Estimation of the spawning stock and recruitment relationship of *Octopus vulgaris* in Asturias (Bay of Biscay) with generalized depletion models: implications for the applicability of MSY

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May 19, 2021

Abstract

We developed a new type of generalized depletion model adapted to the rapid life cycle of *Octopus vulgaris* and the data collection framework put in place in its co-managed small-scale fishery (SSF) in Asturias, northwest Spain. The model uses weekly data from 19 seasons to estimate annual recruitment and female spawners emigration out of the vulnerable stock to attend to their broods. The matched annual spawners-recruitment (SR) magnitudes are then used as observations in a non-Bayesian hierarchical inference framework. The Shepherd SR model was selected among three alternatives. The stock has a high degree of density-dependence, leading to overcompensation. The estimated SR model has an unstable equilibrium point, driving the stock to deterministic cyclic fluctuations under small disturbances. Under those conditions the maximum sustainable yield (MSY) is not applicable, lending further credence to Sidney Holt's opposition to the MSY as a basis for the elaboration of fishery management objectives, with potentially wide relevance to the management of SSF and cephalopod fisheries. We argue that harvest rates based on mean latent productivity, a concept that includes the MSY as a special case, are more adequate and sustainable for fluctuating stocks.

Keywords: stock-recruitment; cephalopod fisheries; small-scale fisheries; hierarchical models; Asturias

1 Introduction

Holt (2020) summarized his opposition to maximum sustainable yield (MSY) as an excessive target yield for fisheries mainly on the grounds of cost-benefit considerations for fishers as economic agents, while also pointing out other benefits of a lower target yield including less need for government subsidies, less by-catch and less harm to ecosystems (Holt and Raicevich, 2018). He further doubted that stocks would produce a constant surplus even at constant abundance because of changes in biological rates (Holt, 2011). Related research in mathematical ecology shows that even stable biological rates under constant environments may lead to widely varying abundance under certain conditions

(May, 1975). The MSY is the constant surplus that occurs when the stock is at the size that maximizes the population growth rate. Fishing that removes the MSY would maintain the stock stable at that level of abundance. Many large stocks may behave so because of demographic inertia creating continuity, especially when they have several cohorts in the age structure. Semelparous populations though, with their weakly-overlapping generations, may behave differently because these populations approximate discrete dynamic nonlinear systems. These may exhibit rich dynamics ranging from stable equilibrium points, to which the MSY concept applies, to cyclic oscillations and chaotic regimes (May, 1975), where the MSY does not apply because the population growth rate, and therefore the yield, are not constant, fluctuating with oscillations in abundance.

MSY as a target yield or as a generator of reference points or proxies is commonly invoked in the management of cephalopod stocks (Quetglas *et al.*, 2015; Ren and Liu, 2020; Sauer *et al.*, 2019; Roa-Ureta *et al.*, 2020; Wang *et al.*, 2020) and small-scale fisheries (SSF) (Giron-Nava *et al.*, 2018; Pomeroy *et al.*, 2009; Gough *et al.*, 2020; Roa-Ureta *et al.*, 2020), although there is general scarcity of stock assessment studies in both cephalopods (Quetglas *et al.*, 2015) and SSF (Lleonart and Maynou, 2003) relative to fish and large-scale fisheries. Cephalopod fisheries and SSF present special challenges to management and stock assessment because of life history traits, data-poor condition, large number of small operators, diverse social and geographic attributes and multiple small stocks (Berkes *et al.*, 2001; Berkes, 2003; Hilborn and Hilborn, 2012; Maravelias *et al.*, 2018). A recent review of cephalopod stock assessment and management (Arkhipkin *et al.*, 2020) recommended innovative depletion models running at rapid time steps because these can handle rapid life histories, short lifespans, and single-cohort population compositions, all important aspects of cephalopod biology. Depletion models are also less data-demanding because they do not require samples of the biological composition or fishery-independent data and so are useful for small-scale data-poor fisheries (Roa-Ureta, 2015; Roa-Ureta *et al.*, 2015, 2019, 2020).

The octopus fishery in Asturias is an SSF that has been managed through a participatory, co-management approach since 2001 (Fernández-Rueda and García-Flórez, 2007). This is a form of governance incorporating local community participation (Basurto *et al.*, 2017; FAO, 2015; Courtney *et al.*, 2020; Roa-Ureta *et al.*, 2020). In Asturias, the resulting management framework was adapted to the fishers' needs, leading to an orderly and agreed upon system of operation and data collection. In 2016, this fishery became the first octopus fishery certified by the Marine Stewardship Council (MSC), which led to increased fishers income (Fernández Sánchez *et al.*, 2020). However, its certification status was conditional on completing studies of octopus abundance, productivity and exploitation status for the implementation of harvest control rules, since these were not available at the time of certification. One aspect of the participatory approach was comprehensive sharing of fishing operational data at the finest time resolution by fishers as willing participators in co-management. These high temporal resolution data offer a source of information on stock status that depletion models can harvest efficiently, offsetting the lack of biological composition and fishing-independent data typical of data-poor and data-limited SSF to a certain extent. In addition to sharing data, management determined a season of operation that included both a recruitment pulse and the brooding emigration of female spawners (Fernández-Rueda and García-Flórez, 2007). Some versions of generalized depletion models, those applied to eel elver fisheries, include immigration and emigration pulses (Lin *et al.*, 2017; Lin and Tzeng, 2018; Lin and Jessop, 2020). Thus the fishery for octopus in Asturias provides an opportunity to develop new depletion models that estimate both recruitment and female spawners abundance.

The spawning abundance and recruitment (SR) relationship is a cornerstone of marine population dynamics and stock assessment. In semelparous species such as *O. vulgaris*, the SR relationship plays a conceptually analogous role to surplus production models, with production of recruits replacing productivity and spawners' abundance replacing biomass (Quinn and Deriso, 1999, p. 122). From an SR relationship, MSY (in numbers) occurs at the maximum vertical distance between the replacement line and the SR curve (Quinn and Deriso, 1999, Fig. 3.19). Unfortunately, in addition to the difficulty in determining the SR relationship for stock assessment in general (Hilborn and Walters, 1992, p. 241) cephalopods in particular have weak SR relationships and are strongly impacted by environmental conditions (Arkhipkin *et al.*, 2020). Agnew *et al.* (2000) observed evidence of density-dependence in the SR relationship of the Patagonian squid fished in the Falkland Islands though a re-analysis with different estimates for the same stock obtained a noisy linear trend instead (Roa-Ureta, 2012). Otero *et al.* (2008) provided indirect evidence for density-dependent effects in *O. vulgaris* inhabiting the northern boundary of the Canary-Iberian upwelling system. Here we use the results of the new depletion models fitted to 19 seasons of the *O. vulgaris* SSF in Asturias to estimate the SR relationship, providing direct evidence of substantial density-dependence.

These findings have implications for the use of the MSY as a reference point for sustainable fishing rates in cephalopod fisheries and SSF more generally. In ICES (2020, section 2.3) we proposed the mean latent productivity, a concept that includes the MSY as a special case, as a more adequate reference point for determining harvest rates from the *O. vulgaris* stock in Asturias. Here we discuss these implications in the context of Sidney Holt's long-held opposition to the MSY, suggesting a further reason why the MSY may not be adequate in general: many stocks may tend to undergo deterministic fluctuations under fishing removals.

2 Materials and Methods

2.1 The fishery and data collection

A description of the co-management system, in place since 2000-2001, and results of biological analyses, are presented in Fernández-Rueda and García-Flórez (2007). The most important management measures during this period are: limiting entry to licensed boats from any of eight legally-recognized fishers' associations, seasonal closures, gear and boat regulations, minimum landing octopus weight, and a maximum catch per boat-season. This SSF is a single-species fishery operated by a varying number of authorized boats, currently around 40. Fishing is conducted with baited traps during a season that since 2004-2005 extends between December and July, and previously it started in November (2004-2005), January (2003, 2004) or December and ended in May (2004-2005), August (2000-2001, 2001-2002) or July. Most boats operate with 2 fishers (65% of all fishing trips as average over the last three seasons) though some had a single fisher (9%) and others carry three fishers (25%). On any given fishing trip, a maximum of 125 traps are lifted per fisher in 1-fisher and 2-fishers boats while a total maximum of 350 lifts per boat applies to boats with three fishers. These traps usually stay at sea, are lifted in the morning of a fishing day, and in good days fishers may lift the traps a second time. For these fishers, good days are days with good catch and good weather, since weather is a major factor for small boats. The total area of operation covers the western half of the coast of Asturias and has been estimated in the range of 228 to 397 km^2, with the lower bound coming from geographic data of radio-tagged boats and the upper bound from the total area between the coast line and the 50 m isobath. This area is divided into dozens of fishing grounds with varying extension, located between the coastline and 50-m depth isobath in south-western Bay of Biscay (Fig. 1). Although the magnitude of by-catch by other fleets has not been evaluated, sales data that can be traced to specific boats reveal that boats operating with gears other than the traps land very little octopus. A minimum landing weight of 1 kg per individual octopus has also been agreed upon in the co-management system regulations. When traps capture smaller octopuses they are returned to sea alive and in good conditions, as witnessed by scientific observers. In other trap fisheries, discarded octopus have also been observed returning to sea in good condition (Conners and Levine, 2016; Conrath and Sisson, 2018). Furthermore, the biological sampling program yielding weight data supports the notion that fishers are in general complying with the minimum landing weight regulation (Fig. 2) although under-sized octopus in the landings have been observed occasionally.

