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REVIEWS

Surplus production models: a practical review of recent approaches

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Abstract Increasing the knowledge of approaches to estimate the status of data-limited stocks is of crucial importance since the vast majority of stocks are data-limited, i.e., there is not enough data to conduct a fully integrated statistical catch-at-age or at-length assessment. Among the different data-limited methods, surplus production models (SPMs) are usually considered the most complete data-limited assessment methods since they are the only method that provides a full stock assessment. Due to high interest in the application of SPMs for assessing data-limited stocks, our contribution focuses on providing a practical review of these models and their corresponding characteristics. Additionally, we review the use of the surplus production concept in the "known biomass production models", highlighting their potential through examples of relevant applications. After a general introduction to the formulation of SPMs, their framework and features, this review focuses on the SPMs most frequently applied by well-known marine research organisations: ASPIC (a stock-production model incorporating covariates), SPiCT (surplus-production model in continuous time) and JABBA (just another Bayesian biomass assessment). For each model, we provide details of its formulation and main features, in addition to evaluating the quality and characteristics of the available software. Based on this information, our comparative study highlights the advantages and disadvantages of each of the three SPMs. The conclusion provides recommendations for their use in the assessment of data-limited stocks, facilitating a decision about whether SPMs constitute an appropriate tool for guidance on and assessment of specific stocks. Finally, we evaluate which of the SPMs considered in this paper should be applied.

Keywords Data-limited stock assessment · ASPIC · SPiCT · JABBA · Known-biomass production models

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Introduction

The vast majority of fish stocks are data-limited: there is not enough data to conduct a fully integrated statistical catch-at-age or at-length assessment (Costello et al. 2012) and, in most cases, there is considerable

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uncertainty over the stock status and its trajectory. Recent years have seen increasing research efforts aimed at developing methods that can improve the reliability of stock assessment in data-limited situations. As a result, a number of approaches for estimating the status of data-limited stocks have been proposed, and data-limited assessment methods are increasingly used for management purposes (Carruthers and Hordyk 2018; Chong et al. 2020). Selecting the most appropriate data-limited assessment method depends on the type of data available. The International Council for the Exploration of the Sea (ICES) workshop on the "Development of Quantitative Assessment Methodologies based on Life-history Traits, Exploitation Characteristics and other Relevant Parameters for Data-limited Stocks" (WKLIFE V), ICES (2015), identified and discussed three categories of data-limited approach: (1) length-based methods, (2) catch-only methods, and (3) catch and CPUE (catch-per-unit-effort), or other fishery-independent biomass index-based methods. The latter group of methods is represented by surplus production models (SPMs). The initial production models developed in the 1950s used differential equations to describe a single stock constrained by its carrying capacity (Fox 1970, 1975; Pella and Tomlinson 1969; Schaefer 1954, 1957). Surplus production models are the only data-limited method that provide a full fish stock assessment, i.e. evaluation of exploitation and stock status based on maximum sustainable yield reference points and catch predictions based on alternative scenarios. For this reason SPMs are the focus of the current review. Although the ICES classifies SPMs within the category of data-limited methods, it is important to bear in mind that there is no globally accepted definition of "data-limited", and hence, other regions or organisations may classify SPMs as data-moderate (Bouch et al. 2020).

Surplus production models estimate the temporal evolution of aggregated biomass (targeted by fishing) by combining the general effects of growth, recruitment and mortality (all aspects of production) into a single production function. That is, SPMs estimate the changes in biomass as a function of the biomass of the previous year, the surplus production in biomass (the sum of new recruitment and the growth of individuals already in the population minus those dying naturally), and the catches. This is why SPMs are also known as biomass dynamics models (Hilborn and Walters 1992). The somatic growth, reproduction, natural mortality, and associated density-dependent processes that define the surplus production are inseparably captured in the interplay between the two major parameters: the intrinsic rate of population increase r and carrying capacity K. A finite carrying capacity represents one possible mechanism for surplus production. According to this scenario, in an unfished population, the biomass expands to the maximum level that can be sustained. Theoretically, the biomass can be held indefinitely at a level below carrying capacity, and the fishery can continue to operate on the corresponding surplus production. Essentially, every assessment model of a sustainable fishery implicitly involves the concept of surplus production, although models vary in their detailed descriptions of population dynamics (Hart and Reynolds 2002).

In SPMs, the stock is considered as one large unit of biomass (undifferentiated biomass), i.e. age and size structure, in addition to other characteristics, such as sex differences, are not considered. Consequently, they have been regarded as relatively simple to implement, as well as easy to present and understand from a management point of view, although their adjustment is not necessarily simple. The minimum data required by SPMs are an index of relative exploitable biomass and a time series of associated catch data (observations of commercial catches). The index of relative exploitable biomass is most often commercial catch-per-unit-effort (CPUE), but could be a fishery-independent biomass index (scientific survey data). If only one source of information is available, alternative methods based exclusively on catch data or on the relative biomass index have also been proposed. For example, CMSY estimates maximum sustainable yield (MSY) and associated reference points from catch data and information on resilience (Froese et al. 2017). On the other hand, the abundance maximum sustainable yields method (AMSY) estimates relative population size when no catch data are available using time series of CPUE or other relative biomass indices as the main input (Froese et al. 2019). In contrast, when age and length information is accessible, scientists usually prefer the assessment provided by more complex models (age or length structured). However, Ludwig and Walters (1985, 1989) have shown that, at a fraction of the cost, SPMs may produce conclusions that are just as useful, and sometimes preferable for management purposes, than those produced by more complex models. It is important to emphasise that the accuracy of any model has a direct relationship to how representative the available data are for a fish stock. So, for instance, if the biomass index is informative but the age-structured data are not necessarily representative, an SPM can provide more useful results for management advice (see Chapter 7 of Haddon 2011). The primary indices of biomass for many of the world's most valuable or vulnerable species are based on catch and effort data collected from commercial and recreational fishers. However, these indices can be misleading because changes in catch rates over time may be due to factors other than changes in abundance (e.g., changes in fishing gear or spatial displacements in the stock biomass). Therefore, the first step before entering a biomass index into a stock-assessment model is standardisation of the CPUE in order to eliminate the possible influence of these factors (Maunder and Punt 2004). The standardised index is then suitable for input to the SPM. A problem arises in SPMs when the data are too homogeneous, more precisely, when the catch and effort information is available only for a limited range of biomass levels, in such cases the input data can be uninformative (Hilborn 1979). Surplus production models require contrasted catch series and relative biomass indices; in fact, the lack of contrast can generate identifiability problems and a high correlation between parameter estimates, which makes the estimation unstable (Hilborn and Walters 1992). In addition, the biomass indices must be representative of the part of the stock vulnerable to commercial fleets, what is known as the exploitable stock biomass (ESB). In fact, in biomass indices independent of the fishery, individuals not represented in commercial fleets must be excluded. On the other hand, for CPUEs, an adequate standardisation is crucial to obtain a representative index that extracts reliable information on the biomass contained in the catch and effort data (Walters 2003). In addition to the need for contrast and representativeness of the input time series, a minimum length is also necessary to avoid high assessment uncertainty. Usually, a short time series (i.e. less 10 years) may be insufficient. In fact, both features (contrast and length) must be analysed together since, for instance, a time series of 40 years with almost no contrast may be less informative than a time series of 20 years that covers almost the entire range of the measured variable. It is not possible to provide specific rules for making this decision, however, we should consider that, in practice, the probability of the available series covering many years and having contrast is low. Thus, the approach is to implement an adequate standardisation of the indices to improve their quality before fitting an SPM. Subsequently, SPM convergence and residual diagnostics can help to conclude whether the input information is adequate and if the model can be assumed appropriate or not. At this point, if the information on catches and indices of relative biomass is not sufficient for a proper SPM fit, the researcher can consider inclusion of additional prior information, if available (e.g., a Bayesian SPM), see section "Most relevant SPMs". Naturally, prior knowledge can also be included when no model fitting problems appear.

