

Research Article

Evaluate the power of a modified continuous time D-DM model, using BSPM and ASPM as benchmarks: a case study of a slow-growing tuna species (*Thunnus alalunga* Bonnaterre, 1788)

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Abstract

Delay-difference type models (D-DMs) represent a theoretical bridge between classical surplus-production models and data-rich age-structured models. However, periodic changes of recruitment, growth, and mortality rates can also be accounted for in the continuous time delay-difference models (CTDDMs). Such models incorporate biological processes by considering continuous time delays. In the present study, CTDDMs produced realistic outputs for yield, biomass, and biological reference points (BRPs) based on using data from the southern Atlantic albacore fishery. Simulations of predicted biomass or numbers were carried out using fully age-structured information (covering 30 years) and compared with more complicated age-structured production models (ASPMs). The performance of the CTDDMs was also compared with that of a Bayesian surplus production model (BSPM). BSPM estimates of the BRPs, e.g., r , k and MSY , were used as benchmarks for the respective CTDDMs estimates. The assessed maximum sustainable yields by the two models were approximately 21,600 t and 23,500 t, respectively, while the CTDDMs produced more population parameters estimation. The CTDDMs provided reliable prediction of BRPs for sustainable fisheries management and required fewer data than ASPMs. This study have evaluated the applicability and sensitivity of the continuous-time-type D-DM model. The scalability of these models will be discussed in further research.

Keywords: CTDDM, DDM, Model validation, Bayesian surplus production model, *Thunnus alalunga*

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Introduction

In demonstrations of the composition of aquatic ecosystems, it is often difficult to decide upon, and to justify, the most practical fish growth model to employ (Hilborn and Mangel 1997; Quinn and Deriso 1999). Individual growth rates of fish and their age of maturity often vary with environmental changes (Haddon, 2011; Froese *et al.*, 2014). The classical surplus production model (SPM) lacks biological reality; the age-structured production model (ASPM) requires highly detailed biological information (Quinn and Deriso, 1999), while the delay-difference model (DDM) considers biological information too simplistically (Deriso, 1980; Musick and Bonfil, 2005; Collette *et al.*, 2006). Walters (2011) first proposed a continuous time delay-difference model (CTDDM) in which recruitment, growth, and mortality rates are treated as varying continuously over time. In the CTDDM, the fishing mortality rate is considered to be dependent on the age of the fish from recruitment through older life stages. The model is considered a theoretical bridge between classical surplus-production models and nominally data-rich age-structured models. Therefore, the CTDDM is an appropriate alternative model for assessment of fish stock, which has the capacity to connect between ASPM and SPM (Walters, 2011).

Previously, several types of discrete-time D-DMs have been applied to fish and short life cycle aquatic animals (Pallare and Restrepo, 2003; Walters

and Martell, 2004; Jensen *et al.*, 2009), such as shark-like fishes (Musick and Bonfil, 2005), lobsters (Hall, 1997), prawns (Dichmont *et al.*, 2003) and Moroccan octopus (Robert *et al.*, 2010). Many assessment methods and approaches have been applied to the stock of the southern Atlantic albacore (*Thunnus alalunga*) (Yeh *et al.*, 1990; Sun *et al.*, 2002; Viñas *et al.*, 2004; Vrugt *et al.*, 2009; ISSF, 2011; ICCAT, 2013), but, to date, the literature on CTDDM is sparse. The southern Atlantic albacore (*Thunnus alalunga*) is a comparatively slow growing, long-lived (>13 years) species. It is a commercially important stock, which is widely distributed in tropical and subtropical waters of the Atlantic Ocean, from the tropics to the latitude of approximately 55°S (Yeh *et al.*, 1990; ICCAT, 1999; Sun *et al.*, 2002; Viñas *et al.*, 2004). The International Commission for the Conservation of Atlantic Tunas (ICCAT) has defined three groups of albacore stock in the Atlantic: the northern and southern Atlantic stocks (separated at 5°N), and the Mediterranean stock. Although the status of the southern Atlantic albacore stock is better than that of the northern stock, the former may also face overfishing (ICCAT, 2011). The ICCAT and International Seafood Sustainability Foundation (ISSF) have also reported overexploitation of the southern Atlantic albacore stock based on different maximum sustainable yield (MSY) reference points (ICCAT, 2012; ISSF, 2011). Thus, effective management procedures are badly

needed to protect against further overexploitation of this fishery (ICCAT, 2011; Zhang *et al.*, 2015).

