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# Estimation of the parameters of the Caddy reciprocal M-at-age model for the construction of natural mortality vectors

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**SUMMARY -** In Mediterranean demersal trawl fisheries, for most of the species, recruitment to the gear starts in their first year of life. This is mainly due to the utilization of cod end stretched mesh sizes of 40 mm or lower. Large adult fish are rarely caught with this fishing strategy because the older individuals show a declining availability/vulnerability to the trawl net. Although comparable data is not available for the Mediterranean, in a study of the limited data available on natural mortality rate at age for a variety of invertebrates and fish world-wide, Caddy (1991) showed that a simple reciprocal relationship reasonably describes the decline in natural mortality with age to the adult value of M used in assessments of mature fish. Considering that many Mediterranean demersal species recruit to the ground in the first year of life, it would be misleading to model yield due to fishing assuming constant death rates throughout life. The practical consequences of this assumption are explored for Mediterranean hake (*Merluccius merluccius*) by Abella *et al.* (in press) by means of yield per recruit calculations assuming rapid declines in M with age in the first few years of life to a relatively low constant mortality, as well as declining availability to trawls of the few individuals surviving to maturity. It is speculated that these combined phenomena may be in part responsible for the continued productivity of some small mesh Mediterranean fisheries for juvenile fish, despite intensive trawling. This should also be linked to the refugium concept for older fish and is one of the few hypotheses advanced to explain why the current fish harvests are sustained, despite the intensive fishery with small mesh trawls on narrow shelves. In this paper, new approaches to "fitting" a reciprocal function for M-with-age for hake are described. Two of them, similar to the method proposed by Caddy (1996), are based on estimates of mean life-time fecundity, mean age at egg production and existing estimates of adult M. The third one is based on stock productivity assumptions. Even if no direct estimates of M-at-age exist for Mediterranean demersal fish, all vectors generated were similar to M-at-age estimates for related North Sea demersal fish as determined from MSVPA.

**Key words:** Caddy M-at-age model, stock assessment.

***RESUME -*** *"Estimation des paramètres de la fonction inverse M par âge pour la construction des vecteurs de mortalité naturelle". Dans les pêcheries démersales méditerranéennes, pour la majorité des espèces, le recrutement au métier (filet de fond) commence dans la première année. Ce recrutement précoce est principalement dû à l'utilisation d'une maille au sac très petite (<= 40 mm). Les poissons adultes de grosse taille sont rarement capturés avec cette stratégie de pêche parce que les plus vieux individus sont caractérisés par une réduction graduelle de leur vulnérabilité/disponibilité relative au métier. Compte tenu qu'il n'y a pas d'informations comparables pour la Méditerranée, comme résultat d'une étude des données disponibles au regard du taux de mortalité naturelle par âge pour invertébrés et poissons provenant de plusieurs régions du monde, Caddy (1991) a démontré qu'une simple relation inverse permet de décrire raisonnablement la diminution de la mortalité naturelle avec l'âge vers la valeur de M stabilisée communément utilisée pour les individus adultes dans les évaluations. En considérant que la plupart des espèces recrutent au fond à la première année de vie, il serait inadéquat de modéliser des rendements dus à la pêche en admettant des taux constants de mortalité à travers toute la vie. Les conséquences pratiques de ces hypothèses ont été explorées pour le merlu méditerranéen* (Merluccius merluccius) *par Abella* et al. *(in press). Pour faire les calculs on utilise des modèles de rendement par recrue qui présument : (i) une rapide diminution de M en relation à l'âge pour les premières années et la tendance, pour les années suivantes, vers une valeur de mortalité relativement basse et constante ; et (ii) une réduction graduelle de leur disponibilité aux engins de pêche utilisés pour le nombre réduit d'individus survivants de taille supérieure. On suppose que ces phénomènes combinés peuvent être en partie responsables de la productivité soutenue découlant des très intensives activités halieutiques méditerranéennes qui utilisent des filets de fond de petit maillage et adressées à des poissons jeunes. Ceci peut être lié au concept de "refuge" pour les poissons plus âgés et constitue une des hypothèses très peu probables proposées pour expliquer pourquoi les captures actuelles sont soutenues malgré l'activité intensive de la pêche avec les filets de petite maille au sac réalisée sur des aires de plate-forme continentale particulièrement restreintes. Dans cet article, de nouvelles propositions pour "arranger" la fonction réciproque de M en relation à l'âge pour le merlu sont présentées. Deux méthodes, semblables à la méthode proposée par Caddy (1996) sont basées sur des estimations de la fécondité moyenne à travers la vie ("mean life-time fecundity"), de l'âge moyen de production des oeufs ("mean age eggs production") et des estimations de M pour les adultes ; la troisième se base sur des assomptions en regardant la production des stocks. Même s'il n'existe pas d'estimation directe de M par âge pour les espèces démersales de* *la Méditerranée, tous les vecteurs obtenus résultent semblables aux vecteurs de M par âge déterminés, à travers les analyses des populations virtuelles multispécifiques, pour certaines espèces de la Mer du Nord phylogénétiquement apparentées avec le merlu.*