Today, SPMs are extensively used for the assessment of data-limited stocks of different fish species. Furthermore, the number of articles published on SPMs has increased in the last decades, whereas research on the topic was practically inexistent in the 1980s (Fig.1). The reason for this low use of SPMs was the scientific community's realisation that the equilibrium assumption used to estimate model parameters was problematic (Fox 1975). The equilibrium assumption, which implies that for each level of fishing effort there is an equilibrium sustainable yield, and that the yield taken is equal to the surplus production of a population in equilibrium, can lead to catch recommendations that are not sustainable in the long term. Indeed, the use of SPMs based on the equilibrium assumption contributed to a number of major fishery collapses

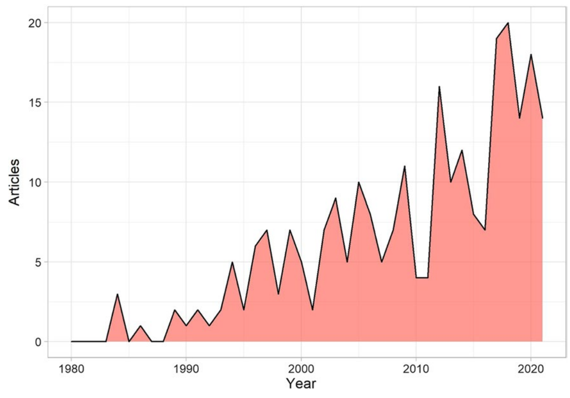

Fig. 1 Annual scientific production. Numbers of articles related to SPMs published each year. Information derived from SCOPUS database search (details in the Supplementary Material)

(Borema and Gulland 1973; Larkin 1977), including the famous Peruvian anchovy collapse of the 70s (Hilborn and Walters 1992). Consequently, equilibrium methods were no longer recommended, and research on these models was reactivated only in the 1990s, with the proposal of fitting methodologies that did not require equilibrium.

Given the interest of SPMs for assessing data-limited stocks, the aim of this article is to review the most commonly used of these methods. Section "SPMs general overview" introduces the general SPM formulation, framework and features, along with the possible fitting methodologies and a brief description of the main model outputs. The SPM research carried out in recent years has provided a huge collection of different SPM implementations; in practice, therefore, it can be difficult to decide which is best suited for assessing a particular stock. Thus, section "Most relevant SPMs" focuses on the three SPMs currently considered most relevant for assessing stocks of interest in Europe, which is the focus of this review. The first method is the classic ASPIC (a stock-production model incorporating covariates) (Prager 1992, 1994), one of the first SPMs proposed after their fall from favour in the 1980s. Its adequate performance has led to its application for the assessment of many data-limited stocks over the years. The other two SPMs described in section "Most relevant SPMs" are SPiCT (surplus production model in continuous time), proposed by Pederseen and Berg (2017), and JABBA (just another bayesian biomass assessment), proposed by Winker et al. (2018). Both models have been widely used in recent years. The wide variety of case studies that implement ASPIC, SPiCT and JABBA are testimony to the relevance of these methods, and can also be used as a guide for future applications: for examples of ASPIC, see Baro et al. (2018), Carbonell and Azevedo (2003), Davis et al. (2006) and Noman et al. (2009), for SPiCT see e.g. Angelini et al. (2021), Geraci et al. (2021) and Kathena et al. (2018) and for JABBA see e.g Chang et al. (2020) and Choi et al. (2021). Although some recent examples exist of comparisons between SPiCT and JABBA (Kolesidis and Tserpes 2020; Soto et al. 2022 or ICES 2021b), we are not aware of any articles that simultaneously compare the results of the three methods in a case study. Section "Stock assessments based on SPMs" summarises the use of different SPMs in some major marine research organizations, and provides details of the number of stocks evaluated by each SPM. Note that, even though some databases classify the CatchMSY method (Martell and Froese 2013) as a biomass dynamics model (for example, in the RAM Legacy Stock Assessment Database 2020), our article does not consider it an SPM since it does not follow the general framework of section "SPMs general overview". Subsequently, section "Known-biomass production models" introduces an application of surplus production models based on biomass time series derived from data-rich models (termed known biomass production models, MacCall 2002). Their potential is also highlighted through examples of several relevant applications. Finally, section "Final recommendations" discusses the advantages of SPMs, providing recommendations for their use in the assessment of data-limited stocks.

SPMs general overview

This section provides an overview of SPMs. First, we describe the general structure of an SPM, including the most popular formulations of the biomass production function (section "Surplus production formulation"), before discussing and explaining the different fitting methodologies and their performance. Finally, this section lists the main outputs of an SPM used for management purposes and stocks status description.

Surplus production formulation

Russell (1931) described the change in biomass of an exploited fish stock in terms of a balance between recruitment, growth, fishing mortality and natural mortality:

$$B_{t+1} = B_t + (R_t + G_t) - (C_t + M_t),$$

B_t is the stock biomass in year t, R_t is the total weight of all individuals recruiting to the stock in year t, G_t is the total growth in biomass of individuals already recruited to the stock during the year, C_t is the total weight of all fish caught, and M_t is the total weight of all fish that die of natural causes during the year.

The general structure of SPMs (discrete form) relates directly to Russell's formulation of stock dynamics, as shown below. Note that discrete form means that the variation in biomass is formulated as the difference between B_t and B_{t+1} instead of using a differential equation to describe how biomass varies continuously over time (sections "A surplus-production model incorporating covariates (ASPIC)" and "Surplus production model in continuous time (SPiCT)" show continuous formulations).

$$B_{t+1} = B_t + f(B_t) - C_t \tag{1}$$

where B_{t+1} is the stock biomass at the beginning of year $t+1$, B_t is the stock biomass at the start of year t, C_t is the biomass caught during year t, and $f(B_t)$ is the production of biomass function.

The population dynamics Eq. (1) is linked with the observations through the relation between the catches and the stock biomass across the catchability coefficient q, defined as the proportion of the total stock taken by one unit of effort. Set E_t, the effort associated to the catch C_t, then

$$\hat{I}_t = C_t / E_t = qB_t \tag{2}$$

where I_t is an index of relative biomass for year t, notation $\hat{}$ denotes an estimated value, and q is the catchability coefficient which scales the modelled stock biomass to match the trends in catch rates. Equation (2) establishes that the catch rates relate to the stock biomass in a linear way, which is a strong assumption that must be considered carefully when SPMs are applied, especially when the quality of the available data is not good. Furthermore, (2) implies that q remains constant over time. However, due to regular improvements in fishing techniques q must be variable over time.