During the period of co-management (2000-2001 to 2018-2019), the data collection system included a census of daily catch in weight and fishing effort measured as the number of boats operating on any single day. The number of fishers per boat has just become available in the last three fishing seasons so we could not use the number of fishers or number of trap lifts per day as fishing effort. In addition to these census data, biological samples are taken on some days of the season. For the purposes of this work, biological samples provide data of mean individual weight in the catch to transform catch in weight to catch in numbers. Considering the extension of the season (normally 7 months) and the sparsity of biological sampling, we grouped the raw data into weekly time steps to fit intra-annual generalized depletion models to each season's data. Fishing effort was the total number of fishing days by all boats operating in any given week. The complete raw data available for modelling are shown in Fig. 2. During the first few years (2000-2001 to 2007-2008), total annual landings averaged 180 tons and total annual effort normally exceeded 3000 days of fishing, but later (2008-2009 to 2018-2019) landings decreased, averaging 102 tons, and effort decreased as well to less than 2000 days (Supplementary Fig. SM1).

2.2 Weekly mean weight model

One important shortcoming of the data was that the biological sampling of mean weight did not occur in all weeks of the 19 seasons and yet individual weight data are necessary to transform from catch in weight to catch in numbers in all weeks (Supplementary Table SM1). As in previous cases with missing biological sampling (Roa-Ureta, 2015; Roa-Ureta *et al.*, 2019, 2020) the missing mean individual weight was replaced with predictions from an accessory model fit with the available data. First, we fitted a simple model of mean weight change through the weeks of the year with a cubic spline smoother, function *loess* in R 3.6.1 (R Core Team, 2019). Little inter-annual variability was observed in the seasonal pattern of the mean individual weight (Fig. 2) and this pattern was similar to results presented in Fernández-Rueda and García-Flórez (2007). Thus we used the pooled data from all 19 seasons to estimate the weekly mean weight model (n=275). In the fit of this accessory model we created a predictor variable spanning the range of week numbers in a year (1 to 53), then we used the data to fit the smoother with a span parameter equal to 1 (equivalent to using the data from all weeks to predict the model at each week), and finally to predict the expected mean weight and its standard error for all weeks within a season (Supplementary Fig. SM2). Secondly, we predicted the mean weight for each week in each season from a truncated normal distribution defined by the predicted weekly mean weight ± 2 standard errors using R package Runuran (Leydold and Hörmann, 2019) (Supplementary Fig. SM2). In this manner we obtained a complete vector of mean weight matching the catch and effort data while introducing noise due to sampling variation in the biological data.

2.3 Generalized depletion model with spawning emigration

During the fishing season, two main events occur in the fishing dynamics of the Asturian octopus that affect the stock abundance that is vulnerable to fishers. Firstly, a cohort of young octopuses experiencing rapid growth become vulnerable to fishing by reaching the minimum size (1 kg) that the fishers can retain. This is a recruitment pulse, i.e. a positive pulse of abundance. Secondly, at a later time, females that have mated and spawned become no longer vulnerable to fishing because they stop searching for food to spend all their time caring for their eggs in dens (Garci *et al.*, 2015). Although traps continue to be deployed in areas where spawning females are searching for dens, these females almost never lay their eggs in traps because they are unstable, being hauled every day by fishers. Some other traps that remain at sea untouched for longer times occasionally catch females with eggs, but this type of gear is not used in Asturias. Therefore, from the point of view of the fishing dynamics, female spawners constitute emigration, a negative pulse of abundance whose magnitude is the size of the female spawning stock. This latter negative pulse is apparent in Fernández-Rueda and García-Flórez (2007, Tables 1, 2), who showed a decreasing proportion of females in the catch and an increasing proportion of sexually mature females towards the end of the season..

Given these specific features, we developed a new generalized depletion model to fit to the data from each fishing season separately. It includes immigration and emigration like a previous model developed for the glass eel fishery of Taiwanese estuaries (Lin *et al.*, 2017) but differs in an important aspect. In the case of the glass eel fishery, all surviving immigrants from any pulse of recruitment leave the estuary at the time of emigration (they are in transit), and therefore the magnitude of each emigration pulse is completely predetermined by other parameters or data in the model. Conversely, in the present case the magnitude of the emigration pulse is not predetermined because it involves an unknown fraction of the stock, the mated female fraction. Thus, in the Asturian octopus SSF the magnitude of the emigration pulse is a new free parameter in the model to be estimated from the data.

Given those features, in any fishing season the total catch at week t can be modelled as

$$\begin{aligned} C_t &= kE_t^{\alpha} N_t^{\beta} = kE_t^{\alpha} m f_t(M, N_0, C_{i<t}, R, S) \\ &= kE_t^{\alpha} m \left(N_0 e^{-Mt} - m \left[\sum_{i=1}^{i=t-1} C_{i,i} e^{-M(t-i-1)} \right] + \sum_{j=1}^{j=u} I_j R_j e^{-M(t-\tau_j)} - \sum_{l=1}^{l=v} J_l S_l e^{-M(t-\nu_l)} \right)^{\beta} . \end{aligned} \tag{1}$$

where $m = exp(-M/2)$ is an adjustment that makes all catch happen instantaneously at mid-week. All variables and parameters in this model are described in Table 1. Essentially, this model says that the expected catch on any week of the season is determined by a proportionality constant (the scaling k) and two predictor variables, the fishing effort E, which is observed exactly, and the stock abundance N, which is latent. Both predictors are modulated by power parameters that measure non-linear effects, the effort response α and the abundance response β. These are the continuum from effort saturation ($\alpha < 1$) through proportionality ($\alpha \approx 1$) to synergy ($\alpha > 1$) and the continuum from abundance hyperstability ($\beta < 1$) through proportionalyty ($\beta \approx 1$) to hyperdepletion ($\beta > 1$). The latent predictor N is made manifest with Pope's recursive formula plus the effect of recruitment minus the effect of the female spawning emigration, which kick-in at different weeks as determined by indicator variables I and J, which are zero before the event (either recruitment or spawning emigration) and 1 afterwards. There might be a range of time steps across which either recruitment or spawning female emigration might take place. Episodes spread over several time steps are less precise because of fewer degrees of freedom for optimization. The timing of recruitment and spawning emigration events are also unknown parameters. In these models, the number and timing of recruitment and spawning emigration events are non-differentiable free parameters. To identify these parameters, the model is run with alternative values. The values that maximize the likelihood (when the likelihood model is comparable across model fits) and/or are best according to other criteria (see below), are chosen. In this work we fitted models with one or two recruitment and spawning emigration events and four options for the timing of these events. When fitting models with two recruitment or spawning events the timings were put on adjacent weeks (t and t+1), thus assuming an extended event taking place over two weeks. Good candidate values for the timings were determined by examination of the non-parametric catch spike statistic, defined as (Roa-Ureta, 2015),

$$Spike_t = 10\left(\frac{\chi_t}{max(\chi_t)} - \frac{E_t}{max(E_t)}\right) \tag{2}$$

where χ is the observed catch. It highlights time steps with excessively high or excessively low catch for the effort at that time step. Thus large positive spikes suggest recruitment and large negative spikes suggest emigration.

The model in Eq. 1 is the deterministic process for the expected catch under the model. The statistical framework is completed by taking the observed catch as a random variable whose mean time series is Eq. 1 with realized time series coming from any of a number of distributions. These distributions define the likelihood function that is to be maximised. Among these, the normal and lognormal distribution have simple formulas for the adjusted profile likelihood, an approximation that eliminates the dispersion parameter from the estimation problem. A total of six alternative likelihood functions or approximations were employed in the estimation of parameters. These are all listed in Roa-Ureta *et al.* (2019, Table 2).

