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Re-evaluation of Georges Bank yellowtail flounder natural mortality based on life history approaches

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ABSTRACT

We investigate several approaches based on life history approaches to estimate natural mortality (M) for Georges Bank yellowtail flounder *Limanda ferruginea*. Currently, a value of 0.2 is assumed for all ages in the stock assessment. A range of M estimates based on maximum age, growth, maturity and weight were derived from both age dependent and age independent approaches applied to a variety of data sources. Further, an alternative approach to the traditional maximum age methods was explored based on the premise of estimating the average maximum age in the population. Results from our analyses indicated that M is higher than 0.2 and likely ranges from 0.3 to 0.5. While M appears higher than the current assumption in the stock assessment, we do not believe that the results of this study will change the perception of the stock nor will it resolve retrospective problems for Georges Bank yellowtail flounder.

Introduction

Georges Bank yellowtail flounder currently assumes a constant rate of natural mortality of M = 0.2 (Legault et al. 2012). This assumption was based on historical tagging studies in the late 1950's and (Lux 1969a) and an analyses relating changes in total mortality to effort (Brown and Hennemuth 1971). Hoenig's commonly used approach also known as "the rule of thumb" (Hoenig 1983) also suggests that natural mortality for yellowtail is approximately 0.2 based on observed maximum age from historical U.S. NEFSC surveys. However, Hewitt and Hoenig's (2005) reformulation of Hoenig's (1983) linear regression model suggest that M for yellowtail flounder is 0.3. While these longevity approaches to estimating natural mortality yielded similar values, observations at oldest ages tend to be very limited and beg the question about the representativeness of these M estimates relative to the rest of the population. In this paper, we evaluated the sufficiency of the current M assumption for Georges Bank yellowtail flounder through life history analyses of natural mortality. For the purpose of our analyses, we considered life history-based methods that describe the relationship between M and traits such as age, growth and weight. Gunderson's approach based on fish reproductive effort was also explored based on histological analyses of yellowtail flounder ovarian development. Finally, we explored a size-dependent approach to estimating natural mortality by modeling the relationship between length and estimated mean age of the population based on the U.S. fishery and survey biological data.

Methods

Data

Over 108,000 age samples of Georges Bank yellowtail flounder from 1963-2013 were used in our analyses, derived from a variety of data sources including the U.S. NEFSC spring and autumn trawl surveys, U.S. observer port samples and commercial landings. Retrieval of age samples from the database were based on U.S. survey strata and fishery statistical area for Georges Bank yellowtail flounder. The distribution and number of ages samples used in this study are presented in Tables 1 and 2 and Figure 1. Age-length keys (ALK's) were generated for each of the age datasets. Because yellowtail flounder are sexually dimorphic, the survey age samples were further separated to allow for sex specific analyses. Ages derived from the survey were converted to decimal ages by accounting for the approximate timing of the spring and fall survey (i.e. April = age + 0.3 and September = age + 0.75) which also allowed for the construction of seasonal growth progression from one age group to the next in our ALK's. For simplicity, survey decimal ages were used as a proxy for both the observer and landings ALK's.

Growth parameters were re-estimated based on the von Bertalanffy growth model using the NEFSC bottom trawl survey data. Several different data sources were used for estimating growth parameters (i.e. factors include sex, season and a combination of both) for Georges Bank yellowtail. However, for simplicity, the von Bertalanffy growth parameters used in this study were based on the combined spring and fall survey data (Table 3). For maturity, parameter estimates were borrowed from O'Brien (1993) and catch mean weights-at-age were derived from the most recent Georges Bank yellowtail flounder TRAC assessment (Legault et al. 2012).

For the Gunderson approach, GSI estimates were based on fish sampled primarily from commercial vessels participating in the Northeast Fisheries Science Center, Northeast Cooperative Research program (NEFSC-NCRP) Study Fleet. Supplemental samples were obtained from other vessels participating in NEFSC-NCRP field research studies. Yellowtail flounder were obtained in the months leading up to and during spawning. Flounder were processed in the laboratory for body and individual organ masses.

