



Biphasic versus monophasic growth curve equation, an application to common sole (*Solea solea*, L.) in the northern and central Adriatic Sea

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ABSTRACT

Traditionally, growth patterns are described as constant throughout life using von Bertalanffy's equation. However, a change in growth due to a reallocation of energy during an individual's lifespan is to be expected. Following this hypothesis, back-calculation measurements obtained from SoleMon survey data were used to fit and compare monophasic and biphasic growth curves for common sole in the northern and central Adriatic Sea. Moreover, individual variability in growth was considered through nonlinear mixed-effect models in which the individual parameters were considered as a random effect. The analyses performed in this study revealed systematic age-specific discrepancies in the monophasic curve and demonstrated that the fit of the biphasic curve was superior (Δ AIC: 329; Δ BIC: 310), confirming the theory that growth in size would decrease as a consequence of reproductive effort. Finally, since common sole is routinely assessed using models that rely on growth to derive assessment estimates and related management reference points, a stock assessment simulation was performed to compare the two growth alternatives. The results showed how the biphasic alternative was preferable to the conventional alternative and how the use of the monophasic pattern would result in an overly optimistic view of stock status (+40% in SSB/SSB_{target} and -35% in F/F_{target} compared to the biphasic pattern), thereby increasing the risk of overfishing.

1. Introduction

Fish growth is a consequence of the intake of energy and material resources from the environment, conversion into body mass, and allocation between maintenance, development, and reproduction (Carbonara et al., 2018; Meekan et al., 2006; Sibly et al., 2015). Specifically, growth depends on a complex interaction between energy allocation, foraging strategy, predation risk, reproductive behavior, short- and long-term density dependence effects and the incidence of senescence (Carbonara et al., 2022). It is common practice in fisheries science to describe the growth pattern using a monophasic function (such as the conventional von Bertalanffy's equation; von Bertalanffy, 1938) relying on the assumption of constant growth throughout life (Helsler and Lai, 2004; Pardo, Cooper, and Dulvy, 2013). This type of curve tends to be

straightforward to fit, and the approach has been particularly common and used for decades as standard descriptor of fish growth (Ricker, 1975; Froese, Pauly, 2022). However, this approach often results in a simplification of reality, and several criticisms have been raised. For example, the limited inferences on life history and ecological information and the energetic justification for this model are problematic (Quince et al., 2008; Wilson et al., 2017). In particular, the conventional monophasic function has proven unable to account for the energetic costs of maturation and reproduction (Day and Taylor, 1997), which in female fish could exceed 15% of somatic energy allocation (Shuter et al., 2005). An alternative approach that has been proposed is to fit a biphasic model that is capable of accounting for differential energy allocation at different ages (Day and Taylor, 1997; Lester et al., 2004; Charnov, 2008; Alós et al., 2010; Wilson et al., 2017). Although fitting a biphasic model

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can be more challenging, it has been proven to be statistically and biologically more valid than monophasic models (Lester et al., 2004; Alós et al., 2010; Moe, 2015). In the literature, there are a considerable number of studies on multistage or multiphase growth theory, according to which one or more changes in the growth parameter occur at some point during the life of an individual (Iles, 1974; Hernandez-Llamas and Ratkowsky, 2004; Rogers-Bennett and Rogers, 2016). In a review by Wilson et al. (2017), the authors summarized and analyzed the factors that lead to a different allocation of energetic costs between somatic growth and other bioecological processes. One of the key factors is direct or indirect reproductive investment (Day and Taylor, 1997; Lester et al., 2004; Manabe et al., 2018), which is based on the concept that sexual maturation should negatively affect growth (e.g., gonadal development, nesting, displaying, and metabolic costs of storing gonads). Other factors may be related to species genetics and physiology (Grønkvær, 2016), environmental drivers (Matthias et al., 2018), habitat changes (Laslett, Eveson and Polacheck, 2002; Tracey and Lyle, 2005), dietary changes (Paloheimo and Dickie, 1965; Soriano et al., 1992), or human exploitation (fishing pressure; Kraak et al., 2019; Carbonara et al., 2022). More likely, many of these factors participate as contributing causes (Enberg et al., 2012). Conventional growth models assume that population growth can be described by average growth parameters, but given natural variability, it is unrealistic to assume that individuals belonging to the same wild population follow the exact same growth trajectory (Smith et al., 1997; Pilling et al., 2002; Pardo, Cooper, and Dulvy, 2013). In fact, individual growth is the result of an interaction between potential growth (at the genetic level of the species) and environmental conditions and can vary from individual to individual (Carbonara et al., 2022). While traditional size-at-age observations are pulled together to fit an overall population growth curve (Haddon, 2011), individual growth trajectories can be back-calculated from the width of the annual increments recorded in the otoliths (Campana, 1990; Fossen et al., 1999). Assuming that each specimen is randomly sampled from the same population of individuals, maximum likelihood or Bayesian methods can be used to explicitly treat individual growth variation as a component of size-at-age variability (Lorenzen, 2016). Pooling data through a shrinkage process that combines population averages with individual data has been shown to produce more reliable and generally less variable estimates of growth parameters (Pilling et al., 2002).

Reliable modeling of fish growth is an essential component of many fishery stock status assessments (Reeves, 2003; Gebremedhin et al., 2021). Growth parameters are key factors in describing fish population dynamics affecting biomass production, natural mortality and fishing mortality (Lorenzen, 2000; Francis, 2016; Sampson, 2014; Gebremedhin et al., 2021). They are crucial for using size composition data in stock assessment, which, to date, remains more frequently available than age-frequency data (Lorenzen, 2016; Minte-Vera et al., 2016). In this context, the most accurate estimates of growth patterns are essential for performing short-term projections of stock status (Punt et al., 2008; Eero et al., 2015; Hüsey et al., 2016) and guiding decisions and management plans regarding future regulation of harvests (Hilborn and Walters, 1992; Lorenzen, 2016). Conversely, biased estimates can result in an overly optimistic or pessimistic view of stock status (Kuparinen et al., 2016; Stawitz et al., 2019), which in some extreme cases led stocks to collapse (Beamish and McFarlane, 1995; Liao et al., 2013). Most fish stock assessments treat growth with a firm focus on constant growth curves (Hilborn and Walters, 1992; Quinn and Deriso, 1999; Haddon, 2011). This is the case for common sole stock in the Adriatic Sea. The stock assessment is routinely performed by the General Fisheries Commission for the Mediterranean, hereafter GFCM, using an externally fixed conventional von Bertalanffy growth curve to convert length composition data into age within the model (FAO-GFCM, 2021). Nevertheless, in recent years, the sensitivity of management advice to variations in growth patterns has been demonstrated (Thorson et al., 2015), and the demand for comparative studies between the conventional curve and alternative formulations has consequently increased

(Minte-Vera et al., 2016). In this context, a more precise estimate of growth obtained by means of biphasic models could improve the use and interpretation of length–composition data in highly structured age-based stock assessments (Edwards et al., 2012; Methot and Wetzel, 2013). In line with this, the GFCM specifically requested further analyses regarding the exploration and application of the biphasic growth model for common sole in the Adriatic Sea (FAO-GFCM, 2021). Therefore, the study was divided into two parts: a growth analysis and a stock assessment application for common sole in the central and northern Adriatic Sea (GSA17). The aim of the first part was to detect potential differences in growth by comparing monophasic and biphasic von Bertalanffy growth functions and to examine them in terms of best fit on the observed data using back-calculated, length-at-age survey data. Individual growth variability was considered using a mixed-effect model. In the second part, an example of a practical application within common sole assessment models was presented to investigate the impact of the two growth patterns on main assessment outcomes and scientific advice.