***Mots-clés :** Modèle de Caddy M-par-âge, évaluation des stocks.*

## Introduction

Over the last 15 years, assessment and management of demersal fish stocks in the Mediterranean have been based on a conventional paradigm for analytical assessments described for North Atlantic fisheries (Beverton and Holt, 1957). This assumes that due to the utilization of large meshed trawl cod ends of 70-100 mm stretched mesh, groundfish becomes fully available to the fishery at or around the age of maturity (between the second and fifth year of life) remaining thereafter fully vulnerable to trawling. By first recruitment, the natural mortality rate has already dropped to a more or less constant annual value, typically of the order of M = 0.1-0.3. The conventional "North Sea" paradigm also assumes that the fishery is targeted to adults and that small fish are without market value. They are presumed to escape through the mesh to survive, or to be discarded dead.

Yield per recruit and virtual population analysis calculations on Mediterranean demersal stocks have been almost always performed assuming constant M and full availability to the gear from just before sexual maturity onwards. In this area, however, fisheries are aimed at juveniles (hake size at 50% retention by a 40 mm stretched mesh is of the order of 12 cm: roughly equivalent to age 1 year). Individuals less than 3 years old constitutes almost all the commercial trawl catch. The above assumptions are obviously unsuitable for performing realistic stock assessments on small-mesh fisheries for juveniles as is common in the Mediterranean. They do not apply either for the North Sea fisheries. In fact, following co-operative ICES studies in the 1980's (ICES, 1988) of stomach contents of the groundfish community, leading to the so-called MSVPA [Multi-Species Virtual Population Analysis: e.g., Gislason and Sparre (1987)] it has been demonstrated that mortality rates drop steeply from very high values early in the first year of life towards a low value for adults, that can reasonably be assumed as constant. Given that high research budgets are needed for the detailed stomach sampling studies that underlie MSVPA estimates, these are not available for many world fisheries, including those in the Mediterranean. There is a need therefore to develop other approaches to obtaining indicative M-vectors for use in yield modelling approaches, which however imprecise, are at least more realistic than assuming constant M from birth.

Assessments "with constant M" have continued to be applied because of the general lack of methodologies for assessing natural mortality at age. Given that corresponding MSVPA data from the Mediterranean is lacking, we propose several approaches to obtaining indicative values for natural mortality rate at age that are not incompatible with experience elsewhere, and which assume the reciprocal M-at-age model proposed in Caddy (1991). To refer to this process as "fitting" the reciprocal model is to use the word "fitting" in a loose sense. We are looking for indicative vectors of M that do not contravene what we know about the life history of hake and other groundfish species, and are ecologically more reasonable than the classic "constant M" assumption. These are of course difficult to confirm directly, but seem the most reasonable "research + management hypothesis" to follow at the present moment.

## Material and methods

Data used in this study relate particularly to fisheries for hake in the Northern Tyrrhenian Sea. In this paper, the results from Abella *et al.* (in press) based on data proceeding from trawl-surveys utilizing commercial trawl gears as well as landing samplings have been utilized. They suggest that in the Tyrrhenian Sea there is a peak in vulnerability to trawling around 11-14 cm. All analyses show a steady decline in availability to the fine mesh (40 mm or smaller) trawl cod-end mesh in common use; the older hake becoming more available later in life to longline and other gears. Many other authors have observed declining availabilities at age for different Mediterranean hake populations (Martin, 1989; Oliver *et al.*, 1990; Aldebert *et al.*, 1993), but in general, they seem to share the same general pattern of decline with age.

In this paper we have used the values for von Bertalanffy growth and length-weight relationships given in Abella *et al.* (1995) (see Table 1). Growth rates of hake, were traditionally considered low but recent estimates are rather higher (Orsi *et al.*, 1992; Aldebert and Recasens, 1995; Alemany and Oliver, 1995) and are similar to those utilized here.

Table 1. Values for von Bertalanffy growth and length-weight relationships

| | $L_\infty$ | K | $t_0$ | a | b |
|---|---|---|---|---|---|
| Males | 53.4 | 0.272 | 0 | 0.0050 | 3.157 |
| Females | 79.1 | 0.185 | 0 | 0.0041 | 3.192 |

Age at maturity for females of hake has been fixed following Cesarini (1994) at a total length of about 46 cm (around 5 years old).