The new generalized depletion model was programmed in a new version of the R package CatDyn (Roa-Ureta, 2019). In CatDyn all parameters are free parameters to be estimated and none of them can be fixed at arbitrary values. The latest version also estimates fishing mortality per time step by using a numerical resolution (R function *uniroot*) of Baranov's catch equation from estimates of abundance, natural mortality and catch per time step. CatDyn depends on package optimx (Nash and Varadhan, 2011), which makes it simple to call several numerical optimization routines as alternatives to minimise the negative log-likelihood. In this work we tried the spg, CG, Nelder-Mead and BFGS routines because these have yielded reliable results in previous applications. The combination of options for number of recruitment and spawning emigration events, timing of those events, likelihood function, and numerical optimization routine led to fitting dozens of alternative model settings for each season of data. Some of these model fits did not pass built-in numerical quality control checks. From the remaining fits, we selected the best model by employing numerical, biological and statistical criteria. Firstly, all fits returning a numerical gradient higher than 1 for any parameter were eliminated. This is commonly employed in stock assessment (Lee *et al.*, 2011; Anderson *et al.*, 2014; Hurtado-Ferro *et al.*, 2015; Thorson *et al.*, 2015). Secondly, all fits that produced a biologically unrealistic estimate of weekly natural mortality ($M > 0.1\ week^{-1}$ or $M < 0.01\ week^{-1}$) were also eliminated. In these models, unrealistic natural mortality estimates are connected with solutions that also return unrealistic abundance estimates. Thirdly, from the short list of model fits, the best fit was selected as the one with the lowest standard errors and with histogram of correlation coefficients between parameter estimates more concentrated around zero. The histogram of correlation coefficients presents the distribution of pairwise correlations between parameter estimates. It is desirable that these correlations are as far away from 1 or -1 as possible because that means that each parameter was a necessary component of the model. Information theory model selection methods such as the Akaike Information Criterion (AIC) are not useful at this stage because the models to select from have been fitted with different likelihood functions or approximations to the likelihood.

2.4 Inference on stock-recruitment

In the dynamics of populations with non-overlapping generations, all individuals alive in the next time step are recruits. If the octopus population had completely non-overlapping generations, then recruitment from generalized depletion models would be quantified as the sum of the N_0 estimate and the back-calculated (to the first week of the fishing season) in-season pulse of recruitment R. Under this scenario, the in-season recruitment pulse R would be interpreted as a second wave of recruitment from the same cohort. However, it is highly likely that some octopuses from last year cohort are alive at the time of the start of the new fishing season, when N_0 is estimated. Lifespan of *O. vulgaris* from several regions in the Atlantic frequently exceed one year and may reach a maximum of nearly two years (Jereb *et al.*, 2015; Katsanevakis and Verriopoulos, 2006). Therefore, the safest assumption is that the N_0 estimate is composed of both new recruits as well as surviving octopuses from the previous cohort. It is for this reason that in order to have a clean recruitment magnitude of year $y+1$ to match with female spawning abundance in year y, we used recruitment estimates from the in-season positive pulses exclusively, which almost surely were fully composed of new recruits. This means that our recruitment estimates probably are under-estimates and consequently, the MSY from the SR model would also be an under-estimate. From a management point of view, under-estimating MSY entails a conservative stance. Nevertheless, we fitted SR models using N_0 plus the back-calculated recruitment pulse and results are reported in the Supplementary Data (see section 3.2 below).

Graphical examination of the relation between $\hat{S}_y$ and $\hat{R}_{y+1}$ indicated that there was strong overcompensation. Therefore, we fitted three stock-recruitment models with overcompensation: 2-parameters Ricker's (Ricker, 1954),

$$R_{y+1} = S_y e^{a\left(1-\frac{S_y}{S_R}\right)}, \quad a > 0, S_R > 0 \tag{3}$$

3-parameters Shepherd's (Shepherd, 1982),

$$R_{y+1} = \frac{bS_y}{\left(1 + \left(\frac{S_y}{Q}\right)^{\gamma}\right)}, \quad b > 0, Q > 0, \gamma > 0 \tag{4}$$

and 3-parameters Saila-Lorda's (Saila *et al.*, 1988),

$$R_{y+1} = S_y^{\gamma} e^{a\left(1-\frac{S_y}{S_R}\right)}, \quad a > 0, S_R > 0, \gamma > 0 \tag{5}$$

A comparative analysis of these three models as applied to flatfish can be found in Iles (1994).

From a statistical point of view, these stock-recruitment models are nonlinear response-predictor models with the complication that both the predictor and the response are random variables. This problem has been recognized in the context of stock-recruitment modelling by Quinn and Deriso (1999, Chapter 3, p. 108), calling it the measurement error approach although no specific solution was offered. In the statistical literature this topic is called errors-in-variable (EIV) regression and our case here corresponds to a non-linear, non-classical errors EIV with continuous random predictor. We develop here a new solution within the non-Bayesian hierarchical modelling framework based on hybrid likelihood functions (Roa-Ureta, 2010). First, note that the observations, the estimates $\hat{S}_y$ and $\hat{R}_{y+1}$, form a 36-dimensional vector $\hat{\boldsymbol{\mu}} = [\hat{S}_{01}, \hat{R}_{02}, \hat{S}_{02}, \hat{R}_{03}, \hat{S}_{03}, ..., \hat{R}_{19}]$ where the sub-index shows the last two digits of the main year of all 19 fishing seasons, all coming from the fits of the 19 best intra-annual generalized depletion models (Eq. 1). Second, note that $\hat{R}_y$ and $\hat{S}_y$ are obtained from the same model fit, and therefore from the hierarchical inference point of view they are bivariate random variables. Thus, the covariance matrix for the complete observations is block-diagonal as follows,

$$\hat{\mathbf{\Sigma}}_{SR} = \begin{bmatrix} \Sigma_{\hat{S}_{01}} & 0 & 0 & 0 & 0 & \cdot & 0 \\ 0 & \Sigma_{\hat{R}_{02}} & \Sigma_{\hat{S}_{02},\hat{R}_{02}} & 0 & 0 & \cdot & 0 \\ 0 & \Sigma_{\hat{S}_{02},\hat{R}_{02}} & \Sigma_{\hat{S}_{02}} & 0 & 0 & \cdot & 0 \\ 0 & 0 & 0 & \Sigma_{\hat{R}_{03}} & \Sigma_{\hat{S}_{03},\hat{R}_{03}} & \cdot & 0 \\ 0 & 0 & 0 & \Sigma_{\hat{S}_{03},\hat{R}_{03}} & \Sigma_{\hat{S}_{03}} & \cdot & 0 \\ \cdot & \cdot & \cdot & \cdot & \cdot & \cdot & \cdot \\ 0 & 0 & 0 & 0 & 0 & 0 & \Sigma_{\hat{R}_{19}} \end{bmatrix} \tag{6}$$

Conceptually, our solution treats the sequence $S_y \rightarrow R_{y+1} \rightarrow S_{y+1} \rightarrow R_{y+2} \rightarrow S_{y+3} \rightarrow \ \ldots$ as a Markov chain with infinitely many state spaces, where the steps from S_y to R_{y+1} are controlled by Eq. 3, Eq. 4 or Eq. 5, which are of interest, and the steps from R_y to S_y are controlled by another model which is of no interest. In fact, graphical examination of the relation between $\hat{R}_y$ and $\hat{S}_y$ suggest that an adequate dummy model for $S_y = f(R_Y)$ is a constant, the average $\hat{S}_y$. Third, considering asymptotic properties of maximum likelihood estimates $\hat{R}_y$ and $\hat{S}_y$, it is reasonable to assume that the vector $\hat{\boldsymbol{\mu}}$ is multivariate normal. From these considerations, the hybrid (marginal-estimated) likelihood function for the observations $\hat{\boldsymbol{\mu}}$ is

$$\begin{gathered} L_{HL}(\boldsymbol{\theta}_{SR}|\hat{\boldsymbol{\mu}}) \propto |\hat{\mathbf{\Sigma}}_{SR}|^{-1/2} exp\left[-\frac{1}{2}(\hat{\boldsymbol{\mu}} - \boldsymbol{\mu}(\boldsymbol{\theta}_{SR}))^T \hat{\mathbf{\Sigma}}_{SR}^{-1}(\hat{\boldsymbol{\mu}} - \boldsymbol{\mu}(\boldsymbol{\theta}_{SR}))\right], \\ \boldsymbol{\theta}_{SR} = [a, S_R, \bar{S}_y] \quad \vee \quad [b, Q, \gamma, \bar{S}_y] \end{gathered} \tag{7}$$

where $\hat{\mathbf{\Sigma}}_{SR}$ replaces the unknown covariance matrix of $\hat{\boldsymbol{\mu}}$.

The statistical models described from Eq. 3-7 were programmed in ADMB-IDE (Magnusson, 2009; Fournier *et al.*, 2012). Some parameters were estimated under unbounded optimization while others were fit within bounds. Acceptable solutions had estimates from bounded optimization falling within the interval, not at any of its bounds. Templates for Shepherd model and data file, including the covariance matrix, are shown in Supplementary Fig. SM3 and SM4.