2. Materials and methods

2.1. Species under analysis

The common sole (*Solea solea*; Linnaeus, 1758) is a demersal species that is particularly abundant on relatively low-depth sandy and muddy bottoms in the Mediterranean Sea and the North–Eastern Atlantic (Quéro et al., 1986). The species is commercially important in the northern and central Adriatic Sea (GSA17; FAO Geographical Sub-Area 17) (Vallisneri et al., 2000; Grati et al., 2013), where the stock is shared between Italy, Slovenia and Croatia, representing approximately 2000 tons and over 20 million euros in terms of landing value (FAO-GFCM, 2021). Spatial distribution data reveal that distribution is a function of age, with progressive migration of spawners from shallow coastal waters, characterized by a high concentration of nutrients, to deeper waters outside the western coast of Istria (Scarcella et al., 2014). In the Mediterranean Sea, reproduction of common sole occurs from December to May (Fisher et al., 1987). Within the framework of the SoleMon project, it has been observed that reproduction occurs from November to March in the central and northern Adriatic Sea. The literature reports that size at first sexual maturity in the Mediterranean is approximately 25 cm (Vallisneri et al., 2000), while more recent age-based maturity derived directly from data collected during the Adriatic Sea survey showed a shift in the proportion of mature fish from 28% to 78% between Age 1 and Age 2 (FAO-GFCM, 2019).

2.2. Sampling and age determination methods

All sole samples used in this study were collected during the *rapid* trawl surveys (SoleMon) conducted in the northern and central Adriatic Sea by the National Research Council (CNR-IRBIM, Italy) in cooperation with the National Institute for Environmental Protection and Research (ISPRA, Italy), the Institute of Oceanography and Fisheries (IOF, Croatia), and the Fisheries Research Institute of Slovenia (FRIS, Slovenia). The survey was selected because it was specifically designed to provide a representative sample of the entire GSA17 stock. Common sole otolith sampling was divided into three areas – stations south of Ancona, north of Ancona, and in international waters – to maximize the coverage of its spatial distribution and involved collecting 10 otoliths per cm class in each area. Sampling design and technical features are detailed in reference papers and manuals (Grati et al., 2013; Anonymous, 2019; ICES, 2019). A dataset of 563 individuals collected between 2014 and 2020 (TL: 72–380 mm) was available for this study.

For age estimation, the right sagitta of each specimen was selected to be transversely sectioned down to the core. The otoliths were burned in a muffle furnace at 350 °C for 10 min. Thereafter, burned otoliths were embedded in resin (Crystalbond 509 Amber), ground on abrasive paper and polished with alumina powder. The burning technique was used to

improve the quality of the observations by enhancing the contrast of the growth rings (Panfili et al., 2002). Sections were immersed in fresh water and viewed under a stereomicroscope (Leica DM4000B) with reflected light against a black background (10x magnification). Images of the sections were taken using a charge-coupled device camera (Leica DFC 420) connected to a digitized computer video system (Leica Application Suite 4.3.0).

To analyze the relationship between total fish length and otolith size, radius length (R_{cpt}) was measured in the entire dataset (Fig. 1). The images from individuals with a total length (TL) ≥ 270 mm who were aged at least 4 years old were analyzed to measure opaque rings distances from the core (R1, R2, R3, etc.; Fig. 1), which are relevant for the back-calculation aging process discussed in the next paragraph. The a priori decision to focus on adult fish was made in order to obtain as balanced a sample size per annual ring as possible and to avoid poor fitting due to a large number of fish for which fewer age observations than parameters were available (e.g., Alós et al., 2010). Moreover, focusing on adult fish, for whom interannual growth had begun to decrease, can provide a more reliable estimate of asymptotic body sizes (Kuparinen et al., 2016). Finally, considering flatfish sexual dimorphism and the lack of male specimens, the subset was restricted to 38 females only (271–370 mm; age maximum of 15 years). Fig. 2 shows the spatiotemporal distribution of this final dataset by sampling station and year. Common sole in the Adriatic Sea is characterized by an opposite pattern of deposition compared to other fishes in temperate and cold waters: an opaque ring in winter/spring and a transparent ring in summer/autumn (Froglia and Giannetti, 1985). One opaque and one transparent ring are considered an annual growth (annulus) (Carbonara and Follesa, 2019). Considering the ring deposition pattern and the spawning period (autumn-winter), the age at each opaque growth increment was assigned as follows: 1st increment 0.5 years (age 0+); 2nd increment 1.5 years (age 1+); 3rd increment 2.5 years (age 2+); and so on. Image processing and age-related measurements were conducted by adhering to the workflow recommendations of the open-source R package *RfishBC* (Ogle, 2022. *RfishBC*. R package Version 0.2.4.9000, <https://doi.org/10.5281/zenodo.6058214>).

2.3. Growth analyses

Back-calculation allows to infer the length of a fish at previous ages from the width of the annual increments recorded in the otoliths (Campana, 1990; Fossen et al., 1999). However, only when there is a strong relationship between otolith length and fish body length is it possible to reconstruct individual growth trajectories through back-calculation techniques (Pilling et al., 2002).

Lengths at age were back-calculated using the Fraser–Lee method (Fraser, 1916; Lee, 1920). The method's underlying concept is that the growth increment of the calcified structure (ratio of R_i to R_{cpt}) is, on average, a constant proportion of the growth increment in length of the fish (ratio of L_i to L_{cpt}).

$$L_i = a + (L_{cpt} - a) \frac{R_i}{R_{cpt}} \quad (1)$$

where R_i and L_i are the radius and length at age i , respectively, R_{cpt} and L_{cpt} are the radius and length at the time of capture, respectively, and a is the intercept of the fitted “L-on-R” linear regression. An alternative nonlinear relationship hypothesis was also tested, but there was no evidence to reject the simpler model. Models comparison and validation are shown in the Supplementary Materials (S.1.1).

To account for individual variability, the back-calculated, length-at-age data were fitted to a nonlinear mixed-effect model of longitudinal data (Pilling et al., 2002; Alós et al., 2010) using the modern and efficient stochastic approximation maximization (SAEM) algorithm (Delyon, Lavielle, and Moulines, 1999; Kuhn and Lavielle, 2005). This algorithm is considered a state-of-the-art method for fitting nonlinear models and is available as an open-source R package available on CRAN (Comets et al., 2017). The use of mixed-effect models makes it possible to take into account both population parameters (fixed effects) and interindividual variability, treating the parameters for each individual as a random effect. For the purpose of this study, growth trajectories were summarized by two different von Bertalanffy (VB) growth models: a monophasic form based on three parameters (Eq. (2); hereafter VB 3-par) and a biphasic implementation that allows for a change in the growth parameter at a specific moment of the lifespan (Eq. (3); hereafter VB 5-par).

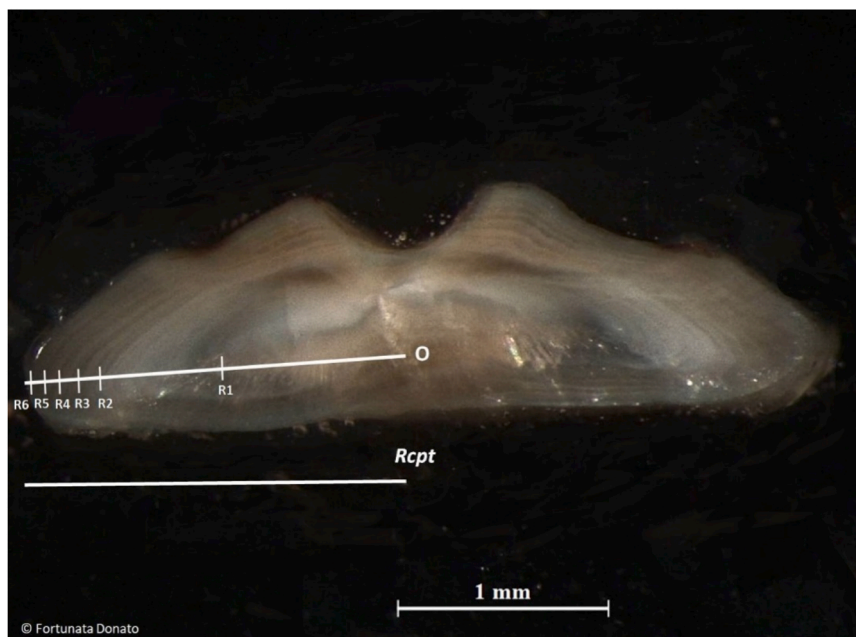


Fig. 1. Sagittal otolith of a 6-year-old common sole. Definition of the measurements taken during the aging process: radius length (R_{cpt}) and the distance of opaque rings from the core (R1, R2, R3, etc.).

