Iranian Journal of Fisheries Sciences 20(6) 1740-1756 2021
DOI: 10.22092/ijfs.2021.125487

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)

Liao B.[1]; Karim E.[2, 3*]

Received: June 2019 Accepted: November 2019

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*

1-Department of Mathematics, Shandong University, Weihai 264209, China
2-Bangladesh Fisheries Research Institute, Mymensingh 2201, Bangladesh
3-Fisheries College, Ocean University of China, Qingdao 266003, China
*Corresponding author's Email: ehsan_tony@yahoo.com

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 (We_k) and $k-1$ ($We_{(k-1)}$) 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) We_k=(1-k)(16.56-10.64k)/(1+1.88k+0.88(k^2)) dW/da = κ(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:

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

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

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

$$dW/da = \kappa(W_{\infty} - w(a)) \qquad (4)$$

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)+εC_t(Y, X). The sensitivity of λ (ε) in the perturbed model was defined as:

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

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

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):

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

$$\breve{I}_t = \begin{cases} q_t \sum_{p,k} S^*_{t,k} N_{p,t,k} e^{-\tau Z_{p,t,k}} \sum_{l} \phi_{p,k,l} S^*_{t,l} & \text{For } \textit{indexes} \text{ in } \textit{numbers} \\ q_t \sum_{p,k} S^*_{t,k} N_{p,t,k} e^{-\tau Z_{p,t,k}} \sum_{l} \phi_{p,k,l} S^*_{t,l} w_l & \text{For } \textit{indexes} \text{ in } \textit{mass} \end{cases} \qquad (14)$$

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; $\breve{I}$ 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):

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

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.

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

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:

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

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

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

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
$B_{MSY}/(10^4\text{t})$	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***	$\boldsymbol{R_{yeild}}$	$\mathbf{R^2}$
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_{vield} 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 form 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.