The SOLVER routine in EXCEL 5.0 was used to arrive at vectors of M-at-size or M-at-age. In this spreadsheet, the availability of routines for non-linear solving permits the user to set one or more mathematical constraints which need to be satisfied in seeking numerical values for population parameters. In the case in point iterations were made following two main different sets of assumptions. Both of them assume a reciprocal relationship between M(t) and age t of the type described in Caddy (1991).

Three different fitting procedures were followed, which all had in common the following:

The change of M-at-age can be represented by $M_t = A + B/t$ (Caddy, 1991), where A was referred to as the asymptotic natural mortality rate but is not equivalent to conventional adult M (see Caddy, *op. cit.*) and B is a parameter that determines the concavity of the curve. Caddy's equation is empirical, and was first fitted directly by linear regression for cases where several estimates of $M_t$ were available at different ages; a situation that does not yet apply for Mediterranean fishery resources; hence, the simulation approach used here. Regression fits can result in negative values of A, and caution must be exercised in the use of this equation in these cases for older fish. The equation will only give positive values for $M_t$ up to a maximum age ($t_\lambda$) in the population if the values of A and B obtained satisfy $A + B/t_\lambda > 0$.

In order to estimate the M values for different life history stages, the mean M is determined for each interval $t_1$ - $t_2$ by the integration of equation 10 of the above mentioned paper ($M_t = A + B/t$):

$\bar{M} = I / (t_2 - t_1)$ where:

$$I = \int_{t_1}^{t_2} (A + B/t)\, dt$$

$$I = \int_{t_1}^{t_2} A\, dt + \int_{t_1}^{t_2} (B/t)\, dt \quad \text{so that:}$$

$$\bar{M} = [1/(t_2 - t_1)]\, [B \ln(t_2/t_1) + A(t_2 - t_1)]$$

and finally we obtain:

$$\bar{M} = [B/(t_2 - t_1)] \ln(t_2 / t_1) + A \quad (\text{for } t > 0)$$

Parameters $L_\infty$, K and $t_0$ of the von Bertalanffy Length Growth equation, and a and b of the length/weight relationship are assumed.

The computations estimate survivals for a cohort expressed as a length frequency which is split up into equivalent non-uniform time intervals by the von Bertalanffy equation:

$$t = 1/K \ln (1 - L_t / L_\infty) + t_0$$

All calculations were carried out on a spreadsheet that specifies the following operations for each length group:

(i) The time spent to grow from the size at the start of an interval $L_{t_1}$ to the end of the interval $L_{t_2}$

$$\Delta_t = (t_2 - t_1) = (1 / K) \ln [(L_\infty - L_{t_1}) / (L_\infty - L_{t_2})]$$

(ii) The number of survivors at length = $N_{t_2} = N_{t_1} * \exp(-M\Delta_t)$

(iii) The fecundity by length equation from Cesarini (1994):

$$\text{No. eggs} = 2.55 * TL^{3.07}$$

where TL is Total length in cm.

## Program PROBIOM

In order to maintain a stable biomass, overall losses of biomass in the unfished population must be equal to gains in production through the cohort life history. For the computations the number lost by natural causes is approximated by:

$D_t = N_t (1\text{-}\exp(-M_t\Delta_t))$ for all age classes,

and the mean individual weight of each class interval is:

$$\bar{w}_t = (1/(L_{t_2} - L_{t_1})) * ](a / (b+1)) * [ L_{t_2}^{(b+1)} - L_{t_1}^{(b+1)} ]$$

the biomass lost due to natural mortality between $L_{t_1}$ and $L_{t_2}$ is

$\Delta B_t = M_t * \bar{N}_t * \bar{w}_t \ (t_2 - t_1)$ for each age class

and the biomass of survivors is calculated as $\bar{B}_t = \bar{N}_t * w_t$

The production for each length interval $L_{t_1}$ -$L_{t_2}$ is then calculated as the product of the instantaneous rate of growth $G = (\ln w_{t_2} - \ln w_{t_1})$ and the mean biomass:

$$P_t = G * \bar{B}_t$$

The overall production summed over the life history will then be given by:

$$OP = \sum_{t = t_1}^{t_\lambda} P_t$$

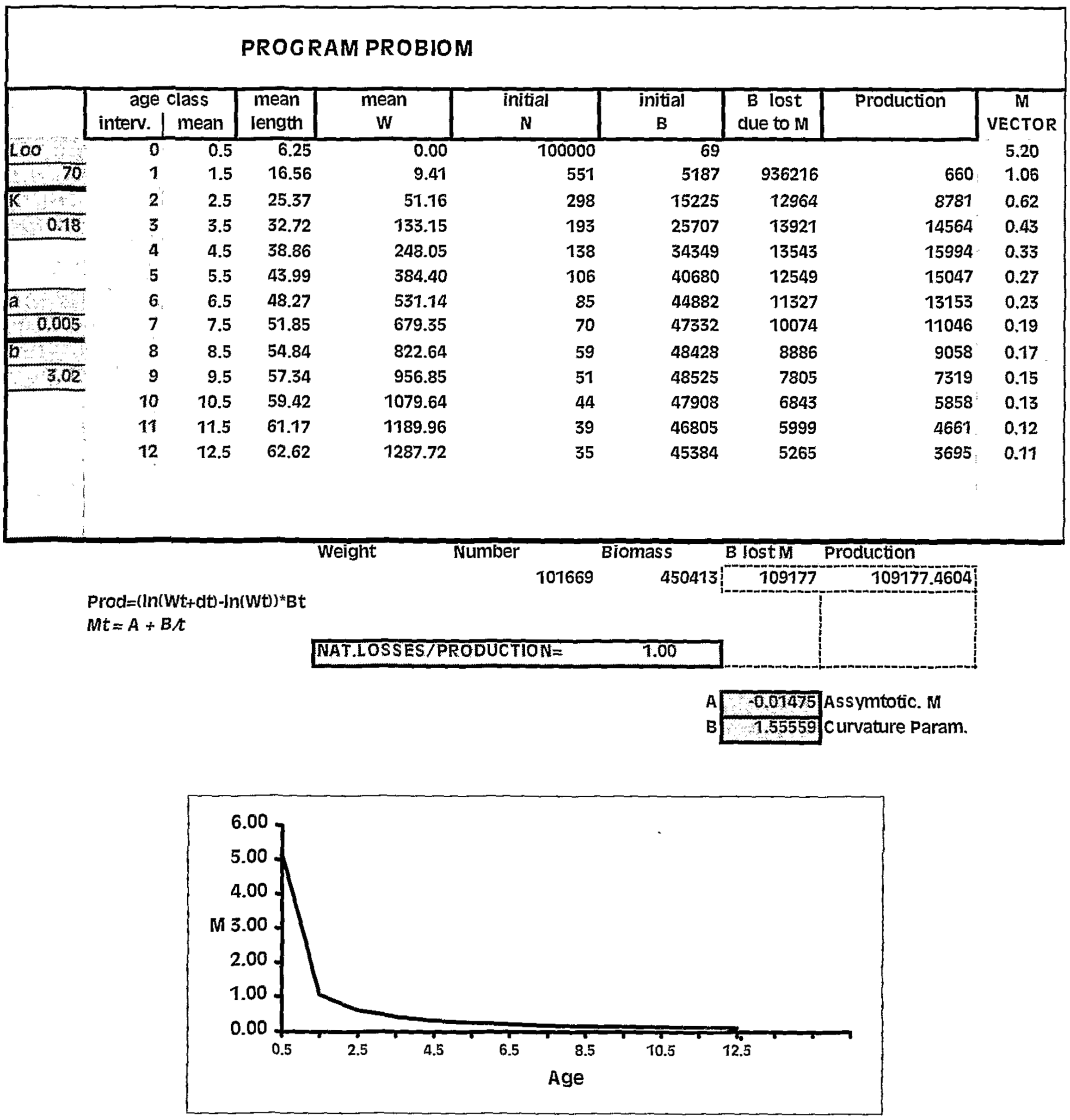
Where the overall losses in biomass due to natural mortality between the first interval $t_1$ and the maximum age $t_\lambda$, is given by:

$$OBL = \sum_{t=t_1}^{t_\lambda} M_t \, B_t \, \Delta t$$

The estimation of the parameters A and B of the reciprocal M equation is performed by the SOLVER option of the EXCEL5 spreadsheet, with the goal of obtaining identical values for Overall Biomass Losses (OBL) and Overall Production (OP) by the instructions: "set the cell corresponding to OP/OBL = 1 by changing the values in the cells of the A and B parameters".

Due to the nature of the equation used for the estimation of the mean M, a very short positive time delay has to be imposed in arbitrarily setting the lower limit of the first time interval. This avoids the indeterminate nature of equation 10 of Caddy (1991) when the first time interval starts at time t = 0. In practice, this initial time value has no significant influence on the estimates of the A and B parameters.

An application of the PROBIOM program is shown in Fig. 1.