There are many formulations of the production of biomass function $f(B_t)$. Schaefer (1954) provided the first simple model through the use of a logistic curve to describe the production of biomass.

$$f(B_t) = rB_t\left(1 - \frac{B_t}{K}\right), \tag{3}$$

where B_t is the stock biomass at time t, r is the population growth rate parameter (intrinsic rate of natural increase), and K is the maximum population size for growth to be positive (the virgin biomass concept related to carrying capacity). In Schaefer's formulation, maximum production is attained at $K/2$ since the logistic curve generates

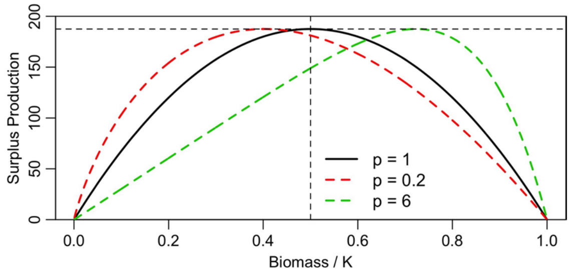

Fig. 2 Influence of the parameter p on the discrete Pella–Tomlinson version of SPM. When $p = 1$, the equation is equivalent to the Schaefer model, and thus has a symmetrical production curve around 0.5. Values of $p < 1$ skew the curve to the left and values > 1 skew it to the right

a symmetric production curve (see Fig. 2). Due to this fact, Schaefer's formulation can be considered too restricted, hence Pella and Tomlinson (1969) introduced a new parameter p in the logistic formulation allowing asymmetry in the production curve.

$$f(B_t) = \frac{r}{p} B_t\left(1 - \left(\frac{B_t}{K}\right)^p\right). \tag{4}$$

Using (4), maximum production can take place at different fractions of K (see Fig. 2). The inclusion of p modifies the interpretation of the remaining parameters, that is, the parameter values obtained using Schaefer's model cannot be directly compared to the ones derived from Pella and Tomlinson curve. The asymmetry parameter, p, is difficult to estimate accurately, then, in practice, a sensitive analysis of this parameter should be carried out.

Finally, although it is less frequently applied than (3) and (4), another popular option is Fox (1970), which is

$$f(B_t) = Ln(K)rB_t\left(1 - \left(\frac{Ln(B_t)}{Ln(K)}\right)\right),$$

and becomes equal to Pella and Tomlinson (1969) when p tends to zero.

Fitting methodology

Throughout the development of SPMs a large number of fitting methodologies have been proposed in order to overcome the equilibrium assumption. Current fitting methodologies can be differentiated depending on whether residual errors are associated to the population dynamics or to the observations. More precisely, we have the following estimators:

- Process error estimators. Assume that all observations were made without error and that all error was in Eq. (1).
- Observation error estimators. Assume that all residual errors are in the catch or biomass index (2) and that Eq. (1) is deterministic and without error.

Recent proposals provide estimators that combine both forms of error. To model the two errors simultaneously, we need additional information, such as an estimate of the ratio of the respective variances of the two processes. This assumption is weaker than the assumption made by choosing to model only one of the errors while assuming that the variance of the unmodeled error is zero (Thorson and Minto 2015). For this reason, the use of models that consider both types of errors is increasing, and it is recommendable to run sensitivity analyses of the information about the ratio of the respective variances of the two processes. Section "Most relevant SPMs" gives SPiCT and JABBA as examples of proposals that combine both types of error in the fitted methodology, whereas ASPIC only assumes observation errors in the fitting methodology.

Polacheck et al. (1993) compared different estimators using real and simulated data sets: process-error estimators, observation-error estimators and effort-averaging methods, which assume that the stock is in equilibrium relative to the weighted average fishing effort $\overline{E}_t = \left(kE_t + (k-1)E_{t-1} + \cdots + E_{t-k+1}\right)/(k + (k-1) + \cdots + 1)$ where k is the number of age classes being fished. Their results suggested that observation-error estimators were preferable, whereas effort-averaging methods should be abandoned, and that process-error estimators should only be applied in simulation studies and/or when practical experience suggests that they will be superior to observation-error estimators. Almost 10 years later, Williams and Prager (2002) pointed out that the equilibrium approximation method was still often used for the Pella-Tomlinson model. After an extensive study, the conclusion reached by Williams and Prager (2002) was that equilibrium methods had played an important role when computer power was far less available, but thanks to advances in computing they should be abandoned completely, and their recommendation was fully accepted by the scientific community.

SPM outputs

There are many possible outputs from fish stock assessment models that can be useful for management or for analysing fisheries performance. The two classical performance measures derived from SPMs are maximum sustainable yield (MSY) and the corresponding effort (E_{MSY}), biomass (B_{MSY}) and fishing mortality (F_{MSY}). Furthermore, the trajectories of estimated biomass and fishing mortality can also be reported relative to reference values B_{MSY} and F_{MSY}, respectively, and the ratio of the current biomass with respect to K or B_0, among others. As equilibrium is not assumed, MSY is defined the maximum catch given the dynamics of the current regime, acknowledging it may change over a longer time horizon.

Most relevant SPMs

Section "A surplus-production model incorporating covariates (ASPIC)" focuses on ASPIC, which is a continuous non-equilibrium surplus production model implemented as an observation error estimator, section "Surplus production model in continuous time (SPiCT)" describes SPiCT, a continuous time state-space model, and finally JABBA, a Bayesian discrete state-space model, is described in section "Just another Bayesian biomass assessment (JABBA)".

A surplus-production model incorporating covariates (ASPIC)

ASPIC (A stock-production model incorporating covariates) is a continuous non-equilibrium surplus production model implemented as an observation error estimator (Prager 1992, 1994). An observation error term is in the equation describing how the index relates to the biomass, implying that the biomass index is subject to error (see section "Fitting methodology"). However, ASPIC considers a deterministic equation for describing stock biomass dynamics, that is, no random term (process error) is included to take into account unmodelled variability.

The ASPIC framework could be applied to the three functions of biomass production, Schaefer (1954), Pella and Tomlinson (1969) and Fox (1970), but using Schaefer (1954) a closed expression for the yield (analytical solution) is attainable, whereas for Pella and Tomlinson (1969) numerical integration needs to be performed. Hence, following Prager (1994) the population's rate of change given Schaefer's production function is given by

$$\frac{dB_t}{dt} = \left(r - F_t\right)B_t - \frac{r}{K}B_t^2. \tag{5}$$

In order to solve Eq. (5), time is divided into constant, or nearly constant, periods, F_t, and a solution is found for each period. In this presentation we consider general periods from $t = h$ to $t = h + \delta$. Then, once the solution of Eq. (5) is available, the yield (catches) Y_h taken from $t = h$ to $t = h + \delta$ involves the following integration:

$$Y_h = \int_{t=h}^{h+\delta} F_h B_t d_t, \tag{6}$$

For illustrative purposes, below, we include the steps of a parameter estimation algorithm that uses effort to estimate yield. Firstly, we obtain starting guesses for the parameters and for the biomass at the beginning of the series. Then, the solution of Eq. (5) is used to project the population over time, and the estimated yield is computed using the solution of (6). Hence, the objective function to be minimized is (assuming multiplicative error structure in yield):

$$\sum_{\tau=1}^{T} \left[\log(Y_\tau) - \log(\hat{Y}_\tau)\right]^2, \tag{7}$$

where T is the total number of time periods. Finally, if convergence is achieved, the parameter estimation algorithm ends. Otherwise, the parameter estimates are revised and the algorithm is applied again.