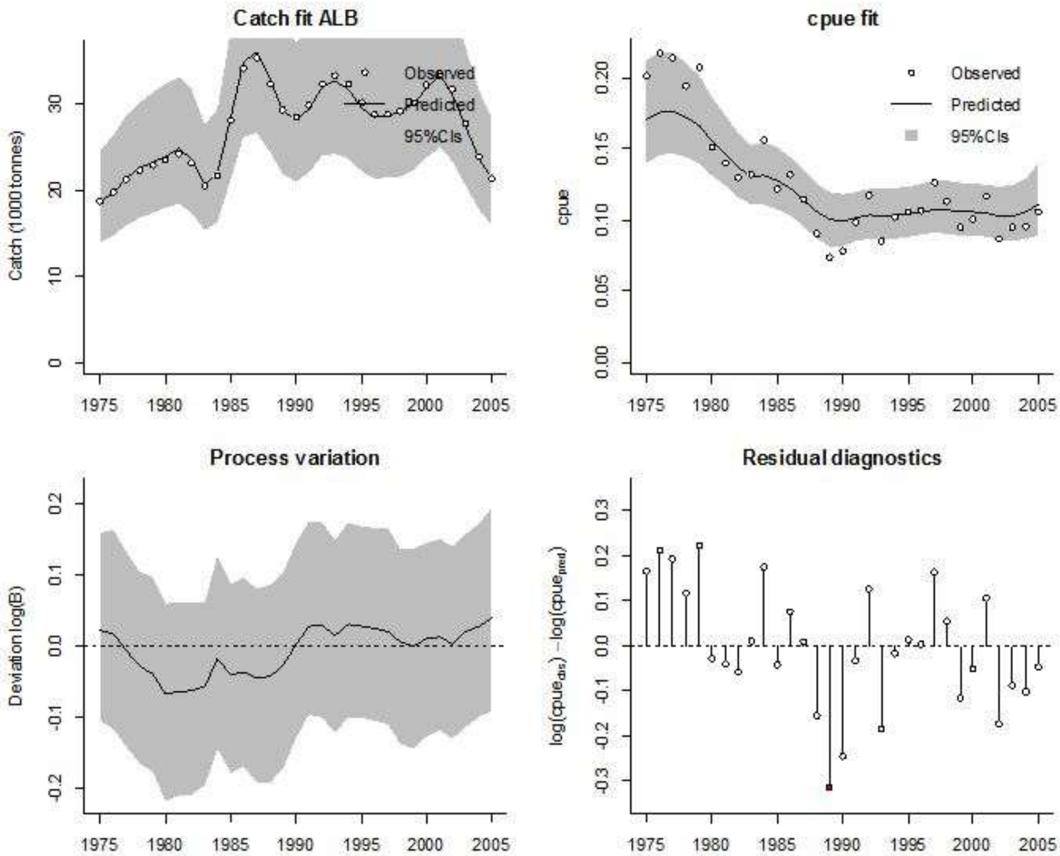

Figure 1: Analytical graph for BSPM analysis of the southern Atlantic albacore (*T. alalunga*) fishery, showing the fit of the predicted to the observed catch, the fit of predicted to the observed CPUE, the deviation from observed to predicted biomass, and an analysis of the log-CPUE residuals.

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).

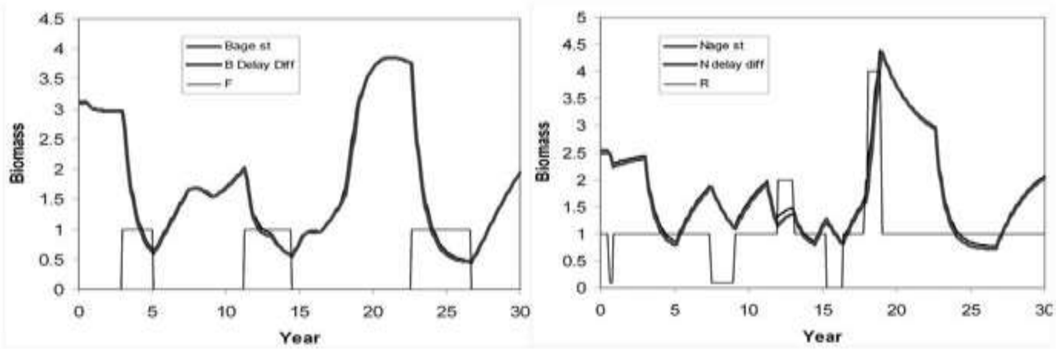

Figure 2: An example on how the continuous time delay-difference type model tracks the total biomass/numbers predicted from the fully age-structured ASPM accounting based on the simulated age-structured data (modified from Walters (2011)).

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 ×10^4 t, 15.27 ×10^4 t)						

Note: ASPM represents age-structured population model.

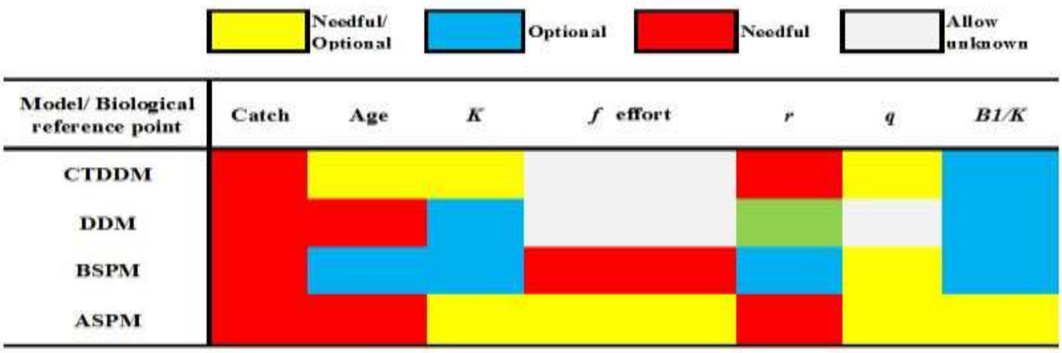

Figure 3: Summary statistics for the needful/optional data information in CTDDM vs. other stock assessments, and comparison of the estimated sustainable yields from these methods for the southern Atlantic albacore (*T. alalunga*) stock.

