Variability of Natural Mortality Estimates–the Case of Selected Demersal/Deep Water Species from Azores (ICES Xa2)

Priscila Silva[1]*, Helena Krug[2,3,4], Ana Novoa-Pabon[3,4] and Mário Rui Pinho[2,3,4,5]

ABSTRACT

Natural mortality (M) is a powerful parameter in fisheries stock assessment and management; however, its precise estimation is extremely difficult. There is still a lack of estimates for several stocks. That is the case of demersal/deep-water species from the Azores archipelago, where demersal species are the second most important fishery based on landings and the most important in value. Species with higher commercial value and lacking M data were selected: *Pagellus bogaraveo, Phycis phycis, Beryx splendens, Pontinus kuhlii, Helicolenus dactylopterus, Pagellus acarne, Beryx decadactylus* and *Pagrus pagrus*. Life history parameters were gathered from literature. A literature review was performed to summarize all published indirect methods that are commonly used, as a simple and low-cost way to estimate M. This study aims to demonstrate the variability of natural mortality estimates based on the input parameters. It also constitutes the first attempt of M estimation for the most commercially important Azorean species. Twenty-six indirect methods were applied and about 70 % of the selected species had an average mortality estimate between 0.22 and 0.34 per year. The most well-studied species (*Pagellus bogaraveo* and *Helicolenus dactylopterus*) provided more accurate mean estimations (M = 0.30 and M = 0.27, respectively). Independent methods based on T_{max} alone, or combined with L_∞ or W_∞, lowered the values. Methods based on reproduction parameters alone, or combined with growth, inflated the estimations. From the selection of life history parameters to the final estimation of M, the results of this study can fill the existing gap and represent a starting point for further studies.

Keywords: Azores, Commercial species, Data-limited, Life history, Methods, Natural mortality (M)

INTRODUCTION

Natural mortality (M) is among the main parameters in fish stock assessment and management (Cadima, 2003). The importance of M is directly defined by stock productivity, yields that can be obtained, optimal exploitation rates, management quantities and reference points (Brodziak *et al*., 2011). However, estimating this parameter with useful accuracy is extremely difficult (Kenchington, 2014). Natural mortality is the result of every cause of death except fishing, so truly direct estimates of this parameter can only be obtained from completely unfished stocks. In exploited fish stocks, M values may be the result of subtracting fishing mortality (F) from total mortality (Z) (Pauly, 1980) or of different direct estimation approaches that are data-intensive (e.g., mark and recapture) and non-applicable to

---

[1] MARE - Marine and Environmental Sciences Centre, Faculdade de Ciências, Universidade de Lisboa, Campo Grande, Lisboa, Portugal
[2] IMAR -Institute of Marine Research, University of the Azores, Horta, Portugal
[3] Okeanos R&D Centre, University of the Azores, Horta, Portugal
[4] Faculty of Science and Technology, Department Oceanography and Fisheries, University of the Azores, Horta, Portugal
[5] MARE - Marine and Environmental Sciences Centre, University of the Azores, Horta, Portugal
* Corresponding author. E-mail address: phsilva@fc.ul.pt
Received 17 August 2020 / Accepted 24 January 2021

most of the world's fisheries (Kenchington, 2014). M for a determined population is greatly associated with age, length or weight and may be variable over time. Also, it may have high variation between subpopulations (Vetter, 1988; Kenchington, 2014). In stock assessment, M has traditionally been considered invariable over time, age, length and weight. Thus, it is assumed that a single estimate of the natural mortality rate applies to the entire stock (Vetter, 1988; Johnson *et al*., 2014). Many authors since Beverton and Holt (1959) have proposed less complex, cheaper but also less reliable methods than direct ones to estimate this parameter, assuming both age independence (M constant for all ages) and dependence (M variable with age, length or weight). To develop these estimators, the authors used various combinations of age point estimates, growth parameters, life history theory and M regressions in well-studied populations (Kenchington, 2014). Due to the importance and influence of this parameter in fisheries management, there is an urgent need for its estimation for exploited communities, especially those which are particularly vulnerable to over-exploitation, which is the case for seamount demersal fish communities (Morato *et al*., 2004).

The Azores archipelago is located at the intersection of the European, American and African plates on the mid-Atlantic ridge. The archipelago consists of nine volcanic islands that form three groups, running from WNW-ESE, with latitude from 37 to 40°N and longitude from 25 to 32ºW (Da Silva and Pinho, 2008).

The Azorean fishing fleet is multi-species and multi-gear and is usually divided into two main segments: 1) a small-scale or artisanal fishing fleet that represents 80-90 % of the vessels and 2) a large-scale or semi-industrial fishing fleet (Morato, 2012). The artisanal and inshore fishing fleet operates essentially along the coast near the islands. The large scale segment operates further from the coast and targets mainly large pelagic and deep-water demersal species (Pinho and Menezes, 2009). Except for tuna, all Azorean vessels target demersal species, which is the second most important fishery in landings and the most important in value, and comprises three demersal fish assemblages: shallow-shelf (<200 m), upper-slope (200-600 m) and mid-slope (600-800 m) (Menezes *et al*., 2006). These resources are considered intensively exploited, although the state of fish stocks in the ecoregion is generally unknown, owing to the lack of analytical assessments. There is no management objective defined for almost all the demersal/deep water species (Pinho and Menezes, 2009). Blackspot seabream (*Pagellus bogaraveo*) is the main target species, dominating landings by weight and value, but other species are also commercially important and caught simultaneously (Pinho and Menezes, 2006).

The present study aims to evaluate the variability of natural mortality estimation for some selected economically important marine species based on the input parameters, using different methods (dependent and independent of age). This is the first study to estimate natural mortality for the most important commercial species from the Azores, filling the existing information gap and serving as a starting point for further studies.

MATERIALS AND METHODS

Eight demersal and deep water species were selected, prioritizing species with higher commercial value in the ecoregion and lacking natural mortality data. Demersal species comprised *Phycis phycis* (Forkbeard), *Pagellus acarne* (Axillary Seabream) and *Pagrus pagrus* (Common Seabream) and the deep-water species comprised *Pagellus bogaraveo* (Blackspot Seabream), *Beryx splendens* (Splendid Alfonsino), *Pontinus kuhlii* (Offshore Rockfish), *Helicolenus dactylopterus* (Blackbelly Rosefish) and *Beryx decadactylus* (Alfonsino).