This present work aims to validate this modified method (CTDDM, Walters, 2011; Walters, 2020) based on continuous simulation of biological processes, and to provide a more detailed account of the model's performance characteristics. For assessment of biological reference points (BRPs) of a slow-growing long-lived species, it is essential to determine a reliable method of management of the fishery when data availability is limited (ICCAT, 2012; Froese *et al.*, 2014). Such models would be useful to assess BRPs, to compare yields in different systems, and to set the fishery management for future sustainable development. CTDDM will be compared with conventional SPM population models accomplished by software packages, including catch-effort data analysis (CEDA, Hoggarth *et al.*, 2006), an SPM incorporating covariates (ASPIC, Prager 2005), an age-structured production model (ASPM, Quinn and Deriso, 1999), and a Bayesian surplus production model (BSPM) (Vrugt *et al.*, 2009; Haddon 2011; Carruthers *et al.*, 2012). Through Bayesian analysis, we can analyze the role of alternative information sources in support of decision-making and the effects of alternative decisions on various aims (Han and Carlin 2001; Vrugt *et al.*, 2009; Kuikka *et al.*, 2014). In this study, a justifiable finding showed that the CTDDM produces realistic outputs for yield, biomass, and

BRPs when applied to southern Atlantic albacore fishery data. The CTDDM treats recruitment, growth, and mortality rates as varying continuously over time, and is considered a theoretical bridge between SPMs and ASPMs. The primary aims of this paper were: (i) to explore and apply this generally unfamiliar CTDDM to an important fishery, southern Atlantic albacore (*T. alalunga*), and to promote this model to the fishery's scientific community; (ii) to examine model presentation, validation and application of CTDDM; and (iii) to provide reference information for the sustainable management on southern Atlantic albacore stock.

Materials and methods

Data sources

Catch data (1956–2011) for the south Atlantic albacore fishery were obtained from the ICCAT statistical databases (ICCAT, 2011). For albacore population, total production over the past 30 years ranged from approximately 15,000 t to 40,000 t, mainly from longline fisheries (ICCAT, 2012). According to ICCAT (2013), the Chinese Taipei Longline Fishery Index provides a good indication of the abundance of albacore populations. Standardized catch per unit effort (CPUE) based on the Chinese Taipei longline fishery was used as a relative abundance index of the southern Atlantic albacore fishery (ICCAT, 2013). The length-weight relationship was taken from Penney (1994) and the Von Bertalanffy growth model

(VBGM) parameter K , W_∞ , and mean body weight at age were based on Lee and Yeh (2007) (Table 1).

Table 1: Summary of the distribution functions or true values used for the key parameters of southern Atlantic Albacore (*Thunnus alalunga*) stock.

The distribution functions or true values used for the key parameters	
The point estimates of Von Bertalanffy growth coefficient, K and asymptotic weight, W_∞ , and mean body weight at ages k (W_{e_k}) and $k-1$ ($W_{e_{k-1}}$) from Von Bertalanffy growth equation.	$L_t=147.5(1-\exp(-0.126(t+1.89)))$ $W_t=1.3718(10^{(-5)}) L_t^{(3.0973)}$ $W_{e_k}=(1-k)(16.56-10.64k)/(1+1.88k+0.88(k^2))$ $dW/da = \kappa(W_\infty-w(a))$

CTDDM

In the classical delay-difference model (D-DM), the mean body weight of the fish follows a difference relationship for age $a \geq k$ that leads to the Ford-Brody version of the von Bertalanffy growth model (Hilborn and Walters, 1992). Schnute (1985) proposed that the point estimates of δ , ρ , and mean body weight at age k could be obtained from the von Bertalanffy growth model. According to the suggestion of Schnute (1985) and Fournier and Doonan (1987), the stock-recruitment relationship (SRR) has three parameters. The CTDDM provides an extremely compact and exact simulation of the dynamics of total numbers and biomass for age-structured populations, and is expressed as follows:

$$B(t) = \int_{a=k}^{\infty} N(a,t)w(a,t)da \quad (1)$$

$$dB(t)/dt = w(k)R(t) + \kappa W_\infty N(t) - (Z(t) + \kappa)B(t) \quad (2)$$

$$R(t) = \alpha B(t-k) / (1 + \beta B(t-k)) \quad (3)$$

$$dW/da = \kappa(W_\infty - w(a)) \quad (4)$$

Where $B(t)$ is the stock biomass for year t , $R(t)$ is recruitment for year t in the Beverton-Holt SRR model, and $N_{a,t}$ is stock number, $N_{a,t} = s_{t-1} N_{a-1,t-1}$; k and W_∞ are von Bertalanffy growth coefficients and asymptotic weight, respectively; the recruitment R_∞ are the asymptotic values. The total instantaneous mortality rate $Z(t) = F(t) + M$, was assumed to vary over time with changes in fishing mortality rate $F(t)$. Under constant $R(t)$ and $F(t)$ conditions and taking differential equations (2) and (3) to equal zero, then $C_\infty = FB_\infty$, and $N_\infty = R/Z$, $B_\infty = BPR * R$, where BPR is biomass per recruit; α , and β are the parameters of the Beverton-Holt SRR model. Under these conditions, recruitment $R(t)$ and fishing mortality rate $F(t)$ are treated as step-wise constants over short time intervals Δt , and $N(t+\Delta t)$ is the exact prediction of population number at the end of each interval for the given starting values, and $B(t+\Delta t)$ is the analytical solution of the CTDDM. The analytical solution of the CTDDM used in this study can be expressed as follows:

$$B(t+\Delta t) = B_{\infty} + w_{\infty}[N(t) - N_{\infty}]e^{-Z\Delta t} + \{B(t) - B_{\infty} - w_{\infty}[N(t) - N_{\infty}]\}e^{-(Z+\kappa)\Delta t} \quad (5)$$

$$N(t+\Delta t) = N_{\infty} + [N(t) - N_{\infty}]e^{-Z\Delta t} \quad (6)$$

$$B(t+\Delta t) = s^*(t)[\delta^*N(t) + \rho^*B(t)] + w_k R(t)H^* \quad (7)$$

$$N(t+\Delta t) = s^*(t)N(t) + R(t)(1 - s^*(t))/Z \quad (8)$$

$$H^* = [1 - \rho^*s(t)]/(Z+\kappa) + \kappa W_{\infty}[1 - \rho^*s(t)]/[w_k Z(Z+\kappa)] - W_{\infty}s(t)(1 - \rho^*)/(w(k)^*Z) \quad (9)$$

$$s^*(t) = e^{-(F+M)\Delta t}, \rho^* = e^{-K\Delta t}, \delta^* = W_{\infty}(1 - \rho^*) \quad (10)$$

Where B_{∞} and N_{∞} are the asymptotic values, and H^* and s^* are transitional parameters, while ρ^* and α^* do not change except in cases where the growth curve varies over time.

Model sensitivity

Sensitivity analysis is the assessment of predicted changes and errors and their impacts on conclusions to be drawn from the model (Pannell, 1997; Arlot and Celisse, 2010; Pardo, *et al.*, 2014). To determine how uncertainty in each parameter affects estimates of the stochastic factor, $\lambda(\varepsilon)$, the formula to calculate them was derived by the perturbing kernel $K(Y, X)$ to $K(Y, X) + \varepsilon C_t(Y, X)$. The sensitivity of $\lambda(\varepsilon)$ in the perturbed model was defined as:

$$SSI_{\lambda} = \left. \frac{\partial \lambda(\varepsilon)}{\partial \varepsilon} \right|_{\varepsilon=0} \quad (11)$$

$$\log_{\lambda}(\varepsilon) = \log_{\lambda}(0) + \varepsilon E \left[\frac{\langle v_{t+1}, C_t w_t \rangle}{\langle v_{t+1}, K_t w_t \rangle} \right] \quad (12)$$

Where ε is a small constant, E denotes expectation, v_t and w_t are the stationary reproductive value and population structure sequences, respectively, and C_t is the function preserving the model assumptions stated above for small ε (Pannell, 1997; Pardo, *et al.*, 2014).

SPM (accomplished by CEDA and ASPIC), BSPM, and ASPM

The CEDA (Catch-effort data analysis, Hoggarth *et al.*, 2006) software package was used to evaluate the values of production parameters for the SPM (surplus production model). ASPIC (A surplus-production model incorporating covariates, Prager, 2005) software package was also used to compare the parameter estimates, such as K , r , q , F_{MSY} (i.e. fishing mortality coefficient F at maximum sustainable yield). The BSPM models used in this study was an extension of the SPM, and model selection criterion (BIC) was used to compare the performance among models (see Zhang *et al.*, 2021 for details). Bayesian approach has been increasingly used in ecological applications to quantify multiple sources of uncertainty (Chen *et al.*, 2000; Peterman *et al.*, 2003; Rivot *et al.*, 2004; Christensen and Walters, 2004; Vrugt *et al.*, 2009; Su and Randall, 2012). With the Bayesian framework, it is more straightforward to calculate simultaneous credible intervals for multiple parameters, and to construct intervals around model predictions (Cowles and Carlin 1996; O'Hara and Sillanpää 2009; Wulff, *et*