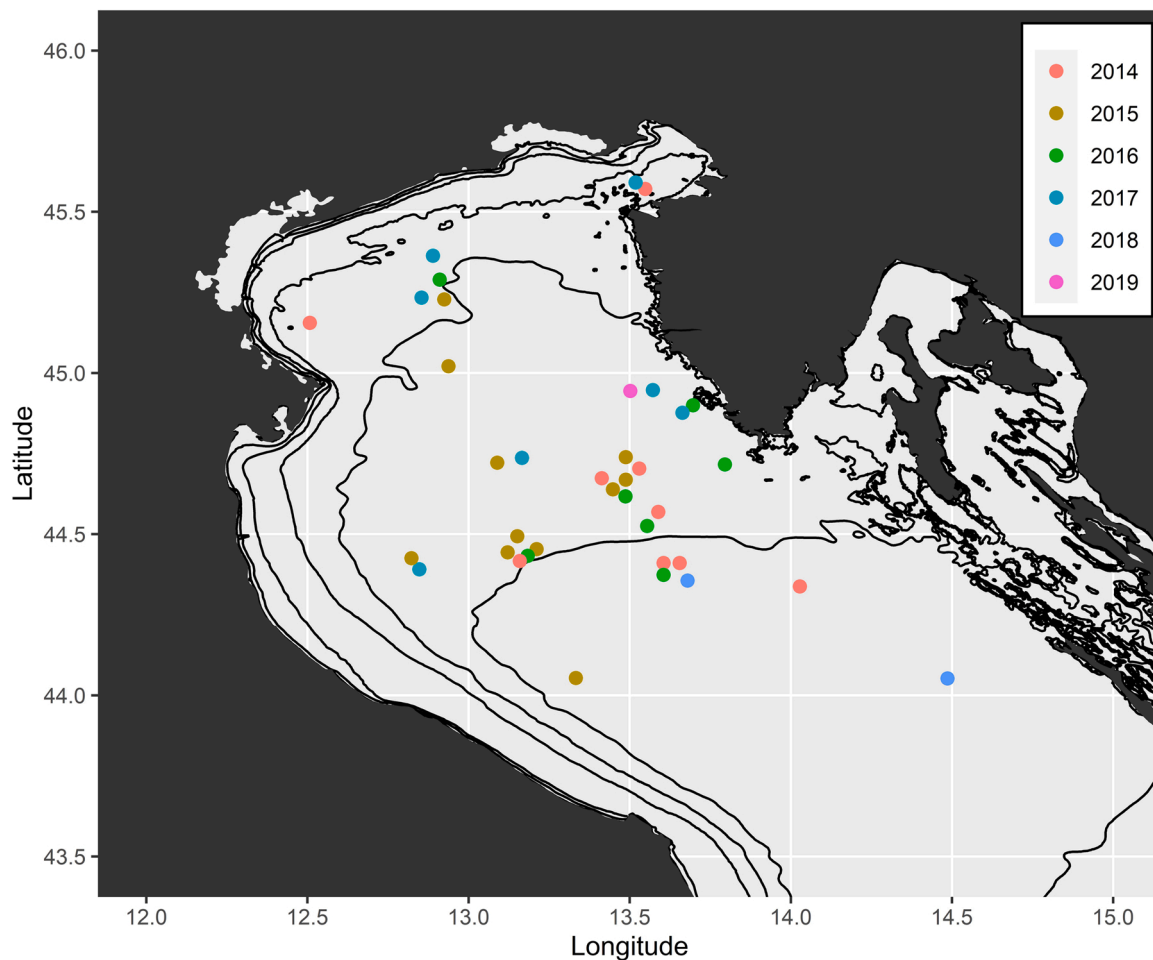


Fig. 2. Spatiotemporal distribution of back-calculated individuals by year from the SoleMon survey in the northern-central Adriatic Sea. Colors correspond to different years.

$$L_{ij} = L_{\infty i} (1 - \exp(-k_i(t_{ij} - t_{0i}))) + \varepsilon_{ij} \tag{2}$$

where L_{ij} is the size of fish i at age j , $L_{\infty i}$ is the asymptotic length of fish i , k_i is the intrinsic growth rate of fish i , t_{ij} is the age j of fish i , t_{0i} is the time when the size of fish i is zero, and ε_{ij} is a normally distributed error.

$$L_{ij} = L_{\infty i} (1 - \exp(-k_{0i}(t_{ij} - t_{0i}))) + \varepsilon_{ij} \text{ for } t_{ij} < t_{1i} \tag{3}$$

$$L_{ij} = L_{\infty i} (1 - \exp(-k_{0i}(t_{1i} - t_{0i}) - k_{1i}(t_{ij} - t_{1i}))) + \varepsilon_{ij} \text{ for } t_{ij} > t_{1i}$$

where k_{0i} and k_{1i} are the growth parameters before and after the time of growth change (t_{1i}).

In the models, the individual parameters were derived by applying a transformation to the random parameters sampled from a multivariate normal distribution (Comets et al., 2017). In this case, we applied the logarithmic function for L_{∞} , k_0 , k_1 and t_1 (to ensure positive values) and the identity function for t_0 (to allow for negative values). To optimize convergence, initial values for the population parameters (fixed effects) were provided considering the plausibility of the specie's life histories (Froese, Pauly, 2022) and information from previous analyses (i.e., FAO-GFCM, 2021): 380 mm for L_{∞} , 0.3 years^{-1} for k_0 , -0.5 years for t_0 , 0.2 years^{-1} for k_1 and 1.8 years for t_1 . However, since nonlinear optimization algorithms are known to be quite sensitive to starting values, a sensitivity analysis on initial values of the parameters was performed on the 5-par VB parametrization. Alternative values tested were: + 20% and - 20% of the abovementioned initial values and the female growth parameters from Vallisneri et al. (2000) (available only for L_{∞} , k_0 and t_0). Model validation and selection between the two alternative growth

formulations were based on visual inspection of individual prediction residual plots, in which predictions are computed using the conditional mode of the parameter's distribution (or maximum a posteriori; MAP) and normalized prediction distribution errors (NPDE), a simulated residual specifically adapted to nonlinear mixed-effect models (Brendel et al., 2006; Comets et al., 2017). Moreover, models were compared using the Akaike information criterion (AIC) and the Schwarz's information criterion (BIC). The model that minimized both estimators was retained as the best growth function. Finally, a comparison with a model without random effects (fitted by a nonlinear least-squares model) was performed on the biphasic formulation to test and verify the foreseen improvement in parameter estimation due to the intrinsic ability of the mixed-effect model to explicitly account for and treat individual variation in growth. All growth analyses were implemented in the R statistical software (Core Team, 2022) using the *saemix* library. Full details of the SAEM algorithm's R implementation can be found in Comets et al. (2017).

2.4. Stock assessment application

The same assessment model used in the FAO-GFCM working group (Stock Synthesis, SS; Methot and Wetzel, 2013) was used to compare and discuss the potential effects of applying the two growth curves (3-par vs. 5-par VB) on estimates of management quantities. Stock Synthesis is programmed in the ADMB C++ software and searches for the set of parameter values that maximize the goodness-of-fit, then calculates the variance of these parameters using the inverse Hessian matrix and

provides estimates for biomass, recruitment, fishing mortality and selectivity. For practical reasons, the overall model structure was kept the same as the reference model of the ensemble grid used during the last FAO-GFCM benchmark session in 2021 (FAO-GFCM, 2021). The model configuration and setting are presented in detail in the [Supplementary Materials](#) (S.2.1), together with a summary of the input data and functional forms used. The SS models used were a one-area yearly models in which the population consisted of 20+ age classes (with age 20 representing a plus group) with sexes combined (males and females were considered together). The models relied on historical GSA17 landings data from 1958 divided by fleet, while tuning data were provided by the SoleMon survey (Table S.2.1.1 in the [Supplementary Materials](#)). Numbers at length in the fleets and survey data were converted into ages within the model using the von Bertalanffy growth model. Following the configuration of the benchmark reference run, time-invariant dome-shaped selectivity was set for all fleets. Natural mortality was based on the average value of vectors by age from Gislason and Chen Watanabe, and the steepness of the stock-recruitment relation was fixed at 0.9 (Table S.2.1.2 in the [Supplementary Materials](#)). The only major changes made for the purposes of this study were the fixed-growth parameters L_{∞} , k_0 and k_1 , which, based on the growth pattern being analyzed, were replaced within each SS model with those resulting from the growth analyses conducted in this study (at the population level). The change in growth in the biphasic model was handled through a specific SS option that allows the user to create age-specific k multipliers from a certain age onward. However, since the software does not enable the use of intermediate ages (i.e., $t_1 = \text{age } 1.5$), the change in growth was approximated to age = 2. Specifically, the k_0 value was used for the juvenile phase, while the ratio between intrinsic growth rates was used as a multiplier of k_0 from Age 2 onward ($k_1/k_0 = 0.35 \text{ year}^{-1}$; see Table S.2.1.2 in the [Supplementary Materials](#)). Finally, the CVs of old individuals were set so that the 95% distribution of length-at-age around the estimated SS growth curve matched as closely as possible the individual L_{∞} distributions obtained from the growth analyses. A selection of multiple diagnostic tests (i.e., the diagnostic toolbox described by [Carvalho et al.,](#)