**PROGRAM PROBIOM**

| | age class interv. | age class mean | mean length | mean W | initial N | initial B | B lost due to M | Production | M VECTOR |
|---|---|---|---|---|---|---|---|---|---|
| Loo | 0 | 0.5 | 6.25 | 0.00 | 100000 | 69 | | | 5.20 |
| 70 | 1 | 1.5 | 16.56 | 9.41 | 551 | 5187 | 936216 | 660 | 1.06 |
| K | 2 | 2.5 | 25.37 | 51.16 | 298 | 15225 | 12964 | 8781 | 0.62 |
| 0.18 | 3 | 3.5 | 32.72 | 133.15 | 193 | 25707 | 13921 | 14564 | 0.43 |
| | 4 | 4.5 | 38.86 | 248.05 | 138 | 34349 | 13543 | 15994 | 0.33 |
| | 5 | 5.5 | 43.99 | 384.40 | 106 | 40680 | 12549 | 15047 | 0.27 |
| a | 6 | 6.5 | 48.27 | 531.14 | 85 | 44882 | 11327 | 13153 | 0.23 |
| 0.005 | 7 | 7.5 | 51.85 | 679.35 | 70 | 47332 | 10074 | 11046 | 0.19 |
| b | 8 | 8.5 | 54.84 | 822.64 | 59 | 48428 | 8886 | 9058 | 0.17 |
| 3.02 | 9 | 9.5 | 57.34 | 956.85 | 51 | 48525 | 7805 | 7319 | 0.15 |
| | 10 | 10.5 | 59.42 | 1079.64 | 44 | 47908 | 6843 | 5858 | 0.13 |
| | 11 | 11.5 | 61.17 | 1189.96 | 39 | 46805 | 5999 | 4661 | 0.12 |
| | 12 | 12.5 | 62.62 | 1287.72 | 35 | 45384 | 5265 | 3695 | 0.11 |

| Weight | Number | Biomass | B lost M | Production |
|---|---|---|---|---|
| | 101669 | 450413 | 109177 | 109177.4604 |

Prod=(ln(Wt+dt)-ln(Wt))*Bt

*Mt = A + B/t*

NAT.LOSSES/PRODUCTION= 1.00

A -0.01475 Assymtotic. M

B 1.55559 Curvature Param.

Fig. 1. An example of utilization of the PROBIOM program on EXCEL5 spreadsheet.

## Program FOREM

For a population in equilibrium for which the sex ratio is assumed constant through life, Caddy (1991) assumed that one female and one male survive to the Mean Parental Age (MPA) (or equivalent length) from an initial cohort size at age t = 0, which is equivalent to the Mean Lifetime Fecundity (MLF). (This is mathematically equivalent to the more conventional assumption that if half of the eggs are female, one female survives to spawn at MPA.) In order to perform calculations for the estimates of MPA and MLF (average egg production throughout life) have to be estimated. The weighted mean age at spawning MPA was calculated and this then allowed the estimation of the lifetime fecundity by summing the eggs produced by a female from $t_m$ (age at first maturity) to the mean age of spawning. An average lifetime fecundity of 3,182,000 eggs was estimated for female hake under unexploited conditions. It corresponds to the number produced on average by a female surviving to maturity through its reproductive life history. This departure value of "recruits" (eggs) is set for the first age class or length class and the program uses the classical survival equation to calculate the number of survivals through each age (length) interval which would result in two survivors at the estimated mean age (length) of reproduction (8 years or near 61 cm of total length) as a result of changing the values of the A and B parameters of the Caddy (1991) equation. The main assumptions and equations utilized in this program are the same as were described above for PROBIOM. The FOREM approach, as well as that referred to below as BACKM, are based on female life histories, and therefore female growth parameters have been used. In consequence, the results of the M vectors obtained by these two methods strictly speaking apply to females, although a similar declining M trajectory is expected for males also. PROBIOM is based on other considerations however, and could in theory allow separate estimation of $M_t$ values by sex, but as used here, applies to the two sexes combined.

An application of program FOREM is shown in Fig. 2.