al., 2012). MCMC techniques bypass the need to evaluate the high dimensional integral in posterior distribution by generating dependent values from the posterior distribution via Markov chains (Jiao *et al.*, 2010). Programs and Bayesian analysis were run in Visual Basic for Applications (Ver 7.1) and R (ver 3.3.3). The convergence diagnostic analysis for any model based-upon Markov Chain Monte Carlo (MCMC) is important, which supposed that N chains of MCMC different initial conditions and the length of G , each chain included m (Number of parameters) of a vector of length G for any parameters were estimated (Gelman and Rubin 1992; Brooks and Roberts 1998). Based on the Gelman-Rubin Statistic (1992), the average variance in

the inter-chain/intra-chain were calculated Scale Reduction Factor (SRF) method (Gelman *et al.*, 2004; Han and Carlin, 2011) (see Zhang *et al.*, 2021 for details). An example of presentation on how the CTDDM tracks the total biomass (or numbers) predicted from the fully age-structured ASPM accounting (Catalano and Allen, 2010; Cope, 2013; Allen, 2017).

The dynamics of the ASPMs modeled population account for mortality due to fishing and natural causes as well as growth, recruitment, and ageing at the end of the year (Quinn and Deriso 1999; Cope, 2013). The ASPMs have an annual time step that leads to the following equation for the population dynamics for an age-cohort (Catalano and Allen, 2010; Allen, 2017):

$$N_{p,t,k} = \begin{cases} R_t \omega_p & \text{If } k=0 \\ N_{p,t-1,k-1} e^{-Z_{p,t-1,k-1}} & \text{If } 1 \leq k < k_{\max} \\ N_{p,t-1,k_{\max}} e^{-Z_{p,t-1,k_{\max}}} + N_{p,t-1,k_{\max}-1} e^{-Z_{p,t-1,k_{\max}-1}} & \text{If } k = k_{\max} \end{cases} \quad (13)$$

$$\check{I}_t = \begin{cases} q_t \sum_{p,k} S_{t,k}^* N_{p,t,k} e^{-\tau Z_{p,t,k}} \sum_l \phi_{p,k,l} S_{t,l}^* & \text{For indexes in numbers} \\ q_t \sum_{p,k} S_{t,k}^* N_{p,t,k} e^{-\tau Z_{p,t,k}} \sum_l \phi_{p,k,l} S_{t,l}^* W_l & \text{For indexes in mass} \end{cases} \quad (14)$$

Where N is the number of animals, k_{\max} is the maximum age-class, R_t is the total number of age-0 animals during year t , ω_p is the proportion of the total number of age-0 animals that settle to platoon (p) in size-class l (assumed to be time-

variant), $Z_{p,t,k,l}$ is the total mortality on animals of age (k) in platoon (p) that are in size-class l during year t ; \check{I} is the model-estimate corresponding to the index of abundance, $S_{t,k}^*$ is the survey selectivity-at-age for animals of age (k)

during year t , q_t is the catchability coefficient for year t , τ is the time during the year corresponding to the index, and $\phi_{p,k,l}$ is the proportion of fish of age (k) in platoon (p) that are in size-class l .

Bayesian surplus production model (BSPM) used in this study was an extension of the surplus production model. The models were used as the basic model structure (Buckland *et al.*, 2004; Jiao *et al.*, 2009; Haddon, 2011; Carruthers *et al.*, 2012):

$$\begin{cases} E(B_{t+1}) = B_t + rB_t(\ln(K) - \ln(B_t)) - C_t \\ E(U_{i,t}) = q_i B_t, \quad r \sim N(\bar{r}, \sigma^2) \end{cases} \quad (15)$$

Where B_t and C_t are the population abundance and the total catch in year t , respectively; q_i is the catch-ability coefficient for i -th type of relative abundance index U_i , r is the population intrinsic growth rate, and the carrying capacity (K). The ASPIC (A surplus-production model incorporating covariates, Prager, 2005) uses time series of indices of abundance and catch biomass to estimate stock status and uses bootstrapping to construct sampling distribution for a statistic of interest, e.g. stock status, the biomass that would provide the maximum sustainable yield (B_{MSY} and MSY). CEDA (Catch-effort data analysis, Hoggarth *et al.*, 2006) software package was used to evaluate the values of production parameters for the Fox surplus production model.

