

FABIO FIORENTINO, VITA GANCITANO, SALVATORE GANCITANO,  
PIETRO RIZZO & SERGIO RAGONESE

AN UPDATED TWO-PHASE GROWTH MODEL FOR DEMERSAL  
FISH WITH AN APPLICATION TO RED MULLET  
(*MULLUS BARBATUS* L., 1758) (*Perciformes Mullidae*)  
OF THE MEDITERRANEAN

SUMMARY

The appropriateness of using the von Bertalanffy model to describe the growth of fishes throughout their lifecycle has been repeatedly questioned in both historical and recent fishery literature. The main criticism is that juveniles and adults grow at different rates, which cannot be expressed by a unique function. On the basis of knowledge gathered in the Mediterranean, a new growth model for demersal fish is proposed, adapting previous biphasic and size-at-maturity-dependent models. According to this new model, young of the year and early immature juveniles (j) and adults (a) tend to the same asymptotic size ( $L_{\infty} = L_{\max \text{ ever}}$ ), but follow two distinct growth trajectories characterized by a decreasing completion rate ( $K_j > K_a$ ). According to findings of literature, the individual length at maturity ( $L_{m50}$ ) is assumed to be the point of discontinuity. The new two-phase growth model is illustrated using data for red mullet, *Mullus barbatus*, L., 1758 from the Central Mediterranean.

*Parole chiave:* Pesci demersali, modello di crescita bifasico, Mar Mediterraneo

RIASSUNTO

Un aggiornamento del modello di crescita bifasico per i pesci demersali, con un'applicazione alla triglia di fango (*Mullus barbatus* L., 1758) del Mediterraneo. L'adeguatezza del modello di Von Bertalanffy nella descrizione della crescita dei pesci è stata più volte messa in discussione in letteratura. Sulla base delle conoscenze acquisite nel Mediterraneo, si propone un nuovo modello di crescita bifasico per i pesci demersali, utilizzando come taglia di variazione del tasso di crescita quella corrispondente alla maturità sessuale ( $LM_{50}$ ). Il modello assume che i giovanili (j) e gli adulti (a) tendano alla stessa dimensione asintotica ( $L_{\infty} = L_{\max \text{ ever}}$ ), seguendo due fasi di accrescimento distinte, caratterizzate da un tasso di crescita decrescente ( $K_j > K_a$ ). Il modello di crescita proposto, applicato alla triglia di fango, *Mullus barbatus*, L., 1758 del Mediterraneo centrale, viene discusso alla luce delle note incongruenze tra conoscenze biologiche e risultati del modello di Von Bertalanffy nella descrizione della crescita dei pesci.

*Key words:* Demersal fish, biphasic growth model, Mediterranean Sea

## INTRODUCTION

The difficulty of applying a unique, one-phase, growth curve to the whole lifecycle of an *iteroparous* fish is well known. Many studies have shown that growth rates vary throughout the lifecycle (larvae, post larvae, young of the year, immature juveniles and adults). The periods in which growth rates are relatively constant are called “*stanzas*” (Vasnetsov in RICKER, 1979), and the final “*stanza*” usually begins during the achievement of sexual maturity (JONES, 1989; DAY & TAYLOR, 1997; STAMPS *et al.*, 1998; PORCH *et al.*, 2002; TRACEY & LYLE, 2005; ARAYA & CUBILLOS, 2006; CHARNOV 2008; QUINCE *et al.*, 2008a,b).

Almost all the proposed biphasic (and even multi-phase) growth models, however, have requirements that are almost never met by Mediterranean demersal fish, which are characterized by a short recruitment/juvenile period and a quick rarefaction of the adult fraction of the stock due to a chronic although steady state of growth overfishing (MAYNOU & LEONART, 2003).

This article presents a new approach for describing the growth of Mediterranean demersal stocks, which integrates the theoretical aspects of the discontinuous models and might allow the computation of growth parameters that are more coherent with the biology and resilience of the stocks.

To illustrate our approach we used a dataset containing the mean length-at-age of the red mullet, *Mullus barbatus*, L., 1758. This species was chosen since there is general agreement in the literature that the VBGF model provides a good fit for fish older than age group 2 and excessively large negative values of  $t_0$  (VOLIANI *et al.*, 1998; BIANCHINI & RAGONESE, 2011; CADDY, 2009).

## THE BIPHASIC GROWTH MODEL

The new growth model (herein NGM) is based on the most general parameterization of a two-phase von Bertalanffy growth function (cf. CRAIG, 1999; PORCH *et al.*, 2002):

$$L_t = \begin{cases} L_\infty (1 - e^{-K_j(t-t_{0j})}) & \text{with } t < t_p \\ L_\infty (1 - e^{-K_a(t-t_{0a})}) & t \geq t_p \end{cases}$$

$$\text{and } t_p = \frac{K_a t_{0a} - K_j t_{0j}}{K_a - K_j}$$

within the NGM, where:

- $L_t$  is the mean length (total length, TL) of a given age class (year,  $y$ ).
- $L_\infty$  is the asymptotic length herein defined as the longest possible length ( $L_{\max \text{ ever}}$ ) a fish will achieve if it continued to live and grow infi-

nately under the given conditions (BEVERTON & HOLT, 1957; RICKER, 1958, 1975). This is assumed to be the result of phylogeny, in other words, the genetically driven or pre-recorded growth programme (cf. PAULY, 1984; FREEDMAN & NOAKES, 2002) and is constant for a given species/stock in a given environment, and independent from food availability, water temperature and fishing pressure (BEVERTON, 1987; MANGEL & ABRAHAMS, 2001; REZNICK *et al.*, 2002). In the model  $L_{\infty}$  is fixed at the largest documented size of the species ( $L_{\infty} = L_{\max \text{ ever}}$ ).