To quantify the stability properties of the best SR model fitted to spawning and recruitment abundance we conducted two further calculations. Firstly, we estimated the largest Lyapunov exponent of the SR dynamics. This parameter is a measure of the rate of divergence of trajectories of dynamical systems under small separations of initial position. When the parameter is >0, the map is chaotic to a certain degree. This was done with R package DChaos (Sandubete and Escot, 2019). We re-programmed the *logistic.ts* function in the package to replace the simple logistic map by the SR map selected in this study, including the specific parameter estimates obtained here but with abundance trajectories confined to the unit interval. Secondly, the dynamics following small perturbations from equilibrium points were mapped using Verlhust diagrams (also known as cobweb plots) to illustrate the kind of behaviour that could be expected from fishing removals. Using the selected SR model we predicted next year's recruitment with this year's spawning abundance. In the time between recruitment and spawning of the same year, we set a 2/3 survival rate, which was the mean rate observed in the 19 seasons. The stock was started 5% under the spawning abundance at replacement and 5% under the spawning abundance at the MSY and was followed over 19 generations. These starting abundances were selected because they represented small perturbations away from interesting and potentially stable points, namely the spawning abundance that produces the MSY and the equilibrium spawning abundance, so if the population did not return to these potentially stable points under those perturbations then it would not return under most perturbations. On the other hand, if the system were stable, starting at 5% under the spawning abundance at replacement, it would return to the equilibrium point, which is the point of crossing of the replacement diagonal and SR curve, forming a cobweb structure with the center at the crossing.

3 Results

3.1 Intra-annual generalized depletion models

We run 90 generalized depletion model versions in 15 out of 19 fishing seasons; in the rest, the number of version runs ranged from 36 in 2003-2004 to 408 in 2001-2002 (Supplementary Table SM2). Amongst these, none of the versions with more than one recruitment week and one spawning emigration week passed the basic numerical requirements in CatDyn so these were not considered further. After the selection criteria of biological realism, statistical quality and numerical diagnostics, a short list of between 2 to 14 fits for each season were finally considered. This short list contained models that, within each season, did not differ much in parameter estimates (Supplementary Table SM3). Tables of these estimates for the 19 selected models, as well as plots demonstrating the close fit of the model to the data, are shown in Supplementary Figs. SM5 to SM23 and Table SM4. These estimates had moderately low correlations in 9 out of 19 seasons (Supplementary Fig. SM24).

Further insights into how identifiable these depletion models are can be gleaned by examining the fit of the models to data from Season 2001-2002. This was the most difficult season to model, with 408 model versions fitted (Supplementary Table SM2). As shown in Fig. 3, top-right panel, six weeks were tried as the timing of the spawning emigration pulse, but the model with the pulse set at season 65 (counting from the first week of the season in December 2001) was selected. Of particular interest is a contrast between fits with the emigration pulse set at week 64 and 65, since they are contiguous and the spike catch statistic shows a downward trend (consistent with emigration out of the vulnerable stock) that includes these two weeks, so they seem indistinguishable at first sight. We fitted the depletion model to data from Season 2001-2002 setting the emigration pulse at week 64 or 65 (as noted above, setting both weeks as spawning emigration weeks did not yield convergence) while all other settings (initial parameter values, timing of recruitment pulse, likelihood model and numerical optimization method) were equal in both fits. The ratio of parameter estimates of the model with the spawning emigration week set at week 64 over the same estimates from the model with the emigration set at week 65 were very close to 1 except for natural mortality, which was close to 1.5. Second order properties however differed much more. The model with the emigration pulse at week 64 failed to produce standard errors for N_0 and the recruitment pulse while the selected model produced standard errors for all parameter estimates. Likewise, the model with the emigration pulse at week 64 produced standard errors for the effort response and the abundance response parameters that were 2 and 3 times higher, respectively, than those from the model with the emigration pulse set at week 65, whereas the standard errors for the remaining estimates were very similar between the two settings. These results show that the objectively best depletion model can be identified even when alternative timings for immigration or emigration pulses are very close.

In all models, the recruitment pulse of octopuses that reached 1 kg occurred earlier than the spawning emigration pulse by a minimum of 2 weeks (2007-2008) and a maximum of 18 weeks (2003-2004), which is to be expected since a single cohort has individuals growing first and maturing later. In some of the tried models we set the pulse of emigration before the pulse of recruitment to challenge the previous reasoning (Fig. 3) but in all instances they failed to perform better. Recruitment generally happened in January while the spawning emigration tended to occur in February-March.

Parameter estimates show high natural mortality (M), scaling (k) generally in the order of 10^{-6} thousand octopuses per unit effort and unit abundance, slightly synergistic effort response (α) and proportional abundance response (β) (Fig. 4). Statistical precision is generally acceptable or good, except in season 2008-2009 for natural mortality, scaling and abundance response. The selected model for each of the 19 seasons predicted minimum and maximum escapement abundances, weekly fishing mortality, and weekly exploitation rate of 162 thousands (2016-2017) to 1265 thousands (2003-2004), $8.5x10^{-4}$ $week^{-1}$ (2011-2012) to $5.5x10^{-3}$ $week^{-1}$ (2015-2016), and 0.083% to 0.555%, respectively.

In seasons with higher natural mortality (4-times as high in seasons 2008-2009 and 2013-2014 than in seasons 2001-2002, 2004-2005, 2005-2006, 2006-2007, 2009-2010, and 2015-2016) spawners abundance was much lower, while fishing mortality had no apparent effect on spawners abundance (Supplementary Fig. SM25). Natural mortality was much higher than fishing mortality in all seasons and in most weeks in each season, and the annual exploitation rate (total catch over initial biomass) was less than 10% in all seasons except 2001-2002, 2004-2005 and 2015-2106, when it was between 10% and 20% (Supplementary Fig. SM26).

3.2 Stock-recruitment models

Among the three stock recruitment models fitted to the spawning and recruitment abundance observations, the Saila-Lorda model had the lowest AIC but it yielded unrealistic predictions at the extremes. Namely, it predicted virtually 0 recruitment below 80 thousand spawners and over 300 thousand spawners. On those grounds this model was not considered further. The Shepherd model, more versatile than the Ricker model due to a third parameter controlling the degree of overcompensation, had a much lower AIC (5420 versus 5998, respectively).

Fig. 5a presents a scatter-plot of observations of spawners in year y and recruitment in year y+1 as well as the fitted Shepherd model and the replacement line. This surface is complex because (i) it has variance heterogeneity at each point on both axes and (ii) the covariance structure connecting spawners and recruitment in the same year has a large impact on inference but it is not visually represented in the SR surface. In this SR surface, covariances are non-zero for horizontal bands and vertical bands in contiguous years. However, some visual clues can be obtained by noting that (1) at less than 100 thousand spawners all most precise recruitment observations (those with a very short vertical line: 2017, 2018, and 2010) are clustered close to the ascending arm of the fitted SR curve, (2) between 100 and 250 thousand spawners, maximum recruitment occurs, with four very precise recruitment observations (2002, 2005, 2011, 2019) clustered around the top of the SR curve, and (3) with more than 250 thousand spawners all recruitment observations (2003, 2006, 2013) are close to the descending arm of the SR curve and all are very precise. The combination of location and precision of estimates (plus the hidden covariance structure) determine the shape of the SR curve. Thus, on the grounds of lowest AIC, the Shepherd model was selected to describe the stock recruitment relationship of *O. vulgaris* from Asturias. When using N_0 plus the back-calculated recruitment pulse as the recruitment matching the spawning abundance we obtained a similar result, with the Shepherd model selected as the best fit over Ricker's and Saila-Lorda's. This is shown in Supplementary Table SM5 and Fig. SM27.

We computed derived parameters from the Shepherd model according to formulas in Table 2 of Iles (1994). These were the slope at the origin, spawning abundance yielding maximum recruitment, maximum recruitment, and replacement spawning abundance (which also is the inflection point and the equilibrium spawning abundance), shown in

Fig. 5a as the point where the diagonal line crosses the predicted (Shepherd) model. Direct estimates and derived parameters are shown in Table 2. The MSY (in numbers) is estimated at 5 times higher than the mean yield over the last decade. The largest Lyapunov exponent is over 0, hence the stock tends to cycles of abundance or chaotic fluctuations after small perturbations. This is illustrated in Fig. 5b, where recruitment predicted by the Shepherd model -given observations of spawners abundance- follows an irregular cycle of peaks and troughs. It is also illustrated in Fig. 5c, where a small perturbation (comparable to fishing removals) from the equilibrium point at the crossing of the diagonal and the SR curve gets the stock locked into an irregular cycle, not returning to the equilibrium point. In Fig. 5d, where the stock suffers a small perturbation from the point of maximum recruitment, the cycle is regular, with the stock fluctuating among 3 points, never approaching the equilibrium point. In both cases the stock gets locked into fluctuations that are not random and do not dissipate variability as time progresses.

