

SAW 47 Working Paper 8 (TOR 3) – Natural Mortality
A Review of Natural Mortality of Summer Flounder
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This report is a short review of the common models used to estimate natural mortality rates M for use in population dynamics modeling. The natural mortality models were categorized as either longevity- or life-history based estimators of M . Sex and age-specific estimates of M are given in Tables 1-3, calculated from model inputs from current summer flounder age and growth data (1976-2007) from the NMFS trawl survey.

Longevity-Based Estimators of Natural Mortality

Longevity-based estimators of natural mortality are derived from the underlying mathematical

function describing population decline, $\frac{N_t}{N_0} = e^{-Zt}$. For unexploited stocks, 1) $Z = M$, and 2)

$\frac{N_t}{N_0}$ approaches zero as t approaches a stock's maximum longevity. This is the basis for the rule

of thumb (ROT) equation, $M = \frac{-\ln(P)}{t_{\max}}$. Only two variables, therefore, affect M given this ROT

expression, 1) P , which represents some small proportion of the population that survives to a given maximum age, and 2) t_{\max} , which should represent the maximum longevity of the stock (Hewitt and Hoenig 2005). The value of P is often set equal to 5% for population modeling purposes (e.g. blue crabs, summer flounder, tautog, bluefish, etc.) resulting in a more simplified

expression, $M = \frac{\ln(0.05)}{t_{\max}} \approx \frac{3}{t_{\max}}$. However, aside from its common use in assessments, the value

of $P = 5\%$ is not well supported by data (Hewitt and Hoenig 2005). Recently, Hewitt and Hoenig (2005) recommended a more empirically supported value of $P = 1.5\%$ based on a regression of Z and maximum observed age from 134 unexploited fish, mollusk, and cetacean stocks in earlier work by Hoenig (1983). Hoenig's (1983) regression, $\ln(Z) = 1.44 - 0.982 \ln(t_{\max})$,

can be rearranged as $Z = \frac{e^{1.44}}{t_{\max}^{0.982}} \approx \frac{4.22}{t_{\max}}$. Ergo, P roughly equals 1.5% from the equation, $\ln(P) =$

-4.22. Estimates of M using the 5% ROT are 29% lower than the estimates from P = 1.5% (Figure 1). Predictably, outputs from population models are highly sensitive to estimates of M. Lower M inputs typically result in lower abundance estimates from population modeling and lower benchmarks from YPR analysis.

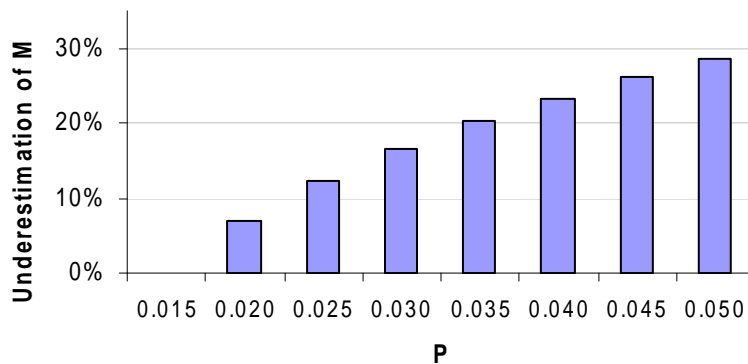


Figure 1. Underestimation of M relative to P = 1.5%.

In addition to the critical importance of P, using a maximum observed age collected from a highly exploited stock produces a biased underestimate of longevity and is in direct violation of the longevity-based M paradigm. As an example of how the maximum observed age can change over a short time period, the maximum observed age of Atlantic croaker increased from 6 to 12 since the early 1990s from age and growth studies in North Carolina, mirroring an increase in stock abundance over this period (pers. comm. R. Gregory, age/growth biologist NC Division of Marine Fisheries). If t_{\max} were solely based on these age samples, the resulting estimates of M (using the 1.5% ROT) would have declined from 0.70 to 0.35 in less than 20 years. Despite the recent occurrence of older age classes, no specimen has yet been observed at the maximum age of 15 y recorded from scattered otoliths found in archaeological shell middens from a period of minimal exploitation (Hales and Reitz 1992).