For each selected species, the necessary life history parameters to estimate each method were collected or calculated: maximum age (T_{max}), asymptotic length (L_∞), growth coefficient (k), hypothetical age of zero length fish (t_0), average length at which fish in a given population is first mature (L_m) and corresponding age ($t_m = t_0 - 1/k \times \ln(1 - L_m/L_\infty)$). Individual weight ($W_i = aL^b$) and asymptotic weight ($W_\infty = aL_\infty{}^b$) were calculated based on each estimated length-weight relationship for the Azores region (Rosa *et al*., 2006), unless the age and growth study selected for each species also provided this parameter. To define T_{max}, growth studies selected for each species were prioritized when this value was available (i.e., *Phycis phycis* and *Helicolenus dactylopterus*). In these cases, it was also considered the maximum age observed under the regional data collection framework covering ICES area X (H. Krug, pers. comm.) to define a range of T_{max} and interpret M variation. For the remaining species, only maximum observed age under regional data collection was available. Dry weight was calculated by assuming it to be 20 % of wet weight, as suggested in the formulation of one of the two methods that required it (Peterson and Wroblewski, 1984).

Preference was given to life history data estimated for the Azores region, published (or observed under regional sampling programs), and based on a representative sample of the population. To create variability of parameters, life history data collected in the regional sampling programs covering ICES area X were used in every possible situation. Fishable size (or length at first capture) (L_c) was also estimated, as average length corresponding to 50 % of the individuals in the accumulated distributions, to define exploitable size range. Information was collected for the combined sexes unless the authors of growth studies reported significant differences between males and females. In this case, M was estimated for sexes separately.

Temperature data were the same for all species considered due to the lack of published information. The average habitat temperature was defined by the depth distribution model based on survey cruises (Menezes *et al*., 2006), and the average temperature corresponding to depth strata was estimated by the depth of the temperature profiles (A. Martins, pers. comm.).

A literature review was performed to summarize all published indirect methods (independent and dependent of age, length or weight) that are often used to estimate natural mortality. Methods applicable to demersal fish were selected, eliminating methods that apply to total mortality (Z) (Hoenig, 1983), or other natural resources such as eggs and larvae (McGurk, 1986), cetaceans (Ohsumi, 1979), pelagic fish (Bayliff, 1967; Sekharan, 1975), or perciforms and reef species (Griffiths and Harrod, 2007). Methods based on the gonadosomatic index were not included because this information was not available for the selected species in the present study. Considering the uncertainty associated with the use of these methods (related to the empirical nature of their formulation), several methods were used, which could have decreased bias related to the application of only one method, as suggested by Kenchington (2014).

Natural mortality was estimated for the combined sexes, unless growth studies showed significant differences between sexes and where the authors suggested using sex-specific values, which is the case for *Pontinus kuhlii* and *Helicolenus dactylopterus*. Five age-dependent methods were also used to estimate natural mortality by age, length or weight. For these methods, age was estimated based on the central point of the length range ($t = t_0 - 1/k \times \ln(1-L/L_\infty)$). We chose not to estimate graphically by age, since our aim is to reveal the variability of M estimations when different life history parameters are considered. As so, an average of M over the exploitable size range was calculated and presented in order to allow the comparison of estimations based on these methods against independent methods.

For each species, the average M of each method was divided by the total mean and converted to a percentage to compare the method's estimation with the species mean. Also, the mean of all species estimations for each method was calculated and presented as percentage, to compare quantitatively the performance of methods.

RESULTS

Table 1 summarizes all indirect methods considered during the literature search that are used in the present study. This represents one of the largest collections of empirical methods to estimate M. Methods are organized by type of parameters needed to estimate them: growth-dependent of age, length or weight or constant over life span; reproduction; or both types of parameters combined.

Table 1. Indirect methods to estimate natural mortality rates.

		References	Equation
Growth	**Constant**	Beverton and Holt (1959)	$M = 5/T_{max}$
		Taylor (1960)	$M = 2.996/T_{max}$
		Tanaka (1960)	$M = 2.5/T_{max}$
		Alverson and Carney (1975)	$M = 3k/(\exp(0.638T_{max}*k-1))$
		Pauly (1980)	$M = \mathrm{Exp}(-0.0066-0.279\mathrm{Log}(L_\infty)+0.6543\mathrm{Log}(K)+0.4634\mathrm{Log}(T))$
			$M = 3/T_{max}$
		Hoenig (1983)	$M = \exp(1.44-0.982\times\ln(T_{max}))$
		Alagaraja (1984)	$M \approx 4.6/T_{max}$
		Ralston (1987)	$M = -0.0666+2.52K \approx 2.5K$
			$M = 1.0661L_\infty^{-0.1172}K^{0.5092}$
		Djabali *et al*. (1993)	$M = 0.8598W_\infty^{-0.0302}K^{0.5280}$
		Pauly and Binohlan (1996)	$M = -0.1778+3.1687K$
		Jensen (1996)	$M = 1.6K$
		Jensen (1996)	$M = 1.5K$
		Cubillos *et al*. (1999)	$M = 1.4K$
		Cubillos *et al*. (1999)	$M = 4.31\ (t0-(\ln(0.05)/k)^{-1.01}$
		Frisk *et al*. (2001)	$M \approx 0.436K^{0.42}$
		Cubillos (2003)	$M = 3K(1-0.62)/0.62$
		Hewitt and Hoenig (2005)	$M = 4.22/T_{max}$
	Dependent of age, length or weight	Peterson and Wroblewski (1984)	$M_w = 1.92w^{-0.25}$
			$M_t = k/(1-e^{-k(t-to)}),\ t \leq tm$
		Chen and Watanabe (1989)	$M_t = K/\ 1-e^{-k(t-to)}[1-k(t-t_m)+0.5K^2(t-t_m)^2],\ t>tm$
		Lorenzen (1996)	$M_w = 3.00W^{-0.288}$
		McCoy and Gillooly (2008)	$M_w = 1.17W^{-0.27}$
		Gislason *et al*. (2010)	$M_L = e^{0.55-1.61LN(L)+1.44LN(L_\infty)+LN(K)}$
	Reproduction	Rikhter and Efanov (1976)	$M = (1.52/tm^{0.72})-0.16$
		Gunderson (1980)	$M = 4.64*IG-0-370$
			$M = 0.03+1.68\ IGS$
		Gunderson and Dygert (1988)	$M = 0.07+1.06K$
		Charnov and Berrigan (1990)	$M = 2/t_m$
		Jensen (1996)	$M = 1.65/t_m$
		Gunderson (1997)	$M = 1.79*IGS$
	Both	Roff (1984)	$M = 3K/e^{tm*K}-1$
		Groeneveld (2000)	$M = K(3L_\infty/lm-3)$
		Zhang and Megrey (2006)	$M = \beta K/e^{K*(tc-to))}-1$