2021) was used to compare and select the best model. The procedure is based on the following four properties as objective criteria for evaluating the plausibility of a model: model convergence and likelihood, fit to the data (run-test and joint residuals), model consistency (retrospective analysis), and prediction skill (hindcasting). The results were examined in terms of estimates of spawning-stock biomass (SSB) and fishing mortality and their ratio to reference points (internally estimated by the SS model and calculated as 40% of the virgin biomass; FAO-GFCM, 2021). The R package *ss3diags* (github.com/JABBAmodel/ss3diags) was used to produce all diagnostic plots and tables related to the stock assessment application.

3. Results

3.1. Growth analyses

The analyses presented in Section S.1.1. of the [Supplementary Materials](#) validated the existence of a linear relationship between total fish length (L_{cpt}) and otolith size at the time of capture (R_{cpt}) ($r^2 = 0.91$, $p \text{ value} < 0.001$). As the $p \text{ value}$ of the intercept was also significant, the Fraser–Lee (FRALE) method was confirmed as the most appropriate method and was used to back-calculate length-at-age data from otoliths. The back-calculated individual growth trajectories are shown in [Fig. 3](#). In addition, plots by year of sampling and age-at-sampling have been added to the [Supplementary Materials](#) (Section 1.2). The colored points of the curves represent the intersection between each annulus measured on the otolith and the back-calculated fish-length value at that time. [Table 1](#) reveals a large fish-length increment between Age 0+ and Age 1+ (67 mm) followed by a stabilization of growth (12 mm on average from Age 2+ onward). This is consistent with the hypothesis of a biphasic growth pattern, in which young individuals grow faster in youth than in adulthood. The standard deviation showed more instability from Age 10+ onward due to the smaller number of data points. Although both 3-par and 5-par VB curves were successfully fitted without major convergence issues in the models, the fit to the data was

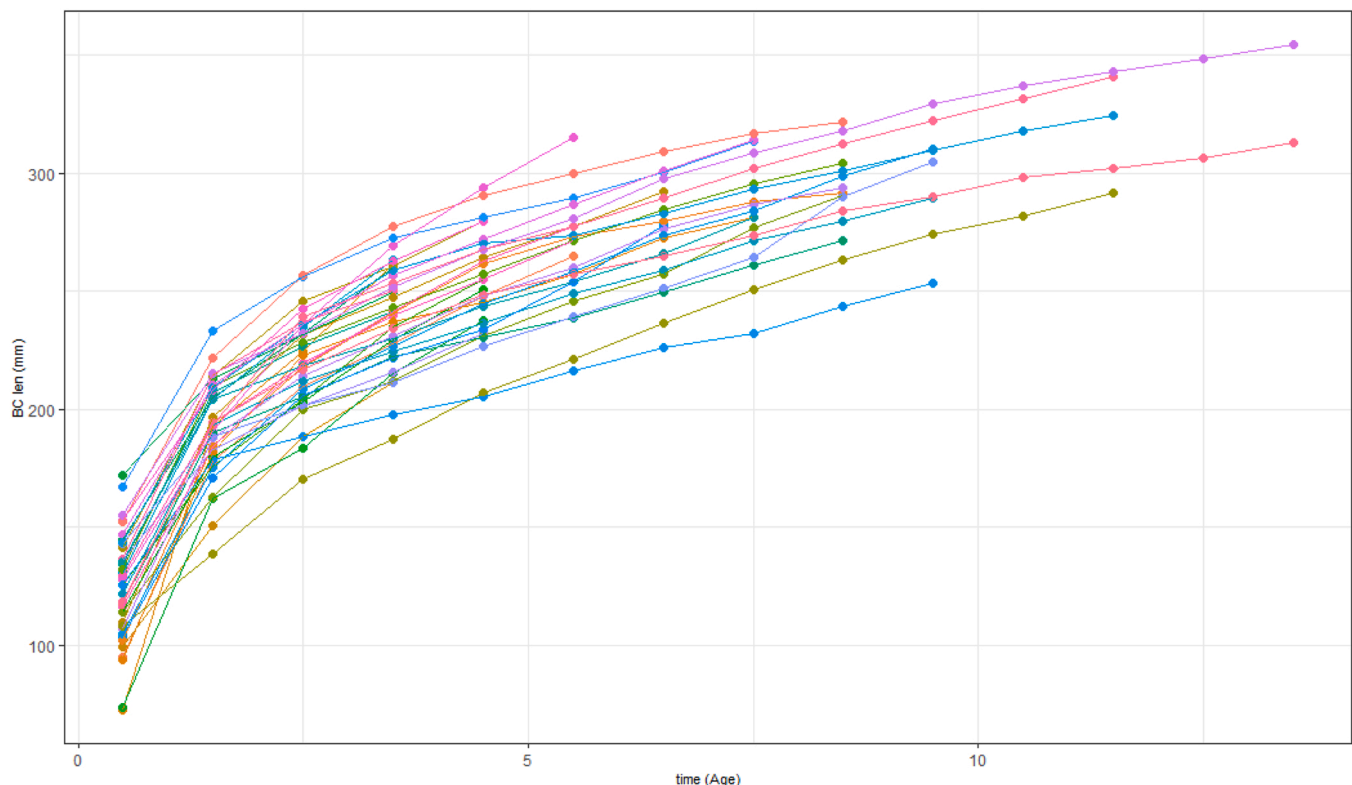


Fig. 3. Individual growth trajectories of common sole back-calculated from the otoliths.

Table 1

Mean back-calculated length for each growth increment for common sole analyzed in the study. SD = standard deviation. MLI = mean length increment between subsequent annual rings (e.g., the back-calculated TL at the 2nd annual ring minus the back-calculated TL at the 1st annual ring, etc.).

N annuli	Reference age	N specimens	Mean length (mm)	SD	MLI (mm)
1	0+	38	124	22.9	-
2	1+	38	192	19.9	68
3	2+	38	219	19.7	27
4	3+	38	239	21.1	20
5	4+	32	252	22	13
6	5+	25	264	22.8	12
7	6+	21	274	21.8	10
8	7+	19	284	22.4	10
9	8+	15	291	20.8	7
10	9+	9	298	23.9	7
11	10+	5	313	23	15
12	11+	5	321	22.9	8
13	12+	2	328	29.7	7
14	13+	2	334	29.4	6

appreciably superior in the biphasic formulation (e.g., ID: 5479; Fig. 4 and Figure S.1.11.1 in the Supplementary Materials). All model diagnostics performed revealed a systematic discrepancy in the 3-par VB (Figures S.1.10.1 and S.1.10.2 in the Supplementary Materials), which is absent in the 5-par formulation (Figures S.1.5.1 and S.1.5.2 in the Supplementary Materials). In particular, the NPDE boxplot showed that the conventional 3-par model had a clear tendency to underestimate Age 1+ and late ages while overestimating intermediate ages (Fig. 5, left side). This error in predicting length-at-age data leads to an overestimation of t_0 (more negative value) and an underestimation of L_∞ . On the other hand, the 5-par VB had no specific trends (Fig. 5, right side). Moreover, model selection by statistical criteria identified the 5-par VB model as the optimal one (Δ AIC: 329; Δ BIC: 310, Table 2), confirming the systematic discrepancy produced by the 3-par VB model. Table 2 list the current value and relative coefficient of variation (CV%) for each parameter effect estimated in the models. All fixed parameters were well estimated, with coefficients of variation below 15%, while the variation around the estimates of the random effects was higher than 30% for both

