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# INDIRECT ESTIMATES OF NATURAL MORTALITY RATES FOR ATLANTIC SKIPJACK (*KATSUWONUS PELAMIS*), USING LIFE HISTORY PARAMETERS

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*SUMMARY*

*This study presents indirect estimates of Atlantic skipjack natural mortality rates (M) based on life history parameters. M is estimated in one hand for the entire population and on the other hand by length size classes, using 7 and 4 different estimators, respectively. For all the M-estimators a Monte Carlo resampling is used to account for uncertainty in life-history parameters. After omitting one of the entire population M-estimator, judged too low with regard to the total mortality value (Z) derived from a mean length method and according to the state of the skipjack stocks currently admitted, the average of the 6 remaining M-estimators gives an estimate of M at 1.27 (95% C. I., 1.04 - 1.52). The 4 M-at-length estimators were then combined with the size independent M to estimate a rescaled M-at-length as follows: Assuming that the global M describes the natural mortality for the most representative size class of skipjack in the catch, (e.g., the 40-45 cm FL class), 4 relative M-at-length vectors were calculated by dividing each M-at-length by the value of M at 40-45 cm FL. Each of these 4 relatives M-at-length vectors was scaled at the estimate of the entire population M value and then averaged by length class in order to provide a unique vector of M-at-length. Combining M for the entire life population and M-at-length allows the integration of several methods and provides a vector of natural mortality at-length which depicts more realistically the decrease in mortality with body size than the simple constant value of 0.8 commonly used by ICCAT in skipjack stock assessments.*

*RÉSUMÉ*

*Cette étude présente des estimations indirectes des taux de mortalité naturelle (M) du listao de l'Atlantique reposant sur les paramètres du cycle vital. M est estimé d'une part pour l'ensemble de la population et, d'autre part, par classes de taille, à l'aide de sept et quatre estimateurs différents, respectivement. Pour tous les estimateurs de M, un rééchantillonnage Monte Carlo est utilisé pour tenir compte de l'incertitude entourant les paramètres du cycle vital. Après avoir omis l'un des estimateurs de M pour l'ensemble de la population, jugé trop faible par rapport à la valeur de la mortalité totale (Z) obtenue d'une méthode de longueur moyenne et conformément à l'état des stocks de listao actuellement admis, la moyenne des six estimateurs de M restants donne une estimation de M de 1,27 (95% CI, 1,04-1,52). Les quatre estimateurs de M par taille ont ensuite été combinés avec le M indépendant de la taille afin d'estimer un M par taille ré-échelonné comme suit: En supposant que le M global décrit la mortalité naturelle pour la classe de taille la plus représentative du listao dans la capture (par exemple la classe de 40-45 cm longueur à la fourche), quatre vecteurs relatifs de M par taille ont été calculés en divisant chaque M par tailles par la valeur de M à 40-45 cm de longueur à la fourche. Chacun de ces quatre vecteurs relatifs de M par taille a été échelonné à l'estimation de la valeur de M pour l'ensemble de la population et on en a ensuite calculé la moyenne par classe de taille afin de fournir un vecteur unique de M par taille. Le fait de combiner M pour toute la population et M par taille permet d'intégrer plusieurs méthodes et fournit un vecteur de mortalité naturelle par taille qui illustre de façon plus réaliste la diminution de la mortalité par taille que la simple valeur constante de 0,8 communément utilisée par l'ICCAT dans les évaluations de stock de listao.*

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*RESUMEN*

*Este estudio presenta estimaciones indirectas de tasas de mortalidad natural (M) del listado del Atlántico basadas en los parámetros del ciclo vital. M se estima por una parte, para la población entera y, por otra, por clases de talla, utilizando 7 y 4 estimadores diferentes, respectivamente. Para todos los estimadores de M, se usa un remuestreo Monte Carlo para tener en cuenta la incertidumbre en los parámetros del ciclo vital. Tras omitir un estimador de M de toda la población que se consideró muy bajo con respecto al valor de la mortalidad total (Z) obtenido a partir de un método de talla media y de conformidad con el estado actualmente admitido de los stocks de listado, los 6 estimadores de M se promediaron y se estimó una M de 1,27 (95% C. I., 1,04-1,52). Posteriormente se combinaron los 4 estimadores de M por talla con la M independiente de la talla para estimar una M por talla reescalada, de la siguiente manera: asumiendo que la M global describe la mortalidad natural para las clases de talla de listado más representativas en la captura (por ejemplo, clase 40-45 cm FL), los 4 vectores relativos de M por talla se calcularon dividiendo cada M por talla por el valor de M en 40-45 cm FL. Cada uno de estos 4 vectores relativos de M por talla se escaló a la estimación del valor de M para toda la población y luego se promediaron por clases de talla para proporcionar un único vector de M por talla. La combinación de M para toda la población y la M por talla permite integrar varios métodos y proporciona un vector de mortalidad natural por talla que refleja con mayor realismo el descenso en la mortalidad por talla que un valor constante simple de 0,8; utilizado habitualmente en las evaluaciones de stock de listado de ICCAT.*