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 a 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.

Acknowledgement
This work was supported in part by the National Key RandD Program of China (Grant No. 2017YFE0104400), the Joint Funds of the National Natural Science Foundation of China (Grant No. U1806202), National Basic Research Program of China (Grant No. 2015CB453303), AoShan Talents Cultivation Program Supported by Qingdao National Laboratory for Marine Science and Technology (Grant No. 2017ASTCP-ES07), China Postdoctoral Science Foundation (Grant

No. 2017M612282), and Shandong Provincial Natural Science Foundation, China (Grant No. ZR201702060096). Specifically, we thank the Drs Harry Taylor, Yan Jiao and Qun Liu for their assistance on earlier drafts of the manuscript, and the two anonymous reviewers for their many helpful comments. We thank Dr. Xiujuan Shan, Dr. Sher Khan Panhwar, and Dr. Kui Zhang, for sharing their expertise on the research.

References

Allen Akselrud, C.I., 2017. Fisheries stock assessments for commercial Alaskan species, accounting for age-size-structured population dynamics (Doctoral dissertation).

Arlot, S. and Celisse, A., 2010. A survey of cross-validation procedures for model selection. *Statistics Surveys*, 4, 40-79.

Bowman, A.W. and Azzalini, A., 1997. Applied smoothing techniques for data analysis: the kernel approach with S-Plus illustrations (Vol. 18). OUP Oxford. pp.10-107

Brooks, S.P. and Roberts, G.O., 1998. Convergence assessment techniques for Markov chain Monte Carlo. *Statistics and Computing*, 8, 319-335. DOI:10.1023/A:1008820505350

Buckland S.T., Newman, K.B. and Thomas, L., 2004. State-space models for the dynamics of wild animal populations. *Ecological Modelling*, 171, 157-175.

Carruthers, T.R., Walters, C.J. and McAllister, M.K., 2012. Evaluating methods that classify fisheries stock status using only fisheries catch data. *Fisheries Research*, 119, 66-79. DOI:10.1016/j.fishres.2011.12.011

Catalano, M.J. and Allen, M.S., 2010. A size- and age-structured model to estimate fish recruitment, growth, mortality, and gear selectivity. *Fisheries Research*, 105(**1**), 38-45. DOI:10.1016/j.fishres.2010.03.002

Chen, Y., Breen, P.A. and Andrew, N.L., 2000. Impacts of outliers and misspecification of priors on Bayesian fisheries-stock assessment. *Canadian Journal of Fisheries and Aquatic Sciences*, 57, 2293-2305.

Christensen, V. and Walters, C.J., 2004. Ecopath with Ecosim: methods, capabilities and limitations. *Ecological Modelling*, 172(**2-4**), 109-139. DOI:10.1016/j.ecolmodel.2003.09.003

Collette, B.B., McDowell, J.R. and Graves, J.E., 2006. Phylogeny of recent billfishes (Xiphioidei). *Bulletin of Marine Science*, 79, 455–468. DOI:10.1139/f80-034

Cope, J.M., 2013. Implementing a statistical catch-at-age model (stock synthesis) as a tool for deriving overfishing limits in data-limited situations. *Fisheries Research*, 142(**6**), 3-14. DOI:10.1016/j.fishres.2012.03.006

Cowles, M.K. and B.P. Carlin, 1996. Markov chain Monte Carlo convergence diagnostics: a comparative review. *Journal of*

American Statistical Association, 91, 883-904. DOI:10.2307/2291683

Deriso, R.B., 1980. Harvesting strategies and parameter estimation for an age-structured model. *Canadian Journal of Fisheries and Aquatic Sciences*, 37, 268-282. DOI:10.1139/f80-034