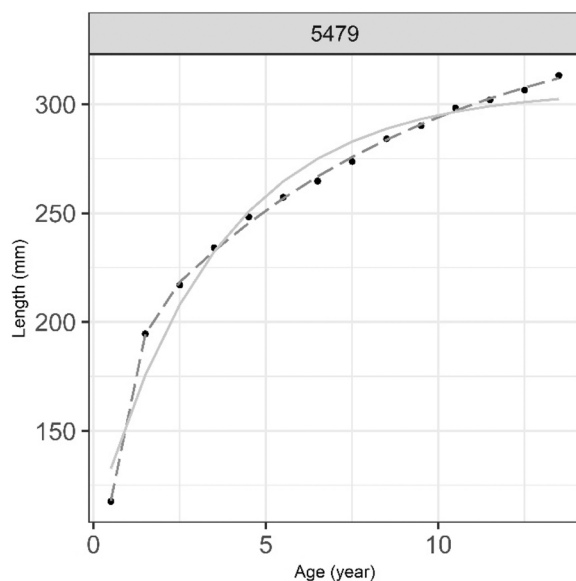


Fig. 4. Individual maximum a posteriori (MAP) predictions for a 13+ year old specimen (ID: 5479). The black dots correspond to observed back-calculated lengths-at-age, the light gray line corresponds to the monophasic von Bertalanffy growth model (3-par VB), and the dark gray dashed line corresponds to the biphasic model (5-par VB).

models. Nevertheless, the standard errors of the in-common fixed effect were smaller in the 5-par VB mixed-effect formulation than in the nonlinear least-square alternative (Section S.1.7 in the Supplementary Materials), advocating the use of a model that included random effects. Although sensitivity analysis revealed small changes in model estimates when alternative sets of initial values were used, the set chosen for the final analysis had the lowest log-likelihood (Table S.1.6.1 in the Supplementary Materials). The distributions of individual growth parameters are shown in Fig. 6. Specifically, L_∞ was lower in the 3-par VB than in the 5-par VB (Fig. 6a; 5-par VB: 307–462 mm, 3-par VB: 253–360 mm). The parameter t_0 varied between -1.42 and 0.05 for the 5-par VB, and between -2.58 and -0.21 for the 3-par VB (Fig. 6b). The parameter t_1 , responsible for the inflection point of the biphasic growth curve, varied from 0.85 to 2.11 years (Fig. 6c). Finally, in terms of intrinsic growth rate, the individual estimates of k_0 using the 5-par VB ranged from 0.14 to 0.51 year^{-1} , whereas estimates based on the 3-par VB, ranged from 0.15 to 0.71 year^{-1} (Fig. 6e). Moreover, the growth rate after the inflection point of the biphasic growth curve (k_1) ranged from 0.04 to 0.3 year^{-1} . Considering the biphasic growth pattern, a general decrease in growth rate from k_0 to k_1 was observed after t_1 (Fig. 6f; ratio k_1/k_0 : 0.13 – 0.82 year^{-1}). Finally, random effects correlation matrices are reported in the Supplementary Materials (Figures S.1.4.1 and S.1.9.1). The analysis showed an overall quite strong correlation among the individual parameters in both growth formulation alternatives. In terms of the relationship between L_∞ and intrinsic growth rate, both k_0 ($r^2 = -0.75$, $p \text{ value} < 0.001$ in 5-par VB; $r^2 = -0.47$, $p \text{ value} < 0.01$ in 3-par VB) and k_1 ($r^2 = -0.53$, $p \text{ value} < 0.001$) showed a strong negative correlation. Moreover, L_∞ and t_0 were slightly negatively correlated ($r^2 = -0.64$, $p \text{ value} < 0.001$ in 5-par VB; $r^2 = -0.49$, $p \text{ value} < 0.01$ in 3-par VB). The parameters k_0 and t_0 showed a positive correlation in both alternatives ($r^2 = 0.61$, $p \text{ value} < 0.001$ in 5-par VB; $r^2 = 0.85$, $p \text{ value} < 0.001$ in 3-par VB). The two intrinsic growth rate parameters, k_0 and k_1 , showed a positive correlation ($r^2 = 0.49$, $p \text{ value} < 0.01$). It is interesting to note that there was no significant correlation between the growth inflection point t_1 and other parameters.

3.2. Stock assessment application

For both SS models (3-par VB and 5-par VB), the convergence gradient was relatively small ($< 1.00E-04$), and the Hessian matrix for the parameter estimates was positively definite (Table 3). The total likelihood of the 5-par VB model was lower than that of the 3-par VB model (167.01 vs. 224.95; $\Delta = 57.94$). More specifically, the difference between the two models was driven by the component of the fit to length data (189.81 vs. 245.06; $\Delta = 55.21$), with the values related to survey and trawl fleet data being significantly lower in the 5-par VB (Table 3). This was confirmed by the LFD plots, in which a slight improvement in model fit was detectable by passing from the three-parameter to the five-parameter growth curve (Figure S.2.2.1 in the Supplementary Materials). The diagnostic tests showed a general improvement in scores when moving from the three to the five parametrizations. The most notable difference was in the model consistency, in which the estimated 3-par VB Mohn's indices for both retrospective (ρ_M) and forecast projections (ρ_F) were above the threshold, indicating an undesirable retrospective pattern for both SSB and fishing mortality (Table 3). Despite detecting no change in the trends of the time series, the 3-par VB model showed a more optimistic status of the stock, characterized by a higher biomass and a lower fishing mortality than the 5-par VB model. This was confirmed by examining the estimates in relation to reference points, in which the increase of the 3-par VB value compared to the 5-par VB value was approximately 40% for SSB (SSB/SSB_{target} : 1.39 for 3-par VB and 0.97 for 5-par VB in 2019; Fig. 7a) and the decrease of F was approximately 35% (F/F_{target} : 0.57 for 3-par VB and 0.87 for 5-par VB in 2019; Fig. 7b).