- $K$  is the rate of approach to  $L_{\infty}$ , or the rate of completion of the growth pattern (BEVERTON & HOLT, 1959); the NGM assumes a  $K_j$  for young of the year and juveniles and a  $K_a$  for maturing and adult specimens. Both completion rates makes no assumptions about dependence on food availability in a given temperature regime (BEVERTON & HOLT, 1957, 1959; BEVERTON, 1987; MANGEL & ABRAHAMS, 2001; REZNICK *et al.*, 2002; SHIN & ROCHET, 1998; LORENZEN & ENBERG, 2001).
- $t_{0j}$  and  $t_{0a}$  represent the theoretical age at zero length according to the VBGF for juveniles and adults, respectively;  $t_{0j} \sim 0$  (CADDY, 2009) and  $t_{0j} \ll t_{0a}$  are expected.
- $t_p$  is the age at which the transition from  $K_j$  to  $K_a$  occurs;  $t_p \sim t_m$  is expected (BEVERTON, 1992; DAY & TAYLOR, 1997; STAMPS *et al.*, 1998; CRAIG, 1999), where  $t_m$  indicates the age corresponding to the length at 50% of sexual maturity ( $L_m$ ).

#### THE FITTING OF THE MODEL PARAMETERS

To fit the biphasic VBGF defined above, two sets of lengths-at-age of red mullet (*Mullus barbatus*, L., 1758) females were used, one from a highly exploited stock off the southern coast of Sicily (LEVI *et al.*, 1993; FIORENTINO *et al.*, 2008a), and the other from a lightly exploited stock in the Gulf of Castellammare (North Sicily), an area that was closed to bottom trawl fishery in 1990 (FIORENTINO *et al.*, 2008b; SIELI *et al.*, 2011). Both modal components and whole otolith readings were employed to compute mean length-at-age and the corresponding standard deviation (sd) (Table 1); the inverse of the sd was used as a weight factor in the non linear regression, and the goodness of fit of the models was based on the Akaike's information criterion (AIC; AKAIKE, 1974), modified for small sample sizes (AICu; MCQUARRIE & TSAI, 1998):

$$AICu = \frac{RSS}{n - k} + \frac{n + k}{n - k - 2}$$

where  $k$  and  $n$  denote the number of parameters and observations in the

Table 1

Mean total length (TL; cm) at age class (AC, year) for the red mullet females from the Strait of Sicily (SoS) and Gulf of Castellammare (GoC). Sd denotes the standard deviation of the mean.

AC (year)	SoS		GoC		AC (year)	SoS		GoC	
	TL (cm)	sd	TL (cm)	sd		TL (cm)	sd	TL (cm)	sd
0.5	8.5	0.9	9.3	1.4	3.5	19.1	1.2		
0.5	10.9	0.9	10.9	2.5	3.5	18	1.1		
0.5	11.1	0.5			3.5	18.6	1.2		
0.5	11.9	0.8			3.5	19.6	1.3		
0.5	12.4	0.5			4.5	19.8	0.6	19.7	2.3
1.5	13.8	1.5	11.6	1.2	4.5	21	0.6	<b>18.4</b>	<b>1.2</b>
1.5	13.3	0.9	<b>12.1</b>	<b>1.5</b>	4.5	20.3	1.3		
1.5	14.1	1.4			4.5	21	0.9		
1.5	14.6	1.1			4.5	21.4	1.2		
2.5	15.6	1.5	14.3	1.6	5.5	21	0.6	21	2.4
2.5	15.7	1.5	<b>15.2</b>	<b>1.2</b>	5.5	22.4	1.2	<b>20.2</b>	<b>2.6</b>
2.5	16.8	1.1			5.5	23.3	0.5		
2.5	17	1.3			6.5	22	1.4	21.3	1.9
2.5	15.7	1.1			6.5			<b>19.8</b>	<b>5.2</b>
2.5	16.2	1.3			7.5			23.2	1.8
2.5	17.1	1			8.5			24.5	2.6
3.5	17.4	1.5	16.9	2.6	9.5			23.5	1.3
3.5	18.9	1.5	<b>17.2</b>	<b>0.8</b>	10.5			24.8	1.8

model, respectively; and RSS is the residual sum of squares, which corresponds to the maximized value of the likelihood function (L) for least square fit, under the assumption that model errors are normally and independently distributed. In order to estimate the one- and two-phase VBGF,  $L_{\infty} = L_{\max}$  ever = 29 cm (recorded for a Tyrrhenian stock; VOLIANI, 1999) and  $L_m = 12$  cm (GANCITANO *et al.*, 2010) were assumed.

## RESULTS

Excluding data from juveniles from estimates of the NGM parameters leads to an improvement in the fitting of the model for both the Strait of Sicily (AICu of 5.929 *vs.* 6.203) and Castellammare (5.758 *vs.* 5.922) (Table 2).