Three variants for Eq. (7) are available: fitting statistically conditioned on yield, fishing effort, or relative biomass. Yield is usually known more precisely than effort or relative abundance; therefore, conditioning on yield is recommended for most analyses (see Prager 1994 for details). In discrete-time formulations, commonly, the catches in the total period are related to the average of the biomass at the start and at the end of the period to mitigate the effect of discretisation, whereas the continuous-time form adopted by ASPIC avoids such approximation.

Further research by Prager and coauthors addressed questions of general interest in the SPM area. Prager et al. (1996) studied whether SPMs should be applied to a stock that exhibits pronounced age structure or changes in selectivity. Their study led to the conclusion that the presence of strong age structure and moderate changes in selectivity should not lead to reject the application of simple SPMs (for stocks similar to the ones simulated in their study). On the other hand, Prager (2002) focused on the estimation of the shape parameter p, and concluded that accurate estimates could be obtained from the Pella-Tomlinson's model if information to specify a prior value of p exists. In other cases, Schaefer's production model can be recommended as a central approximation which can provide estimates when none can be obtained from the Pella-Tomlinson's model.

Prager (2016) provides some executables, among which is ASPIC7, for fitting ASPIC based on Schaefer and Pella and Tomlinson formulations by analysing different data series from catches and indices of relative biomass (http://www.mhprager.com/aspic.html). ASPIC7 can estimate parameters using both frequentist (least squares, least absolute values, or maximum likelihood) and Bayesian (maximum a posteriori) frameworks. In Bayesian frameworks, auxiliary information can be incorporated using so-called informative priors (probability distributions on the model parameters); see Chapter 7 of Zuur et al. (2017) for a introduction to Bayesian statistics. Informative priors usually lead to a more stable fitting and to the reduction of the uncertainty in the model estimates. However, it is worth noting that the information used to define such priors must come from a reliable source, especially for p, r and K (the main parameters for determining management quantities). In practice, it is advisable to perform a sensitive analysis of such prior information. ASPIC7 also computes bootstrapped confidence intervals on estimated quantities using a residual-based bootstrapping method. More precisely, resampled observation is generated by combining the predicted population value with a randomly-chosen normalised inflated residual. After a bootstrap run, the executable ASPICP can be used for projecting trajectories for a period of up to 100 years and, since an SPM implicitly includes a recruitment function, it can be used to make projections based on hypothetical catch or effort values using the same population equations and a proposed set of yields or effort rates.

Additionally, an R package, termed `connectASPIC`, has recently been developed that connects `R` with ASPIC 7 executables, and allows fitting to the model and reading of the results in `R`. The package is available at https://github.com/IMPRESSPROJECT/connectASPIC.

Table 1 presents a quick checklist of ASPIC properties and a comparison to the other SPM methods addressed in the coming sections.

Surplus production model in continuous time (SPiCT)

The straightforward structure of SPMs and their low data demands are useful for data-limited stocks. However, such a structure can be too simple for describing real-world stocks liable to variability in length-structure, recruitment, species interactions, catchability, selectivity, environmental conditions and so on. In order to lessen this effect it is common to add a random term in the equation describing the biomass dynamics, termed process error, as a proxy for the unmodelled variability (see section "Fitting methodology"). The majority of SPMs, except ASPIC which is a continuous time model, adopted the discrete-time form defining state-space models, which simultaneously estimate both types of error, process and observation. Although ASPIC has the advantage of being free from discrete-time average approximations due to its continuous-time formulation, it does not include process error and therefore loses flexibility. Thus, Pederseen and Berg (2017) presented a stochastic surplus production model in continuous time (SPiCT), where both biomass and fishing dynamics are modelled as states that are observed indirectly through biomass indices and commercial catches sampled with error. In addition, SPiCT considers the observation error of both catches and biomass indices, whereas in previous models the catch observations are assumed to be error-free (e.g. ASPIC). Furthermore, SPiCT has also developed seasonal extensions to the fisheries dynamics component of the state-space model to help the use of subannual data that have seasonal patterns.

This section provides an outline of SPiCT formulation. Using the Pella and Tomlinson production function Eq. (4) SPMs can be written as:

$$\frac{dB_t}{dt} = \frac{r}{p}B_t\left(1 - \left(\frac{B_t}{K}\right)^p\right) - F_tB_t \tag{8}$$

which has an intuitive biological interpretation, however, a more stable parametrisation is used to avoid estimation problems.

Table 1 Summary of the main features of three SPMs: ASPIC, SPiCT and JABBA. The properties considered are: inclusion of observation error of both catch and biomass indices, incorporation of dynamics in both biomass and fisheries, and involvement of a seasonal fisheries dynamics component. Finally, inclusion of projection functions related to fisheries management in the corresponding `R` package is also discussed. Note that ✓means that the particular SPM fulfills the corresponding property, whereas ✗represents the opposite situation

	ASPIC	SPiCT	JABBA
R package	`connectASPIC`	`spict`	`JABBA`
Type of formulation	Continuous-time	Continuous-time	Discrete-time
C_t observation error	✗	✓	✗
I_t observation error	✓	✓	✓
B_t process error	✗	✓	✓
F_t process error	✗	✓	✗
F_t seasonal patterns	✗	✓	✗
Projections	✓	✓	✓

$$\frac{dB_t}{dt} = \gamma m \frac{B_t}{K} - \gamma m \left(\frac{B_t}{K}\right)^{p+1} - F_t B_t, \tag{9}$$

where $\gamma = (p+1)^{(p+1)/p}/p$ and $m = (rK)/((p+1)^{p+1/p})$.

A large number of factors have an impact on biomass dynamics (e.g. environmental and ecological factors), however, data related to such factors are not usually available, thus their influence is modelled by adding a stochastic process error term to the deterministic Eq. (9), resulting in:

$$dB_t = \left(\gamma m \frac{B_t}{K} - \gamma m \left(\frac{B_t}{K}\right)^{p+1} - F_t B_t\right) dt + \sigma_B B_t dW_t, \tag{10}$$

where σ_B is the standard deviation of the process noise, and W_t is Brownian motion. The multiplicative error term in Eq. (10) can result in instability problems in the model fitting, and for this reason the equation is transformed, obtaining a additive noise term.

$$dZ_t = \left(\frac{\gamma m}{K} - \frac{\gamma m}{K}\left(\frac{e^{Z_t}}{K}\right)^p - F_t - \frac{1}{2}\sigma_B^2\right) dt + \sigma_B dW_t,$$

where $Z_t = log(B_t)$.