*KEYWORDS*

*Natural mortality, Skipjack*


## Introduction

Natural mortality (*M*) is one of the life history parameters which has a major impact on the stock status diagnosis and, when necessary, on the choice of accurate regulation measures. For instance, protecting juveniles by restricting access to time area strata and/or limiting some fishing practices (e.g. FAD-fishing) may provide benefits in tropical tuna fisheries if their natural mortality is moderate. However, in practice it is often difficult to estimate the *M* of exploited fish populations (Vetter 1988). In this study we explore *M* indirect estimators based on life-history parameters (1) for the entire population and (2) by length size classes. Then (3) we propose a *M* length-specific vector based on relative *M*-at-lengths scaled on the mean estimator performed for the entire population. A Monte Carlo resampling procedure is used to explore the impact of uncertainty in life-history parameters on the *M* estimates.

## Material and methods

### *Data*

Traditional approaches for estimating natural mortality (catch curves, mark and recapture studies) are data intensive and difficult to implement. For this reason many authors have suggested the use of relationships between *M* and life-history parameters to deal with this problem (Pauly, 1980; Hoenig, 1983; Jensen, 1996). Such approaches have been termed indirect methods (Hewitt *et al*., 2007) and have been recently reviewed by Kenchington (2013). Basically, the inputs biological parameters involved in the indirect calculation of *M* are : (i) the length/weight parameters ($\alpha$, $\beta$), (ii) the Von Bertalanffy (VB) growth curve parameters ($K$, $L_\infty$), and (iii) the size at 50% maturity ($L_m$), or the corresponding age at 50% maturity from the inverse of the VB growth curve ($t_m$), as listed in **Table 1**. Although an inverse relationship between longevity and *M* can reasonably be assumed (Hoenig, 1983), we did not use $T_{max}$ - based estimator *M*, because of the uncertainties surrounding maximal ages.

It should be noted that there are some doubts whether the Von Bertalanffy growth curve is the most accurate model for describing the growth of skipjack (Gaertner *et al*., 2012) but due to the potential use of VB parameters in the calculation of *M*, we adopted this growth model. Life-history parameters found in the literature for length-weight relationship, for Von Bertalanffy curve and for size at first maturity (50%) for skipjack in the world Ocean are summarized in **Tables 2, 3 and 4**, respectively.

***Methods***

Based on the tradeoff among growth, reproduction and natural mortality, many indirect estimators of *M* have been developed and discussed (Jensen, 1996, Hewitt *et al*., 2007, Gislason *et al*., 2010, Kenchington, 2013; among others). We selected the following estimators:

Roff's 2nd estimator (Roff, 1984, in Kenchington, 2013)

$$M = \frac{3\ K\ L_\infty \left(1 - {L_m}/_{\infty}\right)}{L_m}$$

Rikhter and Efanov’s first estimator (Rikhter and Efanov, 1976, in Kenchington, 2013)

$M\ = \frac{\beta\ K}{e^{K\,(t_m - t_0)} - 1}$, with $t_m = \ t_0 + \ Ln\ \left(1 - {L_m}/_{L_\infty}\right) / {-K}$

Rikhter and Efanov’s second estimator (Rikhter and Efanov, 1976, in Kenchington, 2013)

$$M\ = \frac{1.521}{t_m^{0.72}} - \ 0.155$$

Griffiths and Harrod (2007)

$M = 1.406\ W_\infty^{-0.096}\ K^{0.78}$, with $W_\infty = \propto L_\infty^{\beta}$

Djabali et al., (1994)

$M = 1.0661\ L_\infty^{-0.1172}\ K^{0.5092}$

Jensen’s first estimator, Jensen (1996)

$$M = 1.5\ K$$

Jensen’s second estimator, Jensen (1996)

$$M = \frac{1.65}{t_m}$$

In addition to *M* estimators assumed to reflect the entire life history of skipjack and thus apply to the entire stock, it was suggested that *M* was length, or weight-dependent (Gulland, 1987). It is reasonably admitted than natural mortality decreases with increasing body size and depending or not if senescence is accounted for, natural mortality by length may be depicted by an L or a U shaped curve. The assumption that natural mortality changes over the different life stages of tunas was reinforced by Hampton (2000) with tagging data. To allow *M* to vary with individual length/weight, different models have been suggested:

Gislason et al. (2010)

$$M_L = 1.73\ L^{-\,1.61}\ L_\infty^{1.44}\ K$$

Charnov et al. (2013)

$$M_L = \ K\ \left({L_\infty}/_{L}\right)^{1.5}$$

Peterson and Wroblewski, (1984)

$M_w = \ 1.28\ W^{-\,0.25}$ , with W = wet weight in gr

Lorenzen (1996)

$$M_w = \ 3\ W^{-\,0.288}$$

To account for the uncertainty in the life-parameters estimates, we used a Monte Carlo sampling procedure. For each equation 1,000 realizations of $L_\infty$, $K$, $L_m$, $\alpha$, $\beta$ were derived from resampling in skipjack tuna historic parameters (i.e., **Tables 2, 3 and 4**). In order to maintain the correlation between some parameters, the VB parameters in one hand and the length-weight parameters on the other hand, were resampled by pair.