The underestimation of longevity is a legitimate concern for stocks whose t_{\max} is observed during a period of heavy exploitation. For example, for summer flounder at the current $t_{\max} = 15$, the effect of potentially underestimating longevity by 1 to 5 years results in an overestimation of M by 6 to 32% (Figure 2). On the other hand, the consequence of using a P value up to 5% is the 29% reduction in M from the 1.5% ROT supported by Hoenig (1983) (Figure 1). The widespread use of $P = 5\%$ for stock assessment purposes, whether intentional or not, automatically accounts for an assumed ~ 4 year underestimation of longevity (assuming that $P = 1.5\%$ is the proper P value for the longevity-based ROT).

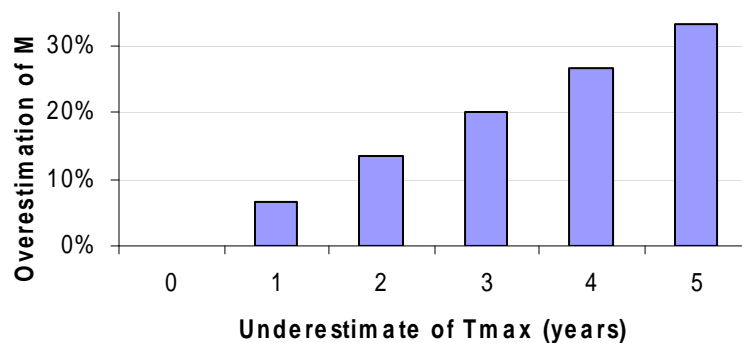


Figure 2. Effect of underestimating longevity by up to 5 years for summer flounder.

Life-History Based Estimators of Natural Mortality

Other methods of estimating M are based on specific life history characteristics from the species in question (Table 1; Figure 3). Pauly (1980) described M using von Bertalanffy growth parameters (L_{inf} , K) and water temperature based on data of 175 fish stocks. Jensen (1996) provides a modification of Pauly's (1980) model based solely on the correlation between M and K , providing the basis for the simplified equation, $M = gK$. The coefficient g was estimated as 1.598 ($r^2 = 0.72$) based on Pauly's (1980) data (Jensen 1996). Gunderson (1997) showed that M

could be predicted from reproductive effort from data of 28 fish stocks by the linear regression, $M = 1.79 * GSI$ ($r^2 = 0.75$). Variance of these life-history based estimates of M can be calculated given the known variances of model inputs (Gunderson et al. 2002).

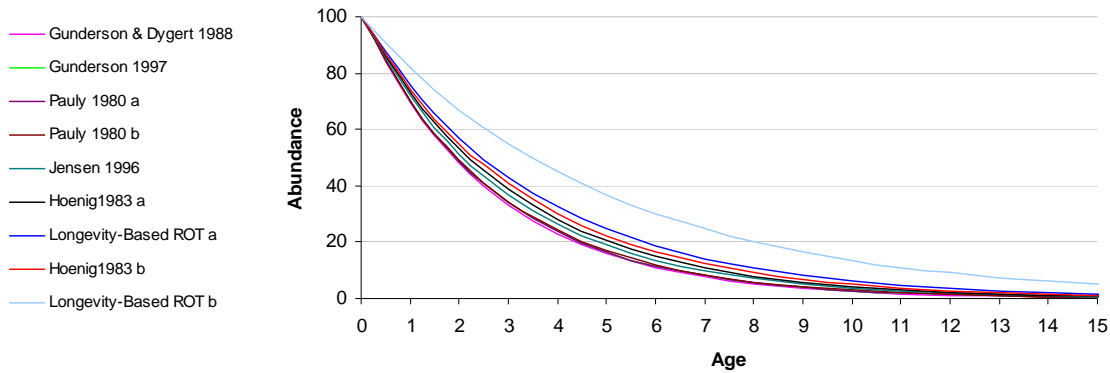


Figure 3. Survival curves from constant M estimates.

Other life-history based estimators of M provide for size-specific or age-based natural mortality rates (Tables 2, 3; Figures 4, 5, 6). Peterson and Wroblewski (1984) describe an inverse relationship between M and dry weight for juvenile and adult fishes. McGurk (1986) complemented this model by describing a steeper inverse M-dry weight relationship specific to fish eggs and larvae based on the linear regression of $\ln(M)$ and $\ln(\text{dry weight})$ ($r = 0.58$, $P < 0.001$). Lorenzen (1996) describes a similar allometric relationship between body weight and natural mortality in juvenile and adult fish across different ecosystems. All of these size-dependent M rates can also be expressed as age-dependent M rates with necessary age and growth data. Chen and Watanabe (1989) estimate age-specific M rates based on known LVB growth parameters, accounting for higher natural mortality rates at early and senescent life history stages. Use of Lorenzen's (2000) approach, which is based on an allometric relationship between body length and M, combined with an assumption of longevity (ala the aforementioned

longevity-based ROTs) can provide for somewhat of a hybrid age-dependent-longevity-based natural mortality model (pers. comm. L. Brooks, NMFS).