Dichmont, C.M., Punt, A.E. and Deng, A., 2003. Application of a weekly delay-difference model to commercial catch and effort data for tiger prawns in Australia's Northern Prawn Fishery. *Fisheries Research*, 65, 335-350. DOI:10.1016/j.fishres.2003.09.024

Fournier, D.A. and Doonan, I.J., 1987. A length-based stock assessment method utilizing a generalized delay-difference model. *Canadian Journal of Fisheries and Aquatic Sciences*, 44, 422-437. DOI:10.1139/f87-051

Froese, R., Thorson, J.T. and Reyes, R.B., 2014. A Bayesian approach for estimating length-weight relationships in fishes. *Journal of Applied Ichthyology*, 30, 78-85. DOI:10.1111/jai.12299

Gelman, A. and Rubin, D.B., 1992. Inference from iterative simulation using multiple sequences. *Statistical Science*, 21, 457-472. DOI:10.1186/1471-2105-7-471

Gelman, A., Carlin, J.B., Stern, H.S. and Rubin, D.B., 2004. Bayesian Data Analysis. London: Chapman and Hall, 368 P.

Haddon, M., 2011. Modelling and Quantitative Methods in Fisheries, Second Edition, London: Chapman and Hall, 499 P.

Hall, N.G., 1997. Delay-difference model to estimate the catch of different categories of the western rock lobster (*Panuliruscygnus*) for the two stages of the annual fishing season. *Marine and Freshwater Research*, 48, 949-958. DOI:10.1016/j.fishres.2003.09.024

Han, C. and B.P. Carlin, 2011. Markov chain Monte Carlo methods for computing Bayes factors. *Journal of American Statistical Association*, 96, 1122-1132. DOI:10.1016/j.jmp.2011.06.004

Hilborn, R.M. and Walters, C.J., 1992. Quantitative Fisheries Stock Assessment: Choice, Dynamics and Uncertainty/ London: Chapman and Hall, 499 P.

Hilborn, R.M. and Mangel, M.M., 1997. The Ecological Detective: Confronting models with data. Monor. *Population Biology*, 28, 11-23. DOI:10.1016/j.jmp.2011.06.004

Hoggarth, D.D., Abeyasekera, S., Arthur, R., Beddington, J.R., Burn, R.W. and Halls, A.S., 2006. Stock assessment for fishery management: A framework guide to the stock assessment tools of the fisheries management and science programme. Food and Agriculture Org, pp. 261-268.

ICCAT (International Commission for the Conservation of Atlantic Tunas), 1999. Detailed report on albacore. *ICCAT*, *Collective Volume of Scientific Papers*, 49(**4**) 1–92.

ICCAT (International Commission for the Conservation of Atlantic Tunas), 2011. ICCAT Statistical Bulletin, Vol. 40. Madrid, Spain, 156 P.

ICCAT (International Commission for the Conservation of Atlantic Tunas), 2012. Report of the 2011 ICCAT south Atlantic and Mediterranean albacore stock assessment sessions. ICCAT, Madrid, Spain, 491 P.

ICCAT (International Commission for the Conservation of Atlantic Tunas), 2013. Report of the 2013 ICCAT north and south Atlantic albacore data preparatory meeting. ICCAT, Madrid, Spain 68 P.

ISSF (International Seafood Sustainability Foundation), 2011. Stock status ratings: status of the world fisheries for tuna Status of the world fisheries for tuna stock. ISSF Technical Report. 36 P.