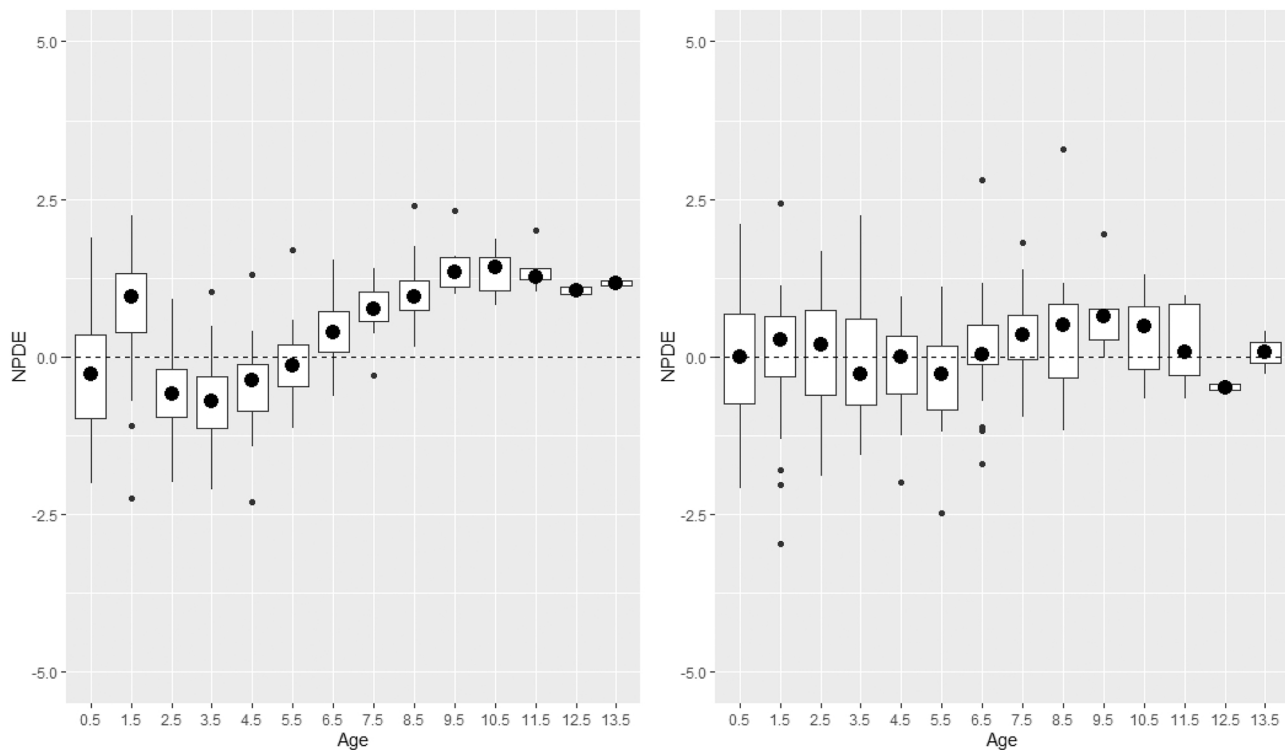


Fig. 5. Normalized prediction distribution errors (NPDE) based on 3-par VB (left) or 5-par VB growth curves (right). The dots are the median values, the boxes are the 25th and 75th percentiles, and the bars are the minimum and maximum nonoutlier values, while the single black dots are the outlier values.

Table 2

Comparison of parameter estimates between monophasic and biphasic von Bertalanffy growth curves. CV: coefficient of variation. AIC and BIC: statistical criteria used in model selection.

Model	Effect	L_{∞} (CV%)	k_0 (CV%)	t_0 (CV%)	k_1 (CV%)	t_1 (CV%)	AIC	BIC
3-par VB	fixed	302 (1.7)	0.35 (6.8)	-1.19 (9.74)	NA	NA	2298	2314
	random	0.01 (32.6)	0.12 (32.8)	0.38 (30.7)	NA	NA		
5-par VB	fixed	397 (3.6)	0.31 (7.4)	-0.76 (9.3)	0.11 (10.5)	1.5 (4.61)	1969	2004
	random	0.02 (46.7)	0.09 (44.1)	0.13 (31)	0.20 (42.5)	0.05 (33.6)		

4. Discussion

In this study, we evaluated and compared two different growth model formulations based on von Bertalanffy’s equation for common sole in the northern-central Adriatic Sea (GSA 17): the conventional three-parameter formulation (3-par VB), which assumes constant growth throughout fish life, and the biphasic alternative (5-par VB), which instead separates the growth into two phases based on the assumption of the reallocation of energy during the individual’s lifespan (Lester et al., 2004; Rogers-Bennett and Rogers, 2016). In agreement with the results presented for other species with similar growth patterns (Alós et al., 2010; Minte-Vera et al., 2016), our analyses confirmed that a biphasic model provided a better fit to length-at-age data for both younger and older ages than the conventional monophasic formulation (Δ AIC: 329; Δ BIC: 310). Using the 3-par VB model, diagnostic plots showed systematic age-specific discrepancies at both the individual and population levels, resulting in a severe underestimation of L_{∞} . This was driven by the assumption of constant intrinsic growth. Conversely, L_{∞} from the biphasic model was more biologically appropriate, displaying a better fit to length-at-age data for older ages and effectively reflected real sampled values in the northern and central Adriatic Sea (i.e., maximum TL: 39.3 cm in survey data, 43 cm in commercial data; Masnadi et al., 2021). The more reliable estimate of asymptotic length was due to the biphasic model’s ability to accommodate rapid growth in the early years (with the growth parameter k_0) and a sharp decline in growth

(with the growth parameter k_1) that occurs after the age of change (t_1), confirming that different growth parameter values are needed for juveniles and adults (Boukal et al., 2014). This change in growth, which occurs approximately in the middle of the second year of life (1.5 year) for Adriatic sole, also allows for a better estimation of t_0 , leading to a better fit to length-at-age data for younger ages. According to the theory that growth would decrease as a consequence of reproductive effort (Lester et al., 2004; Charnov, 2005), the value of t_1 estimated by the biphasic model was consistent with the spatial distribution studies conducted in the Adriatic. Survey data clearly showed a segregation between Age Groups 0–2, primarily characterized by sexually immature specimens occupying shallow coastal waters, and the rest of the mature population migrating toward deeper waters (Scarcella et al., 2014). Parameter correlations from biphasic models were similar to those from monophasic models and were in agreement with previous studies (Helser and Lai, 2004; Minte-Vera et al., 2016; Mollet et al., 2010). Interestingly, the two growth rates of the equation (k_0 and k_1) showed a positive correlation, indicating that a fish displaying fast juvenile growth will also have a high-growth parameter after maturation. However, there was no correlation with the inflection time t_1 , corroborating the hypothesis that sexual maturation seems to be a specific characteristic of the population rather than an individual trait. This may be more related to other factors, such as changes in habitat and diet that occur during the ontogenetic coast-offshore migration of the species (MediSeH - Mediterranean Sensitive Habitats et al., 2013). High