Selected life history and abiotic parameters used to estimate M for our study are also presented with their references for each species. As several sets of parameters were found for each species, life history values are presented as mean and standard deviation (SD) (Table 2). Methods independent and dependent of age were performed for all selected species, resulting in their estimations of M. Methods are grouped by the parameters required (as in Table 1). Methods dependent of age are presented as the mean for the exploitable size range (Table 3). In addition, some methods presented in Table 1 were not applied (Gunderson, 1980; Gunderson and Dygert, 1988–IGS formulation, and Gunderson, 1997) because their formulation is based on the gonadosomatic index and these data were not available for selected species.

An average M from all 26 indirect methods of estimation was calculated for each species and about 70 % of the selected species had an average mortality estimate between 0.22 and 0.34 per year. *Pagellus acarne* presented the highest mean M (0.67), especially for those methods based on reproduction parameters alone or from combined parameters.

Among the eight species, three of them stand out for their comparatively high average values: *Beryx splendens* (0.46), *Pagellus acarne* (0.67) and *Beryx decadactylus* (0.38). It is also clear that a high standard error is associated with some species estimations. It is assumed that the smaller the standard error is, the more representative the sample will be of the overall population. All dependent methods were estimated for combined sexes, including species with sex-specific life history values, since dry and wet weight were calculated based on individual length and weight-length relationship parameters, which did not differ between male and female individuals. None of the dependent methods presented an estimate that was notably higher or lower than from independent methods. The methods of Alverson and Carney (1975) and Roff (1984) produced higher estimates of natural mortality than the corresponding averages for most of the species.

Displaying mean M estimations as a grey scale allowed a visual analysis of method performance (Table 4). In a general way, independent methods based solely on maximum age (T_{max}) or combined with L_∞ or W_∞ provided lower results, below the species average (Gunderson and Dygert, 1988; Djabali *et al.*, 1993; Jensen, 1996; Cubillos *et al.*, 1999; Cubillos, 2003). Of the dependent methods, those based on the growth parameters K and L_∞ also provided estimations lower than the average. On the other hand, methods based on reproduction parameters alone (Charnov and Berrigan, 1990; Jensen, 1996) or combined with growth parameters (Roff, 1984; Zhang and Megrey, 2006) generally provided higher estimations. Methods that produced estimates close to the average were Lorenzen (1996), Groeneveld (2000) and Hewitt and Hoenig (2005).

DISCUSSION

The estimation of von Bertalanffy growth parameters depends on the sample size (n) and the corresponding age and length ranges, so that the growth equation can represent the entire stock instead of just a fraction. However, even if the sample is representative of the population, an error in a parameter calculation can spread throughout the population dynamics model (Andrews and Mangel, 2012). It should be noted that life history parameters may also vary between stocks, so using a single time interval to interpret life history parameters may be unrealistic (Begg *et al.*, 1999). Furthermore, the selected life history parameters should represent the entire population or a management unit, and not a small fraction. Otherwise, the M estimates will not be reliable. Hence, in this study, the selection of life history parameters was a meticulous task; data from the Azores management area and those with a wide size range were prioritized in order to have confidence in the estimates produced. The authors of the estimated weight-length relationship parameters for the Azores area (Rosa *et al.*, 2006) and adopted in the present study warned of their limitations, as the values may not reflect the entire length range due to the selectivity of fishing gears. However, the cited study prevailed as the best weight-length relationship estimated for our study area.

Table 2. Life history and abiotic values for selected species. Parameters are presented as mean±SD where different sets were considered. Weight-length relationship parameters (a, b) were all obtained from Rosa et al., 2006.

Parameters	***Pagellus bogaraveo***	***Phycis phycis***	***Beryx splendens***	***Pontinus kuhlii***		***Helicolenus dactylopterus***		***Pagellus acarne***	***Beryx decadactylus***	***Pagrus pagrus***
	combined	**combined**	**combined**	**F**	**M**	**F**	**M**	**combined**	**combined**	**combined**
L_∞ (cm)	58.53±3.93	76.76±4.37	45.07±9.25	44.65±1.91	68.00±17.25	47.97±10.21	51.17±6.89	28.02±0.02	57.65±9.52	102.00±1.41
k	0.119±0.021	0.116±0.029	0.153±0.071	0.107±0.012	0.065±0.039	0.115±0.069	0.087±0.026	0.383±0.003	0.149±0.069	0.055±0.008
T_o (years)	-1.20±0.69	-2.48±0.95	-3.15±0.39	-1.28±1.00	-2.19±2.31	-1.07±0.87	0.09±0.03	-0.81±0.05	-2.16±1.00	-2.50±1.12
Growth references	a, b, c, d, e	f, g, h	g, i, j	i, j		k, l		j, g	m, k, g	i, n
T_{max} (years) [o]	13	13±3	6	10		23±12	26±13	9	8	12
W_∞ (g) [p]	3896±772	5875±1023	2503±1046	1365±179	5471±3918	2140±1274	2459±998	424±1	4830±2415	21160±838
L_m (cm)	30.40 [a]	38.00 [f]	27.57±6.49 [a,j,r]	20.55±2.90 [j,r]	24.20±8.06 [j,r]	21.40±0.46 [k,r]	27.05±1.21 [k,r]	16.00 [s]	30.80±5.53 [j,t]	29.50 [u]
T_m (years) [p]	5±1	3	4±3	5±1	6±4	5±1	8±1	1	4±1	4
L_c (cm) [p]	30	45	30	32		29		24	35	37
a	0.0172	0.0057	0.0198	0.0115		0.014		0.0158	0.0304	0.0388
b	3.027	3.1881	3.043	3.075		3.058		3.06	2.941	2.856
Temperature (ºC)[q]	12	14	12	13		12		16	11	16