Jensen, O.P., Gilroy, D.J. and Hogan, Z., 2009. Evaluating recreational fisheries for an endangered species: a case study of taimen, Huchotaimen, in Mongolia. *Canadian Journal of Fisheries Aquatic Sciences*, 66, 1707-1718. DOI:10.1139/F09-109

Jiao, Y., Hayes, C. and Corte´s, E., 2009. Hierarchical Bayesian approach for population dynamics modelling of fish complexes without species-specific data. *ICES Journal of Marine Science* 66, 367-377. DOI:10.1093/icesjms/fsn162

Jiao, Y., Reid, K. and Nudds, T., 2010. Consideration of uncertainty in the design and use of harvest control rules. *Scientia Marina*, 74, 371-384. DOI:10.3989/scimar.2010.74n2371

Kuikka, S., Vanhatalo, J., Pulkkinen, H., Mäntyniemi, S. and Corander, J., 2014. Experiences in Bayesian inference in Baltic Salmon management. *Statistical Science*, 29, 42-49. DOI:10.1214/13-STS431

Lee, L.K. and Yeh, S.Y., 2007. Age and growth of south Atlantic albacore-arevision after the revelation of otolith daily ring counts. *Collective Volumes of Scientific Papers - ICCAT*, 60(**2**), 443-456. DOI:10.1093/icesjms/fst093

Lehodey, P., Senina, I., Calmettes, B. and Titaud, O., 2017. Operational real-time and forecast modelling of Atlantic albacore tuna. Collective Volumes of Scientific Papers – ICCAT. 29 P.

Liao, B., Liu, Q., Wang, X., Baset, A., Soomro, S. H., Memon, A.M. and Kalhoro, M.A., 2016a. Application of a continuous time delay-difference model for the population dynamics of winter-spring cohort of neon flying squid (*Ommastrephes bartramii*, Lesueur 1821) in the North-west Pacific Ocean. *Journal of the Marine Biological Association UK*, 96(**7**), 1527-1534. DOI:10.1017/S00253154150018244

Liao, B., Liu, Q., Zhang, K., Baset, A., Memon, A.M., Memon, K.H. and Han, Y., 2016b. A continuous time delay-difference type model (CTDDM) applied to stock assessment of the southern Atlantic albacore *Thunnus alalunga*. *Chinese*

Journal of Oceanology and Limnology, 34(**5**), 977-984. DOI:10.1007/s00343-016-5126-x

Musick, J.A. and Bonfil, R., 2005. Management techniques for elasmobranch fisheries. FAO, Rome. 474 P.

O'Hara, R.B. and Sillanpää, M.J., 2009. A review of Bayesian variable selection methods: what, how and which. *Bayesian Analysis*, 4, 85-117. DOI:10.1214/09-BA403

Pallare, P. and Restrepo, V., 2003. Use of delay-difference models to assess the India bigeye stock. *IOCT Proceedings*, 6, 148-150. DOI:10.1016/j.fishres.2003.09.024

Pannell, D.J., 1997. Sensitivity analysis: strategies, methods, concepts, examples. *Agricultural Economics*, 16, 139-152. DOI:10.1016/0165-0114(93)90298

Pardo, S.A., Cooper, A.B., Reynolds, J.D. and Dulvy, N.K., 2014. Quantifying the known unknowns: estimating maximum intrinsic rate of population increase in the face of uncertainty. *Ices Journal of Marine Science*, 75(**3**), fsx220. DOI:10.1093/icesjms/fsx220

Penney, A.J., 1994. Morphometric relationships, annual catches and catch-at-size for South African caught South Atlantic albacore (*Thunnus alalunga*). *Collective Volumes of Scientific Papers - ICCAT*, 42(**1**), 371-382.

Peterman, R.M., Pyper, B.J. and MacGregor, B.W., 2003. Use of the Kalman filter to reconstruct historical trends in productivity of Bristol Bay sockeye salmon (*Oncorhynchus nerka*). *Canadian Journal of Fisheries Aquatic Sciences*, 60, 809–824. DOI:10.1139/F03-069

Prager, M.H., 2005. A stock production model incorporating covariates (Version.5) and auxiliary programs, CCFHR (NOAA) Miami laboratory document MIA-92/93-55. Beaufort Laboratory Document, BL-2004-01, pp. 12-55.