4 Discussion

The stock assessment of octopus stocks (and cephalolopods more generally) is a special case due to distinct life history features such as short life cycles, semelparous reproduction, high natural mortality rates, rapid growth, and complex population structures (Arkhipkin *et al.*, 2020). At the same time, their importance in fisheries worldwide is increasing due to growing landings (Arkhipkin *et al.*, 2015; Sauer *et al.*, 2019). Yet globally, octopus fisheries are typically running blind because little is known about their productivity (Sauer *et al.*, 2019). Therefore stock assessment models adapted to octopus life history and their fisheries are greatly needed. The conventional approach of using a relative index of abundance from catch per unit of effort (cpue) did not seem adequate in a holobenthic octopus fishery in southeast Australia because the cpue remained stable in spite of expected impact of fishing mortality on recruitment (Leporati *et al.*, 2009). Conventional "closed population" depletion models applied at monthly time steps jointly for 21 years of data provided estimates of annual recruitment and monthly abundance in the Moroccan octopus fishery; the model however, had to include several strong assumptions such a constant and known value of natural mortality during the 21-yr period, known and fixed seasonal cycle of recruitment, and further statistical restrictions (Robert *et al.*, 2010). It would be better to estimate all important parameters within the stock assessment model. In western Australia, Hart *et al.* (2019) used the standardized cpue index of relative abundance, confirmed to be proportional to absolute abundance with local depletion experiments, to derive a harvest strategy taking advantage of records that go back to the very start of the fishery. Our stock assessment methodology followed the advice in Arkhipkin *et al.* (2020) to develop innovative depletion models. Our "open population" depletion models harvest the rich information present in the rapid time step dynamics of the weekly fishing operations to estimate total vulnerable biomass, as well as natural mortality, recruitment and spawning stock for each year of data separately. These results are further combined in a non-Bayesian hierarchical inference approach to model the spawners and recruitment relation in the annual dynamics. This approach of combining a depletion model for the rapid fishing dynamics and a population model for the annual dynamics has been used successfully in data-poor SSF, although in previous cases the annual dynamics was the Pella-Tomlinson logistic map instead of the SR relation (Roa-Ureta *et al.*, 2015, 2019, 2020).

We estimated the timing of the recruitment pulse and spawning emigration pulse in the fit of generalized depletion models (see Fig. 3) and these estimates can be compared with results of biological studies carried out on *O. vulgaris* stocks across European waters. In our models, recruitment to the fishery (reaching 1 kg of body weight) generally happened in mid winter while the spawning emigration tended to occur in late winter-early spring. In coastal Greek waters settlement of larvae to the benthos happened in summer (Katsanevakis and Verriopoulos, 2006) and the main spawning occurred in late winter-early spring. In the Gulf of Cadiz, recruitment to the fishery (reaching 1 kg of body weight) was observed in winter while spawning was inferred to occur between July and October (Sobrino *et al.*, 2011). Comparing the spawning seasons in north-west Portugal (in the Canary-Iberian upwelling system) and southern Portugal Lourenço *et al.* (2012) observed marked differences, with the northern stock spawning from late winter to early summer while the southern stock spawned in summer. Both Otero *et al.* (2007) and Guerra *et al.* (2015) reported that the spawning season in Galician waters occurred in spring. Thus, the timings of recruitment and spawning determined from our models agree well with the findings of the biological studies conducted in the northern part of the Iberian Peninsula. It should be noted though that the measurements of recruitment and spawning differ, particularly the latter. Our estimates of spawning time describe emigration pulses, episodic events happening in a single week each fishing season, while biological studies generally measure gonad maturity progression at monthly time steps. The progression of gonad maturation will be necessarily gradual while the spawning emigration of females could happen more rapidly, as the culmination of maturity progression.

A further comparison of our modelling results with empirical findings in previous studies can be made with regards to octopus density in the field. Considering the area of the fishing grounds off Asturias (228 to 397 km^2) and the abundance estimates from our depletion models, we find that octopuses live at densities ranging from 1250 to nearly 5000 per km^2. Hart *et al.* (2019) used local depletion experiments in unfished areas to estimate *O. tetricus* density between 500 and 800 octopus per km^2, Arechavala-Lopez *et al.* (2018) reported a maximum density of 800 adult octopuses per km^2 in waters that are highly impacted by anthropic activities around the island of Mallorca, southern Spain, Katsanevakis and Verriopoulos (2006) obtained on average around 400 octopus per km^2 in

Greece, Garofalo *et al.* (2010) reported a maximum of 200 recruits and 100 spawners per per km^2 in the Strait of Sicily. Thus, our density estimates are much higher, which could be interpreted as the continental shelf off Asturias being a rich habitat for *O. vulgaris* and/or that fishing pressure has depleted the stock to a lesser degree than in other areas as a positive result of sound co-management policies during the past two decades.

Wide interannual fluctuations in recorded catch of *O. vulgaris* have been observed and analyzed in connection with environmental drivers in West Africa (Faure *et al.*, 2000; Cabellero-Alfonso *et al.*, 2010) and southern Spain (Sobrino *et al.*, 2020; Vargas-Yáñez *et al.*, 2009). In Galicia, a region influenced by the Canary-Iberian upwelling system immediately west of our study area, Otero *et al.* (2008) used additive approximations to analyze the impact of meteorological indices on cpue and concluded that a large fraction of the annual variability in catch could be explained by variability in upwelling, with the link occurring through the impact of upwelling on the survival of planktonic life stages. Remarkably, they also show evidence for density-dependence by obtaining a concave shape of the additive coefficients as a function of a density-dependent proxy, which implies overcompensation in the SR relation. Our study area is close to the Canary-Iberian upwelling system and microsatellite DNA variation have demonstrated genetic homogeneity amongst *O. vulgaris* stocks in this region (Cabranes *et al.*, 2008). Our results confirm Otero *et al.* (2008) implications with regards to density-dependence and overcompensation in *O. vulgaris*, further clarifying the nature of the processes underlying these dynamics. Recently, Sobrino *et al.* (2020) also found a strong effect of environmental processes on abundance in the *O. vulgaris* stock of the Gulf of Cadiz, namely previous year's rainfall having a negative effect on next year's abundance. When combined with a recruit index from surveys, their additive approximation explained nearly 90% of total variability in catches. Our results show that in addition to the strong impact of environmental conditions on the variability of octopus recruitment and catches, intrinsic population dynamic processes determining strong density-dependent and overcompensation cause fluctuations in *O. vulgaris* stocks abundance that need to be considered when designing effective policies for sustainable exploitation.

Given the strong degree of overcompensation observed in the stock-recruitment relationship the question arises as to what might be causing it. Overcompensation is usually understood to be caused by cannibalism or other forms of aggression of individuals in the pre-existing cohorts against individuals from the new cohort of recruits. Escola and Geritz (2007) derived explicit mechanisms involving aggression between individuals from a cohort of adults and a cohort of juveniles and the timing of reproduction, leading in some cases to overcompensation as in the Ricker model. In the present case, given the likelihood of some degree of overlapping generations of *O. vulgaris* considering its longevity, aggression of surviving octopuses from the previous cohort against recruits and among recruits could certainly contribute to overcompensation. However, unlike in iteroparous species, mass mortality of reproducing octopuses would diminish the impact of inter-cohort interactions so the strong degree of overcompensation observed here could also be connected to additional factors of the special population dynamics of octopuses. We hypothesize that availability of good quality dens for egg clutches and the competition to mate further drives the stock into overcompensation. To see this, first let the number of good quality dens for broods be fixed and limiting, such that females that do not secure a good quality den will suffer a higher chance of failing to turn broods into recruits. Second, let the number of females determine the strength of the competition between males to mate such that when there are too many females the strength of the competition to mate is low and virtually all males, even weaker ones, are able to mate. Third, let the quality of male gametes vary such that a substantial number of males, the weakest of them, are poor progenitors. Under these three conditions, a high number of females will cause overcompensation by letting too many of the good quality dens be taken by females impregnated by low quality males, which in turn will lead to many unsuccessful broods thereby undermining next year recruitment. Conversely when the number of females is relatively low and the strength of competition to mate is relatively high then only the strongest males will mate leading to dens being taken by females impregnated by the strongest males, and more successful broods. This hypothesis is supported by some findings of cephalopod reproductive biology. In removal experiments, Hartwick *et al.* (1978) observed that smaller octopus tended to occupy newly dug dens whereas larger octopus occupied natural dens. This suggests that dens are a limiting resource in octopus reproduction. Female cephalopods and female *O. vulgaris* in particular can be impregnated by multiple males leading to clutches of eggs with multiple paternity (Quinteiro *et al.*, 2011), a phenomenon called polyandry. Squires *et al.* (2012) have demonstrated experimentally that polyandry in a squid is advantageous despite the cost of multiple mating because polyandrous females had eggs that developed faster and turned into larger hatchlings relative to egg masses of monandrous females. The authors hypothesized that the increased reproductive rate of polyandrous females could be connected to the chance to receive better quality spermatophores. It is straightforward to see that an over-abundance of opportunities to mate would cause fewer females having the chance to mate multiple times thus decreasing next year recruitment if good quality dens are in limited supply. Thus we suggest that a combination of inter-cohort aggression early during recruitment and less competition to mate under limiting supply of dens later during mating could be driving the fall in recruitment at high spawners abundance.