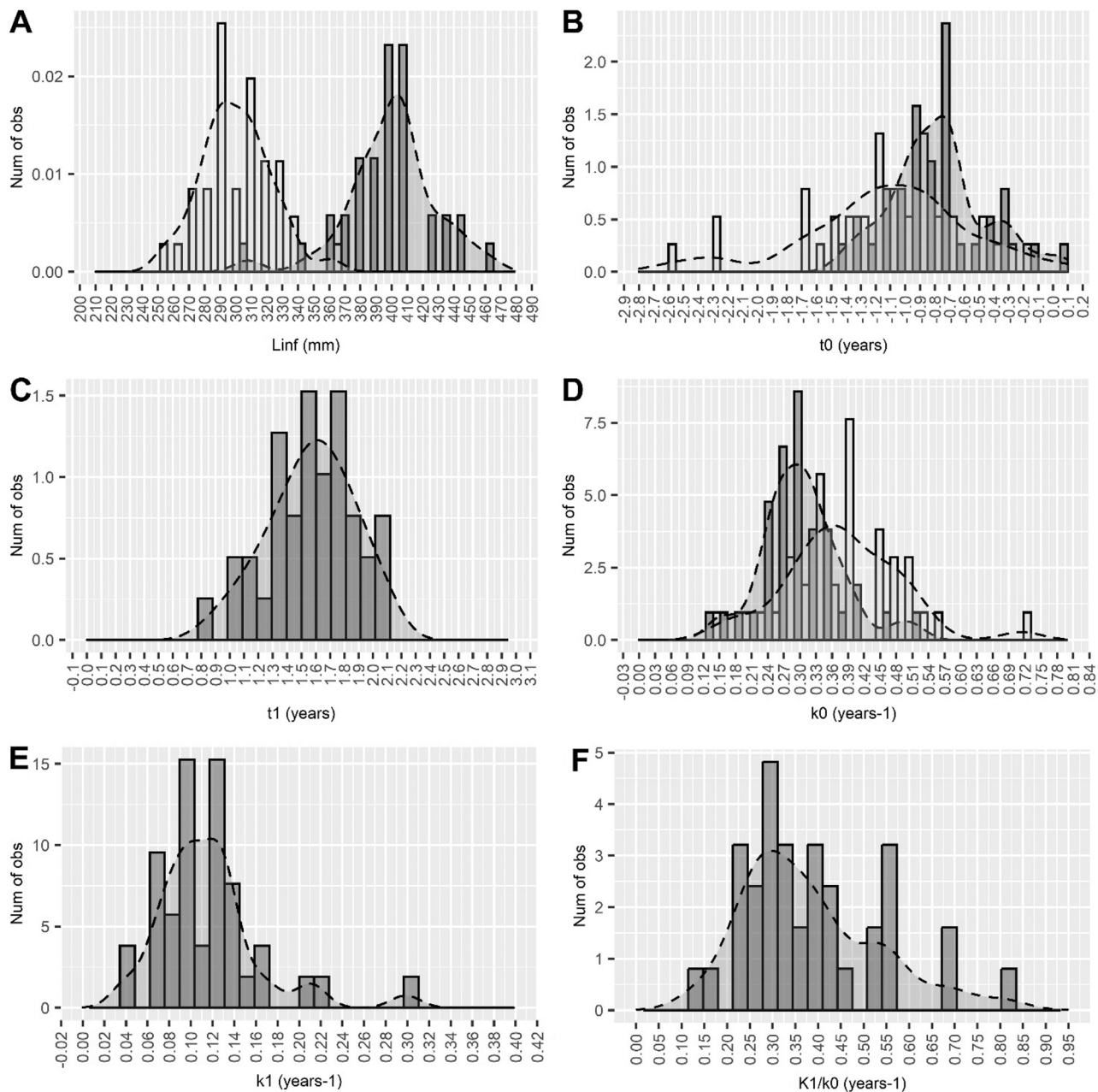


Fig. 6. Frequency distribution of individual parameters from the SAEMIX nonlinear mixed-effect model obtained using the conditional mode of the parameter distribution (or maximum a posteriori; MAP): a) L_{∞} estimated from 3-par and 5-par von Bertalanffy growth models; b) t_0 estimated from 3-par and 5-par von Bertalanffy growth models; c) t_1 estimated from the 5-par von Bertalanffy growth model; d) k_0 estimated from 3-par and 5-par von Bertalanffy growth models; e) k_1 estimated from the 5-par von Bertalanffy growth model; and f) ratio of k_1/k_0 calculated for the 5-par von Bertalanffy growth model. The light gray color corresponds to the monophasic von Bertalanffy growth model (3-par VB), the dark gray color corresponds to the biphasic model (5-par VB).

estimates of among-individual variation in growth parameters should not be viewed as a problem. In fact, studies conducted in the Adriatic Sea have shown a high degree of variability in the growth rate of common sole in general: some specimens grow by 2 cm in one month, while others of the same age group need an entire year to do so (Piccinetti and Giovanardi, 1984). In contrast, the advantage of a mixed-effect model is that it assumes that the estimated growth parameters for each fish in the population represent a subsample of the growth parameters characteristic of the population (Pilling et al., 2002). In this sense, a mixed-effect model applied to back-calculation data (multiple observations of the same individuals over their lifespan) grant the possibility of explicitly considering individual variation in growth as a random effect in the model. As a result, comparison with the method in which no random

effect was considered showed an improvement in the precision of population parameter estimates when individual variability was considered, confirming once again the importance and benefits deriving from such an approach. Comparing growth data from previous studies on the species, mean lengths-at-age obtained from the biphasic formulation fell within the general variability found in the Mediterranean area and in particular in the GSA17 (Vallisneri et al., 2000; Fabi et al., 2009; FAO-GFCM, 2021; see Table S.1.12 in the Supplementary Materials). However, an increase in the difference in mean length with age was found between the biphasic curve reported in this study and the others reported in the literature. The interpretation of the growth bands in common sole can be prone to several sources of error, including the presence of false growth increments and overlapping growth bands in

Table 3

Diagnostic table following the procedure proposed by [Carvalho et al. \(2021\)](#). *Convergence and likelihood*: the final convergence gradient must be relatively small (e.g., < 1.00E-04), and the Hessian matrix for the parameter estimates must be positively definite; the total likelihood of the SS model consists of a number of components, including the fit to the survey index, fishery length frequency data and catch data. *Fit to the data*: run test for residual as judged by the p values computed for each series; the joint-residual indicates a good fit to the data if the RMSE (root mean square error) is less than 30%. *Consistency*: both ρ_M and ρ_F are measures of average bias over the years under evaluation. Following a “rule of thumb” by [Hurtado-Ferro et al. \(2015\)](#), values should fall within a range of – 0.15–0.20 for the longest-lived species. *Prediction skill*: the hindcasting cross-validation technique compares observations with their predicted future values. MASE values lower than one indicate that forecast values under consideration performed better than a naïve baseline. Colors denote the test’s pass (green) or fail (red) according to the above criteria.

		Diagnostic components	3-par VB	5-par VB
Convergence and likelihood	Convergence	Final convergence	2.80E-05	6.69E-05
		Positive Hessian matrix	Yes	Yes
	Likelihood components	Total	224.95	167.01
		Catch	9.90E-12	3.76E-11
		Equil_catch	1.47E-13	7.38E-12
		Survey	-20.1	-20.46
		Recruitment	-0.01	-2.38
		InitEQ_Regime	2.33E-31	2.23E-31
		Length_comp Total	245.06	189.85
		Len_GNS_ITA	38.41	48.88
		Len_TBB_ITA	18.14	17.85
		Len_GTR_HRV	7.21	3.11
		Len_OTB_ITA	41.82	36.46
		Len_DRB_HRV	0.94	0.83
		Len_SoleMon	138.53	82.73
Fit to the data	Run test	Survey Index	Passed	Passed
		Len_GNS_ITA	Passed	Passed
		Len_TBB_ITA	Passed	Passed
		Len_GTR_HRV	Passed	Passed
		Len_OTB_ITA	Passed	Passed
		Len_SoleMon	Passed	Passed
	Joint-residuals	Survey Index	16	15
		Length	3.6	3.2
Consistency	Retrospective analysis	Retro_SSB	0.30	-0.04
		Forecast_SSB	0.27	-0.03
		Retro_F	-0.18	0.03
		Forecast_F	-0.18	0.09
Prediction skill	Hindcasting (MASE)	MASE Index_Survey	0.84	0.58
		MASE GNS_ITA	0.13	0.13
		MASE TBB_ITA	0.27	0.22
		MASE GTR_HRV	0.13	0.17
		MASE OTB_ITA	0.58	0.58
		MASE Len_Survey	0.30	0.26

older specimens ([Carbonara et al., 2018](#); [Etherton et al., 2019](#)). The variability in age data could be due to ecological, physiological, and genetic variability, but it could also be the result of underrepresentation of small or large individuals in the sample ([Neves et al., 2022](#)), different age schemes ([Carbonara and Follesa, 2019](#)), otolith preparation methods ([Smith et al., 1997](#)), age criteria ([Hüssy et al., 2016](#)) and reader

experience ([Kimura and Lyons, 1991](#); [Carbonara et al., 2019](#)), or a combination of all of the above. For example, the use of only adult specimens leads to a greater risk of occurrence of the so-called "Rosa Lee effect", according to which, in historically heavily exploited stocks (such as the one in question), the removal of faster-growing individuals by selective fishing translates into a population dominated by