To combine information provided by the *M* unique estimators (i.e., calculated for the entire population) and a size-dependent process in natural mortality, we followed a procedure adopted for Pacific Blue Marlin by Lee and Chang (2013). We assumed that the constant entire life *M* estimator value describes the natural mortality for the most representative size classes of skipjack in the catch. Consequently, we attributed the averaged value of the entire life history *M* to the class 40-45 cm (FL). For each *M* length-specific equation we performed relative *M*-at-length by dividing each *M* length value by the *M* value of the reference size class (i.e., the 40-45 cm class). Then a rescaled *M*-at-length was calculated as the product of the relative *M*-at-length by the constant *M* estimator. To account for uncertainties in the 4 *M* length-specific equations, the rescaled *M*-at-length values were averaged.

**Results**

The global indirect estimators collectively provided a broad range of *M* estimates (0.52 - 1.73 per year; **Table 5** and **Figure 1**). The lowest estimate was given by the Djabali et al's estimator. Even if this estimator depicts a low variability in comparison with the other ones, it might be biased since it was established with data from Mediterranean fish stocks only. It should be stressed that an *M* value of 0.52 appears very low and unlikely for a tropical tuna species such as skipjack. Furthermore total mortality rates (*Z*) from mean length data in nonequilibrium situations for eastern Atlantic skipjack were estimated at about 2.84 in the nineties (**Figure 2**). Since skipjack was not assumed to be overexploited in the historic period of the fishery, one can reasonably assume that $M > Z/2$ (i.e., an *M* value around 1.4). Consequently we omitted the Djabali *et al.*'s estimate in the calculation of the mean for the entire life history *M*. Omitting this estimator, *M* was estimated at 1.27 (95% C. I. 1.04 -1.52, see **Figure 3**).

Length-specific *M* from the 4 corresponding equations are showed separately in **Figure 4** to depict the uncertainty associated with the variability of the inputs life-history parameters and together with the averaged entire *M* estimator in **Figure 5** for comparison purpose. Both Gislason et al and Charnov et al estimators depicted large range of values between juveniles and adults while Peterson and Wroblewski's estimator showed a moderate range of change in natural mortality over the life stages. Lorenzen's approach represented a median pattern for juveniles but according to this model the main exploited phase of the skipjack stocks (i.e., the 40-80 cm fork length) should support higher natural mortality than estimated by the other 3 models.

The rescaled length-specific *M* estimates which combines entire indirect *M* estimators and *M*- at-length estimators is represented in **Figure 6**. High natural mortality is assumed for 10-15 cm FL skipjack, around 7.7, with a fast decline when body size increases (e.g., 0.7 at 65-70 cm, **Table 6**). As mentioned previously, uncertainty was introduced by the Monte Carlo resampling method, drawing 1,000 realizations of the growth parameters, length at maturity and length-weight relationship coefficients in the calculation of the constant *M* and the *M*-at-length. Nevertheless, the range of plausible *M* values for each size class remains relatively moderate.

**Discussion and conclusion**

*M* values for skipjack found in this study were higher than values commonly used in ICCAT stock assessment (0.8) or found by tagging experiments (e.g., Bousquet *et al*., 2012 in the Indian Ocean), but are lower than values reported in the Western and Central Pacific (9.6 for 21-30 cm and 1.44-1.8 for 51-70 cm; Langley and Hampton, 2008). In the case of the Eastern Pacific, IATTC has used a constant value of 1.5, on an annual basis, for *M* in yield-per-recruit analyses (Anon., 2000). With regard to L vs U shaped form, senescence may exhibit in the later stage of life (Fonteneau and Pallares, 2005) and an increase in natural mortality for individuals up to 10 years old has been reported by Hampton (2000), Langley and Hampton (2008), and recently by Bousquet *et al.* (2012), but here more moderately and after 4 years old only. It is unclear however whether high natural mortality for old skipjack is an artifact of the tagging data due to older fish moving out of the fishery (Maunder, 2012). Notice that escapement is likely to occur in the Eastern Atlantic where large skipjack are scarce in comparison with the Western Atlantic. It should be stressed that the same range of values (0.6-0.8) are also used by ICCAT to depict *M* of yellowfin, despite this species is likely less vulnerable to predation than skipjack, at least during the adult phase.