Note:
[a] ICES, 2012
[b] Krug *et al*., 1994
[c] Menezes *et al*., 1998
[d] Krug, 1997
[e] Krug, 1989
[f] Monteiro, 2014
[g] regional sampling programs covering ICES area X
[h] Abecasis *et al*., 2009
[i] Krug *et al*., 1998
[j] Isidro, 1996
[k] Abecasis *et al*., 2006
[l] Isidro, 1987
[m] Krug *et al*., 2011
[n] Serafim and Krug, 1995
[o] parameter estimated in growth studies or observed under regional sampling programs
[p] parameters calculated in the present study. Each calculation was explained in Methods section
[q] parameter calculated in the present study with information provided by A. Martins (pers.comm.)
[r] Estácio *et al*., 2001
[s] FishBase, 2020 (https://www.fishbase.de)
[t] in this specific case, this parameter was calculated using (n) growth parameters and $t_m = 4$ years
[u] Afonso *et al*., 2008

Table 3. Natural mortality values (mean±SE) of eight fish species obtained from different methods. Invariable methods are grouped by parameters required: (a) reproduction, (b) growth or (c) combining both. Where there was a single set of parameters, M estimate is a single value. Variable methods values for M (d) are presented as the mean for exploitable size range. The mean of all M estimations is also presented for each species.

	Methods	*Pagellus bogaraveo*	*Phycis phycis*	*Beryx splendens*	*Pagellus acarne*	*Beryx decadactylus*	*Pagrus pagrus*	*Pontinus kuhlii* (F)	*Pontinus kuhlii* (M)	*Helicolenus dactylopterus* (F)	*Helicolenus dactylopterus* (M)
(a)	Rikhter and Efanov, 1976	0.32±0.11	0.48±0.27	0.53±0.31	1.04±0.74	0.44±0.25	0.43±0.30	0.35±0.25	0.29±0.21	0.31±0.15	0.20±0.10
	Charnov and Berrigan, 1990	0.40±0.13	0.60±0.34	0.69±0.40	1.43±1.01	0.54±0.31	0.53±0.37	0.44±0.31	0.38±0.27	0.39±0.19	0.27±0.13
	Jensen, 1996	0.33±0.11	0.49±0.28	0.57±0.33	1.18±0.83	0.45±0.26	0.43±0.21	0.36±0.25	0.31±0.22	0.32±0.16	0.22±0.11
(b)	Beverton and Holt, 1959	0.38	0.40±0.24	0.83	0.56	0.63	0.42	0.50	0.50	0.27±0.14	0.24±0.12
	Taylor, 1960	0.23	0.25±0.14	0.50	0.33	0.37	0.25	0.30	0.30	0.16±0.08	0.15±0.07
	Tanaka, 1960	0.19	0.21±0.12	0.42	0.28	0.31	0.21	0.25	0.25	0.14±0.07	0.12±0.06
	Alverson and Carney, 1975	0.45±0.15	0.50±0.29	1.11±0.56	0.42±0.30	0.78±0.45	0.58±0.41	0.64±0.45	0.70±0.49	0.30±0.15	0.27±0.14
	Pauly, 1980	0.25±0.08	0.24±0.14	0.30±0.15	0.75±0.53	0.28±0.16	0.15±0.10	0.27±0.19	0.17±0.12	0.25±0.13	0.21±0.11
	Hoenig, 1983	0.34	0.37±0.21	0.73	0.49	0.55	0.37	0.44	0.44	0.24±0.12	0.22±0.11
	Alagaraja, 1984	0.35	0.38±0.22	0.77	0.51	0.58	0.38	0.46	0.46	0.25±0.13	0.22±0.11
	Gunderson and Dygert, 1988	0.20±0.07	0.19±0.11	0.23±0.13	0.48±0.34	0.23±0.13	0.13±0.09	0.18±0.13	0.14±0.10	0.19±0.10	0.16±0.08
	Djabali *et al*, 1993	0.22±0.07	0.21±0.12	0.26±0.15	0.44±0.31	0.25±0.14	0.14±0.10	0.22±0.15	0.16±0.11	0.22±0.11	0.19±0.10
	Djabali *et al*, 1993	0.22±0.07	0.21±0.12	0.25±0.14	0.43±0.31	0.24±0.14	0.14±0.10	0.21±0.15	0.15±0.11	0.21±0.11	0.19±0.09
	Jensen, 1996	0.19±0.06	0.19±0.11	0.25±0.14	0.61±0.43	0.24±0.14	0.09±0.06	0.17±0.12	0.10±0.07	0.18±0.09	0.14v0.07
	Jensen, 1996	0.18±0.06	0.17±0.10	0.23±0.13	0.57±0.41	0.22±0.13	0.08±0.06	0.16±0.11	0.10±0.07	0.17±0.09	0.13±0.07
	Cubillos *et al*., 1999	0.17±0.06	0.18±0.10	0.26±0.15	0.60±0.43	0.23±0.13	0.08±0.06	0.15±0.11	0.09±0.06	0.16±0.08	0.13±0.06
	Cubillos, 2003	0.22±0.07	0.21±0.12	0.28±0.16	0.70±0.50	0.27±0.16	0.10±0.07	0.20±0.14	0.12±0.08	0.21±0.11	0.16±0.08
	Hewitt and Hoenig, 2005	0.32	0.33±0.24	0.70	0.47	0.53	0.35	0.42	0.42	0.23±0.12	0.21±0.10
(c)	Roff, 1984	0.43±0.14	0.73±0.42	0.88±0.51	1.62±1.15	0.6±0.35	0.71±0.50	0.51±0.36	0.47±0.33	0.42±0.21	0.28±0.14
	Groeneveld, 2000	0.33±0.11	0.35±0.20	0.30±0.17	0.86±0.61	0.33±0.19	0.41±0.29	0.39±0.28	0.37±0.26	0.35±0.17	0.22±0.11
	Zhang and Megrey, 2006	0.47±0.16	0.69±0.40	0.42±0.25	1.37±0.97	0.49±0.28	0.30±0.21	0.48±0.34	0.35±0.25	0.47±0.23	0.32±0.16
(d)	Peterson and Wroblewski, 1984	0.47	0.42	0.47	0.44	0.40	0.34	0.43	0.43	0.49	0.49
	Chen and Watanabe, 1989	0.17	0.15	0.18	0.41	0.18	0.09	0.13	0.08	0.13	0.11
	Lorenzen, 1996	0.38	0.33	0.38	0.57	0.31	0.26	0.33	0.33	0.40	0.40
	McCoy and Gillooly, 2008	0.33	0.23	0.26	0.38	0.21	0.18	0.23	0.23	0.27	0.27
	Gislason *et al*., 2010	0.18	0.16	0.18	0.44	0.17	0.10	0.14	0.09	0.14	0.12
	Mean	**0.30**	**0.34**	**0.46**	**0.67**	**0.38**	**0.28**	**0.32**	**0.29**	**0.27**	**0.22**

Table 4. Comparison of mean M estimations (Table 3) by method, represented as percentage of the species mean. Darker shading highlights higher values. A mean of percentages for each method is presented with horizontal bar relating methods to each other.