The two-phase VBGF indicated higher growth performance and more realistic biological values for  $t_0$  in juveniles than adults (Table 2). The data and growth models are shown in Figs. 1 and 2. The main geographical difference concerned the higher homogeneity of  $K$  and  $t_0$  among adults and combined fits for Castellammare and the better correspondence between  $t_m$  and  $t_p$  for

the Strait of Sicily. The expected age at which the transition from  $K_j$  to  $K_a$  occurs ( $t_p$ , was very close to the indicates the age corresponding to the length at 50% of sexual maturity ( $t_m$ ), in the case of red mullet of the Strait of Sicily. On the contrary  $t_p$  was lower than  $t_m$  in the stock of the Castellammare Gulf.

It is worth noting the differential time required to approach 95% of the  $L_\infty$  with the juveniles or adults  $K$  (~ 7-9 and 15-18 y respectively) (Table 2), figures that are close to the maximum observed age reported for exploited (3-10 y; CAMPILLO, 1992; TSERPES *et al.*, 2002; RIZZO *et al.*, 2005) and virtually unexploited (10–11 y; CAMPILLO, 1992; FROESE & PAULY, 2010; present results for Castellammare) Mediterranean red mullet females.

DISCUSSION

The proposed model assumes that  $L_\infty$  is not dependent on food availability, in contrast with the classic theory of density-dependent growth (BEVERTON & HOLT, 1957, 1959; SHIN & ROCHET, 1998; LORENZEN & ENBERG, 2001).

Conceptually, we believe that the reported variability in literature of  $L_\infty$  estimates reflects the variability in the  $L_m$  figures at hand (STAMPS *et al.*, 1998). In particular, two school of thoughts might be considered in explaining the  $L_m$  variability: the documented inverse interaction between the intensity of food available “*pro capite*” and  $L_m$  (BEVERTON, 1987; MANGEL & ABRAHAMS, 2001; REZNICK *et al.*, 2002) or the supposed inverse relationship between the amount of fishing and  $L_m$  (ROCHET, 1998), due to the “thinning” phenomenon (i.e.

Table 2  
Overall results of one and two phase VBGF analysis for the red mullet females from the Strait of Sicily (SOS) and Gulf of Castellammare (GoC) (Mediterranean Sea).

Location Parameters	SOS			GoC		
	Juveniles	Adults	Combined	Juveniles	Adults	Combined
$L_{\max \text{ ever}}$						
29	29	29	29	29	29	29
k	0.385	0.178	0.187	0.314	0.160	0.159
$t_0$	-0.68	-2.138	-2.05	-0.96	-2.00	-2
$L_\infty$ at 95% $L_{\max \text{ ever}}$	27.6	27.6	27.6	27.6	27.6	27.6
Age at 95% $L_{\max \text{ ever}}$	7.1	14.7	14.0	8.6	17.6	16.8
$L_m$	12			12		
Age 50% at maturity	0.71			0.74		
Expected age at transition	0.57			0.12		

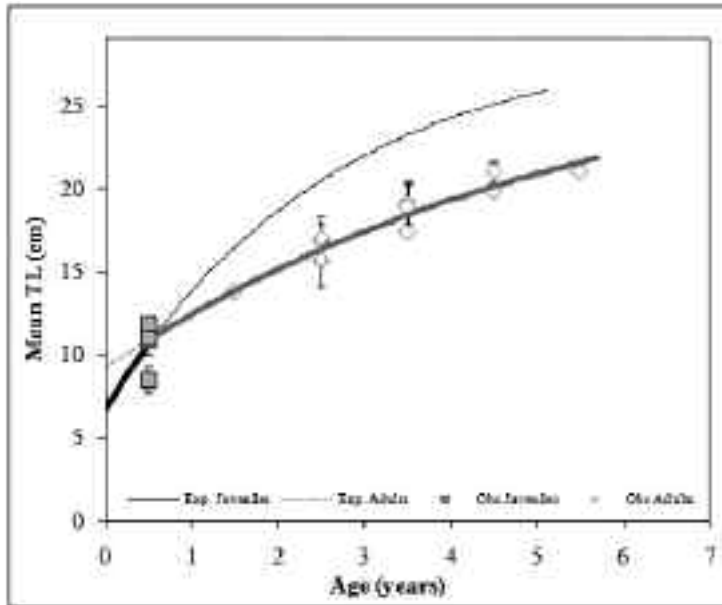


Figure 1 — Scatter-plot of the mean total length (TL; cm) vs. age class (year) and corresponding juveniles and adults fits for the red mullet females from the Strait of Sicily (Western Ionian; Mediterranean Sea). The vertical bars denote the standard deviation of the mean. The two phase growth curve of the red mullet (juveniles in black and adults in grey) is reported as solid line.

reduction of the strength of the cohort) and quick removal of the slower-growing and later maturing component present in the pristine stock.