Although *M* indirect methods rely on parameters that are commonly measured in biological studies, their use in stock assessment has been questioned. One of the major criticism is the fact that indirect methods that have been derived from data on many species to predict M for a single species (Vetter, 1988; Pascual and Iribarne, 1993). However as noted by Hewitt *et al.* (2007), the use of multiple methods may reduce the bias imposed by any one method and other indirect *M* estimators should be explored and added to the models used in this study. In addition, by resampling life-history parameters only we are aware that we are missing the uncertainty associated to the estimates of the coefficients of the different models. All sources of uncertainty should be incorporated in the predictive capacity of the indirect estimators themselves (Pascual and Iribarne, 1993; Quiroz *et al*., 2010).

Another limit mentioned in the Data section, is the use of *M* indirect estimators based on the Von Bertalanffy parameters. Assuming such a growth model might be incorrect for skipjack as suggested from tagging data analysis in the Indian Ocean (**Figure 7**).

The conclusion of this study is that despite these limits the combination of *M* indirect estimators based on life-history parameters gives some insight on plausible range of entire *M* estimate for skipjack, as well as *M*-at-length, and could be used to implement data-poor assessment methods such as Depletion-Based Stock Reduction Analysis (DB-SRA) (Dick and MacCall, 2011).

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**Table 1.** Standard symbols used in this study.

| | |
|---|---|
| $\alpha$ | Parameter of the length-weight relationship |
| $\beta$ | Exponent of the length-weight relationship |
| $L_\infty$ | Asymptotic fish length |
| $K$ | Parameter of the von Bertalanffy growth curve |
| $t_0$ | Parameter of the von Bertalanffy growth curve |
| $l$ | Individual fish length |
| $l_m$ | Length at reproductive maturity |
| $M$ | Natural mortality rate |
| $M_l$ | Natural mortality rate at length l |
| $M_w$ | Natural mortality rate at weight w |
| $t_m$ | Age at reproductive maturity |
| $W_\infty$ | Asymptotic fish weight |
| $w$ | Fish weight |

**Table 2.** Parameters of the length-weight relationship for skipjack (FL in cm, Weight in gr).

| *Area* | $\alpha$ | $\beta$ | *sex* | *Reference* |
|---|---|---|---|---|
| Cuba A | 4.68E-06 | 3.39 | all | Valle *et al*. 1986 |
| Cuba C-D | 1.07E-05 | 3.175 | all | Valle *et al*., 1986 |
| E-Atl | 5.61E-06 | 3.315 | all | Lenarz 1974 |
| all Atl | 7.48E-06 | 3.253 | all | Cayre_Laloe, 1986 |
| Atl E. N 10N Z1 | 8.47E-06 | 3.215 | male | Cayre_Laloe, 1986 |
| Atl E. N 10N Z1 | 9.80E-06 | 3.205 | female | Cayre_Laloe, 1986 |
| Atl E. N 10N Z1 | 5.03E-05 | 2.733 | juvenile | Cayre_Laloe, 1986 |
| Atl E. Trop Z2 | 6.88E-06 | 3.292 | male | Cayre_Laloe, 1986 |
| Atl E. Trop Z2 | 7.15E-06 | 3.282 | female | Cayre_Laloe, 1986 |
| Atl E. Trop Z3 | 6.10E-06 | 3.31 | male | Cayre_Laloe, 1986 |
| Atl E. Trop Z3 | 6.34E-06 | 3.3 | female | Cayre_Laloe, 1986 |
| Atl SW Brazil Z4 | 6.02E-06 | 3.313 | male | Cayre_Laloe, 1986 |
| Atl SW Brazil Z4 | 6.26E-06 | 3.303 | female | Cayre_Laloe, 1986 |
| AtlNE Azores Z5 | 6.87E-06 | 3.283 | male | Cayre_Laloe, 1986 |
| AtlNE Azores Z5 | 7.14E-06 | 3.273 | female | Cayre_Laloe, 1986 |
| Atl SE | 4.12E-06 | 3.409 | all | Pianet, 1974 |
| Atl SW Brazil Z4 | 6.54E-06 | 3.293 | all | Andrade_Oliveira Campos, 2002 |
| Atl SW | 6.87E-06 | 3.287 | all | Vilela Castelo, 1993 |
| Atl SW Brazil | 6.79E-06 | 3.28 | all | Amorim *et al*., 1981 |
| Atl SW Brazil | 3.82E-06 | 3.377 | all | Menezes *et al*., 2010 |
| Atl NW | 2.16E-06 | 3.353 | all | Batts, 1972 |
| IO NW Madagascar | 1.13E-05 | 3.158 | all | Marcille_Stequert, 1976 |
| IO East | 7.81E-06 | 3.226 | all | Thapanand-Chaidee_Pudprommarat, |
| IO Minicoy Islands | 1.98E-06 | 3.356 | male | Mohan_Kunhikoya, 1985 |
| IO Minicoy Islands | 1.00E-06 | 3.463 | female | Mohan_Kunhikoya, 1985 |
| South China Sea | 5.80E-06 | 3.3471 | all | Chu Tien Vinh, 2000 |
| New Zeland | 6.21E-06 | 3.19 | all | Vooren, 1976, in Matsumoto *et al*., 1984 |
| New Zeland | 3.48E-06 | 3.29 | all | Habib, 1978, in Matsumotu *et al*., 1984 |
| Hawaii | 4.81E-06 | 3.368 | all | Nakamura_Uchiyama, 1966 in Wild and Hampton, 1994 |
| E. Pacific | 5.53E-06 | 3.336 | all | Hennemuth 1959 in Wild and Hampton, 1994 |