The Gunderson method, as defined in Gunderson and Dygert (1988) and Gunderson (1997), limited analysis to fish with fully developed gonads, prior to hydration and commencement of spawning. They used egg size or gonad histology, when available, as a criterion for inclusion in the analysis. We used gonad histology to select fish close to but prior to any spawning, as recommended by Gunderson (1997). Flounder were sampled for gonad histology following the protocols of McBride (WP#32). Since, yellowtail flounder release their eggs in batches, to get an estimate of maximum GSI, it is necessary to be certain a fish has not yet started spawning. If postovulatory follicles (POFs) were evident in histology samples, an indication that individuals had commenced spawning, these samples were not used further in the analyses. Next, we refined estimates of GSI during the pre-spawning period by classifying the most advanced oocyte stage (MAOS) for each developing fish. Briefly, the stages were (Figure 3; adapted from Howell 1983):

LC: Late Cortical alveolar – cortical alveoli form a ring around the oocyte periphery
EV: Early vitellogenic - yolk inclusions partially fill cytoplasm
LV: Late vitellogenic, yolk inclusions throughout the cytoplasm
GM: Germinal vesicle migration, nucleus has begun migration to the cell periphery
H: Hydrated, fully hydrated but remains inside the follicle
OV: Ovulated, hydrated eggs outside the follicle

In this scheme, the GM stage is the most appropriate relative to the criteria of Gunderson (1997). Although few individuals were collected in this stage, the GSI values were intermediate to the LV stage prior and below the final oocyte maturation stages, so are a reasonable approximation of the maximal pre-spawning GSI. Fish total mass was measured to the nearest 0.1g and gonad to the nearest 0.001g. The gonnadosomatic index (GSI) was calculated as:

GSI = GM / (BM-GM)

Where GM is the gonad mass, BM is the total body mass. The regression reported by Gunderson (1997) was based on the same GSI formulation, however when possible, they define body mass as body mass less stomach content:

GSI_{ES} = GM / (BM-GM-ES),

where ES is the estimated mass of the stomach contents. Mean stomach contents (MS) from Southern New England yellowtail flounder was used as a proxy for measured ES mass, MS was estimated to be 0.524% of the total body mass determined from 289 fish (SE = 0.034) over months consistent with GSI analyses for Georges Bank fish (Mar-June), sampled during the study. The ES for each fish used in the GSI analysis was calculated as the product of MS and BM. The MS was determined excluding the empty stomach to get an upper bound of the over estimation of BM by excluding stomach mass from the calculation. The traditional calculation of GSI provides the lower bound.

Estimating Natural Mortality

Age Independent Methods

Five commonly indirect age-independent and two age dependent methods were explored to estimate natural mortality for Georges Bank yellowtail flounder (Table 4). For the age independent approaches, the estimated growth rate (k) from the von Bertalanffy growth model and age at maturity (t_{max}) derived from O'Brien (1993) were applied to Jensen (1996). GSI estimates from Georges Bank yellowtail flounder were applied to Gunderson's regression (1997). Values of t_{max} were used to derive M estimates from Hoenig (1983) and Hewitt and Hoenig (2005). Further, an alternative approach to the observed maximum age (t_{max}) was explored by utilizing a size dependent approach to estimate the corresponding average maximum age in the population as a function of the observed maximum size. A power function that relates size to the weighted mean age at length was used to predict the corresponding average maximum age in the population and applied to both Hoenig (1983) and Hewitt and Hoenig (2005) as proxy to estimate natural mortality (Figure 2). Variance estimates for the t_{max} approach were based on the observed maximum size in the population due to very small sample sizes. However, after inspection of data density at the larger size classes, we used a minimum sample size of five as criteria to define bounds around the mean average age in the population (Table 5).

Age Dependent Methods

Recognizing that natural mortality is likely to vary with age and time, we explored the applications of age-specific M approach defined by Lorenzen (1996) and Chen and Wantanabe (1989). The Lorenzen approach is premised on the empirical relationship between fish body weight and natural mortality. Using average catch weights-at-age from of Georges Bank yellowtail flounder from 1973-2012, Rivard Calculations were used to convert to January 1 weights to generate age and year specific M's. Parameters for the model were based on the ocean ecosystem as presented in Lorenzen (1996). However, due to the high M's estimates that were generated using the raw weights at age, probably due to inter-species variation that is not accounted for in the Lorenzen's ecosystem model parameters, the M values were rescaled to allow for some consistency with Georges Bank yellowtail flounder life history. For simplicity, age independent M estimates based on Hewitt and Hoenig (2005) for the combined data source (M = 0.403) was chosen to rescale M. Chen and Wantanabe (1989) on the other hand describe natural mortality having a U-shape curve also known as the "bathtub curve." The model uses two functions, one describing mortality falling early in life and a second describing mortality increasing towards the end of life. Chen and Wantanabe's two function model are based on K and t_0 parameters of the von Bertalanffy growth function. Using Georges Bank growth parameters estimated in this study, M at age was estimated for ages 1-14. However, the application of the analysis resulted in impractical results for ages greater than 10. Hence, the results from this analysis are presented only for illustrative purposes (Table 9, Figure 7)