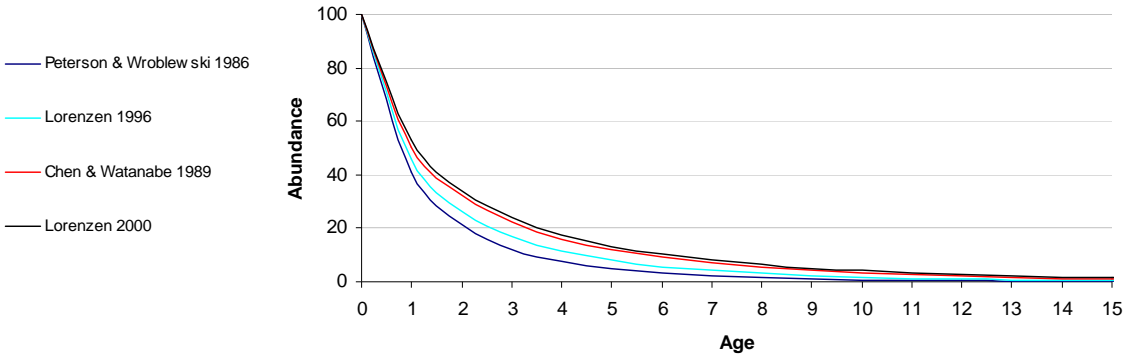


Figure 4. Survival curves from age-specific M estimates.

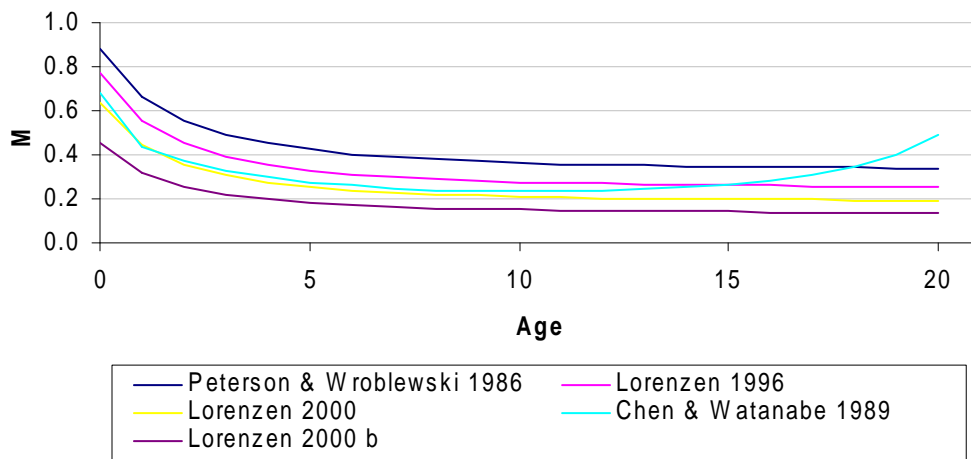


Figure 5. Age-specific M rates. Lorenzen 2000 is based on the 1.5% ROT, Lorenzen 2000 b is based on the 5% ROT.