One of the major issues that Sidney Holt defended during his career in fisheries management was that the MSY is an excessive yield policy. Holt recently elaborated his objections mostly around the arguments that the MSY is economically wasteful for fishers and that it increases by-catch and other harms to the ecosystem (Holt, 2020; Holt and Raicevich, 2018). He also expressed doubts that a stock could be kept producing the same surplus even when having the same total abundance and density because population growth rates vary for other reasons, especially the biological composition and demography of the stock (Holt, 2011). In this work we provide further reasons for a less-than-MSY policy in fisheries management with potentially broad relevance. In our study case the MSY is excessive because the population has intrinsic properties that result in unstable equilibrium points and thus cannot be kept stable at the size that maximizes the population growth rate. The intrinsic factor is the mode of relationship between spawning stock and recruitment. The Shepherd mechanism describing strong overcompensation sets the equilibrium spawners abundance at the inflection point, which is unstable. Any small perturbation, such as modest fishing removals, will set the population trajectory away from stationary for a long time, with the stock oscillating irregularly or cyclically, not declining or increasing. Thus, the concept of removing the maximum sustainable surplus from a stable population is simply not adequate. The MSY can still be calculated with the usual formulas but if removals close to MSY (under a constant harvest policy) or MSY-derived reference points (such as the fishing mortality at MSY) are applied when the stock is at the low points in the trajectory, the risk of fishery decline or collapse is high.

Our results regarding the inadequacy of MSY for fluctuating abundance dynamics could be seen as just having relevance for stocks with the special life history of octopuses and other short-lived species. However, the MSY also resulted excessive in a multi-cohort stock of long-lived sea urchins that fluctuates because of a high intrinsic population growth rate ($r > 3$) in the Pella-Tomlinson logistic map (Roa-Ureta *et al.*, 2015). Thus, one important implication of our results is that the MSY may not be valid for many stocks exploited by small-scale fisheries (SSF) as well as stocks with special characteristics such as cephalopods. This is because these stocks may posses intrinsic properties that make them prone to population dynamics consisting of irregular or cyclic fluctuations. A new sustainable rate of exploitation, less than the rate entailed by the MSY, would need to be defined. In Roa-Ureta *et al.* (2015) we proposed the latent productivity averaged over the peaks and troughs of stock fluctuations as the less-than-MSY sustainable yield. Application of our recommended policy by managers has been accompanied by a long period of stability in the largest sea urchin fishery in the world (FAO, 2021). We applied the same approach of using annual biomass predictions by the depletion models to fit the Pella-Tomlinson logistic map to the Asturias octopus stock (ICES, 2020, section 2.3). Having estimated the Pella-Tomlinson model, we estimated the mean latent productivity as the sustainable harvest rate. This estimate turned out to be close to the maximum landings along the time series and only 44% higher than the historical mean landings since 1990, while the MSY, computed from the estimated Pella-Tomlinson model, was six times higher than mean historical catch and three times higher that the highest recorded catch. Asturias management set the annual global catch as equal to the mean latent productivity minus two times the standard error of the estimate as a precautionary, sustainable and economically viable annual harvest rate. In this connection, it should be noted that the latent productivity is the general surplus production of which the MSY is a special case, the case when the stock has one stable equilibrium. For all other cases, those of stocks that tend to get locked into stable cycles because of intrinsic properties, the MSY is not adequate while the latent productivity, which varies with fluctuations in abundance, is the sustainable surplus production.

Stocks exploited by SSF compose the bulk of the large majority of stocks that remain un-assessed and yet SSF provide most of worldwide landings (Costello *et al.*, 2012) and employment (The World Bank, 2012). Extending stock assessment practices to SSF-stocks will enrich our knowledge of marine population dynamics and will broaden the practice of sustainable fisheries management. Our study shows that a small *Octopus vulgaris* stock presents rich dynamics that result from intrinsic properties of the stock as well as from small perturbations from moderate fishing removals and possibly environmental forces. The greatest difficulty in assessing SSF stocks lies in the paucity of elementary data such as reliable time series of catch and effort (Bañon *et al.*, 2018). Our study shows that when the fishery is co-managed, the data provided by the fishers on their daily operations, complemented with simple biological data that can be obtained at fairly low cost, could be sufficient to understand the fishery and population dynamics, and thus achieve sustainable exploitation at rates that guarantee sufficient supply of seafood and economic returns to fishers.

Acknowledgements. We appreciate the comments and suggestions to improve the manuscript from three anonymous reviewers and editor A. Arkhipkin. These reviews helped greatly to write a more balanced article. We are also grateful to fishers of the Asturias province for contributing with reliable data of their operations for nearly 20 years as willing contributors to sustainable exploitation. Funding was provided by the European Maritime and Fisheries Fund to the government of Spain (García-Flórez, Fernández-Rueda and Roa-Ureta) and Project Ecosifood MCI-20-PID2019-108481RB-I00/AEI/ 10.13039/501100011033 (Acuña, Rivera, González-Gil and Roa-Ureta).

Data availability. The data underlying this article will be shared on reasonable request to Fernández-Rueda or García-Flórez.

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Table 1: Notation used in this work. Phase 1 is the estimation of parameters connected to the data; Phases 2 is the estimation of hyper-parameters as a function of estimated parameters.

Phase	Concept	Notation
Data	Fishing effort	E
	Catch in weight	W
	Mean weight	w
	Time step (week)	t,i,j,l
	Number of seasons	19
Phase 1 Intra-annual generalized depletion models	Number, timing of immigration pulses	u, τ
	Number, timing of emigration pulses	v, ν
	Expected catch in numbers	C
	Observed catch in numbers ($W \div w$)	χ
	Abundance	N
	Scaling	k
	Effort response	α
	Abundance response	β
	Initial abundance	N_0
	Natural mortality	M
	Recruitment magnitude	R
	Female spawners magnitude	S
	Event indicator, 0 before, 1 otherwise	I,J
	Variance of spawning abundance	Σ_S
	Variance of recruitment	Σ_R
	Covariance of spawning, recruitment	$\Sigma_{S,R}$
Phase 2 Spawners recruitment model	Spawning abundance	S
	Recruitment	R
	Slope at start	$e^a, 1/b$
	Replacement spawning abundance	S_R
	Threshold spawning abundance	Q
	Degree of compensation	γ

Table 2: Parameter estimates of the Shepherd spawning stock and recruitment model fitted to the spawning and recruitment abundance observations in the fishery for *Octopus vulgaris* in Asturias, north-west Spain.

Parameter	Estimate	Standard error
b	2.5251	0.0033
Q (thousands)	311.3700	5.6508
γ	8.0132	0.6090
Slope at the origin	0.3960	0.0051
Spawning abundance at maximum recruitment (thousands)	244.1800	4.4739
Maximum recruitment (thousands)	539.6362	12.670
Maximum spawning abundance at replacement (thousands)	321.2733	6.3023
MSY (thousands)	295.4544	9.8369
Largest Lyapunov exponent	0.3564	0.0217

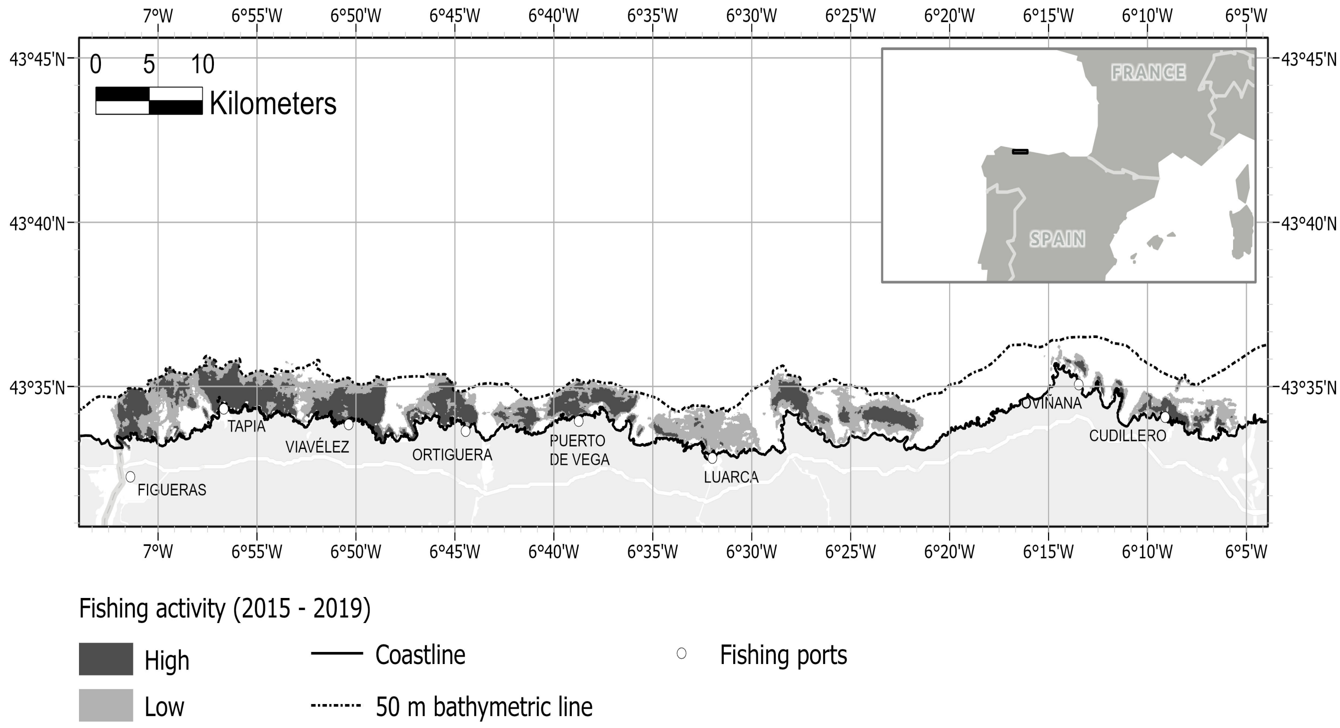

Figure 1: Fishing grounds for *Octopus vulgaris* in Asturias, north-west Spain.