Results and Summary

The use of multiple indirect relationships for estimating the rates of natural mortality resulted in fairly similar estimates of M for each approach. Estimates from the age-independent approaches ranged between 0.27 – 0.745. The highest age-independent estimates of M were provided by Jensen's K-based approach, but were the least variable (0.73-0.76) based on the 95% confidence derived from von Bertalanffy K estimates. However, Jensen's estimate appears to be unusually high and is not consistent with the expected rate of natural mortality based on current age observations in the survey or commercial data. M estimates from the Gunderson (1997) approach resulted in the lowest age-independent M estimates. M estimated based on the 95% confidence limits of the mean GSI ranged from 0.22 to 0.33. These estimates were similar to SNEMA yellowtail flounder used in the most recent assessment (NEFSC, 2012).

The average maximum age approach resulted in M estimates of approximately 0.31 for the Hoenig estimator and 0.43 for the Hewitt and Hoenig estimator for average age in the population of approximately 10 year old and ranging between 5 and 14 for a 58cm fish. However, when our analyses were adjusted for sample sizes, the resulting M estimates increased slightly from 0.31 to 0.34 for the Hoenig (1983) and from 0.43 to 0.47 for the Hewitt and Hoenig (2005) based on average age in the population of approximately 8.9 yrs, ranging between 6.3 and 11.3 years old for a 56cm fish. Sex specific estimates of M from the average maximum age approach resulted in higher M values for males relative to females. M estimates from both the t_{max} estimators ranged between 0.42 – 0.59 for males average maximum age of 6.3 years and 0.33-0.46 for females with average maximum age of 7.5 years. For M adjusted estimate, natural mortality for males with 95% confidence interval was approximately 0.48 (0.36-0.95) based on Hoenig (1983) and 0.67 (0.51-1.34) for Hewitt and Hoenig (2005). In the case of females, the adjusted M estimates was approximately 0.40 (0.28-0.68) using Hoenig (1983) and 0.56 (0.40-0.96) for the Hewitt and Hoenig (2005).

The age dependent natural mortality estimated by Lorenzen (1996) method declined from a median of 0.85 in the youngest age class to 0.46 for the oldest age group (ages 6+; Figure 6). Evaluation of Lorenzen's M estimates over time shows that M for ages 2 and older were relatively stable around the time series mean with the exception of age 1. The variability observed in age-1 was related to changes observed in the average mean weights in the commercial catch (Figure 5). The Chen and Wantanabe (1989) also yielded high estimates of natural mortality in the youngest age group (0.96 at age-1) and declined to 0.5 for ages 5 and 6 then increased at the oldest age groups. However, given the unrealistic result of the estimator for ages > 10, interpretation of the Chen and Wantanbe estimator should not be considered any further. For an overall summary of the age-independent M estimates explored in this study, see Table 6 and Figure 4 for details.

The results from this study suggest that the assumed natural mortality for Georges Bank yellowtail is likely higher than 0.2. Additionally, our analyses show differences in M estimates between males and females suggesting that females live longer than males. The choice between age dependent and age independent approaches are not substantially different and will likely not have much of an impact on the perception of the stock nor will it solve the retrospective problem. However, based on the available analyses, it is likely that M for Georges Bank yellowtail is in the range of 0.3 to 0.5.

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Tables

Table 1: Number of age samples for Georges Bank yellowtail flounder used for relating age to length, derived from the U.S. NMFS BTS (Fall and Spring), observer port samples, and commercial biological sampling.