Bayesian information criterion (BIC) was used to evaluate the performance or variation among BSPM, CTDDM, and SPM, which could incorporate the

variation among models (Haddon, 2011), and then the smaller Bayesian information criterion (BIC) value mean the better fit.

$$BIC = -2\ln(\text{maximum likelihood}) + m\ln(n) \quad (16)$$

Where m is the number of parameters to be estimated and n is the number of data points. Based on the Gelman-Rubin Statistic (1992), the average variance in the inter-chain/intra-chain and the Scale Reduction Factor (SRF) were calculated as follows:

$$W = \frac{1}{N(G-1)} \sum_{j=1}^N \sum_{g=1}^G (\theta_{gj} - \bar{\theta}_j)^2 \quad (17)$$

$$\bar{B} = \frac{1}{N(G-1)} \sum_{j=1}^N \left(\sum_{g=1}^G \theta_{gj} - \frac{1}{N} \sum_{j=1}^N \sum_{g=1}^G \theta_{gj} \right)^2 \quad (18)$$

$$SRF = \sqrt{\frac{1}{G} \left(G-1 + \frac{\bar{B}}{W} \right)} \quad (19)$$

Where θ_{gj} is the estimated value, $\bar{\theta}_j$ is the mean value of θ in the whole j sequence, W is the weighted value of predictions, and \bar{B} is the average variance of the intra-chain (Bowman and Azzalini 1997; Gelman *et al.*, 2004; Han and Carlin, 2011). The SRF significant difference ($SRF > 1.2$ or $SRF < 1.0$) indicates the parameters whether achieve the convergence for that chain (Gelman *et al.*, 2004; Han and Carlin, 2011).

Results

The BRPs of the southern Atlantic albacore (*T. alalunga*) stock were evaluated using the CTDDM using catch data (1956–2011) and growth information for the longline fishery (Table 2). The model also assessed the carrying capacity (K), the biomass at

MSY (B_{MSY}), and the intrinsic growth rate (r). The ratios of catch (C) against MSY (C/MSY), and effort (E) against E_{MSY} (E/E_{MSY}), of the stock in 2011 were 1.07 and 0.94, respectively. SPM

generated a value for MSY with 80% confidence intervals of 23,630–27,390 t for this stock. The B_{2009}/B_{MSY} ratio was 1.18 from ASPIC, and the F_{2009}/F_{MSY} ratio was 1.42 using CEDA.

Table 2: Summary statistics of Biological Reference Points (BRPs) from the classical SPM accomplished by software package Catch-Effort Data Analysis (CEDA, Hoggarth *et al.* 2006) and A Surplus-production Model Incorporating Covariates (ASPIC, Prager 2005). Summary statistics of model outputs of the CTDDM for the southern Atlantic albacore fishery; and comparison of the obtained estimates of population parameters (r and k) and biological reference points (BRPs) using different methods.

Models (using CEDA)	Fox			Schaefer				
Parameters	Normal	Long normal	Gamma	Normal	Long normal	Gamma		
R^2	0.653	0.708	0.317	0.506	0.573	0.521		
K	190280	178755	8290	158718	118698	118735		
q	3.44E-90	3.74E-09	8.38E-09	3.33E-09	4.69E-09	4.59E-09		
r	0.403	0.434	0.999	0.725	1.001	1.001		
MSY	28242	28520	30497	28778	29697	29697		
R_{yield}	28111	28519	28606	26660	29275	29299		
B_{2011}	74247	75877	104714	74120	75802	100720		
F_{2011}	0.415	0.324	0.302	0.418	0.325	0.301		
F_{MSY}	0.386	0.301	0.281	0.386	0.301	0.281		
B_{MSY}	91325	93330	128800	90321	92310	120500		
Models (using ASPIC)	Fox			Logistic				
B_1/K		0.86			0.86			
R^2		0.863			0.834			
q		3.32E-09			3.18E-09			
r		0.2844			0.2844			
MSY		28300			28680			
B_{2011}		70023			69153			
F_{2011}		0.548			0.556			
F_{MSY}		0.386			0.387			
B_{MSY}		32908			81600			
Models/BRPs	CTDDM				BSPM			
BSPs	Mean (SE)	Median	2.5% quantile	97.5% quantile	Mean (SE)	Median	2.5% quantile	97.5% quantile
F_{MSY}	0.163(0.13)	0.161	0.138	0.231	0.18(0.12)	0.182	0.14	0.23
$F_{0.1}$	0.159(0.13)	0.157	0.125	0.191	0.16(0.12)	0.161	0.12	0.21
F_{2011}/F_{MSY}	0.386(0.11)	1.382	1.021	1.713	1.34(0.11)	1.342	1.04	1.62
$B_{MSY}/(10^4t)$	15.35(0.12)	14.68	12.4	19.21	15.27(0.11)	14.94	12.4	19.45
B_{2011}/B_{MSY}	0.178(0.11)	1.175	1.087	1.689	1.204(0.11)	1.203	1.102	1.71
Parameter/BRPs	K	q	r	R_{yield}	R^2			
CEDA	375 755	3.74E-10	0.434	28 519	0.71			
ASPIC	387 300	4.314E-10	0.391		0.86			
SPM (Classical)	MSY (23 630-29 700)		B_{2011}/B_{MSY} (0.813-1.02)		F_{2011}/F_{MSY} (0.75-1.07)			
ICCAT (used by)	MSY (21 500-28 700)		B_{2011}/B_{MSY} (0.813-1.02)		F_{2011}/F_{MSY} (1.07-1.098)			

Note: R_{yield} is the replacement yield, q is the catchability coefficient, and R^2 is the coefficient of determination.