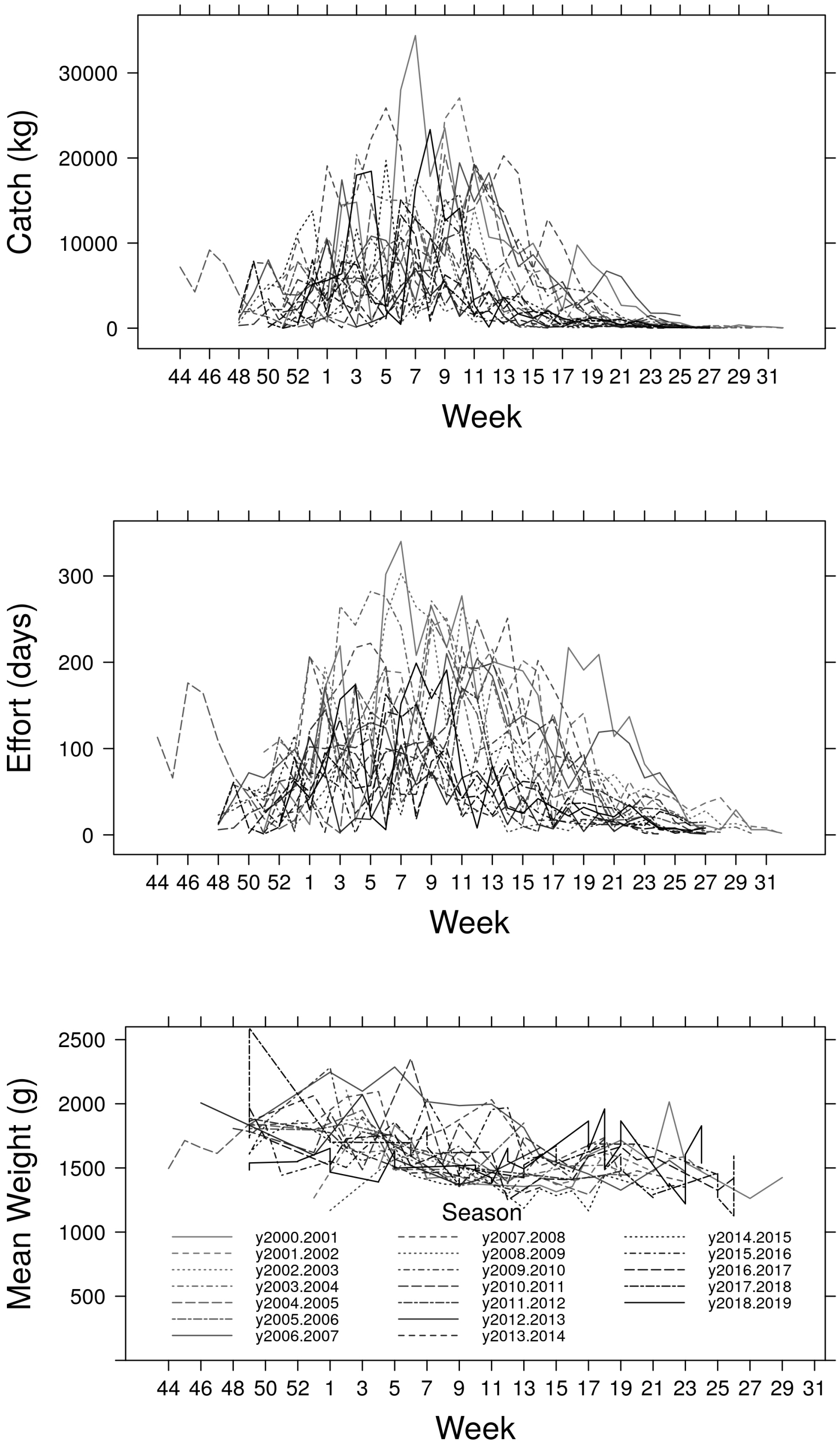

Figure 2: Raw catch, fishing effort and mean weight data from 19 seasons of the fishery for *Octopus vulgaris* in Asturias, north-west Spain.

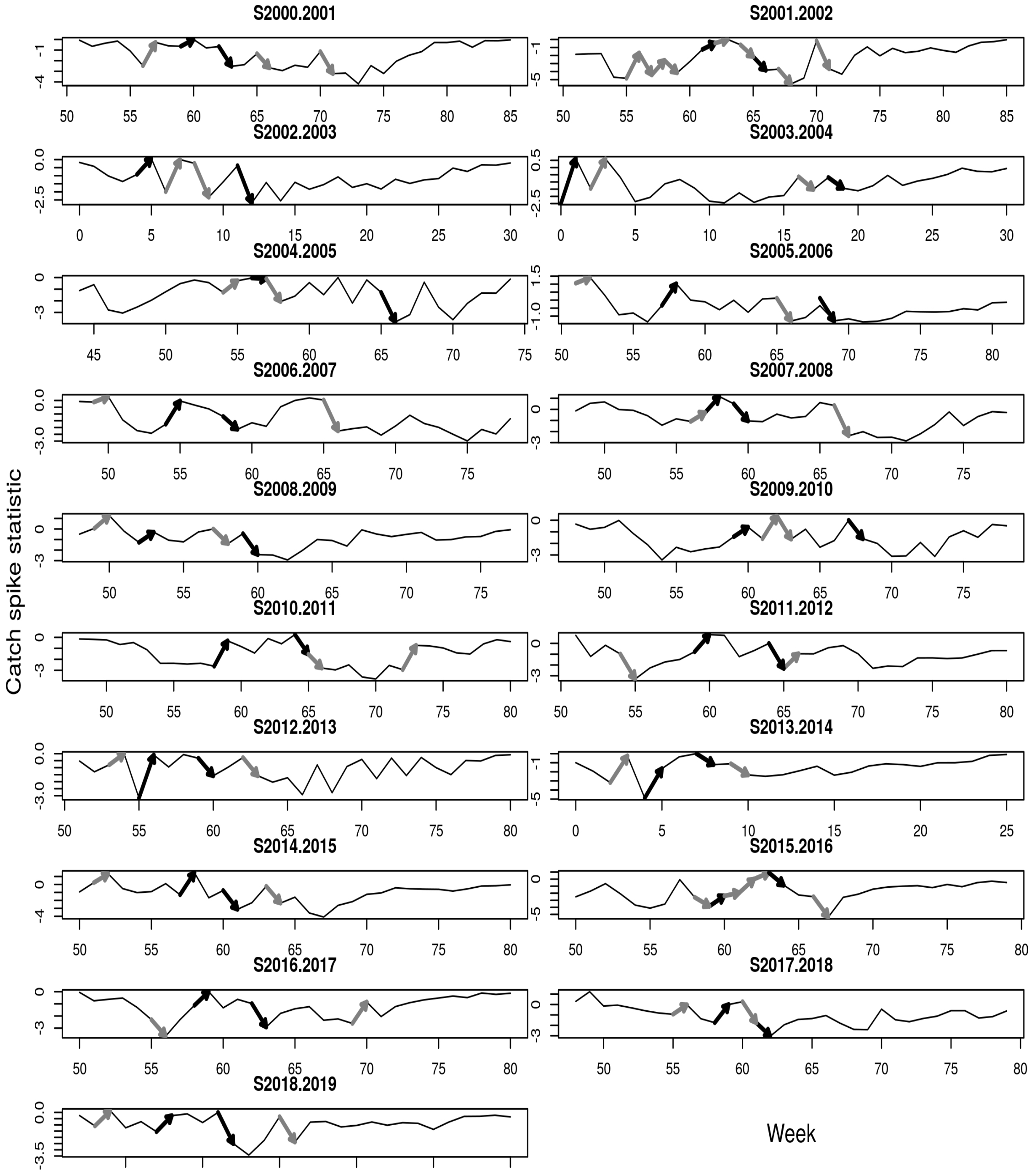

Figure 3: Catch spike statistic and the location of recruitment week (ascending black arrows) and spawning emigration week (descending black arrows) in the fishery for *Octopus vulgaris* in Asturias, north-west Spain. Alternative weeks of recruitment (ascending gray arrows) and spawning emigration (descending gray arrows) from model configurations that were discarded are also shown. The weeks are counted since the calendar week at the start of the season.