There is some evidence that  $L_{max}$  is not a reliable estimator of  $L_{\infty}$  (MATH- EWS & SAMUEL, 1990). The estimation of  $L_{\infty}$  in the classical VBGF model is strongly influenced by the present  $L_{max}$ , which generally reflects the level of exploitation exerted on the stock and the almost linear growth after reproduction (cf. ABELLA *et al.*, 1997). In such a situation, it is difficult to accurately estimate  $L_{\infty}$  (cf. BLISS, 1970), and the scientist involved in the analysis may use more or less conscious subjective forcing to figure out a compromise. Consequently, it is likely that current Mediterranean VBGF parameters are strongly affected by the different  $L_{max}$  arising due to the interaction between the rate of removal by fisheries and the more or less slow convergence to a unique asymptotic size (cf. ALDRICH & LAWLER, 1996). More concisely, it is possible that  $L_{max} - L_{\infty}$  instead of the “true”  $L_{\infty}$  is the parameter that is influenced by food availability and fishing pressure and consequently also the  $K$ . This new interpretation might also explain the contradictions apparent among the unit stock differentials in red mullet (cf. LEVI *et al.*, 1992; SONIN *et al.*, 2007) despite their relatively high genetic homogeneity (GAROIA *et al.*, 2004;

ARCULEO *et al.*, 2005). The curves in Figs. 1 and 2 closely resemble Fig. 1 in STAMPS *et al.* (1998), the difference being that the NGM predicts that very old adults will converge very slowly towards a unique  $L_{\infty}$ . Practically, the two-phase VBGF gives a more unambiguous and objective ( $L_{\infty}$  is fixed at the upper documented size limit) and realistic (higher growth and  $t_0 \sim 0$  in juveniles) growth pattern, with a marginal departure from the adult trajectory described by the one-phase curve parameters.

It is well known that growth depends on a complex interaction between energy allocation, foraging strategy, risk of predation, reproductive behaviour, short and long-term density dependence effects and the incidence of senescence (cf. RAGONESE, 2004), i.e. the overall physiological performance becomes poorer as specimens become older independently from the biotic and abiotic environmental conditions (CUSHING, 1981; ROFF, 1983; REZNICK *et al.*, 2002).

Females of the Mediterranean red mullet are generally considered as non-territorial low trophic species (BADALAMENTI *et al.*, 2000) that have evolved a saturation reproductive pattern (production of large numbers of eggs) (GARROD & HORWOOD, 1984), a high initial growth rate, precocious

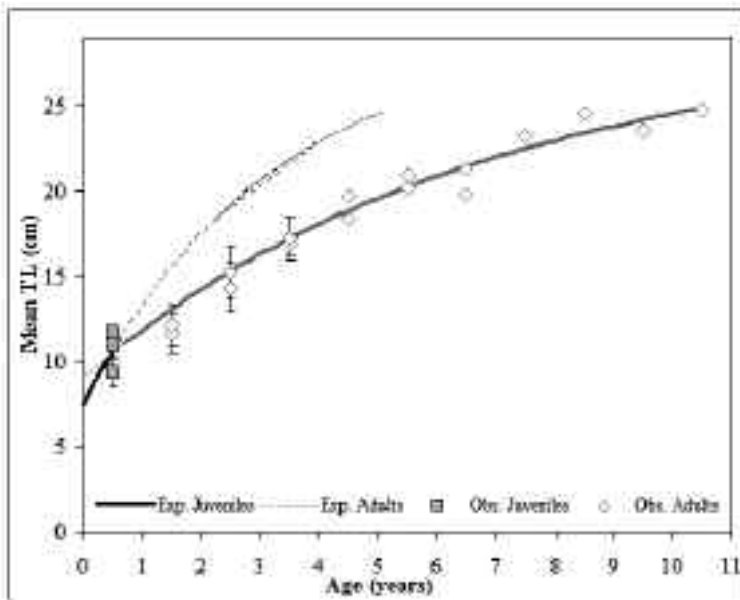


Figure 2 — Scatter-plot of the mean total length (TL; cm) vs. age class (year) and corresponding juveniles and adults fits for the red mullet females from the Gulf of Castellammare (Southern Tyrrhenian; Mediterranean Sea). The vertical bars denote the standard deviation of the mean. The two phase growth curve of the red mullet (juveniles in black and adults in grey) is reported as solid line.

maturity and a reduction in growth thereafter (FIORENTINO *et al.*, 1998; TSERPEDES *et al.*, 2002; SONIN *et al.*, 2007). Such life history traits reflect partially the stress induced by the oligotrophic, warm and salty Mediterranean waters where the species lives (PAULY, 1981, 1984) but most likely they are the results of adaptation to other factors. Another explanation was the diversion of energy from somatic growth to reproduction and a reduction in foraging to reduce the risk of predation (ROFF, 1983), but since the general rule is that minimum food intake occurs around and during the spawning period, and that in non-territorial fish females are larger than males, other explanations are possible, such as that more time is devoted to mating, more room is left for the enlarging ovary, and limiting factors (such as oxygen requirements) other than food limitations may be present (PAULY, 1981, 1998).

Size and age at maturity trajectories in fish also reflect the interaction between genetic and phenotypic plasticity, pristine stock abundance and distribution, and the response to stress encountered in the changing environments in which fish have evolved and live. Whatever the cause, reproduction costs represent an increasing strain on the metabolism of maturing and mature fish as they grow larger and older, decreasing the resources available for somatic growth. Consequently, it is not surprising that  $L_m$  might be reduced in heavily exploited stocks (ROCHET, 1998), along with the median size, leading to the so-called “tropicalization” of highly depleted resources (STERGIOU, 2002).

The abovementioned problems hamper the use of a one-phase growth model for the whole lifecycle and the assumption of constant parameters, which on the contrary may vary according to the life phase.