Quinn, T.J. and Deriso, R.B., 1999. Quantitative fish dynamics. New York: Oxford University Press, 542 P.

Rivot, E., Prevost, E. and Parent, E., 2004. A Bayesian state-space modeling framework for fitting a salmon stage-structured population model to multiple time series of field data. *Ecological Modelling*, 179, 463-485. DOI:10.1016/j.ecolmodel.2004.05.011

Robert, M., Faraj, A. and McAllister, M.K., 2010. Bayesian state-space modelling of the De Lury depletion model: strengths and limitations of the method, and application to the Moroccan octopus fishery. *ICES Journal of Marine Science*, 67(**6**), 1272-1290. DOI:10.1093/icesjms/fsq020

Schnute, J.T., 1985. A general theory for analysis of catch and effort data. *Canadian Journal of Fisheries Aquatic Sciences*, 42, 414–429. DOI:10.1139/cjfas-53-10-2157

Su, Z. and Randall, M.P., 2012. Performance of a Bayesian state-space model of semelparous species for stock-recruitment data subject to measurement error. *Ecological Modelling*, 224, 76-89. DOI:10.1016/j.ecolmodel.2011.11.001

Sun, C.L., Ehrhardt, N.M. and Porch, C.E., 2002. Analyses of yield and spawning stock biomass per recruit for the South Atlantic albacore (*Thunnus alalunga*). *Fisheries Research*, 56, 193-204. DOI:10.1016/S0165-7836(01)00320-4

Viñas, J., Bremer, J.R. and Pla, C., 2004. Inter-oceanic genetic differentiation among albacore (*Thunnus alalunga*) populations. *Marine Biology*, 145, 225-232. DOI:10.1007/s00227-004-1319-5

Vrugt, J.A., Ter Braak, C.J., Gupta, H.V. and Robinson, B.A., 2009. Equifinality of formal and informal Bayesian approaches in hydrologic modelling. *Stochastic Environmental Research and Risk Assessment*, 23, 1011-1026. DOI:10.1007/s00477-008-0284-9

Walters, C.J. and Martell, S.J., 2004. Fisheries Ecology and Management. New Jersey: Princeton University Press, 448 P.

Walters, C.J., 2011. The continuous time Schnute-Deriso delay-difference model for age-structured population dynamics. http://www.fisheries.ubc.ca/biblio/author/2. Accessed on 2020-11.

Walters, C.J., 2020. The continuous time Schnute-Deriso delay-difference model for age-structured population dynamics, with example application to the Peru anchoveta stock. This working paper is made available by the Institute for the Oceans and Fisheries, University of British Columbia, 2202 Main Mall, Vancouver, BC, V6T 1Z4, Canada Accessed on 2021-10

Wulff, F., Field, J.G. and Mann, K.H., 2012. Network analysis in marine ecology: methods and applications (Vol. 32). Springer Science and Business Media. pp. 3–12.

Yeh, S.Y., Liu, H.C. and Tsou, T.S., 1990. Assessment of the south Atlantic albacore resource by using surplus production models, 1967–1988. *Collective Volumes of Scientific Papers -ICCAT*, 31, 236-240. DOI:10.1016/j.fishres.2003.09.024

Zhang, K., Liu, Q. and Muhsan, A.K., 2015. Application of a Delay-difference model for the stock assessment of southern Atlantic albacore (*Thunnus alalunga*). *Journal of Ocean University of China*, 14(**3**), 557–563. DOI:10.1007/s11802-015-2517-0

Zhang, K., Li, J., Hou, G., Huang, Z., Shi, D., Chen, Z. and Qiu, Y., 2021. Length-based assessment of fish stocks in a data-poor, jointly exploited (China and Vietnam) fishing ground, northern South China Sea. *Frontiers in Marine Science*, 8, 718052. DOI:10.3389/fmars.2021.718052