**Table 3.** Estimates of growth parameters for skipjack.

| *Area* | $L_\infty$ | *K* | *Method* | *Reference* |
|---|---|---|---|---|
| E. Atlantic G. of Guinea | 80 | 0.32 | Tagging | Bard and Antoine, 1986 |
| E. Atlantic N. trop | 80 | 0.60 | Tagging | Bard and Antoine, 1986 |
| E. Atlantic G. of Guinea | 86.7 | 0.31 | Spines | Chur and Zharov, 1983 |
| E. Atlantic Senegal | 62 | 2.08 | Tagging | Cayré *et al*., 1986 |
| E. Atlantic Cap Vert | 60 | 1.54 | Tagging | Cayré *et al*., 1986 |
| E. Atlantic Senegal | 97.26 | 0.25 | Tagging | Hallier and Gaertner, 2006 |
| W. Atlantic Caribbean sea | 94.9 | 0.34 | Length-freq | Pagavino and Gaertner, 1995 |
| W. Atlantic Brasil | 87.12 | 0.22 | Spines | Vilela and Costello, 1991 |
| Indian Ocean | 60.6 | 0.93 | Length-freq | Marcille and Stequert, 1976 |
| Indian Ocean Maldives | 64.3 | 0.55 | Tagging | Adams, 1999 |
| Indian Ocean Maldives | 82 | 0.45 | Length-freq | Hafiz, 1987, in Adams 1999 |
| Indian Ocean Sri Lanka | 85 | 0.62 | Length-freq | Amarasiri and Joseph, 1987 |
| Indian Ocean Sri Lanka | 77 | 0.52 | Length-freq | Sivasubramanium, 1985; in Adams, 1999 |
| Indian Ocean Minicoy | 90 | 0.49 | Length-freq | Mohan and Kunhikoya, 1985; in Adams, 1999 |
| Indian Ocean | 82.91 | 0.24 | Tagging | De Bruyn and Murua, 2008 |
| Indian Ocean | 76.88 | 0.28 | Tagging | Gaertner *et al*., 2011 |
| E. Pacific | 85 | 0.7 | Tagging | Rothschild, 1966 |
| E. Pacific | 79 | 0.64 | Tagging | Josse *et al*., 1979 |
| E. Pacific N | 96.3 | 0.52 | Tagging | Bayliff, 1988 |
| E. Pacific S | 66.5 | 1.81 | Tagging | Bayliff, 1988 |
| E. Pacific | 73 | 0.82 | Tagging | Joseph and Calkins, 1969 |
| E. Pacific | 107 | 0.42 | Length-freq | Joseph and Calkins, 1969 |
| E. Pacific | 75.5 | 0.772 | Tagging | Sibert *et al.*, 1983 |
| W. Pacific | 61.3 | 1.25 | Tagging | Sibert *et al.*, 1983 |
| W. Pacific | 65.5 | 0.95 | Tagging | Josse *et al*., 1979 |
| W. Pacific Vanuatu | 60 | 0.75 | Length-freq | Brouard *et al*., 1984 |
| W. Pacific Trop. & Jap. | 93.6 | 0.43 | Otolith | Tanabe *et al*., 2003 |
| W. Pacific Japan | 76.6 | 0.60 | Length-freq | Yao, 1981; in Wild and Hampton, 1994 |
| W. Pacific Taiwan | 103.6 | 0.30 | Vertebrae | Chi and Yang, 1973; in Wild and Hampton, 1994 |
| Central Pacific | 102.2 | 0.55 | Otolith | Uchiyama and Struhsaker, 1981 |
| Central Pacific | 80 | 0.95 | Grouped L-freq | Brock, 1954; in Adams, 1999 |
| Central Pacific West | 74.8 | 0.52 | Length-freq | Wankowski, 1981 |
| Central Pacific West | 62.17 | 2.373 | Otolith | Leroy, 2013 |
| Hawaii | 82.3 | 0.77 | Tagging | Rothschild, 1984 |
| South China Sea | 77.67 | 0.299 | Length-freq | Chu Tien Vinh, 2000 |
| Philippines | 74 | 0.77 | Length-freq | Tandog-Edralin *et al.*, 1990 |