These limitations have led to the development and proposal of different two-phase growth models (CHARNOV, 1993; PORCH *et al.*, 2002; TRACEY & LYLE, 2005; CHARNOV, 2008; QUINCE *et al.*, 2008a,b). The application of these models, however, generally requires representative size-at-age samples (cf. PORCH *et al.*, 2002) and a prolonged “juvenile” phase (cf. QUINCE *et al.*, 2008b). Such requirements are difficult to meet when considering Mediterranean demersal bony fish resources, which are characterized by precocious sexual maturity and for which it is difficult to obtain representative samples of the highly depleted adult fraction of the stock (LEONART, 2005; PAPA-CONSTANTINOU & FARRUGIO, 2000; CADDY, 2009; GFCM, 2010).

Furthermore, to our knowledge, all discontinuous VBGF versions assume only one (CRAIG, 1999) or different (STAMPS *et al.*, 1998) asymptotic sizes for the adults. The latter approach gives a sound explanation for the discrepancy between the asymptotic and the maximum-ever size; unusually large sizes might reflect rare cases of “always juveniles”, later maturing and very lucky old mature specimens which have had the opportunity to achieve the



full growth potential of the stock.

The “always juveniles” category deserves some comment: there is growing evidence that both skipping spawning after the onset of sexual maturity (cf. RIDEOUT *et al.*, 2005) and the existence of large and old specimens with atresic and undeveloped gonads (FREEDMAN & NOAKES, 2002) in iteroparous fish are more frequent phenomena than previously believed.

On the contrary, by considering  $L_{\infty}$  as a genetically fixed parameter, the new growth paradigm assumes that growth rates in the case of red mullet remain relatively high in the first 1–2 years of life and then decline after the transition to the adult stage; at 1.5 years of age, present estimates indicate a mean length of 13–16 and 12–14 cm for juveniles and adults respectively, size limits that encompass the majority of specimens caught by bottom trawling (median length 14–16 cm; SAMED, 2002).

We believe our approach to describing the growth of fish may also help solve the apparent contradiction of growth parameters of VBGF derived from samples covering different phases of fish populations. In the Mediterranean, it is well known that the nets used by trawlers mainly catch juvenile hake while long-line fishing mainly captures adults (OLIVER & MASSUTI, 1995; ABELLA *et al.*, 1997). The selection of different life phases in samples used to study the growth of this species can therefore affect the results, producing biased estimates in favour of juvenile or adult patterns on the basis of the age groups from which the length/age data are obtained.

On the other hand the recent contrasting results that form the basis of the debate on hake growth in the Eastern Atlantic and in the Mediterranean, based on VBGF parameters obtained by tagging, could be reconstructed in the light of our novel approach using a two-phase growth model. Following publication of the study by DE PONTUAL *et al.* (2006) and examining the growth of hake in the Bay of Biscay (Eastern Atlantic Ocean), MELLON-DUVAL *et al.* (2010) proposed a new growth pattern for hake in the Gulf of Lions (Western Mediterranean). Fixing  $L_{\infty}$  at values estimated by ALDEBERT & RECASENS (1995) (100.7 and 72.8 cm TL for females and males respectively), MELLON-DUVAL *et al.* (2010) estimated the K parameter as the mean value of individual increments of length within a known time interval. Since the length at 50% of mature fish is 38.0 cm TL for females and 28.8 cm TL for males (RECASENS *et al.*, 1998), the recorded mean growth rate (0.04 cm d<sup>-1</sup>) derived from juveniles fish, being TL lower than 24 cm in 96 out 108 individuals. These growth rates produced a K value that was double that reported by ALDEBERT & RECASENS (1995). In the light of our NGM, the new K estimated by MELLON-DUVAL *et al.* (2010) (K=0.236) should be interpreted as  $K_1$  while the old value, obtained from otolith readings including many adult

specimens and reported by ALDEBERT & RECASENS (1995) ( $K=0.124$ ), should be considered as  $K_a$ .

In conclusion, our novel approach to the two-phase growth model may help not only with estimations of more realistic description of growth, but also improve the reconstruction of more accurate age structures when length distributions from surveys or catch data will be sliced by using growth curve to stock assessment purpose. Finally, it is well known that natural mortality (M) is one of the main “critical” parameter in analytical stock assessment (MERTZ & MYERS, 1997) and its estimation is often obtained by VBGF parameters (cf. RAGONESE *et al.*, 2002). The estimation of separate K for fast growing (juveniles) or low growing (adults) phases of fish life can allow to the a more reliable estimation of natural mortality, to be considered in assessing the potential productivity of commercial stocks.