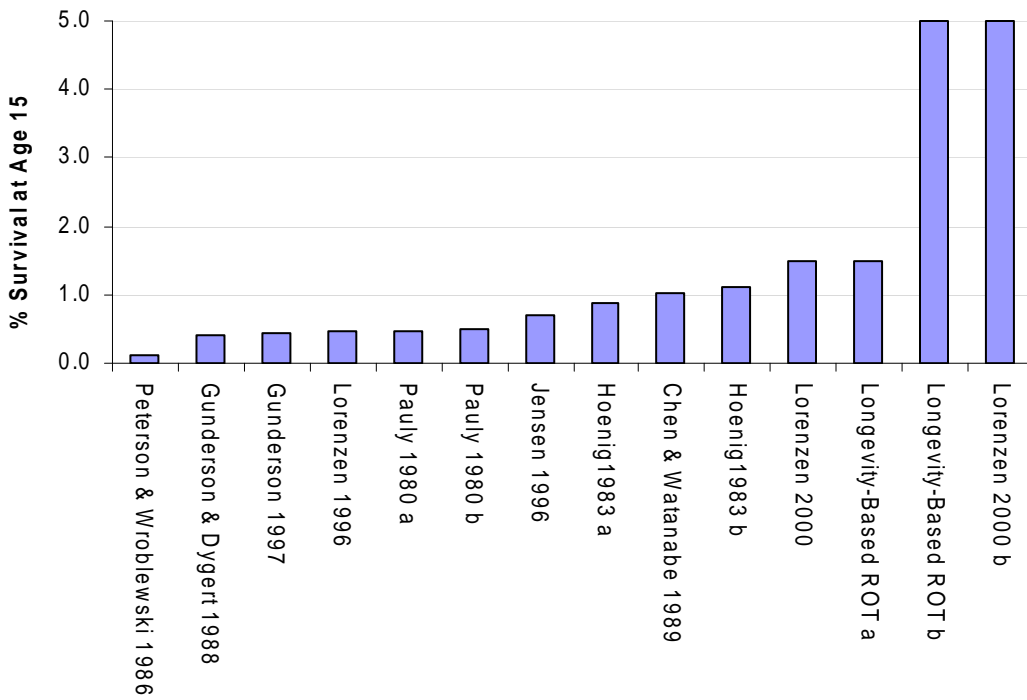


Figure 6. Percent survival at age = 15y.

Male-to-female demographics are very important considerations when combined-sex M rates are calculated. For example, size-at-age inputs for M models will likely differ from a combined-sex LVB growth trajectory versus the sex-weighted mean size-at-age observed in the population (Figure 6), resulting in potentially different M rates. Also, the time step chosen for calculating age-based M estimates can be influential particularly when estimates of natural mortality are much higher at early life stages. For example, survival after one year is 46% using a 1 year time step versus 44% using a 1/4 year step from size-based M rates calculated from the Lorenzen (1996) model (using the size at the mid-point of each time step).

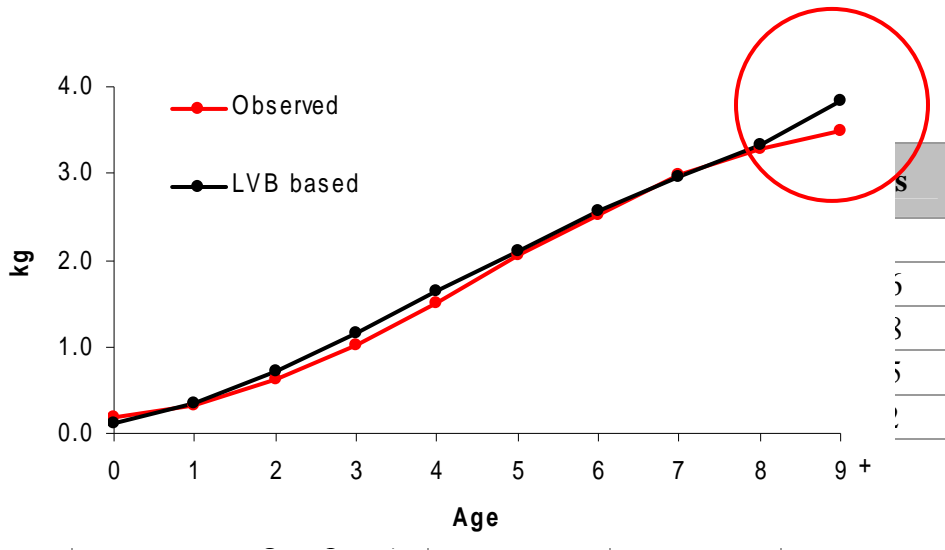


Figure 7. Observed mean weight-at-age from the NMFS trawl survey versus weight-at-age based on LVB length-at-age and L:W relationship.

Table 1. Estimates of constant natural mortality rates for summer flounder.

Model	Formula	M (combined- sex)	M (females)	M (males)
Hoenig (1983)	$Z = \exp(1.44-0.982*\ln(tmax));$ 134 mixed stocks	0.295	0.295	0.340
	$Z = \exp(1.46-1.01*\ln(tmax));$ 84 fish stocks	0.279	0.279	0.323
Longevity-Based ROTs	$Z = \ln(1.5\%)/tmax$ or $4.22/tmax$	0.280	0.280	0.323
	$Z = \ln(5\%)/tmax$ or $3/tmax$	0.200	0.200	0.230
Pauly (1980)	$\ln(M) = -0.0066-$ $0.279*\ln(Linf)+0.6543*\ln(K)+0.4634*\ln(T)$	0.358	0.419	0.452
	$\ln(M) = -0.0152-$ $0.279*\ln(Linf)+0.6543*\ln(K)+0.4634*\ln(T)$	0.355	0.416	0.448
Jensen (1996)	$M = gK; g = 1.598$	0.331	0.414	0.428
Gunderson & Dygert (1988)	$M = 0.03 + 1.68*GSI$		0.368	
Gunderson (1997)	$M = 1.79*GSI$		0.360	

Table 2. Age or size-based estimates of M.