The simulation is presented here as an example to illustrate the convergence of the diagnostic analysis in relation to the scale reduction factor (SRF) that was used to evaluate the convergence of the Bayesian estimator. Based on prior

input of the above information, the BSPM was analyzed using the Markov chain Monte Carlo estimator. The BSPM obtained MSY with an 80% confidence interval of 22135–24007 t. The estimated C/MSY from the BSPM

was approximately 1.0 for the past few years, whilst the relative fishing mortality ratio (F_{2011}/F_{MSY}) was greater than 1.0. When value of the SRF coefficient is greater than 1.0, the Markov chains for the parameters have converged; in this example, the values of SRF were 1.0265 and 1.0586. The BRPs estimates from BSPM analysis of this fishery are showing the fit of the

predicted to the observed catch, the fit of predicted to the observed CPUE, the deviation from observed to predicted biomass, and an analysis of the log-CPUE residuals (Fig. 1). BSPM estimates of the BRPs and fishery reference points were used as benchmarks for the respective CDTTM estimates.

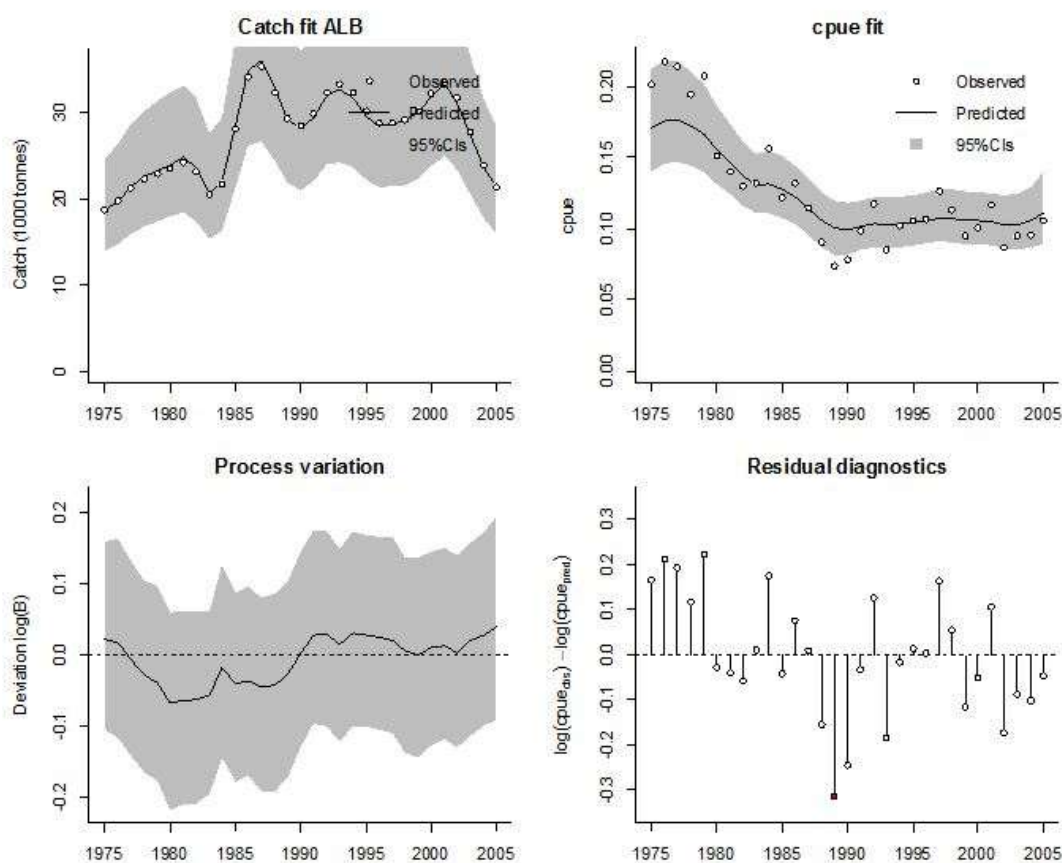


Figure 1: Analytical graph for BSPM analysis of the southern Atlantic albacore (*T. alalunga*) fishery, showing the fit of the predicted to the observed catch, the fit of predicted to the observed CPUE, the deviation from observed to predicted biomass, and an analysis of the log-CPUE residuals.