#### REFERENCES

- ABELLA A., CADDY J.F. & SERENA F., 1997. Do natural mortality and availability decline with age? An alternative yield paradigm for juvenile fisheries, illustrated by the hake *Merluccius merluccius* fishery in the Mediterranean. *Aquat. Liv. Res.*, 10: 257-269.
- AKAIKE H., 1974. A new look at the statistical model identification. *IEEE Transactions on Automatic Control*, 19 (6): 716-723. doi:10.1109/TAC.1974.1100705.
- ALDEBERT Y. & RECASENS L., 1995. Estimation de la croissance du merlu du Golfe du Lion par l'analyse des fréquences de tailles. *Rapp. Comm. Int. Mer Médit.*, 34: 236.
- ALDRICH J.C. & LAWLER I.F., 1996. The model-free analysis of growth curves. *Mar. Ecol.*, 17 (1-3): 491-500.
- ARAYA M. & CUBILLOS L.A., 2006. Evidence of two-phase growth in elasmobranchs. *Environ. Biol. Fish.*, 77: 293-300.
- ARCULEO M., LO BRUTTO S., MAGGIO T. & TERRANOVA S.M., 2005. Identificazione di stock mediante analisi del DNA nucleare e mitocondriale nelle specie ittiche *Merluccius merluccius* (Nasello), *Mullus barbatus* (Triglia di fango) e *Seriola dumerili* (Ricciola) catturate lungo le coste siciliane. *Naturalista Sicil.*, 29 (1-2): 19-36.
- BADALAMENTI F., PINNEGAR J. K., POLUNIN N. V. C. & D'ANNA G., 2000. Estimates of trophic level in the red mullet *Mullus barbatus*: a comparison between gut-contents and stable-isotope data. Pp. 19-21 in: Briand F. (ed.), *Fishing Down the Mediterranean Food Webs? Series No. 12. CIESM Workshop*, Kerkyra.
- BEVERTON R.J.H. & HOLT S.J., 1957. On the Dynamics of Exploited Fish Populations. Fishery Investigations (Series II, Vol. XIX). Ministry of Agriculture, Fisheries and Food, *Her Majesty's Stationery Office*, London, 533 pp.
- BEVERTON R.J.H. & HOLT S.J., 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. Pp. 142-180 in: Wolstenholme G.E.W. & O'Connor M. (eds.), *The Lifespan of Animals*, CIBA Foundation, colloquia on ageing Vol. 5. *J. & A. Churchill*, Ltd.
- BEVERTON R.J.H., 1987. Longevity in fish: some ecological and evolutionary perspectives. Pp. 161-186 in: Woodhead M., Witten K. & Thompson A.D. (eds.), *Ageing Processes in Animals*. *Plenum Press*, New York.

- BEVERTON R.J.H., 1992. Patterns of reproductive strategy parameters in some marine teleost fishes. *J. Fish Biol.*, 41 (Supplement B): 137-160.
- BIANCHINI M. & RAGONESE S., 2011. Establishing length at age references in the red mullet, *Mullus barbatus* L. 1758 (Pisces, Mullidae), a case study for growth assessments in the Mediterranean Geographical Sub Areas (GSA). *Medit. Mar. Sci.*, 12 (2): 316-332.
- BLISS C.I., 1970. Statistics in Biology, Vol. II. *McGraw-Hill Book Company*, New York, 639 pp.
- CADDY J.F., 1993. Toward a comparative evaluation of human impacts on fishery ecosystems of enclosed and semi-enclosed seas. *Rev. Fish. Sci.*, 1: 57-96.
- CADDY J.F., 2009. Practical issues in choosing a framework for resource assessment and management of Mediterranean and Black Sea fisheries. *Medit. Mar. Sci.*, 10/1: 83-119.
- CAMPILLO A., 1992. Les pêcheries françaises de Méditerranée: synthèse des connaissances. Report No. RIDRV-92/019-RH, Ifremer, Sète. 206 pp.
- CHARNOV E.L., 1993. Life history invariants. Some Explorations of Symmetry in Evolutionary Ecology. *Oxford University Press*, Oxford. 167 pp.
- CHARNOV E.L., 2008. Fish growth: Bertalanffy  $k$  is proportional to reproductive effort. *Environ. Biol. Fishes*, 83 (2): 185-187.
- CRAIG P.C., 1999. The von Bertalanffy growth curve: When a good fit is not good enough. *NAGA, the ICLARM quarterly*, 22 (4): 28-29.
- CUSHING D.H., 1981. Fisheries Biology: A Study in Population Dynamics, 2nd ed. *The University of Wisconsin Press*, Madison, 295 pp.
- DAY T. & TAYLOR P.D., 1997. Von Bertalanffy's growth equation should not be used to model age and size at maturity. *Am. Nat.*, 149: 381-393.
- DE PONTUAL H., GROISON A.L., PINEIRO C. & BERTIGNAC M., 2006. Evidence of underestimation of European hake growth in the Bay of Biscay, and its relationship with bias in the agreed method of age estimation. *ICES J. Mar. Sci.*, 63: 1674-1681.
- FIorentino F., BEN MERIEM S., BAHRI T., CAMILLERI M., DIMECH M., EZZEDDINE-NAJA S., MASSA F., JARBOUI O. & ZGOZI S., 2008a. Synthesis of information on some target species in the MedSudMed Project area (central Mediterranean). GCP/RER/010/ITA/MSM-TD-15. *MedSudMed Technical Documents*, No. 15: 67 pp.
- FIorentino F., BADALAMENTI F., D'ANNA G., GAROFALO G., GIANGUZZA P., GRISTINA M., PIPTONE C., RIZZO P. & FORTIBUONI T., 2008b. Changes in spawning-stock structure and recruitment pattern of red mullet, *Mullus barbatus*, after a trawl ban in the Gulf of Castellammare (central Mediterranean Sea). *ICES J. Mar. Sci.*, 65 (7): 1175-1183.
- FIorentino F., ZAMBONI M., ROSSI M. & RELINI G., 1998. The growth of red mullet (*Mullus barbatus*, L. 1758) during the first years of life in the Ligurian Sea (Mediterranean). *Cahiers Options Méditerranée*, 35: 65-78.
- FREEDMAN J.A. & NOAKES D.L.G., 2002. Why are there no really big bony fishes? A point-of-view on maximum body size in teleosts and elasmobranchs. *Rev. Fish Biol. Fish.*, 12: 403-416.
- FROESE R. & PAULY D., 2010. FishBase. World Wide Web electronic publication. Available at [www.fishbase.org](http://www.fishbase.org) [Last accessed: 15 April 2010].
- GANCITANO V., BASILONE G., BONANNO A., CUTTITTA A., GAROFALO G., GIUSTO G.B., GRISTINA M., MAZZOLA S., PATTI B., SINACORI G. & FIORENTINO F., 2010. GSA16 - Stretto di Sicilia. Pp. 93-116 in: Mannini A. & Relini G. (eds.), Rapporto Annuale sullo Stato delle Risorse Biologiche dei Mari Italiani. Anno 2008. *Biol. Mar. Medit.*, 17 (suppl. 3).
- GAROA F., GUARNIERO I., PICCINETTI C. & TINTI, F., 2004. First microsatellites loci of red mullet (*Mullus barbatus*) and their application to genetic structure analysis of Adriatic shared stock. *Mar. Biotech.*, 6: 446-452.
- GARROD D.J. & HORWOOD J.W., 1984. Reproductive strategies and the response to exploitation. Pp. 367-384 in: Potts G.W. & Wootton R.J. (eds.), *Fish Reproduction: Strategies and Tactics*. *Academic Press*, London.