Data	Years	Age Samples	% Age Samples
NMFS Fall	1963-2012	10,783	10%
NMFS Spring	1968-2013	10,423	10%
U.S. Observer	1992-2003	3,293	3%
U.S. Comm.	1964-2012	84,396	78%
All	1963-2013	108,895	100%

Table2: Number of age samples by age group derived from the U.S. NMFS BTS, observer port samples and commercial catch biological sampling

Age	NMFS_Fall	NMFS_Spr	Obs	Comm	Total
0	157	-			157
1	2,215	344	107	280	2,946
2	3,304	3,006	1,162	17,123	24,595
3	3,236	3,668	1,064	32,051	40,019
4	1,260	2,234	526	21,297	25,317
5	429	840	236	8,774	10,279
6	118	221	104	3,089	3,532
7	47	83	42	1,139	1,311
8	9	21	32	395	457
9	6	3	15	176	200
10	-	2	4	58	64
11	1	1	1	11	14
12	-	-		3	3
13	-	-			-
14	1	-			1
Total	10,783	10,423	3,293	84,396	108,895

Table3: Biological parameters used in deriving instantaneous rates of natural mortality for Georges Banks yellowtail flounder

Parameter	Symbol	Unit	Est.	Source
Growth Coefficient	k	year-1	0.47	NMFS Spring and Fall Survey (1963-2013)
Asymptotic Length	Linf	cm	44.85	NMFS Spring and Fall Survey (1963-2013)
Age at Zero Length	t0	year	-0.42	NMFS Spring and Fall Survey (1963-2013)
Age at (50%) Maturity	A50	Year	Males= 1.3, Females = 1.8	O'brien et al. 1993
Age at 100% Maturity	tmat	Year	3	O'brien et al. 1993

Table 4: Corresponding age (years) at length (cm) calculated from a length-at-age power function for Georges yellowtail flounder. Estimated ages are provided for both observed maximum length in the population and the adjusted upper size limit conditioned on a minimum sample age size >= 5. Sample size (n) is the number age samples for a given length bin. Values in parenthesis are the observed range of ages at the maximum length or adjusted length. Note that decimal ages were used as a proxy for seasonal growth progression based on the U.S. Spring and Fall BTS (April and September).

	n	Obs. Max Len (Cm)	Est.A Age (yrs)	nadj	Adj. Max Len (cm)	Adj. Est. Age (yrs)
NMFS Surv_Male	1	58	14.75 (NR)	8	47	3.82 (3.75-4.30)
NMFS Surv_Female	2	55	7.53 (6.30-8.75)	6	54	7.71 (6.75-9.30)
NMFS_Sur_All	1	58	14.75 (NR)	6	54	7.71(6.75-9.30)
U.S. Observer	1	56	7.30 (NR)	7	52	8.87 (8.30-10.30)
U.S. Comm	1	58	5.3 (NR)	5	56	9.17 (6.30-11.30)
ALL	2	58	10.03 (5.30-14.75)	6	56	8.86 (6.30-11.30)

Table 5: Methods used to determine rates of instantaneous rates of natural mortality (M) from Georges Bank yellowtail flounder

Method	Functional Relationship
Age-independent methods	
Hoenig (1983)	$M = 3/t_{max}$
Hewitt and Hoenig (2005)	$M = 4.22/t_{max}$
Jensen (1996)	$M = 1.65/t_{mat}$
Jensen (1996)	$M = 1.5k$
Gunderson (1997)	$M = 0.03 + 1.68GSI$
Age-dependent methods	
Lorenzen (1996)	$M(t) = 3.69\ Wt^{-0.305}$
Chen and Waantanbe (1989)	$M(t) = \begin{cases} \dfrac{k}{1-e^{-k(t-t_0)}}; t \le t_M \\ \dfrac{k}{a_0 + a_1(t-t_M) + a_2(t-t_M)^2}; t \ge t_M \end{cases}$ $\begin{cases} a_0 = 1-e^{-k(t_M-t_0)} \\ a_1 = ke^{-k(t_M-t_0)} \\ a_2 = -0.5k^2 e^{-k(t_M-t_0)} \end{cases}$ $t_M = -\dfrac{1}{k}\ln\left[1-e^{kt_0}\right] + t_0$

Table 6: Estimates of instantaneous rates of natural mortality for Georges Bank yellowtail flounder based on age independent approaches. Note that M estimates from both the Hoenig (1983) and Hewitt and Hoenig (2005) were based on the expected age in the population from a power function (See figure 2) either at the maximum length observed in the population or at the adjusted upper size limit for age samples >=5