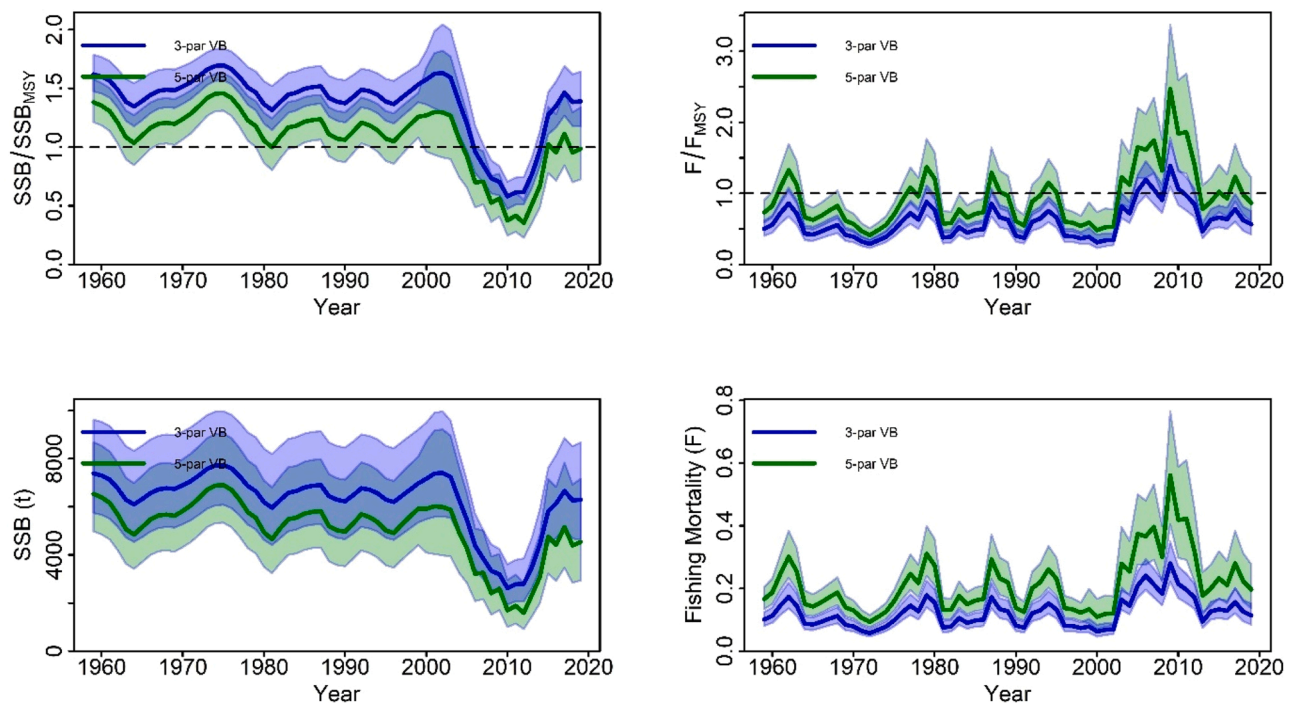


Fig. 7. Comparison of stock status trajectories based on Stock Synthesis assessment models: a) biomass outcomes in absolute value (SSB) and relative to the reference point (SSB/SSB_{target}); and b) fishing mortality outcomes in absolute value (F) and relative to the reference point (F/F_{target}). The blue line represents the 3-par VB model results, while the green line represents the 5-par VB results. Shaded areas represent the 95% confidence intervals.

slower-growing individuals (Lee, 1912). Ignoring this demographic effect would most likely lead to an underestimation of the true average growth parameters of the population under analysis. In a simulation framework, this phenomenon has been proven to introduce bias in the estimation of relevant quantities used for fishery advice (Kraak et al., 2019). Another precondition that may reduce result's reliability was the assumption that the back-calculation procedure produced length-at-age measurements without error. In fact, even with the use of standardized and semi-automated reading processes (i.e., the *RfishBC* R package) by trained experts, the possibility of observation error is very plausible. According to growth theory, length variability should be lower among younger individuals and then increase with age. In contrast, the observed range of growth trajectories shown in this study remains fairly constant and independent of age. This is probably the result of more uncertain measures for annuli that are further away from the age of capture, since back-calculation did not undergo any validation process. However, a full validation process using direct, semidirect or indirect methods (Campana, 2001) requires considerable effort and must be properly designed with this as a central goal (Vigliola and Meekan, 2009; Carbonara et al., 2018). Error propagation related to the back-calculation method could be investigated with the help of a much larger dataset and more readers. Moreover, in a situation in which data are lacking for very old individuals, such as most historically overfished stocks in the Mediterranean Sea, L_{∞} is more susceptible to strong reliance on model structure and data on younger fish. This suggests that the true value of the asymptotic length may be different from that estimated using this constrained dataset. In this context, it is even more important to promote the choice of a biphasic model structure that has been proven to be statistically sound in comparison to the conventional one. Aware of the limitations presented, the results remain valid when contextualized in relation to the comparison between the monophasic and biphasic growth equations, which remains unrelated to the age validation per se. Indeed, since the two alternative models were fitted to the same dataset, the comparison is independent of possible sources of error deriving from the procedure used to derive the age backwards.

As a final step of this study, a simplified stock assessment comparison

was performed on the Adriatic sole stock to quantify and discuss the effects of the two alternative growth models (monophasic vs. biphasic) on the stock assessment outcomes. To our knowledge, this is one of the first attempts to analytically analyze the effect of biphasic growth implementation in a highly structured stock assessment model such as Stock Synthesis. While emphasizing that this study's objective was not to provide management advice for the species under analysis, the results presented here confirmed that incorrect growth specifications within integrated models can have a significant impact on biomass and fishing mortality estimates. In age-based assessment models that rely on size observations, in which growth parameters are used to better fit the expected length composition to the observed length data and to translate them into population numbers-at-age, this change in growth pattern can directly affect biomass estimates (Maunder and Piner, 2015) and related management reference points, such as spawning stock biomass at MSY (Lorenzen, 2016). In this particular case, a higher mean length of the oldest age in the 5-par VB (i.e., due to a higher L_{∞}) caused the estimated relative abundance of the oldest ages to decrease to fit the length composition of the largest fish. This phenomenon led to an increase in the estimated fishing mortality and, consequently, a lower estimate of SSB (Maunder and Piner, 2015). It is important to remember that the reduction in abundance of the oldest ages is not always associated with higher fishing mortality but can also be explained by the appearance of cryptic biomass that can be the result of the selectivity pattern used (Maunder and Piner, 2015). Despite this, the use of the same dome-shaped selectivity in both models ruled out the possibility that it played a substantial role in the observed disparities. Even if there were no drastic differences between the diagnostics of the two models, retrospective analyses clearly indicated a lack of predictive ability of the 3-par VB formulation. This, along with the improvement in the likelihood component, confirmed and reinforced the results of the previous conducted growth analyses, which clearly demonstrated how the biphasic curve was statistically and biologically more appropriate than the conventional curve. In relation to reference points, the analyses showed that the 3-par VB estimate would result in a substantial overestimation of 40% of SSB/SSB_{target} and an underestimation of 35% of

F/F_{target} providing an overly optimistic view of stock status. This indicates that the use of a monophasic growth pattern would critically underestimate the risk of overfishing compared to a biphasic growth pattern. These findings are consistent with studies demonstrating that reference points are highly sensitive to biological parameters (Maunder, 2012) and, in particular, to asymptotic length (Aires-da-Silva et al., 2015). However, how the growth component affects results can vary differently based on data availability, assessment model choice and assumptions about process submodels (Lorenzen, 2016). It is therefore important to contextualize these results specifically for the type of assessment model under discussion. Models based purely on age observation may be affected differently by growth misspecification than models based on size-composition observation (i.e., the type presented in this paper). Moreover, according to the assessment models' descriptions, only the growth pattern was changed in the parameterization of the two models compared to the reference run used during the FAO-GFCM benchmark assessment conducted in 2021 (Masnadi et al., 2021). In this regard, it has been demonstrated that, the use of fixed steepness and natural mortality values, may introduce bias into the estimated derived quantities of interest (Mangel et al., 2013). In this sense, a simulation study conducted by Thorson et al. (2015) highlighted that the sensitivity of reference points to changes in growth parameters was higher than that of recruitment parameters but smaller than that of natural mortality. More in-depth studies conducted with the use of operating models in a proper simulation framework (e.g., the *ss3sim* R package by Anderson et al., 2014) would be preferred and recommended.

5. Conclusion

Although the results are quite regional (Adriatic Sea) and being aware of the abovementioned caveats and limitations of the study, we believe that the comparison between the two sets of VB parameters presented herein is sufficient to provide general information, indications, and food for thought, leading to a more careful selection of growth alternatives when building up specific cases of stock assessment models. Despite being a simplification, our analyses confirmed that, due to the greater flexibility of the biphasic model, a more precise estimate of the growth curve, particularly for older ages, can have a substantial impact on stock assessment results and scientific advice. This is especially true in management contexts in which biomass estimates are used to calculate total allowable catches (TACs) for subsequent years (e.g., the ICES advisory framework). As a final suggestion, stock assessment experts should give greater consideration to the use of biphasic growth curves in size-based assessment models when, on a case-by-case basis, they have proven to have a better fit than traditional curves.

CRedit authorship contribution statement

Francesco Masnadi and Pierluigi Carbonara conceived, designed and developed the study. Francesco Masnadi implemented the growth and stock assessment analyses with the assistance of Massimiliano Cardinale for setting up the SS models. Fortunata Donato, Laura Sabatini, and Giulio Pellini provided otolith readings and biological information. Giuseppe Scarcella supervised and organized the SoleMon survey. Francesco Masnadi and Pierluigi Carbonara wrote the manuscript with contributions from all authors. All the authors examined the results and contributed to the revision.

Declaration of Competing Interest

The authors declare that they have no known competing financial interests or personal relationships that could have appeared to influence the work reported in this paper.

Data availability

Data will be made available on request.

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Appendix A. Supporting information

Supplementary data associated with this article can be found in the online version at [doi:10.1016/j.fishres.2023.106694](https://doi.org/10.1016/j.fishres.2023.106694).

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