- GFCM 2010. General Fisheries Council for the Mediterranean reports. Available at: <http://www.icm.csic.es/rec/projectes/scsa/documents>.
- JONES R., 1989. Towards a general theory of population regulation in marine teleosts. *J. Cons. Int. Explor. Mer.*, 45: 176-189.
- LEVI D., ANDREOLI M.G. & RIZZO P., 1992. Growth curves from representative samples of fish populations as possible hints for the identification of unit stocks. The case study of red mullet from the Sicilian Channel. Pp. 299-306 in: Colombo G., Ferrari L., Ceccherelli V.U. & Rossi R. (eds.), Marine Eutrophication and Population Dynamics. *Olsen & Olsen Publ. and Printers*, Helstedsvej, Fredensborg, Denmark.
- LEVI D., ANDREOLI M.G. & GIUSTO G.B., 1993. An analysis based on trawl survey data of the state of the "Italian" stock of Sicilian Channel, including management advice. *Fish. Res.*, 17: 333-341.
- LEONART J., 2005. Mediterranean and Black Sea. Pp. 49-64, 220-221, 235 in: Review of the State of World Marine Fishery Resources. *FAO Fish. Tech. Pap.*, 457.
- LEONART J. & MAYNOU F. 2003. Fish stock assessments in the Mediterranean: state of the art. *Sci. Mar.* 67(SUPPL.1): 37-49.
- LORENZEN K. & ENBERG K., 2001. Density-dependent growth as a key mechanism in the regulation of fish populations: evidence from among-population comparisons. *Proc. R. Soc. Lond. Series B Biol. Sc.*, 269: 49-54.
- MANGEL M. & ABRAHAMS M.V., 2001. Age and longevity in fish, with consideration of the ferocious trout. *Exp. Gerontol.*, 36: 765-790.
- MATHEWS C.P. & SAMUEL M., 1990. The relationship between maximum and asymptotic length in fishes. *Fishbyte*, 8 (2): 14-16.
- MCQUARRIE A. D. R. & TSAI C. L., 1998. Regression and Time Series Model Selection. *World Scientific*, 480 pp.
- MELLON-DUVAL C., DE PONTUAL H., MÉTRAL L. & QUEMENER L., 2010. Growth of European hake (*Merluccius merluccius*) in the Gulf of Lions based on conventional tagging. *ICES J. Mar. Sci.*, 67: 62-70.
- MERTZ G. & MYERS R.A., 1997. Influence of errors in natural mortality estimates in cohort analysis. *Can. J. Fish. Aquat. Sci.*, 54: 1608-1612
- OLIVER P. & MASSUTI, E., 1995. Biology and fisheries of western Mediterranean hake (*M. merluccius*). Pp. 181-202 in: Alheit J. & Pitcher T.J. (eds.), Hake: Biology, Fisheries and Markets. Fish and Fisheries Series, 15, *Chapman and Hall*, London, 478 pp.
- PAPACONSTANTINO C. & FARRUGIO H., 2000. Fisheries in the Mediterranean. *Medit. Mar. Sci.*, 1: 5-18.
- PAULY D., 1981. The relationship between gill surface area and growth performance in fish: a generalization of von Bertalanffy's theory of growth. *Meresforschung, Rep. Mar. Res.*, 28 (4): 251-282.
- PAULY D., 1984. Fish Population Dynamics in Tropical Waters. A manual for use with programmable calculators. ICLARM Studies and Reviews (Vol. 8). *Int. Centre Liv. Aquatic Res. Manage.*, Manila.
- PAULY D., 1998. Tropical fishes patterns and propensities. *J. Fish Biol.*, 53 (Supplement A): 1-17.
- PORCH C., WILSON C.A. & NIELAND D. L., 2002. A new growth model for red drum (*Sciaenops ocellatus*) that accommodates seasonal and ontogenic changes in growth rates. *Fish. Bull.*, 100: 149-152.
- QUINCE C., ABRAMS P.A., SHUTER B.J. & LESTER N.P., 2008a. Biphasic growth in fish I: Theoretical foundations. *J. Theor. Biol.*, 254, 197-206.
- QUINCE C., SHUTER B.J., ABRAMS P.A. & LESTER N.P., 2008b. Biphasic growth in fish II: Empirical assessment. *J. Theor. Biol.*, 254: 207-214.
- RAGONESE S., 2004. Growth and senescence interaction in fish: the state of art. *Biol. Mar. Medit.*, 11 (2): 91-106.