	Methods	***Pagellus bogaraveo***	***Phycis phycis***	***Beryx splendens***	***Pagellus acarne***	***Beryx decadactylus***	***Pagrus pagrus***	***Pontinus kuhlii (F)***	***Pontinus kuhlii (M)***	***Helicolenus dactylopterus (F)***	***Helicolenus dactylopterus (M)***	**Mean**
(a)	Rikhter and Efanov, 1976	108	144	115	156	116	154	109	101	117	92	121
	Charnov and Berrigan, 1990	135	180	150	214	143	190	137	133	147	124	155
	Jensen, 1996	111	147	124	177	119	154	112	108	121	101	127
(b)	Beverton and Holt, 1959	128	120	180	84	167	151	156	175	102	111	137
	Taylor, 1960	77	75	109	49	98	90	93	105	61	69	83
	Tanaka, 1960	64	63	91	42	82	75	78	87	53	55	69
	Alverson and Carney, 1975	151	150	241	63	206	208	199	245	113	124	170
	Pauly, 1980	84	72	65	112	74	54	84	59	95	97	80
	Hoenig, 1983	114	111	158	73	145	133	137	154	91	101	122
	Alagaraja, 1984	118	114	167	76	153	136	143	161	95	101	126
	Gunderson and Dygert, 1988	67	57	50	72	61	47	56	49	72	74	61
	Djabali *et al*, 1993	74	63	56	66	66	50	68	56	83	88	67
	Djabali *et al*, 1993	74	63	54	64	63	50	65	52	79	88	65
	Jensen, 1996	64	57	54	91	63	32	53	35	68	65	58
	Jensen, 1996	61	51	50	85	58	29	50	35	64	60	54
	Cubillos *et al*., 1999	57	54	56	90	61	29	47	31	61	60	55
	Cubillos, 2003	74	63	61	105	71	36	62	42	79	74	67
	Hewitt and Hoenig, 2005	108	99	152	70	140	125	131	147	87	97	116
(c)	Roff, 1984	145	219	191	242	159	255	159	164	159	129	182
	Groeneveld, 2000	111	105	65	129	87	147	121	129	132	101	113
	Zhang and Megrey, 2006	158	207	91	205	130	108	149	122	178	147	150
(d)	Peterson and Wroblewski, 1984	158	126	102	66	106	122	134	150	185	226	138
	Chen and Watanabe, 1989	57	45	39	61	48	32	40	28	49	51	45
	Lorenzen, 1996	128	99	82	85	82	93	103	115	151	184	112
	McCoy and Gillooly, 2008	111	69	56	57	56	65	72	80	102	124	79
	Gislason *et al*., 2010	61	48	39	66	45	36	44	31	53	55	48
	Mean	**0.30**	**0.34**	**0.46**	**0.67**	**0.38**	**0.28**	**0.32**	**0.29**	**0.27**	**0.22**	

A beneficial approach to estimating M is to apply various methods, but also to use different datasets for life history parameters. As stated above, it was concluded that the variability in the input life history data led to variability of M estimates by method. Over- or under-estimating the average prediction value was associated with the relation between M and the variables (Silva *et al*., 2015).

When considering the most important species for the Azorean fleet (and, consequently, the most well-studied), *Pagellus bogaraveo*, ICES Working Group (ICES, 2019) considered its M value as 0.2. This does not differ greatly from the mean of 0.3 estimated in the present study. It is also important to highlight that there have been considerably more age and growth studies for this species. Thus, lower variability of life history parameters expected for well-studied species could reduce M variability and standard error associated with its mean. Another species for which M values and standard errors presented lower values was *Helicolenus dactylopterus*. Not surprisingly, this is the second-most well-studied species in our study area and four different sets of life history values were available from the two cited growth studies. These cases lead us to suggest that well-studied species provide more accurate estimations with lower associated error. Natural mortality varies with time, age, sex, cohort, environmental conditions, predation, and inter- and intraspecific competition (Vetter, 1988; Kenchington, 2014; Hamel, 2015), and therefore led us to adopt life history parameters estimated specifically for the stocks under analysis.

From all the indirect methods considered, Alverson and Carney (1975) and Roff (1984) produced higher estimates of natural mortality than the corresponding averages for most of the species. In fact, Then *et al*. (2015) stated that Alverson and Carney's (1975) method brought no additional advantage when compared to estimators based only on T_{max}, and therefore was not recommended. The estimates of M below the species average came from independent methods based solely on maximum age (T_{max}) or combined with L_∞ or W_∞. Lower estimates also resulted from some of the dependent methods based growth parameters (K, L_∞), which is related to the previous conclusions about T_{max}-based estimators performing better than others reviewed (Kenchington, 2013). Despite the fact that variable methods have been developed to depict mortality for the entire lifespan, it is widely accepted by the scientific community that a single value for M can provide an accurate image of mortality over much of the exploitable lifespan of a species (Then *et al*., 2015). And in fact, none of the methods presented estimations that stood out as noticeably higher or lower than those from independent methods.

The indirect methods adopted in the present study empirically estimated natural mortality rates for demersal/deep-water species based on life history parameters. Although these methods are an easy and cheap way to estimate M, authors have claimed that they have many limitations, such as inaccurate estimates of life history parameters and consequent bias in empirical relationships (Kenchington, 2014; Hoenig *et al*., 2016).

Methods used to estimate M are seen as only useful within the life-history parameter ranges used to establish them. Consequently, authors have assumed that M estimates based on these methods are often very inaccurate and the prediction errors are large (Pascual and Iribarne, 1993). Many studies employing empirical estimators, with the present work included, have had a wide range of results. The wide variation of M estimates from different empirical predictors remains unexplained, and therefore it is unknown which should be preferred. The real M of a fish remains unknown, and this will remain the main issue when comparing and validating estimations (Then *et al*., 2015). Even if there are some accurate M values for a fish species available from another ecosystem, it is not appropriate to use them to compare or validate estimations (Maunder and Wong, 2011).