Inputs	Combined-sex	Females	Males	Model	Formula
Maximum Observed Age	15	15	13	Peterson & Wroblewski 1984	$M^d = 5.26 \cdot (10^{-3}) \cdot W^{-0.25}$
K	0.207	0.259	0.268	Chen & Watanabe 1989	$M1 = K / (1 - \text{EXP}(-K \cdot (t - t_0)))$; early life stages
L _{inf}	76.95	73.97	61.15		$M2 = K / (a_0 + a_1 \cdot (t - t_m) + a_2 \cdot (t - t_m)^2)$; senescence
T0	-1.24	-0.92	-1.32	Lorenzen 1996	$M = 3.00 \cdot W^{(-2.88)}$
L:W Parameter a	4.08E-06	3.68E-06	4.51E-06	Lorenzen 2000	$M = Mr \cdot (Lr/Lt)$, assuming 1.5% survival ROT
L:W Parameter b	3.241	3.266	3.218		
a0	0.773	0.787	0.702		
a1	0.047	0.055	0.080		
a2	-4.87E-03	-7.13E-03	-1.07E-02		
Lr	33.35	34.48	32.43		
Mr	0.443	0.434	0.456		

Table 3. Age-variable M rates for fluke.

Age	Lorenzen 2000			Lorenzen 1996			Chen & Watanabe 1989			Peterson & Wroblewski 1986		
	Combined-sex	Females	Males	Combined-sex	Females	Males	Combined-sex	Females	Males	Combined-sex	Females	Males
0	0.634	0.656	0.627	0.775	0.796	0.759	0.685	0.840	0.694	0.886	0.908	0.871
1	0.443	0.434	0.456	0.554	0.540	0.566	0.441	0.516	0.500	0.663	0.648	0.675
2	0.356	0.344	0.378	0.452	0.434	0.475	0.373	0.432	0.418	0.555	0.536	0.580
3	0.307	0.297	0.334	0.393	0.377	0.423	0.329	0.378	0.369	0.492	0.475	0.525
4	0.276	0.268	0.306	0.356	0.343	0.391	0.298	0.343	0.340	0.452	0.437	0.490
5	0.255	0.250	0.288	0.331	0.321	0.370	0.275	0.320	0.323	0.424	0.412	0.466
6	0.240	0.237	0.276	0.313	0.305	0.355	0.260	0.304	0.316	0.404	0.395	0.450
7	0.229	0.228	0.267	0.300	0.295	0.344	0.248	0.295	0.316	0.389	0.383	0.439
8	0.221	0.222	0.261	0.290	0.287	0.337	0.241	0.290	0.325	0.378	0.374	0.430
9	0.215	0.217	0.256	0.283	0.281	0.331	0.236	0.291	0.343	0.369	0.368	0.424
10	0.210	0.213	0.253	0.277	0.277	0.327	0.234	0.296	0.375	0.363	0.363	0.419
11	0.207	0.211	0.250	0.272	0.274	0.324	0.235	0.306	0.427	0.357	0.359	0.416
12	0.204	0.209	0.248	0.269	0.271	0.322	0.238	0.323	0.516	0.353	0.356	0.413
13	0.202	0.207	0.247	0.266	0.269	0.320	0.244	0.348	0.688	0.350	0.354	0.411
14	0.200	0.206	0.246	0.263	0.268	0.319	0.254	0.386	1.124	0.347	0.353	0.410
15	0.198	0.205	0.245	0.262	0.267	0.318	0.267	0.443	4.066	0.345	0.351	0.409
16	0.197	0.205	0.244	0.260	0.266	0.317	0.286	0.536		0.344	0.350	0.408
17	0.196	0.204	0.244	0.259	0.265	0.316	0.312	0.703		0.342	0.350	0.407
18	0.195	0.204	0.243	0.258	0.265	0.316	0.350	1.085		0.341	0.349	0.407
19	0.195	0.203	0.243	0.257	0.264	0.315	0.404	2.727		0.340	0.349	0.406
20	0.194	0.203	0.243	0.257	0.264	0.315	0.491			0.340	0.348	0.406
21							0.643					
22							0.974					
23							2.222					