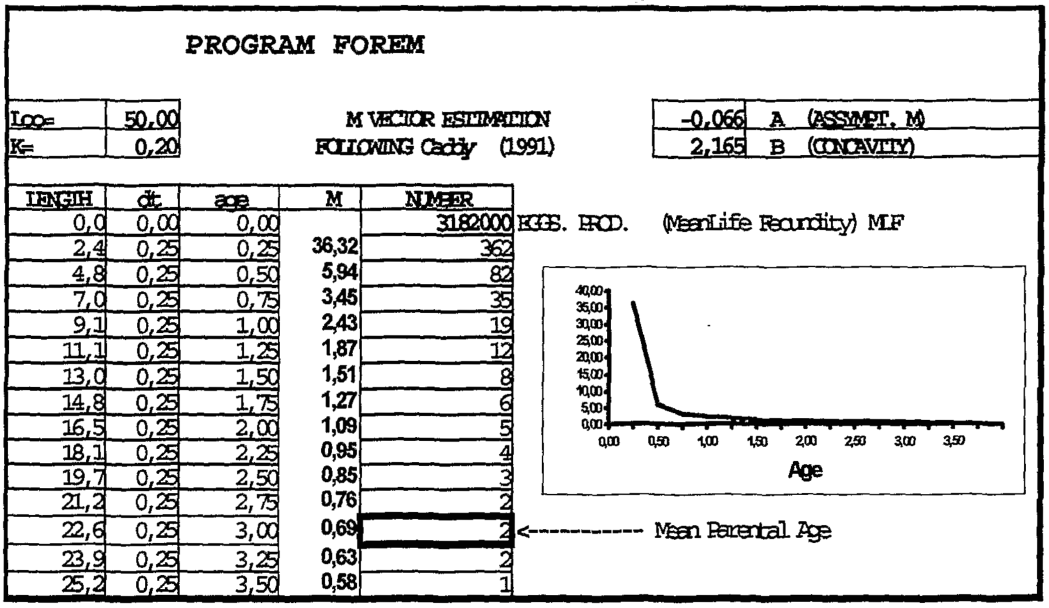
## Program BACKM

The assumptions followed are the same as for FOREM, but the inverse procedure is utilized: departing from 2 surviving individuals at the MPA (length), back-calculation involving a change in sign of the survival equation should result in 3,182,000 individuals (egg production) being generated. The SOLVER routine is set equal to the estimated mean lifetime production of eggs. For the cell corresponding to the MLF, beginning with two individuals at the mean age or length of reproduction (8 years or around 61 cm of T.L.), the initial fecundity is reconstructed by changing the values of the cells corresponding to A and B in the Caddy (1991) equation until the initial number equals the MLF.

The results of the three fitting procedures were compared with estimates of M-at-age for 3 species of North Sea groundfish (from Sparholt, 1990). The North Sea species were cod, haddock and whiting. North Sea data combined for natural survivorship of these 3 gadoids similar to the Mediterranean hake provide a broad standard for interspecies comparison for demersal fish.

In order to estimate the Mean Lifetime Fecundity, the adult population structure for females was reconstructed assuming a constant natural mortality rate of 0.2 for individuals older than the age of maturity. This value is generally accepted for adult natural mortality for Mediterranean hake in the literature where values in the range M = 0.17 to 0.35 can be found. These values are generally obtained by using empirical formulas such as those in Rikhter and Efanov (1976) and Pauly (1980). From successive trials, it seems the method is robust and does not critically depends on the above approximation methods for adult M estimates. This makes the choice of a suitable adult M not very critical for the estimation of the Mean Lifetime Fecundity (MLF) or Mean Age of Spawning (MPA). Notwithstanding that changes in input M produce different estimates of MLF and MPA, any pair of values of MLF and MPA determined on the basis of a reasonable wide range of adult M from 0.05-0.4, gave practically identical results for the parameters of the reciprocal equation as demonstrated by Abella *et al.* (in press).

An application of program BACKM is shown in Fig. 2.