Traditionally, M has been set based on a priori considerations (as the conventional assumption of M = 0.2 $year^{-1}$) or based on empirical methods, catch-curve analysis or occasionally, tagging methods. All these approaches make some assumptions; therefore, the value of M used in stock assessments will ultimately be incorrect because any method used to estimate M is biased and imprecise

(Punt *et al*., 2021). Direct methods probably provide more reliable M estimates, but require more detailed information about the resource, which is usually not available (Maunder and Wong, 2011). Even given all the advances in data collection methods and analytical techniques, M remains hard to estimate (Punt *et al*., 2021).

For all their faults and limitations, these estimates are the values used in practice (e.g., for assessment and management of resources, ecosystem modelling) (Maunder and Wong, 2011). Also, in data-poor situations, like the present study, only the empirical methods may be viable (Punt *et al*., 2021). Thus, an indirect estimate may be better than a direct estimate if the direct estimate is poorly done (Hoenig *et al*., 2016). These estimations, as previous detailed, are extremely important to stock assessments. Thus, assuming that natural mortality and fishing mortality are additive, stocks with higher natural mortality rates are more productive and are capable of sustaining higher exploitation rates (Hewitt *et al*., 2007).

For precautionary use of our empirical estimations, and considering all the consequences of their use mentioned above, we do recommend the use of underestimated values. The present estimated average value of M for each of the eight species evaluated suggests a reasonable value, similar to the conventional assumption ($M = 0.2\ \text{year}^{-1}$) in all except *Pagellus acarne*. In this particular case, again to emphasize caution, lower rates should be considered. Therefore, assuming lower natural mortality rates, stocks are considered less productive and less capable to tolerate higher exploitation rates. Nonetheless, the best option still is to introduce variability in M in stock assessments, as previously discussed.

CONCLUSION

This study constitutes the first attempt of natural mortality estimation for the most commercially important Azorean fish species, and can help fill the existing information gap. As in previous studies, we recommended that a sensitivity analysis be performed using various empirical methods and life history parameters, to minimize errors and expose atypical values. Our results lead us to suggest that the best-studied species provide more accurate estimations with lower associated error. In response to this study objective, there is obvious variability of estimations associated with different parameters and methods. Moreover, it was observed that over- or under-estimating the average prediction value is associated with the relation between M and the variables. Generally, independent methods based only on T_{max}, or combining it with $L\infty$ or $W\infty$, lowered the estimations, whereas methods based on reproduction parameters alone, or combined with growth parameters, inflated estimations. Nonetheless, the estimated average values of M for almost all the selected species in this study are reasonable, and close to the conventional assumption. However, we do recommend the use of more conservative (i.e., lower) estimations. Also, our estimations should be carefully applied, due to the importance and power of M values for stock assessment, and being often updated and improved with continuous species study.

ACKNOWLEDGEMENTS

Authors acknowledge the support from Fundação para a Ciência e a Tecnologia (FCT) (UIDB/04292/2020). Priscila Silva was supported by an FCT Ph.D. grant (SFRH/BD/04416/2020). Ana Novoa-Pabon was funded by an FCT Ph.D. fellowship (SFRH/BD/124720/2016).

LITERATURE CITED

Abecassis, D., A.R. Costa, J.G. Pereira and M.R Pinho. 2006. Age and growth of bluemouth, *Helicolenus dactylopterus* (Delaroche, 1809) from the Azores. **Fisheries Research** 79: 148–154.

Abecasis, A.R.C., A. Canha, D. Reis, M.R. Pinho and J. Gil-Pereira. 2009. Age and growth of the forkbeard *Phycis phycis* (Gadidae) from the Azorean archipelago. **Journal of the Marine Biological Association of the United Kingdom** 89(3): 629–633.

Afonso, P., F. Tempera and G. Menezes. 2008. Population structure and habitat preferences of red porgy (*Pagrus pagrus*) in the Azores, central north Atlantic. **Fisheries Research** 93: 338–345.

Alagaraja, K. 1984. Simple methods for estimation of parameters for assessing exploited fish stocks. **Indian Journal of Fisheries** 31: 177–208.

Alverson, D.L. and M.J. Carney. 1975. A graphic review of the growth and decay of population cohorts. **ICES Journal of Marine Science** 36: 133–143.

Andrews, K.I. and M. Mangel. 2012. Asymptotic size and natural mortality of long-lived fish for data poor stock assessments. **Fisheries Research** 127-128: 45–48.

Bayliff, W. 1967. Growth, mortality, and exploitation of the Engraulidae, with special reference to the anchoveta, *Cetengraulis mysticetus*, and the Colorado, *Anchoa naso*, in the eastern Pacific Ocean. **Bulletin of the Inter-American Tropical Tuna Commission** 12: 367–408.

Begg, G.A., J.A. Hare and D.D. Sheehan. 1999. The role of life history parameters as indicators of stock structure. **Fisheries Research** 43: 141–163.

Beverton, R.J.H. and S.J. Holt. 1959. **A review of the lifespans and mortality rates of fish in nature and their relation to growth and the other physiological characteristics.** In: CIBA Foundation Colloquium on Aging. Vol. 5. The Lifespan of Animals (eds. G.E.W. Wolstenholme and M. O’Connor), pp. 142–180. J&A Churchill Ltd., London, UK.

Brodziak, J., J. Ianelli, K. Lorenzen and R.D. Methot. 2011. **Estimating Natural Mortality in Stock Assessment Applications.** NOAA Technical Memorandum NMFS-F/SPO-119. Alaska Fisheries Science Center, Seattle, Washington. 38 pp.

Cadima, E.L. 2003. **Fish Stock Assessment Manual.** FAO Fisheries Technical Paper. No. 393. Food and Agriculture Organization of the United Nations, Rome, Italy. 161 pp.

Charnov, E.L. and D. Berrigan. 1990. Dimensionless numbers and life history evolution: age of maturity versus the adult lifespan. **Evolutionary Ecology** 4: 273–275.

Chen, S. and S. Watanabe. 1989. Age dependence of natural mortality coefficient in fish population dynamics. **Nippon Suisan Gakkaishi** 55: 205–208.

