system, where abundance can only decay during the fishing season due to fishing and natural mortality, and a linear relation between catch rate and its predictor, effort and abundance. Then at any given time the true number of fish  $N(t)$  is the initial number that have survived natural mortality minus those that have been caught by fishermen and that would have survived natural mortality had they been not caught by fishermen,

$$(A1) \quad C(t) = q \int E(t) N(t) dt = q E(t) \int_0^t \left( N_0 e^{-Mt} - \int_0^{t-\delta t} C(\tau) e^{-M(t-\delta t)} d\tau \right) dt$$

for a very small  $\delta t$ ,  $M$  the instantaneous natural mortality rate (assumed the same for all  $0 \leq t \leq \tau$ ), and  $N_0$  the initial abundance in numbers. The observations of catch and effort are actually discrete, recorded by time step such as day or week. The discrete model corresponding to eq. (2) is the Leslie-Davies-Chapman depletion model (Leslie and Davies, 1939; Chapman, 1974; Rosenberg et al., 1990; McAllister et al. 2004; Roa-Ureta and Arkhipkin 2007),

$$(A2) \quad C_t = q E_t N_t e^{-M/2} = q E_t \left( N_0 e^{-Mt} - e^{-M/2} \sum_{i < t} C_i e^{-(t-i-1)M} \right) e^{-M/2}$$

where the catch is assumed to occur exactly at mid time step. To drop the assumption of proportionality adopt instead a power model for both effort and abundance. To drop the assumption of a closed population introduce into the expanded abundance term a further additive term accounting for episodic pulses of abundance. Then eq. (2) follows.

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