PROGRAM FOREM

| | |
|---|---|
| Loo= | 50,00 |
| K= | 0,20 |

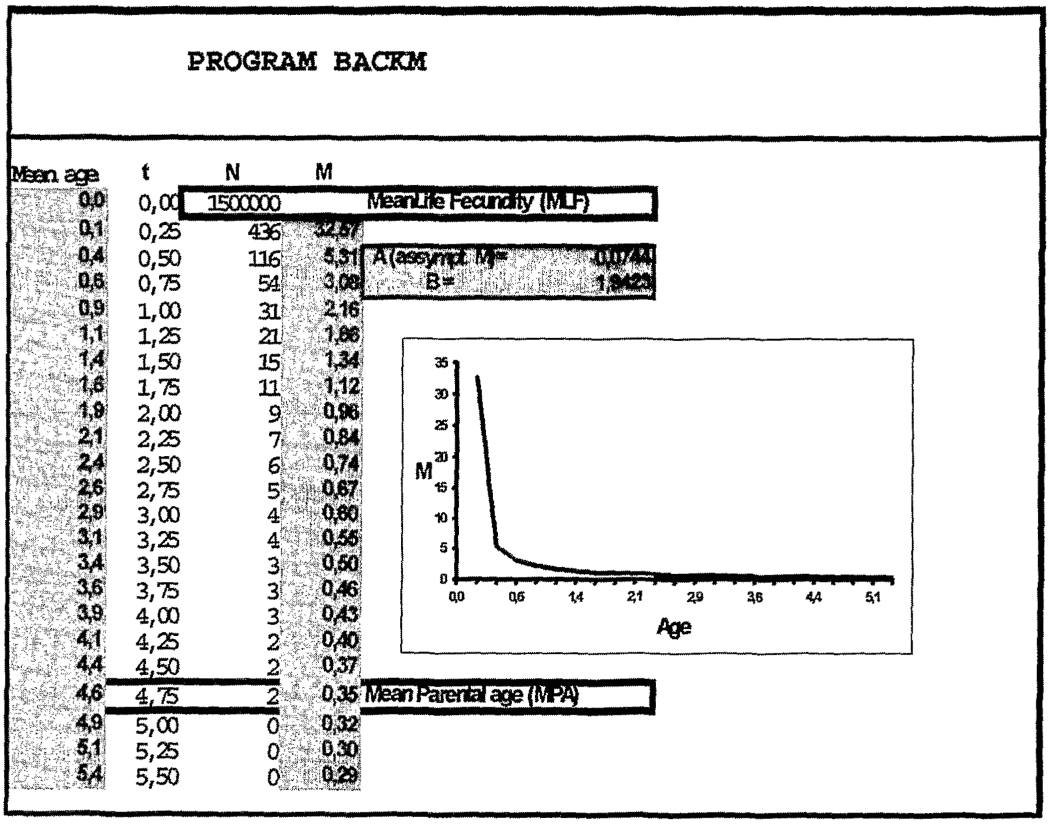
M VECTOR ESTIMATION
FOLLOWING Caddy (1991)

| | | |
|---|---|---|
| -0,066 | A | (ASSYMPT. M) |
| 2,165 | B | (CONCAVITY) |

| LENGTH | dt | age | M | NUMBER |
|---|---|---|---|---|
| 0,0 | 0,00 | 0,00 | | 3182000 |
| 2,4 | 0,25 | 0,25 | 36,32 | 362 |
| 4,8 | 0,25 | 0,50 | 5,94 | 82 |
| 7,0 | 0,25 | 0,75 | 3,45 | 35 |
| 9,1 | 0,25 | 1,00 | 2,43 | 19 |
| 11,1 | 0,25 | 1,25 | 1,87 | 12 |
| 13,0 | 0,25 | 1,50 | 1,51 | 8 |
| 14,8 | 0,25 | 1,75 | 1,27 | 6 |
| 16,5 | 0,25 | 2,00 | 1,09 | 5 |
| 18,1 | 0,25 | 2,25 | 0,95 | 4 |
| 19,7 | 0,25 | 2,50 | 0,85 | 3 |
| 21,2 | 0,25 | 2,75 | 0,76 | 2 |
| 22,6 | 0,25 | 3,00 | 0,69 | 2 |
| 23,9 | 0,25 | 3,25 | 0,63 | 2 |
| 25,2 | 0,25 | 3,50 | 0,58 | 1 |

EGGS. PROD. (MeanLife Fecundity) MLF

<------------ Mean Parental Age



PROGRAM BACKM

| Mean age | t | N | M |
|---|---|---|---|
| 0,0 | 0,00 | 1500000 | |
| 0,1 | 0,25 | 436 | 32,57 |
| 0,4 | 0,50 | 116 | 5,31 |
| 0,6 | 0,75 | 54 | 3,08 |
| 0,9 | 1,00 | 31 | 2,16 |
| 1,1 | 1,25 | 21 | 1,66 |
| 1,4 | 1,50 | 15 | 1,34 |
| 1,6 | 1,75 | 11 | 1,12 |
| 1,9 | 2,00 | 9 | 0,96 |
| 2,1 | 2,25 | 7 | 0,84 |
| 2,4 | 2,50 | 6 | 0,74 |
| 2,6 | 2,75 | 5 | 0,67 |
| 2,9 | 3,00 | 4 | 0,60 |
| 3,1 | 3,25 | 4 | 0,55 |
| 3,4 | 3,50 | 3 | 0,50 |
| 3,6 | 3,75 | 3 | 0,46 |
| 3,9 | 4,00 | 3 | 0,43 |
| 4,1 | 4,25 | 2 | 0,40 |
| 4,4 | 4,50 | 2 | 0,37 |
| 4,6 | 4,75 | 2 | 0,35 |
| 4,9 | 5,00 | 0 | 0,32 |
| 5,1 | 5,25 | 0 | 0,30 |
| 5,4 | 5,50 | 0 | 0,29 |

MeanLife Fecundity (MLF)

A (assympt. M)= 0,0744
B= 1,8423

Mean Parental age (MPA)

Fig. 2. An example of utilization of the FOREM program (top) and BACKM (bottom) on EXCEL5 spreadsheet.