Population parameters and BRPs from the SPM, BSPM, and CTDDM are shown in Table 2. The CTDDM obtained an MSY with an 80% confidence interval of 21,510–23,118 t for this stock. Population parameters

and BRPs obtained from the SPM, BSPM, and CTDDM are shown in Table 2. The 80% confidence interval of MSY obtained from the CTDDM was 21510–23118 t for this stock. A simulation on the predicted biomass (or

numbers) from ASPM were carried out using fully age-structured information to compare with the CTDDM (Fig. 1). The Bayesian information criterion

(BIC) values for the BSPM, CTDDM, and SPM models were 81.36, 85.21, and 102.19, respectively (Table 3).

Table 3: Summary statistics for model selection results (using BIC) and the MSY estimates (80% confidence interval, CI) from the Fox SPM, BSPM, and CTDDM.

Model	BIC	Negative Log-likelihood
CTDDM	81.36	40.41
BSPM	85.21	42.53
Fox Model	102.19	50.19

	MSY estimates (80% CI)	MSY (80% CI) used by ICCAT
CTDDM	21 510-23 118	
BSPM	22 135-24 007	21 500-28 700
Fox Model	23 630-27 390	

Thus, the CTDDM provides a reliable prediction of BRPs for sustainable fisheries management comparable with that of the classical full stock assessment methods. The predicted biomass (or numbers) from the

CTDDM exactly tracked the fully age-structured (ASPM) simulation. The biomasses summed over age for the CTDDM precisely tracked the ASPM predictions as the age-time increment became smaller (Fig. 2).

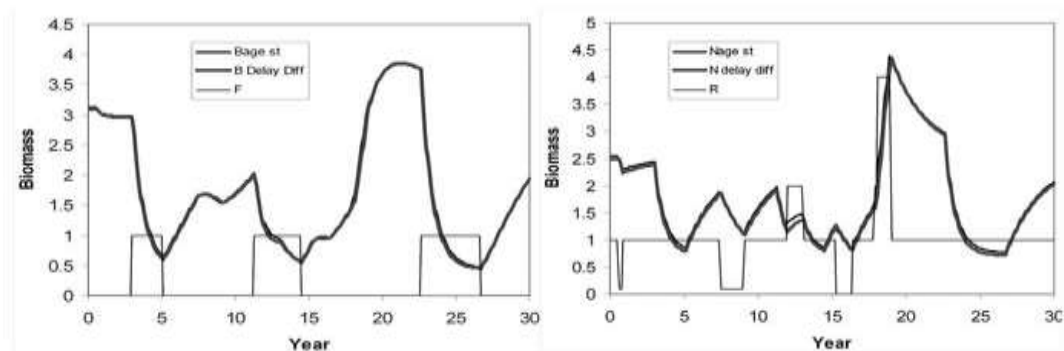


Figure 2: An example on how the continuous time delay-difference type model tracks the total biomass/numbers predicted from the fully age-structured ASPM accounting based on the simulated age-structured data (modified from Walters (2011)).

The CTDDM provided reliable prediction of BRPs for sustainable fisheries management, and used fewer data compared with ASPMs. The Bayesian information criterion (BIC) values for the BSPM, CTDDM, and SPM were 81.36, 85.21, and 102.19, respectively (Table 3). The BSPM fits exhibited a lower variance (i.e., the

expected log predictive density for a new data point) than that given by the CTDDM, and the expected $Lppds$ (i.e., log pointwise predictive densities) of the BSPM were higher than for the CTDDM. A comparison of the needful and optional data information in CTDDM vs. other stock assessments was shown in Table 4. CTDDM used

fewer data than DDM method in the analysis process, and provided reliable prediction of BRPs for sustainable fisheries management (especially

compared with ASPM, the advantages are more obvious) (Fig. 3).

Table 4: Summary statistics for the needful/optional data information in CTDDM vs. other stock assessments, and comparison of the estimated sustainable yields (e.g., B_{MSY}) using different methods for the subject fishery.

Model	Effort	Catch	k	B_1/k	r	q	Age
CTDDM	Optional	Needful	Optional	Optional	Needful	Optional	Optional
DDM	Optional	Needful	Optional	Optional	Optional	Optional	Needful
BSPM	Needful	Needful	Optional	Optional	Optional	Needful	Optional
ASPM	Needful	Needful	Needful/ Optional	Needful	Needful	Optional	Needful

B_{MSY} estimates	
CTDDM	14.35×10^4 t (CV=0.11)
DDM	15.50×10^4 t
ASPM	\
BSPM	$(12.40 \times 10^4$ t, 15.27×10^4 t)

Note: ASPM represents age-structured population model.