The majority of the previous SPMs do not model the process of instantaneous fishing mortality rate. In discrete-time models F_t is often assumed equal to C_t/B_t, where C_t is the catch in year t and B_t the mean biomass in the same period (for example, Punt 2003). Hence, if the catch observations are assumed error-free then, if such error exists, it spreads directly to the F_t process, producing an effect on the conclusions about fishing pressure. SPiCT overcomes this issue by modelling F_t as an unobserved process, as is done for B_t. Furthermore, this approach allows estimation of F_t at any time even if catch observations are not available at such a time. SPiCT models F_t as the product of seasonal and random components (S_t and G_t respectively):

$$\begin{aligned} F_t &= S_t G_t \\ d\ \log G_t &= \sigma_F dV_t, \end{aligned}$$

where dV_t is standard Brownian motion and σ_F is the standard deviation of the noise. Note that $S_t = 1$ if only annual data is used. On the other hand, if subannual data are available, two models for seasonal variation in the fishing are proposed. The first is the use of a cyclic spline to describe the seasonal variation. The disadvantage of this is that it is not able to adapt to changes in amplitude and timing (phase) of the real seasonal fishing pattern. The second proposal overcomes this limitation by employing a system of stochastic differential equations (SDEs), whose solutions oscillate periodically to represent the seasonal variation in fishing. Of course, this second model is more complex than the previous one, and difficulties to obtain model convergence can appear.

After modelling the instantaneous fishing mortality rate, SPiCT considers the following integral in continuous time plus noise for modelling the observed catch:

$$\log(C_t) = \log\left(\int_t^{t+\Delta_t} F_s B_s ds\right) + \epsilon_t,$$

where C_t is the cumulative catch over a time interval Δ_t and $\epsilon_t \sim N(0, \sigma_C^2)$ are the independent catch observation errors.

Finally, the observed series of indices of exploitation biomass, $I_{t,i}$, $i = 1, \ldots, N_i$, scientific or commercial catch-per-unit-of-effort data, are modelled as follows, considering them as "snapshots" related to the time point t:

$$\log(I_{t,i}) = \log(q_i B_t) + e_{t,i},$$

where $e_{t,i} \sim N(0, \sigma_{I,i}^2)$ are independent normal errors and $\sigma_{I,i}$ is the standard deviation of the i-th index observation error, and q_i is a catchability parameter for the i-th index.

SPiCT parameters can be estimated using both frequentist and Bayesian frameworks. In the former, model parameters are estimated by maximizing the log-likelihood function. In the latter, auxiliary information can be incorporated using informative priors, which are multiplied by the likelihood function to obtain the posterior distribution, the maximum of which defines the Bayesian maximum a posteriori parameter estimates.

The SPiCT model can be applied easily using the `R` package `spict` which contains a detailed user manual available at https://github.com/DTUAqua/spict. Basic functionality of the `spict` package by default includes confidence intervals of the estimated quantities, whereas advanced functionality allows direct use of the effort data instead of exploitable biomass indices, the calculation of retrospective plots and scaling the uncertainty of individual data points, among other available options. On the other hand, `spict` can also apply different management scenarios to explore the effect of different management strategies on the recommended total allowable catch (TAC), predicted fishing mortality or biomass. It also includes functions to compute TAC based on an accepted SPiCT assessment and several implemented harvest control rules (HCR), such as the hockey-stick MSY rule.

Table 1 also includes a summary of SPiCT features.

Just another Bayesian biomass assessment (JABBA)

As mentioned above, an advantage of the Bayesian framework is the use of informative priors to incorporate additional information and reduce the uncertainty of the resulting estimates. A large number of slightly different Bayesian SPMs have been proposed over the years. Of these models, the ones that are most applied are those for which a specific software has been developed and published.

In particular, the deterministic Bayesian surplus production (BSP) model detailed in McAllister and Babcock (2006) has been widely used by the International Commission for the Conservation of Atlantic Tunas (ICCAT) to conduct several stock assessments. Since the BSP model only considers observation error terms, McAllister (2014) improved its implementation to include process error, naming it Bayesian surplus production 2 (BSP2).

One of the problems that Winker et al. (2018) found is that programmes are improved slowly since their maintenance depends only on a few developers. For this reason, fisheries scientists usually decide to programme their own code, and modify the models as necessary, which may lead to implementation errors. In response to this, Winker et al. (2018) developed a new open-source modelling software entitled "just another Bayesian biomass assessment" (JABBA) which implements a generalised Bayesian state-space SPM. The name is a reference to JAGS (just another gibbs sampler, Plummer 2003), which is the language in which the Bayesian algorithm is executed. However, JABBA software is presented in an `R` package termed `JABBA` that provides a user-friendly `R` to JAGS interface for fitting these generalised models that generate reproducible stock status estimates and diagnostics for fisheries (`R JABBA` package is available at https://github.com/jabbamodel/JABBA). It is worth mentioning that the `JABBA R` package also allows forecasting under constant catch scenarios. JABBA automatically compares the difference between the last assessment year and the present year. The difference between these years is projected forward under the current catch, which could, for example, be determined based on updated catch information or by assuming an average catch based on the three most recent assessment years.

In JABBA formulation, the biomass B_t is expressed as a proportion of K (i.e. $P_t = B_t/K$) to improve the efficiency of the estimation algorithm that estimates the Bayesian posterior distributions of all quantities of interest by means of a Markov Chains Monte Carlo (MCMC) simulation. Winker et al. (2018) noted that the surplus production function formulated according to Pella and Tomlinson (1969) allows the surplus production per unit biomass to approach infinity even when biomass approaches zero. Hence, JABBA provides the option of combining surplus production with a generic "hockey stick" recruitment function, which assumes that the recruitment becomes increasingly impaired below a given biomass ratio ($P_{lim} = B_{lim}/K$), with P_{lim} ranges of 0.2–0.25 having been widely adopted as thresholds for recruitment overfishing.

$$
\begin{aligned}
P_t =& \phi e^{\eta_t} \quad \text{if} \quad t = 1 \\
P_t =& \left(P_{t-1} + \frac{r}{p} P_{t-1} \left(1 - P_{t-1}^{p}\right) - \frac{\sum_f C_{f,t-1}}{K} \right) e^{\eta_t} \\
& \text{if} \quad P_{t-1} \geq P_{lim} \quad \& \; t = 2, 3, \ldots, T \\
P_t =& \left(P_{t-1} + \frac{r}{p} P_{t-1} \left(1 - P_{t-1}^{p}\right) \frac{P_{t-1}}{P_{lim}} - \frac{\sum_f C_{f,t-1}}{K} \right) e^{\eta_t} \\
& \text{if} \quad P_{t-1} < P_{lim} \quad \& \; t = 2, 3, \ldots, T
\end{aligned}
$$

where T is the total numbers of years, η_t is the process error, with $\eta_t \sim N(0, \sigma_\eta^2)$, and $C_{f,t}$ is the catch in year t by fishery f. Note that the corresponding biomass for year t is $B_t = P_t K$, so the observation equation is given by

$$
I_{i,t} = q_i B_t e^{\epsilon_{t,i}}, \quad t = 1, 2, \ldots, T.
$$

where q_i is the estimable catchability coefficient associated with the biomass index i, and $\epsilon_{t,i}$ is the observation error, with $\epsilon_{t,i} \sim N(0, \sigma_{\epsilon_{t,i}}^2)$.

From the above formulation we can conclude that JABBA has two main disadvantages with respect to SPiCT: (1) JABBA is based on the assumption that catch observations are error-free, whereas SPiCT models the harvest rate as a separate and unobserved process, and (2) JABBA is a discrete time model while SPiCT is continuous in time. Additionally, SPiCT allows the direct use of effort data in the model instead of exploitable biomass indices, whereas we are not aware of this functionality in JABBA. Table 1 provides a quick review of JABBA's properties to aid comparison of the features of ASPIC, SPiCT and JABBA.