In order to avoid multiple solutions, some reasonable constraints can be introduced into the computations of anyone of the 3 above described programs. For instance, if we have reliable estimates of the natural mortality rate for adults, it is possible to take this into account, and constrain the choice of the A and B parameters by SOLVER. This can be achieved by first calculating for each age (length) class above the age of maturity, the squared deviations between this chosen value and the values predicted for each age (length) for the input values of A and B currently being used. Secondly, the sum of these deviations can be minimized in the SOLVER dialogue box such that values of A and B are chosen that produce 2 survivals at MPA, but also minimize the sum of the deviations of the predicted from the observed value of M.

A more simple procedure can be to constrain the program to select the couple of parameters A and B that produces, for a given time interval, an M value considered reliable.

## Results and conclusions

The results of the 3 main methods of fitting the Mortality-at-age reciprocal relationship for Mediterranean hake are shown in Fig. 3, where they are compared with the North Sea groundfish data for cod, whiting and haddock from the MSVPA experiments. The agreement between the North Sea data and the simulations presented here shown for ages 1 and 2 and ages 5 onwards appear reasonable. Apparently, slightly higher values of M-at-age are suggested for intermediate aged (3+ and 4+) fish by the proposed procedures, and the reader is left to judge whether these are realistic. One comment must be made with respect to the North Sea data however, namely the "hybrid" nature of these vectors: North Sea data for early age groups are from MSVPA, and for the older specimens from earlier "constant M" estimates; presumably resulting from fitting total mortality against annual effort using the Paloheimo (1958) or similar procedures. All 3 new procedures described here showed similar trends in relative values of natural mortality at age to those for the North Sea data, but the fitting with PROBIOM seems to show the overall closest correspondence.

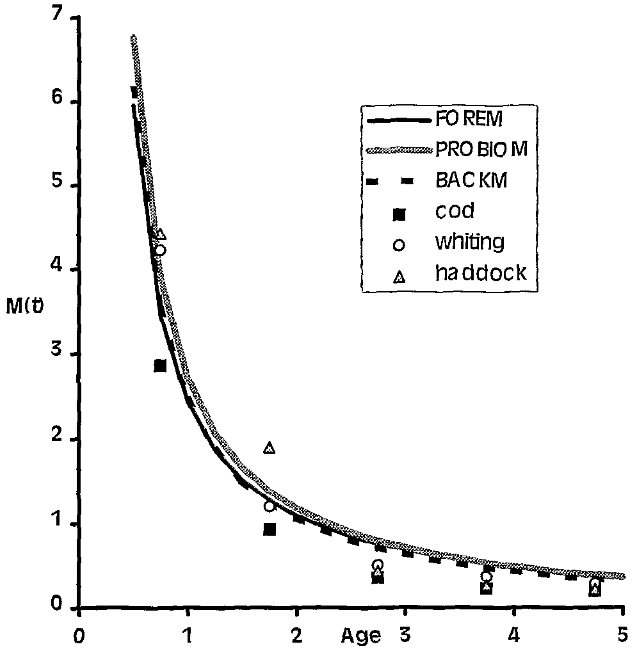


Fig. 3. Comparison of results of the 3 main methods of fitting the Mortality-at-age reciprocal relationship for Mediterranean hake with the North Sea groundfish data for cod, whiting and haddock from the MSVPA experiments.

Several different methods of arriving at an indicative vector of M with age using the reciprocal model are proposed here. At this early stage in applying a new methodology, it is difficult to decide which is the most realistic. A general similarity to the values obtained empirically for (M0+M1+M2) for North Sea groundfish offered one of the few standards of comparison, and seems to confirm that our results are realistic, at least if current perceptions of similar longevity and growth rates of Atlantic and Mediterranean groundfish species are confirmed.

The application of this reciprocal model in most fisheries must still be considered a hypothesis, but is certainly ecologically more realistic than the current assumption of constant natural mortality rate at age for 0+ to 2+ age groups: the age groups that are numerically most important in many Mediterranean demersal fisheries. In the opinion of the authors, it becomes positively dangerous, and in fact contrary to our knowledge of the role of predators in all marine food webs to assume that a constant natural mortality rate applies during the first few years of life. We feel therefore that it is justifiable and precautionary to explore the results of the assumption that natural mortality in the Mediterranean demersal stocks follows a reciprocal relationship with age, and to consider some of the implications it points to.

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