**Table 4.** Size at 50% maturity for skipjack.

| *Area* | $L_m$ | *sex* | *Reference* |
|---|---|---|---|
| Atl all | 42 | female | Cayre_Farrugio, 1986 |
| Atl all | 45 | male | Cayre_Farrugio, 1986 |
| Atl NE | 44 | female | Cayre, 1981 |
| Atl NE | 46 | male | Cayre, 1981 |
| Atl NW | 50 | all | Batts, 1972, in Cayre et Farrugio, 1986 |
| Atl SW | 51 | female | Vilela_Castello, 1993 |
| Atl SW | 52 | male | Vilela_Castello, 1993 |
| Atl equat | 45 | female | Hazin_*et al.*, 2001 |
| Atl equat | 48 | male | Hazin_*et al.*, 2001 |
| W et C Pacific | 47.9 | male | Ashida *et al.*, 2010 |
| Philippines | 43 | all | Tandog-Edralin_*et al.*, 1990 |
| West IO | 39.9 | female | Grande, 2013 |
| West IO | 40 | male | Timohina_Romanov, 1996 |
| West IO | 43 | female | Timohina_Romanov, 1996 |
| West IO | 42 | female | Stequert_Ramcharrun, 1976 |
| West IO | 43.5 | male | Stequert_Ramcharrun, 1976 |

**Table 5.** Estimates of natural mortality (M) for skpijack from different entire population indirect estimators. Djabali *et al.* estimator was omitted in the calculation of the Great Mean value (see text).

| *Estimator* | *Roff* | *Rikhter Efanov 1* | *Rikhter Efanov 2* | *Griffiths Harrod* | *Djabali et al* | *Jensen 1* | *Jensen 2* | *Great Mean* |
|---|---|---|---|---|---|---|---|---|
| Mean | 1.59 | 1.73 | 1.16 | 0.81 | 0.52 | 1.01 | 1.35 | 1.27 |
| 95% L.C.I. | 1.29 | 1.40 | 0.98 | 0.67 | 0.46 | 0.80 | 1.10 | 1.04 |
| 95% U.C.I. | 1.93 | 2.11 | 1.35 | 0.96 | 0.58 | 1.25 | 1.63 | 1.52 |

**Table 6.** Estimates of rescaled *M*-at-length for skipjack (a 10 cm size class means a 10-15 cm interval).

| *L (cm)* | *10* | *15* | *20* | *25* | *30* | *35* | *40* | *45* | *50* | *55* | *60* | *65* | *70* | *75* | *80* | *85* | *90* | *95* | *100* |
|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|---|
| M | 7.66 | 4.43 | 3.04 | 2.28 | 1.81 | 1.49 | 1.27 | 1.10 | 0.97 | 0.87 | 0.78 | 0.71 | 0.65 | 0.60 | 0.56 | 0.52 | 0.49 | 0.46 | 0.44 |
| L. C.I. | 6.26 | 3.62 | 2.48 | 1.86 | 1.48 | 1.22 | 1.04 | 0.90 | 0.79 | 0.71 | 0.64 | 0.58 | 0.53 | 0.49 | 0.46 | 0.43 | 0.40 | 0.38 | 0.36 |
| U.C.I. | 9.17 | 5.31 | 3.64 | 2.73 | 2.17 | 1.79 | 1.52 | 1.32 | 1.16 | 1.04 | 0.94 | 0.85 | 0.78 | 0.72 | 0.67 | 0.63 | 0.59 | 0.55 | 0.52 |

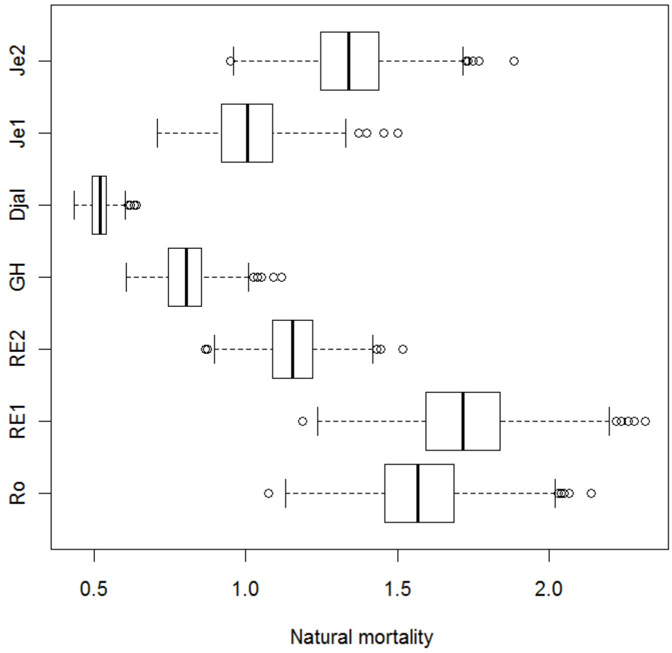


**Figure 1.** Skipjack *M* entire population estimators from different models. Ro= Roff's estimator, RE1 = Rikhter and Efanov's first estimator, RE2= Rikhter and Efanov's second estimator, GH= Griffiths and Harrod's estimator, Djal= Djabali *et al*.'s estimator, Je1= Jensen's first estimator, Je2=Jensen's second estimator.