An interesting feature of JABBA is that the future line of research mentioned in Winker et al. (2018) to improve the comparability between age-structured models and JABBA was developed in Winker et al. (2020). In order to do this, they introduced "JABBA-Select", which incorporates life history parameters and fishing selectivity, in addition to distinguishing between exploitable biomass (used to fit indices given fishery selectivity) and spawning biomass (used to predict surplus production). Application of JABBA-Select involves the use of an age-structured equilibrium model to convert the input parameters into multivariate normal priors for surplus-production productivity parameters.

Stock assessments based on SPMs

There are many marine research organisations that focus on ensuring the long-term conservation and sustainable use of fishery resources. To do so, they carry out stock assessments providing knowledge to understand the population dynamics of these resources and generate advice for meeting goals in conservation, management, and sustainability. The aim of the current section is to analyse the use of SPMs in the stock assessments of the main marine research organisations: ICES (International Council for the Exploration of the Sea), ICCAT (International Commission for the Conservation of Atlantic Tunas), NAFO (Northwest Atlantic Fisheries Organisation) and GFCM (General Fisheries Council for the Mediterranean).

Information on the SPMs used for stock assessment in each of these organisations during the last two years has been collected from stock assessments and executive summaries of ICES expert group reports https://www.ices.dk, scientific reports of NAFO https://www.nafo.int/About-us, ICCAT https://www.iccat.int and finally GFCM data which comes from SAC (2019a) and SAC (2019b). Figure 3 reports this information in a barplot where, for each model, the height of the bar represents the number of stocks assessed with the model.

ASPIC (section "A surplus-production model incorporating covariates (ASPIC)") was one of the first continuous non-equilibrium surplus production models proposed in the 1990s, and consequently was widely used for the assessment of different stocks over the years. However, nowadays, ASPIC is only applied for the assessment of three species (two in ICCAT and one in NAFO); as we see in Fig. 3.

SPiCT ('section "Surplus production model in continuous time (SPiCT)") is currently the most used SPM at both the GFCM and ICES; see Fig. 3. Furthermore, the number of species evaluated by SPiCT is expected to continue increasing in coming years since several stocks are not yet assessed by means of SPiCT, but preliminary analyses have been conducted for its use in future assessments. This is the case of hake GSA 20,22, 23 or Sardine GSA 3 stocks assessed by the GFCM.

Bayesian surplus production models (BSP and BSP2) and JABBA, which improves on the previous implementations, are widely used by the ICCAT (Fig. 3). More precisely, six stocks are assessed using BSP and four with the application of BSP2 (one stock is assesed using both BSP and BSP2), and five through JABBA. As the scientific community learns more about JABBA software, its increased use instead of BSP and BSP2 is to be expected because the optimisation procedure for the Bayesian state-space model is an improvement on the previous models.

Figure 3 also shows other less common SPMs that the ICES, ICCAT, GFCM and NAFO use to assess their stocks. Biodyn, which the GFCM uses to assess one stock, refers to Punt and Hilborn (1996) user's manual of biomass dynamics models, which provides implementations of the described models in EXCEL spreadsheets. Among the different models described in Punt and Hilborn (1996) a simple biomass dynamic Schaefer production model is the one the GFCM applies. The `mpb` software that the ICCAT applies is an `R` package included in the larger project known as FLR https://flr-project.org/. FLR is a collection of

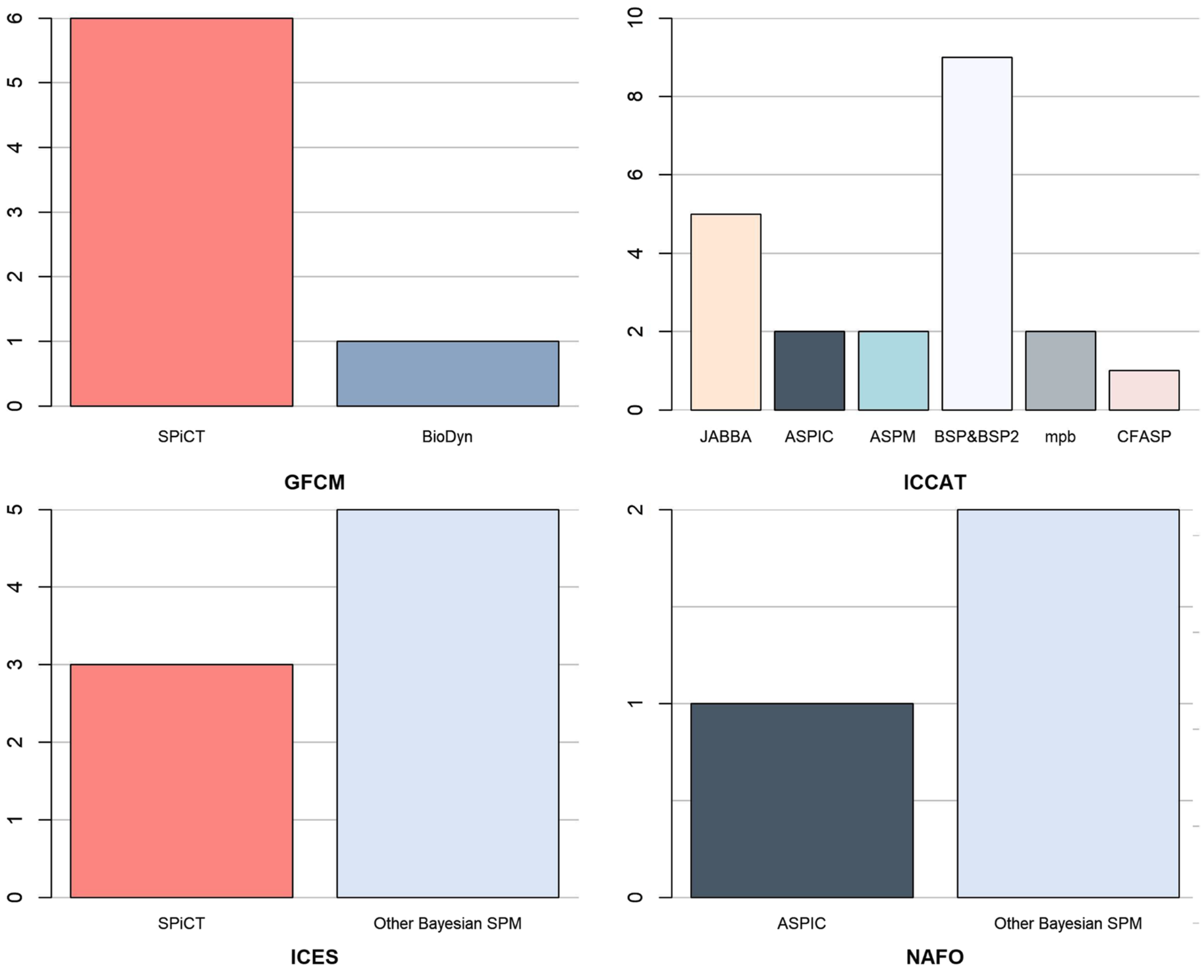

Fig. 3 Barplot showing the SPMs used by each of the organisations (ICES, GFCM, ICCAT, and NAFO). For each model the height of the bar represents the number of stocks assessed by means of the corresponding SPM based on the latest assessments available in April 2021 (data collection month). Take into account that the category "Other Bayesian SPM" includes different Bayesian formulations