Cubillos, L.A. 2003. An approach to estimate the natural mortality rate in fish stocks. **Worldfish Center Quarterly** 26(1): 17-19.

Cubillos, L.A., R. Alarcon and A. Brante. 1999. Empirical estimates of natural mortality for the Chilean hake (*Merluccius gayi*): evaluation of precision. **Fisheries Research** 42: 147–153.

Da Silva, H.M. and M.R. Pinho. 2008. **Small-scale fishing on Seamounts.** In: Seamounts: ecology, fisheries and conservation (eds. T.J. Pitcher, T. Morato, P.J.B. Hart, M.R. Clark, N. Haggan and R.S. Santos), pp. 335–360. Fisheries and Aquatic Resource Series, Blackwell Scientific, Oxford, UK.

Djabali, F., A. Mehailia, M. Koudil and B. Brahmi. 1993. Empirical equations for the estimation of natural mortality in Mediterranean teleosts. **Naga, the ICLARM Quarterly** 16: 35–37.

Estácio, S., A. Mendonça, H. Krug, G.M. Menezes, J. Branco and M.R. Pinho. 2001. Aspects of the reproduction of six demersal fishes captured in the Azores Archipelago. **Arquipelago Life and Marine Sciences** Supplement 2B: 83–94.

Frisk, M.G., T.J. Miller and M.J. Fogarty. 2001. Estimation and analysis of biological parameters in elasmobranch fishes: A comparative life history study. **Canadian Journal of Fisheries and Aquatic Sciences** 58: 969–981.

Gislason, H., N. Daan, J.C. Rice and J.G. Pope. 2010. Size, growth, temperature and the natural mortality of marine fish. **Fish and Fisheries** 11: 149–158.

Griffiths, D. and C. Harrod. 2007. Natural mortality, growth parameters and environmental temperature in fishes revisited. **Canadian Journal of Fisheries and Aquatic Sciences** 64: 249–255.

Groeneveld, J.C. 2000. Stock assessment, ecology and economics as criteria for choosing between trap and trawl fisheries for spiny lobster *Palinurus delagoae*. **Fisheries Research** 48: 141–155.

Gunderson, D.R. 1980. Using r-K selection theory to predict natural mortality. **Canadian Journal of Fisheries and Aquatic Sciences** 37: 2266–2271.

Gunderson, D.R. 1997. Trade-off between reproductive effort and adult survival in oviparous and viviparous fishes. **Canadian Journal of Fisheries and Aquatic Sciences** 54: 990–998.

Gunderson, D.R. and P.H. Dygert. 1988. Reproductive effort as a predictor of natural mortality rate. **ICES Journal of Marine Science** 44: 200–209.

Hamel, O.S. 2015. A method for calculating a meta-analytical prior for the natural mortality rate using multiple life history correlates. **ICES Journal of Marine Science** 72(1): 62–69.

Hewitt, D.A. and J.M. Hoenig. 2005. Comparison of two approaches for estimating natural mortality based on longevity. **Fishery Bulletin** 103: 433–437.

Hewitt, D.A., D.M. Lambert, J.M. Hoenig, R.N. Lipcius, D.B. Bunnell and T.J. Miller. 2007. Direct and indirect estimates of natural mortality for Chesapeake Bay blue crab. **Transactions of the American Fisheries Society** 136(4): 1030–1040.

Hoenig, J.M. 1983. Empirical use of longevity data to estimate total mortality rates. **Fishery Bulletin** 82: 898–903.

Hoenig, J.M., A.Y.H. Then, E.A. Babcock, N.G. Hall, D.A. Hewitt and S.A. Hesp. 2016. The logic of comparative life history studies for estimating key parameters, with a focus on natural mortality rate. **ICES Journal of Marine Science** 73(10): 2453–2467.

International Council for the Exploration of the Sea (ICES). 2012. **Report of the Working Group on the Biology and Assessment of Deep-sea Fisheries Resources (WGDEEP), 28 March-5 April, Copenhagen, Denmark.** ICES CM 2012/ACOM:17. 9. International Council for the Exploration of the Sea, Copenhagen, Denmark. 29 pp.

International Council for the Exploration of the Sea (ICES). 2019. **Working Group on the Biology and Assessment of Deep-sea Fisheries Resources (WGDEEP).** ICES Scientific Reports. 1: 21. International Council for the Exploration of the Sea, Copenhagen, Denmark. 988 pp.

Isidro, E.J. 1987. **Age and Growth of the Bluemouth, *Helicolenus dactylopterus* (De la Roche, 1809) Off the Azores.** International Council for the Exploration of the Sea CM 19871G: 63. International Council for the Exploration of the Sea, Copenhagen, Denmark. 6 pp.

Isidro, E.J. 1996. **Biology and population dynamics of selected demersal fish species of the Azores Archipelago.** Ph.D. Thesis, University of Liverpool, Isle of Man, UK. 249 pp.

Jensen, A.L. 1996. Beverton and Holt life history invariants result from optimal tradeoff of reproduction and survival. **Canadian Journal of Fisheries and Aquatic Sciences** 53: 820–822.

Johnson, K.F., C.C. Monnahan, C.R. McGilliard, K.A. Vert-pre, S.C. Anderson, C.J. Cunningham and C.S. Szuwalski. 2014. Time-varying natural mortality in fisheries stock assessment models: identifying a default approach. **ICES Journal of Marine Science** 72(1): 137–150.

Kenchington, T.J. 2014. Natural mortality estimators for information-limited fisheries. **Fish and Fisheries** 15: 533–562.

Krug, H. 1989. The Azorean blackspot seabream, *Pagellus bogaraveo* (Briinnich, 1768) (Teleostei, Sparidae): Age and growth. **Cybium** 13(4): 347–355.

Krug, H. 1994. **Biologia e avaliação do stock açoreano de goraz, *Pagellus bogaraveo*.** Ph.D. Thesis, University of the Azores, Horta, Portugal. 193 pp.

Krug, H., D. Carvalho and J.A. González. 2011. Age and growth of the alfonsino *Beryx decadactylus* (Cuvier, 1829) from the Azores, Madeira and Canary Islands, based on historical data. **Arquipelago: Life and Marine Sciences** 28: 25–31.

Krug, H., D. Rosa, G. Menezes and M.R. Pinho. 1998. **Age and Growth of Some Demersal Species of the Azores.** International Council for the Exploration of the Sea, Copenhagen, Denmark. 11 pp.