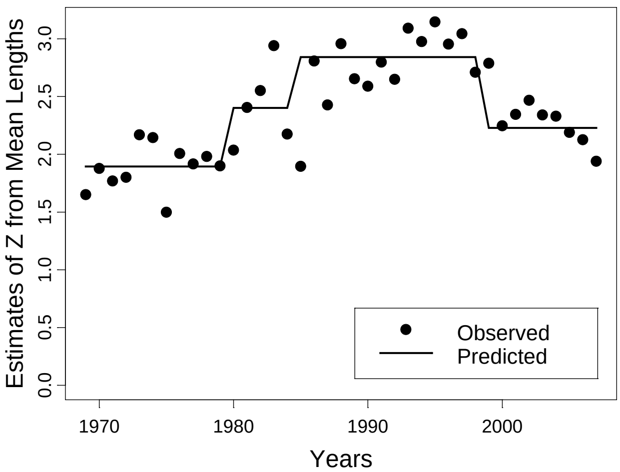


**Figure 2.** Estimates of skipjack mortality rates ($Z$) in the eastern Atlantic from 1969 to 2007. Observed values correspond to the Beverton-Holt estimator. Predicted line corresponds to the mortality estimates by the transitional model of Gedamke-Hoenig in nonequilibrium situations (from Gaertner, 2010).

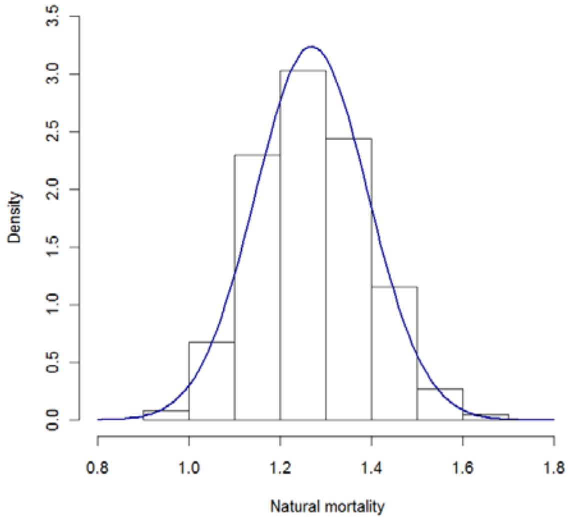


**Figure 3.** Histogram of the averaged estimates of skipjack natural mortality from different entire population indirect estimators and obtained by Monte Carlo resampling (1000 runs * 7 models) of life-history parameters.

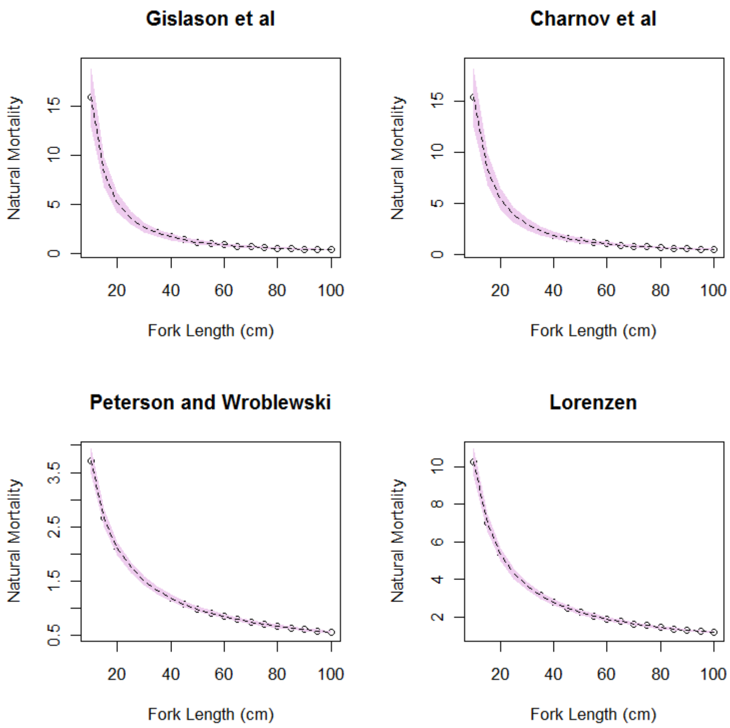


**Figure 4.** Relationships between fork length and natural mortality (*M*) estimated from different models for skipjack. *M* uncertainty at length was obtained by 1000 Monte Carlo resamplings of the corresponding life-history parameters.