tools for quantitative fisheries science that facilitates the construction of bio-economic simulation models of fisheries systems. The `mpb` package allows us to run and perform simulation-testing biomass-based stock assessment models. The ICCAT also assesses three species by means of an ASPM (an age-structured production model; see Brooks et al. 2002) and a CFASPM (catch-free age-structured production model; Porch et al. 2006). Both of these represent more complex models than the classic formulations of an SPM, since they can incorporate age-specific differences into the model parameters such as growth, fecundity, and gear vulnerability (selectivity). Thus, both models are outside of the framework of the SPMs described in section "SPMs general overview", and hence far from the focus of the current review. Finally, the category "other Bayesian SPM" includes different Bayesian formulations, such as known Bayesian SPMs that fisheries scientists have slightly adapted to their specific needs. The two-stage biomass dynamic model of Ibaibarriaga et al. (2008) or the Bayesian nonlinear state–space models of Meyer and Millar (1999) are examples of this.

To conclude, the percentage of stocks that each organisation evaluates using SPMs is as follows: 66.67% in ICCAT, 13.64% in NAFO, 8.97% in GFCM and 3.03% in ICES. Such values allow us to conclude that SPMs are widely used in ICCAT, where more

Table 2 Summary of the SPMs mentioned in section "Stock assessments based on SPMs". The full names, acronyms and main references are provided. * both models are outside of the framework of SPMs described in section "SPMs general overview", since they represent a step-up in model complexity from the classical formulations of an SPM, since they can incorporate age-specific differences in model parameters such as growth, fecundity, and gear vulnerability (selectivity)

SPM name	Acronym	References
A surplus-production model incorporating covariates	ASPIC	Prager (1992, 1994)
Surplus-production model in continuous time	SPiCT	Pederseen and Berg (2017)
Just another Bayesian biomass assessment	JABBA	Winker et al. (2018)
Bayesian surplus production	BSP	McAllister and Babcock (2006)
Bayesian surplus production 2	BSP2	McAllister (2014)
Simple biomass dynamic model	BioDyn	Punt and Hilborn (1996)
Simulation testing biomass based stock assessments	`mpb` package	https://flr-project.org/
An age-structured production assessment model	ASPM	Brooks et al. (2002)*
Catch-free age-structured production model	CFSAPM	Porch et al. (2006)*
Other Bayesian Models:		
Two-stage biomass dynamic model	–	Ibaibarriaga et al. (2008)
Bayesian nonlinear state–space models	–	Meyer and Millar (1999)

than half of the stocks are assessed by means of SPMs, whereas their use has less importance for the GFCM, NAFO and ICES. However, as mentioned, its relevance in ICES is increasing, see ICES (2021a).

Finally, Table 2 summarises the SPMs mentioned in section "Stock assessments based on SPMs", including their full names, acronyms and the main references.

Known-biomass production models

Traditional SPMs, like those mentioned in section "Most relevant SPMs", relate historical series of catches to historical fishing effort or indexes of relative biomass such as CPUE (catch-per-unit-effort). These SPMs require the estimation of a catchability coefficient to relate the biomass index to an (inferred) true biomass. This parameter is often difficult to accurately estimate using production models and consequently, it introduces uncertainty in other parameters estimated by the SPM. An alternative line of research based on surplus production models, named known-biomass production models (KBPM), was developed (MacCall 2002). The basis of this model is the idea that annual surplus production in an unfished stock is equal to $B_{t+1} - B_t$, and that, for a fished stock, the calculation of surplus production depends on catch (see Eq. 1). In contrast to traditional SPMs, KBPMs use a biomass time series produced by other stock assessment models as input data, and thereby avoid the imprecision associated with estimating the catchability coefficient. Surplus production is calculated with the known biomass and the observed catches and the production curve is fitted in the usual manner (e.g. Schaefer or Pella-Tomlinson).

The changes in known stock biomass are fully as informative as the history of catches, nearly doubling the information content in the time series of data. Thus, KBPMs were not developed to assess data-limited stocks because these models require a biomass time series that is usually estimated with a data-rich assessment model. But if we already have a data-rich model that reports the stock status, why do we need to use a KBPM? In order to answer this question, we provide several examples of interesting applications of KBPM over the years in the paragraphs that follow.

KBPM formulations can be used to perform a sensitivity analysis of the catchability coefficient (q) by exploring the consequences of different biomass values. More precisely, it is possible to compute the entire series of surplus production using alternative hypotheses of the current stock size that correspond to alternative values of the q parameter, and thus evaluate the robustness of the general pattern of estimated surplus production. Hilborn (2001) considered this analysis for the monkfish (*Lophius* *americanus*) in the eastern United States, concluding that the general pattern of surplus production was robust to alternative assumptions about current stock size.

Jacobson et al. (2002) compare two ways to estimate the surplus production curve and MSY reference points: (1) the "external" method which estimates production model parameters after a data-rich assessment model is fitted (i.e. KBPM), and (2) the "internal" method which fits a more complicated assessment model and an SPM simultaneously adding a likelihood that compares observed and predicted surplus production. The advantage of both approaches is that a single model, using all of the available information, provides the information needed for status determination (biomass and fishing mortality rate estimates) and estimation of MSY reference points. Note that if separate models are used to estimate biomass (e.g., virtual population analysis) and MSY parameters (e.g., traditional SPM), then reconciling and linking the two sets of estimates may be problematic (e.g., due to fishery selectivity assumptions). KBPM can provide an estimation of MSY reference points without fitting a stock-recruitment function and can serve as a cross-check on the sensibility of stock-recruitment model results (MacCall 2002) and the derived values such like MSY, F_{MSY} or B_{MSY}.

KBPM's are also part of the pragmatic approach proposed by Sparholt et al. (2020) to include density dependence in the estimation of management reference points where the fishing mortality corresponding to MSY, F_{MSY}, was obtained using different methods, including KBPM, and compared to the one derived from a time-series of fishing mortality from the age-based available annual assessments.

On the other hand, Walters et al. (2008) compared the patterns of the relationship between surplus production and stock size derived from KBPM, age-structured population models, and ecosystem models, concluding that the plots of surplus production vs stock size derived from KBPM can provide insights into the fact that nonstationarity in productivity needs to be considered as part of population rebuilding.

Another important point is that KBPM can be used to study whether the hypothesis of excessive fishing is sufficient to explain large stock declines in biomass and failures to recover. With this aim in mind, Hilborn and Litzinger (2009) applied KBPM to Atlantic cod populations, for which many hypotheses have been proposed to explain their failure to recover, including climate variability (Meng et al. 2016) or overexploitation (Hutchings and Myers 1994).

Bundy et al. (2012) and Mueter and Megrey (2006) provide relevant applications of KBPM related to an ecosystem. KBPM can be applied to the dynamics of the total aggregated biomass and catch of all targeted fish species in the ecosystem, thus defining a simple model to assess the ecosystem's status. In addition, aggregate KBPM that includes environmental and biological covariates has been used to consider the dynamic nature of marine ecosystems, which means that their overall productivity responds in a non-linear way to multiple drivers associated with climatic, anthropogenic and ecological influences. Furthermore, these models are also applied to compare the productivity of different ecosystems and the influence of environmental covariables in such productivity.