Krug, H., D. Rosa, H.M. Silva and G. Menezes. 1997. **Age and Growth of Demersal Species from Azores.** Semana das pescas dos Açores, Horta.

Lorenzen, K. 1996. The relationship between body weight and natural mortality in juvenile and adult fish: A comparison of natural ecosystems and aquaculture. **Journal of Fish Biology** 49: 627–647.

Maunder, M.N. and R.A. Wong. 2011. Approaches for estimating natural mortality: Application to summer flounder (*Paralichthys dentatus*) in the U.S. mid-Atlantic. **Fisheries Research** 111: 92–99.

McCoy, M.W. and J.F. Gillooly. 2008. Predicting natural mortality rates of plants and animals. **Ecology Letters** 11: 710–716.

McGurk, M.D. 1986. Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. **Marine Ecology Progress Series** 34: 227–242.

Menezes, G., J. Delgado, H. Krug, M.R. Pinho, H. Silva and D. Carvalho. 1998. **Design Optimization and Implementation of Demersal Survey Cruises in the Macaronesian Archipelagos.** Internal Report Series No. 3/98. University of Azores, Horta, Portugal. 162 pp.

Menezes, G., M.F. Sigler, H.M. Silva and M.R. Pinho. 2006. Structure and zonation of demersal fish assemblages off the Azores Archipelago (mid-Atlantic). **Marine Ecology Progress Series** 324: 241–260.

Monteiro, S.V. 2014. **Ecology and fisheries of the forkbeard *Physis physis* (L., 1776) in the Azores Region ICES(Xa2).** Master Thesis, University of the Azores, Horta, Portugal. 96 pp.

Morato T., W.W.L. Cheung and T.J. Pitcher. 2004. **Additions to Froese and Sampang's checklist of seamount fishes.** In: Seamounts: Biodiversity and Fisheries. Fisheries Centre Research Reports, 12(5), Appendix 1 (eds. T. Morato and D. Pauly), pp. 1–6. Fisheries Centre, University of British Columbia, Vancouver, Canada.

Morato, T. 2012. **Description of Environmental Issues, Fish Stocks and Fisheries in the EEZs around the Azores and Madeira.** Report for the European Commission, Directorate-General Maritime Affairs and Fisheries, Brussels, Belgium. 63 pp.

Ohsumi, S. 1979. **Interspecies relationships among some biological parameters in Cetaceans and estimation of the natural mortality coefficient of the Southern Hemisphere Minke Whale.** In: Report of the International Whaling Commission (ed. E. Donovan), pp. 397–406. International Whaling Commission, Cambridge, UK.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. **ICES Journal of Marine Science** 39: 175–192.

Pauly, D. and C. Binohlan. 1996. **FishBase and AUXIM as tools for comparing the life history patterns, growth and natural mortality of fish: applications to snappers and groupers.** Proceedings of International Center for Living Aquatic Resources Management 1996: 218–243.

Pascual, M.A. and O.O. Iribarne. 1993. How good are empirical predictions of natural mortality? **Fisheries Research** 16: 17–24.

Peterson, I. and J.S. Wroblewski. 1984. Mortality rate of fishes in the pelagic ecosystem. **Canadian Journal of Fisheries and Aquatic Sciences** 41: 1117–1120.

Pinho, M.R. and G. Menezes. 2006. **Azorean deepwater fishery: Ecosystem, species, fisheries and management approach aspect.** Proceedings of Conference on the Governance and Management of Deep-sea Fisheries 2006: 330–343.

Pinho, M.R. and G. Menezes. 2009. Azorean demersal fishery. **Boletim do Núcleo Cultural da Horta** 18: 85–102.

Punt, A.E., C. Castillo–Jordán, O.S. Hamel, J.M. Cope, M.N. Maunder and J.N. Ianelli. 2021. Consequences of error in natural mortality and its estimation in stock assessment models. **Fisheries Research** 233: 105759. DOI: 10.1016/j.fishres.2020.105759.

Ralston, S. 1987. **Mortality rates of snappers and groupers.** In: Tropical Snappers and Groupers: Biology and Fisheries Management (eds. J.J. Polovina and S. Ralston), pp. 375–404. Westview Press, Boulder, USA.

Rikhter, V.A. and V.N. Efanov. 1976. **On One of the Approaches to Estimation of Natural Mortality of Fish Populations.** International Commission for the Northwest Atlantic Fisheries, Kaliningrad, Russia (USSR). 12 pp.

Roff, D.A. 1984. The evolution of life history parameters in teleosts. **Canadian Journal of Fisheries and Aquatic Sciences** 41: 989–1000.

Rosa, A., G. Menezes, O. Melo and M.R. Pinho. 2006. Weight-length relationships of 33 demersal fish species from Azores. **Archipelago Life and Marine Science** 80: 329–332.

Sekharan, K.V. 1975. Estimates of the stocks of oil sardine and mackerel in the present fishing grounds off the West coast of India. **Indian Journal of Fisheries** 21: 177–182.

Serafim, M. and H. Krug. 1995. Age and growth of the red porgy, *Pagrus pagrus* (Linnaeus, 1758) (Pisces: Sparidae) in Azorean Waters. **Arquipelago: Life and Marine Sciences** 13: 11–20.

Silva, P., H. Krug and M.R. Pinho. 2015. **Natural Mortality for the Red Seabream (*Pagellus bogaraveo*) Stock from the Azores (ICES Xa2).** Working document WGDEEP 2015. International Council for the Exploration of the Sea, Copenhagen, Denmark. 25 pp.

Tanaka, S. 1960. Studies on the dynamics and the management of fish populations. **Bulletin of Tokai Regional Fisheries Research Laboratory** 28: 1–200.

Taylor, C.C. 1960. Temperature, growth and mortality the Pacific cockle. **ICES Journal of Marine Science** 26(1): 117–124.

Then, A.Y., J.M. Hoenig, N.G. Hall and D.A. Hewitt. 2015. Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. **ICES Journal of Marine Science** 72(1): 82–92.

Vetter, E.L. 1988. Estimation of natural mortality in fish stocks: a review. **Fishery Bulletin** 86: 25–43.

Zhang, C.I. and B.A. Megrey. 2006. A revised Alverson and Carney model for estimating the instantaneous rate of natural mortality. **Transactions of the American Fisheries Society** 135: 620–633.