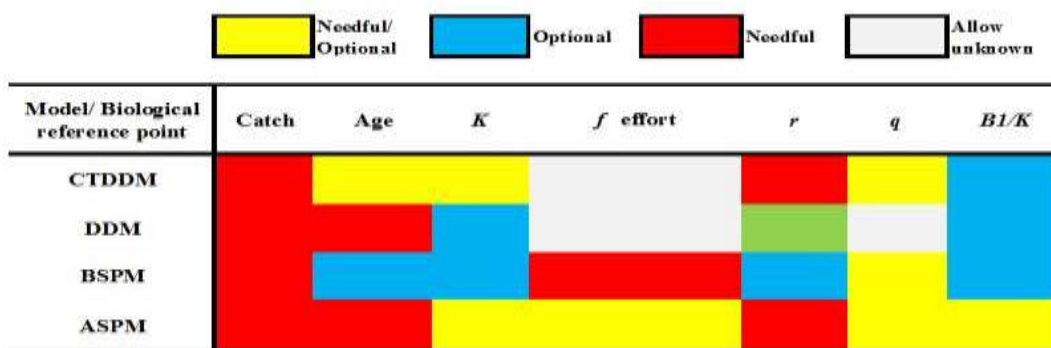


Figure 3: Summary statistics for the needful/optional data information in CTDDM vs. other stock assessments, and comparison of the estimated sustainable yields from these methods for the southern Atlantic albacore (*T. alalunga*) stock.

Discussion

The CTDDM treats recruitment, growth, and mortality rates as varying continuously over time and is considered a theoretical bridge between simple surplus-production models and complicated age-structured models (Walters, 2011). Hilborn and Walters (1992) concluded that a delay-difference model captured cyclic trends better than the Schaefer model for fitting catch and CPUE data to Pacific

cod, *Gadus macrocephalus* (Tilesius, 1810). Various models and approaches have previously been used to assess *T. alalunga* stock, including the SPM, BSPM, DDM, and ASPM (Yeh *et al.*, 1990; Sun *et al.*, 2002; Viñas *et al.*, 2004; Vrugt *et al.*, 2009; ISSF, 2012; ICCAT, 2013; Liao *et al.*, 2016a; Liao *et al.*, 2016b). A validation study showed that the CTDDM produced a realistic output for yield, biomass, and BRPs. The catch stabilized at about

30,000 t from 1988 to 2001, with a peak of 40,630 t, but has since declined to an average of 21,000 t over five years (Zhang *et al.*, 2015). Since the early 2000s, the southern Atlantic stock has been considered to have high potential for development. In the present study, CTDDM and BSPM obtained 80% confidence intervals for MSY of 21,510–23,118 t and 21,756–23,408 t, respectively.

Using an age-structured simulator to generate ‘true’ values is considered the most suitable way of validating the performance of the CTDDM model (Catalano and Allen, 2010; Cope, 2013; Liao *et al.*, 2016a; Lehodey *et al.*, 2017). The biomasses (or numbers) summed over age for the CTDDM did indeed track the ASPM’s predictions precisely as the age-time increment became smaller in the simulator. Simulations that were carried out using fully age-structured information exhibited a different influence on the estimated values of the parameters. With the Bayesian framework, it is relatively straightforward to calculate simultaneous credible intervals for multiple parameters, and to construct intervals around model predictions (Cowles and Carlin 1996; O’Hara and Sillanpää 2009; Wulff, *et al.*, 2012). A Bayesian approach has been increasingly used in ecological applications to quantify multiple sources of uncertainty (Chen *et al.*, 2000; Peterman *et al.*, 2003; Rivot *et al.*, 2004; Christensen and Walters, 2004; Vrugt *et al.*, 2009). The BSPM fits exhibited a lower variance (i.e., the

expected log predictive density for a new data point) than those given by the CTDDM, but the expected log pointwise predictive densities from the BSPM were higher than those from the CTDDM. The CTDDM provides an extremely compact and exact simulation of the dynamics of numbers and biomass for fish populations and produces reliable predictions of BRPs for sustainable fisheries management.

The main purpose of this study is to evaluate the capabilities of the CTDDM model, which is generally not familiar to the fisheries science community.. The CTDDM provides an extremely compact performance of the exact dynamics of numbers and biomass for the fish population, which is considered a theoretical bridge between SPMs and ASPMs. The CTDDM is not well known and has not previously been explored with respect to real fisheries. This study provides an interesting attempt to investigate its properties in a real-world application.

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