Performance of the aggregate KBPM approach has been evaluated using a simulation approach akin to a simple management strategy evaluation cycle. The conclusions indicate that biological reference points have been reasonably well estimated for many ecosystems, and that because environmental variability has an impact on such estimates, the combined impacts of environment must be included (Gaichas et al. 2012).

Final recommendations

This study describes the general structure of surplus production models and the estimation frameworks used, also providing a description of the most frequently used SPMs in ICES, GFCM, ICCAT, and NAFO.

To conclude this review, we created a flowchart to answer the following questions: (1) How do we know whether SPMs are a suitable choice for a particular assessment? and (2) Which of the reviewed models is the best option depending on the data and specific aims?

It is necessary to cautiously consider some general aspects before deciding to use one of the SPMs summarised in Fig. 4. Firstly, the biomass indices (after catch-effort standardisation) should be representative of the part of the stock vulnerable to commercial fleets, what is known as the exploitable stock biomass (ESB). Secondly, in many cases the

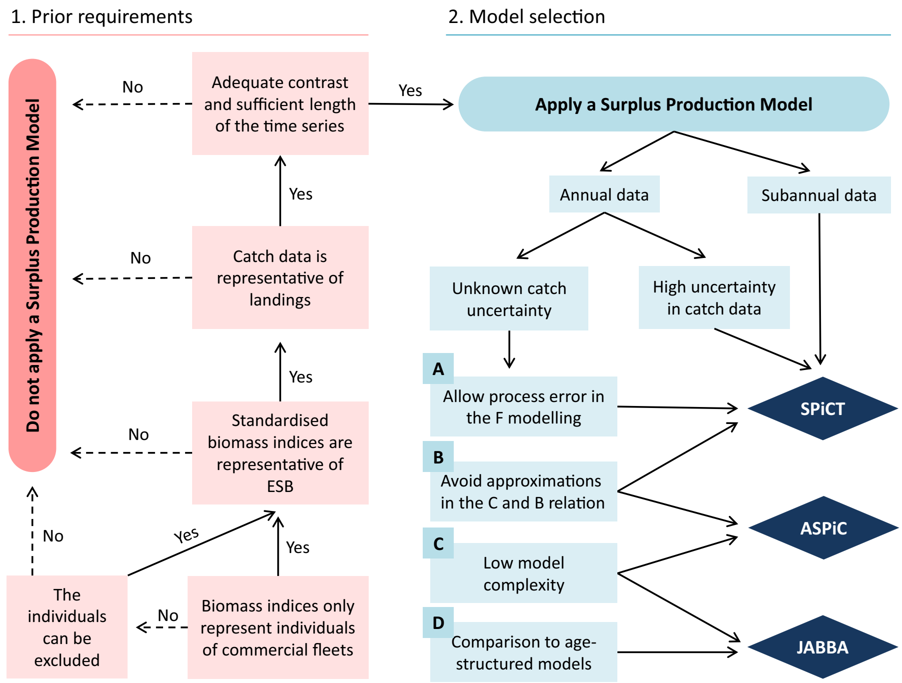

Fig. 4 Flowchart for deciding (1) whether SPM is a suitable choice for a particular assessment. (2) Which of the three models, ASPIC, SPiCT or JABBA may be the best option depending on the data and specific aims. Note that ESB is exploitable stock biomass, *F* is fishing mortality, *C* is catch time series and *B* is biomass time series

gear selectivity of commercial and scientific fleets do not coincide, and thus the biomass indices have to be corrected to exclude individuals that are not represented in commercial fleets. Thirdly, catch data should be representative of total removals (landings, discards and by-catch). Finally, the contrast in the input time series and their minimum recommended length should be analysed in accordance with the recommendations in section "Introduction"; considering the inclusion of additional information through priors if extra information is available.

On the other hand, the flowchart also provides advice for selecting one of the reviewed models (Fig. 4). The SPMs that ICES, GFCM, ICCAT and NAFO use most are SPiCT and JABBA, whose main differences are, in brief, as follows. SPiCT, unlike JABBA, is a continuous time model, free of discrete average approximations. If subannual data is available, SPiCT can model seasonal variation in the fishing since harvest rates are modelled as a separate an unobserved process, whereas JABBA does not include this flexibility. In particular, JABBA assumes that the catch rates relate to stock biomass biomass in a linear way, which is a strong assumption that must be met for its proper use. In addition, JABBA assumes that catch observations are error-free, whereas SPiCT considers catch observation errors. This leads to an additional problem because if catch observation error exists JABBA spreads it to fishing pressure since, rather than modelling the fishing mortality rate (as SPiCT does), JABBA derives the rate from catch information. On the other hand, JABBA's extensions provide a direct comparison to age-structured production models which can be useful depending on the aim of the application. In conclusion, although SPiCT overcomes some assumptions/simplifications considered in other models, such as JABBA, the price to pay is an increase in model complexity, which may or not be helpful depending on the data available and the assumptions satisfied by the stock.

Many factors can act and interact to affect catchability and thus the relationship between the relative biomass index and the biomass, leading to hyper-stability or hyper-depletion relations instead of a linear one. In some cases, these relationships appear due to the lack of a suitable standarisation of the indices, however, in other cases the explanation is a denso-dependent effect. Commonly, data-rich assessment models, such as Stock Synthesis (Methot and Wetzel 2013) or the Globally applicable Area-Disaggregated General Ecosystem Toolbox (Begley 2005), allow denso-dependent effects, establishing a parameter γ for non-linearity $I_t = qB_t^{\gamma}$. However, none of the SPMs in section "Most relevant SPMs" allow denso-dependent effects or environmental effects on the catchability coefficient estimates. Thus, a suitable catch-effort standardisation is even more relevant in SPMs to make the assumption of linear relation between B_t and I_t and constant catchability more plausible. An additional practice to overcome the assumption of constant catchability is to estimate q for different periods by splitting the time series.

This review has focused on the most frequently used methods as recently applied by well-known marine research organisations. However, this is a rapidly developing field, and the body of knowledge relevant to SPMs is growing. For example, Best and Punt (2020) focus on increasing the efficiency of fitting Bayesian state-space SPMs. Firstly, using NUTS (No-U-Turn Sampler, Hoffman and Gelman 2014) implementation in the Stan software (Carpenter et al. 2017), and, secondly, providing practical recommendations about the efficiency of multiple parameterisations of a state-space biomass dynamics models. Ovando et al. (2021) also proposed a new stock assessment software package, named `sraplus`, which allows the combination of a biomass dynamics model with a variety of data sources (e.g. priors on recent stock status or an index of biomass), and the model fitting is carried out using Rcpp (Eddelbuettel and Francois 2011) and Stan implemented through Template Model Builder (Kristensen et al. 2016).

Finally, although the main use of SPMs is to assess data-limited stocks, they can be applied in data-rich contexts to compare the given results to those obtained by means of age or length structured models (see section "Introduction"). Also in that context, KBPM (section "Known-biomass production models") may be of interest to carry out studies/applications like the ones mentioned there.

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