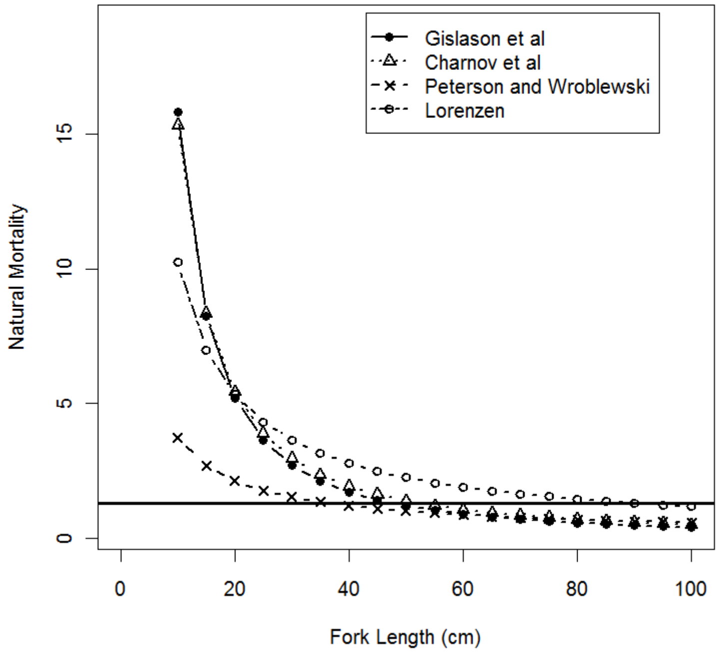


**Figure 5.** Comparison of 4 *M*-at-length estimators and the averaged entire *M* estimator (horizontal line) for skipjack.

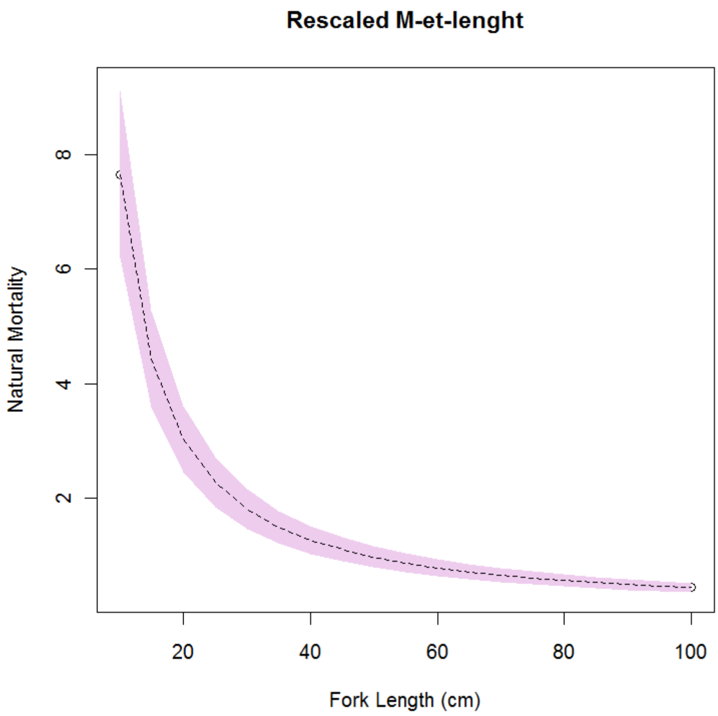


**Figure 6.** Rescaled *M*-at-length estimator for skipjack combining the entire population indirect estimators and *M*-at-length estimators. Uncertainty in life-history parameters was accounted for Monte Carlo resampling of life-history parameters at each equation level.

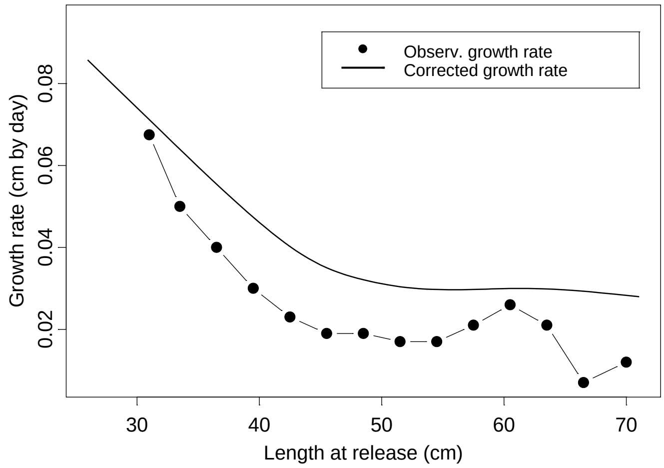


**Figure 7.** Growth rate (cm /day) of skipjack in the Indian Ocean observed from tagging data which suggests that growth does not follow the conventional Von Bertalanffy model. The (GAM) corrected growth rate accounted for the differences in days at sea for each length at release (from Gaertner *et al*., 2012).