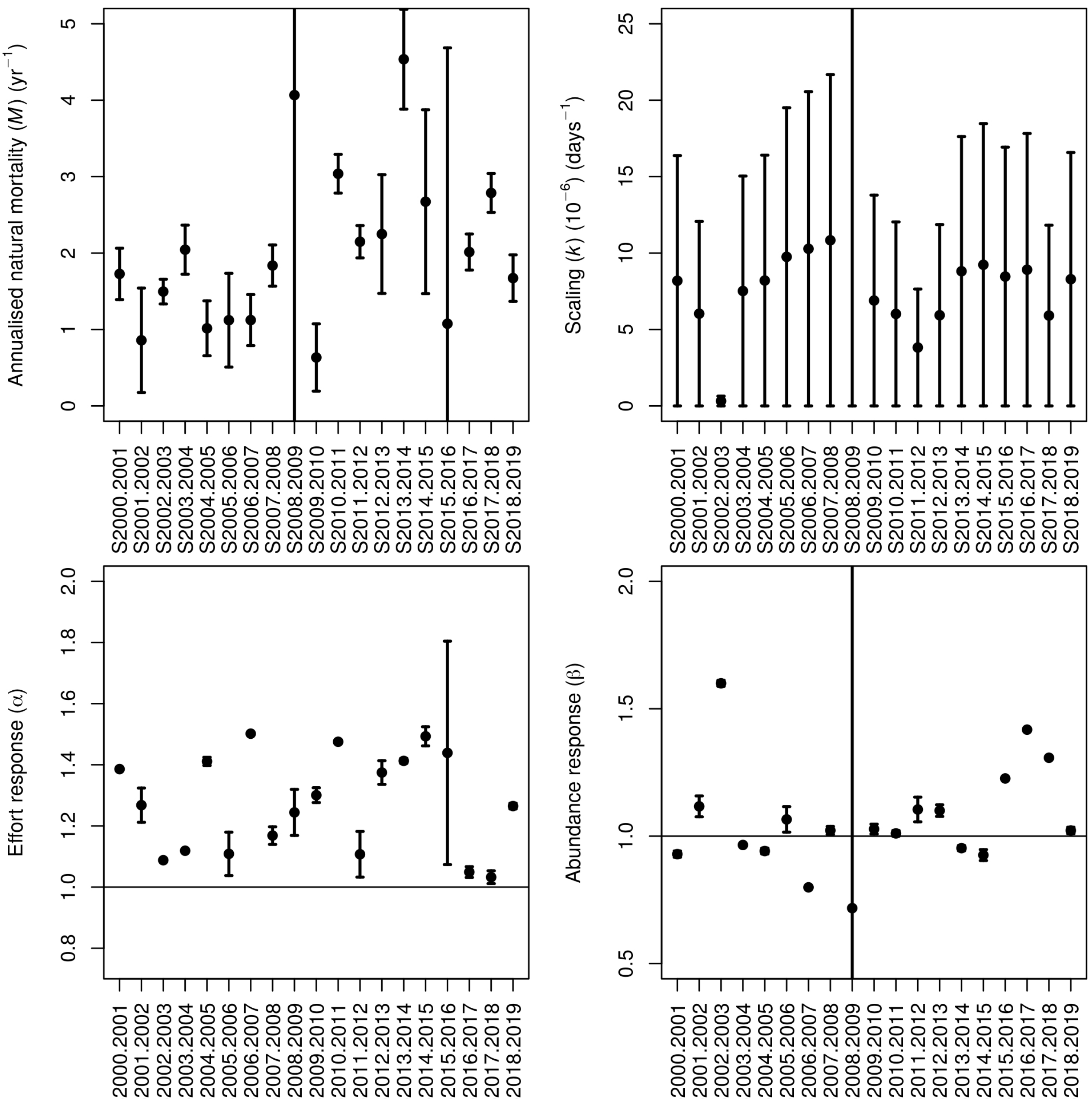

Figure 4: Generalized depletion model estimates ± 1 standard error across 19 seasons in the fishery for *Octopus vulgaris* in Asturias, north-west Spain.

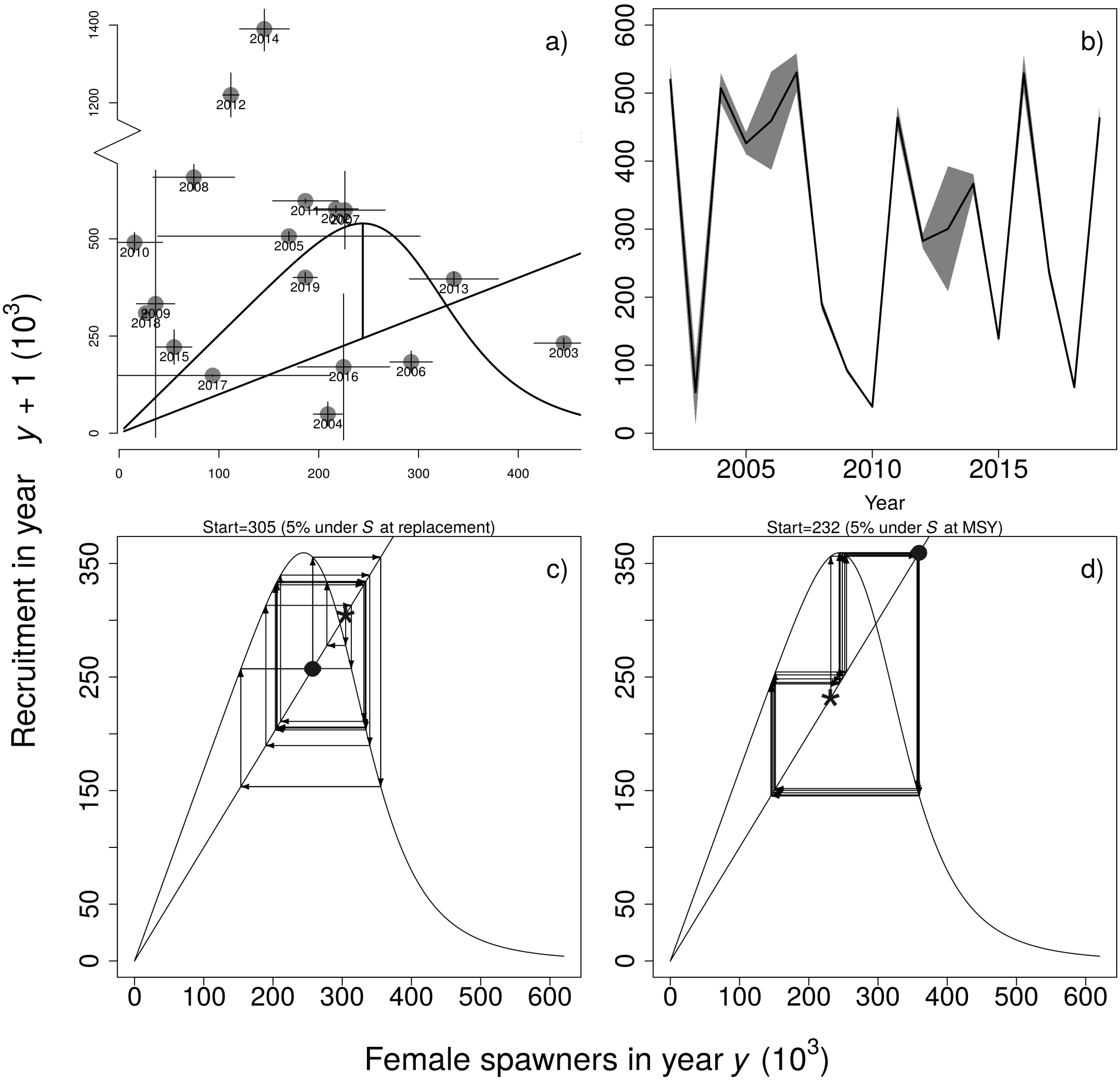

Figure 5: Female spawning stock and recruitment dynamics in *Octopus vulgaris* from Asturias, Northern Spain. a): Spawning stock and recruitment observations from generalized depletion models (dots) ± 0.25 times standard errors bars for the predictor and the response (crosses over dots), fitted spawning stock and recruitment model (line), replacement spawning abundance (diagonal), and MSY (vertical line). Years below dots are recruitment years. b): Predicted recruitment from spawning abundance observations ± 3 standard errors. c) Population trajectory under small perturbations from maximum spawners abundance at replacement. d) Population trajectory under small perturbations from spawners abundance at maximum recruitment. In panels c) and d) the star indicates initial state and the filled circle marks the final state.