- RAGONESE S., ABELLA A., FIORENTINO F. & SPEDICATO M.T., 2006. Methods for estimating the instantaneous rate of natural mortality (M) in fisheries science with particular reference to the Mediterranean. *Biol. Mar. Medit.*, 13 (3): 1-151.
- RECASENS L., LOMBARTE A., MORALES-NIN B. & TORRES G., 1998. Spatiotemporal variations in the population structure of the European hake in the northwestern Mediterranean. *J. Fish Biol.*, 53: 387-401.
- REZNICK D., GHALAMBOR C. & NUNNEY L., 2002. The evolution of senescence in fish. *Mechanisms of Ageing and Development*, 123: 773-789.
- RICKER W. E., 1958. Handbook of computations for biological statistics of fish populations. *Bull. Fish. Res. Board Can.*, 119: 300.
- RICKER W. E., 1975. Computation and interpretation of biological statistics of fish populations. *Bull. Fish. Res. Board Can.*, 191: 382.
- RICKER W. E., 1979. Growth rates and models. Pp. 677-743 in: Hoar W.S., Randall D.J. & Brett J.R. (eds.), *Fish Physiology*, Vol. 8. *Academic Press Inc*, New York.
- RIDEOUT R. M., ROSE G. A. & BURTON M.P.M., 2005. Skipped spawning in female iteroparous fishes. *Fish Fish.*, 6: 50-72.
- RIZZO P., GANCITANO S., BADALUCCO C. & FIORENTINO F., 2005. Age estimation from "hard structures" of exploited marine organisms in the experience of CNR Centre of Mazara del Vallo: the procedures adopted and the maximum ages estimated. Report of the Workshop on Standardization of Fish Age Determination Based on Otolith Samples in the MedSudMed Project Area, GCP/RER/010/ITA/MSM-09. *MedSudMed Technical Documents*. No. 9: 46 pp.
- ROCHET M. J., 1998. Short-term effects of fishing on life history traits of fishes. *ICES J. Mar. Sci.*, 55: 371-391.
- ROFF A., 1983. An allocation model of growth and reproduction in fish. *Can. J. Fish. Aquat. Sci.*, 40: 1395-1404.
- SAMED 2002. Stock Assessment in the Mediterranean. *Final Report EU Project No. 99/047*.
- SHIN Y. J. & ROCHET M. J., 1998. A model for phenotypic plasticity of North Sea herring growth in relation to trophic conditions. *Aquat. Liv. Res.*, 11: 315-324.
- SIELI G., BADALUCCO C., DI STEFANO G., RIZZO P., D'ANNA G. & FIORENTINO F., 2011. Biology of Red mullet, *Mullus barbatus* (L. 1758), in the Gulf of Castellammare (NW Sicily, Mediterranean Sea) subjected to a trawling ban. *J. Appl. Ichthyol.*, 27: 1218-1225.
- SONIN O., SPANIER E., LEVI D., PATTI B., RIZZO P. & ANDREOLI M.G., 2007. Nanism (dwarfism) in fish: a comparison between red mullet *Mullus barbatus* from the south eastern and the central Mediterranean. *Mar. Ecol. Prog. Ser.*, 343: 221-228.
- STAMPS J. A., MANGEL M. & PHILIPS J.A., 1998. A new look at relationships between size at maturity and asymptotic size. *Am. Nat.*, 152: 470-479.
- STERGIOU K.I., 2002. Overfishing, tropicalization of fish stocks, uncertainty and ecosystem management: re-sharpening Ockham's razor. *Fish. Res.* 55: 1-9.
- TRACEY S.R. & LYLE J.M., 2005. Age validation, growth modelling and mortality estimates of striped trumpeter (*Latris lineata*) from southeastern Australia: making the most of patchy data. *Fish. Bull.*, 103: 169-182.
- TSERPES G., FIORENTINO F., LEVI D., CAU A., MURENU M., ZAMBONI A. & PAPACONSTANTINO C., 2002. Distribution of *Mullus barbatus* and *Mullus surmuletus* (Osteichthyes: Perciformes) in the Mediterranean continental shelf: implications for management. *Sci. Mar.*, 66 (Suppl. 2): 39-54.
- VOLIANI A., 1999. *Mullus barbatus*. Pp. 276-291 in: Relini G., Bertrand J. & Zamboni A. (eds.), *Synthesis of the Knowledge on Bottom Fishery Resources in Central Mediterranean (Italy and Corsica)*. *Biol. Mar. Medit.*, 6 (Suppl. 1).

VOLIANI A., ABELLA A. & AUTERI R., 1998. Some considerations on the growth performance of *Mullus barbatus*. Proc. 2nd Meeting of the DYNPOP Working Group, Genoa, 2-5 October 1996. *Cab. Option Mediter.*, 35: 93-106.

*Authors' address* — F. FIORENTINO, V. GANCITANO, S. GANCITANO, P. RIZZO & S. RAGONESE, Consiglio Nazionale delle Ricerche (CNR), Istituto per l'Ambiente Marino Costiero (IAMC) via Luigi Vaccara, 61 - 91026 Mazara del Vallo (TP, I); e-mail: fabio.fiorentino@iamc.cnr.it