Method	Data Source	M Est.	95% LCI	95% UCI	adj. M Est	adj_95% LCI	adj_95% UCI
Hoenig (1983)	NEFSC_Surv Male	0.422	-	-	0.477	0.361	0.950
	NMFS_Surv Female	0.326	0.241	0.573	0.398	0.282	0.680
	NMFS_Survey _All	0.309	-	-	0.369	0.289	0.529
	U.S. Observer	0.301	-	-	0.373	0.271	0.523
	U.S. Comm	0.315	-	-	0.344	0.227	0.604
	ALL	**0.309**	**-**	**-**	**0.337**	**0.245**	**0.540**
Hewitt and Hoenig (2005)	NMFS_Surv Male	0.594	-	-	0.670	0.508	1.336
	NMFS_Surv Female	0.458	0.339	0.806	0.560	0.397	0.957
	NMFS_Survey _All	0.434	-	-	0.518	0.407	0.744
	U.S. Observer	0.423	-	-	0.525	0.381	0.735
	U.S. Comm	0.443	-	-	0.484	0.319	0.850
	ALL	**0.434**	**-**	**-**	**0.474**	**0.345**	**0.760**
Jensen (1996)	VonBert_K	0.745	0.727	0.763	-	-	-
	Age at 100% Maturity	0.550	0.485[1]	0.635[1]	-	-	-
Gunderson (1996)	Study Fleet (GSI_{ES})	0.274	0.219	0.329	-	-	-
	Study Fleet (GSI)	0.273	0.219	0.327	-	-	-

1. 95% CI was based on Female maturity derived from O'Brien (1993).

Table 7: Catch weights-at-age for Georges Bank yellowtail derived from the most recent 2013 TRAC assessment

Year	Age-1	Age-2	Age-3	Age-4	Age-5	Age-6+
1973	0.101	0.348	0.462	0.527	0.603	0.778
1974	0.115	0.344	0.496	0.607	0.678	0.832
1975	0.113	0.316	0.489	0.554	0.619	0.695
1976	0.108	0.312	0.544	0.635	0.744	0.861
1977	0.116	0.342	0.524	0.633	0.780	0.931
1978	0.102	0.314	0.510	0.690	0.803	0.970
1979	0.114	0.329	0.462	0.656	0.736	0.950
1980	0.101	0.322	0.493	0.656	0.816	1.072
1981	0.122	0.335	0.489	0.604	0.707	0.840
1982	0.115	0.301	0.485	0.650	0.754	1.082
1983	0.140	0.296	0.441	0.607	0.740	1.010
1984	0.162	0.239	0.379	0.500	0.647	0.797
1985	0.181	0.361	0.505	0.642	0.729	0.800
1986	0.181	0.341	0.540	0.674	0.854	1.015
1987	0.121	0.324	0.524	0.680	0.784	0.875
1988	0.103	0.328	0.557	0.696	0.844	0.975
1989	0.100	0.327	0.520	0.720	0.866	1.053
1990	0.105	0.290	0.395	0.585	0.693	0.845
1991	0.121	0.237	0.369	0.486	0.723	0.877
1992	0.101	0.293	0.365	0.526	0.651	1.110
1993	0.100	0.285	0.379	0.501	0.564	0.863
1994	0.193	0.260	0.353	0.472	0.621	0.775
1995	0.174	0.275	0.347	0.465	0.607	0.768
1996	0.119	0.276	0.407	0.552	0.707	1.012
1997	0.214	0.302	0.408	0.538	0.718	0.947
1998	0.178	0.305	0.428	0.546	0.649	0.966
1999	0.202	0.368	0.495	0.640	0.755	0.901
2000	0.229	0.383	0.480	0.615	0.766	0.954
2001	0.251	0.362	0.460	0.612	0.812	1.027
2002	0.282	0.381	0.480	0.665	0.833	1.068
2003	0.228	0.359	0.474	0.653	0.824	1.048
2004	0.211	0.292	0.438	0.585	0.726	0.956
2005	0.119	0.341	0.447	0.597	0.763	0.991
2006	0.100	0.310	0.415	0.557	0.761	0.996
2007	0.154	0.290	0.409	0.542	0.784	1.023
2008	0.047	0.302	0.415	0.533	0.675	0.962
2009	0.155	0.328	0.434	0.538	0.699	0.929
2010	0.174	0.323	0.432	0.519	0.661	0.808
2011	0.128	0.337	0.461	0.553	0.646	0.747
2012	0.185	0.339	0.452	0.555	0.671	0.806
Mean	0.147	0.318	0.454	0.589	0.725	0.923

Table 8: Lorenzen estimates of instantaneous rates of natural mortality (M) based on catch weights-at-age for Georges Bank yellowtail flounder

Year	Age-1	Age-2	Age-3	Age-4	Age-5	Age-6+	Mean
1973	0.903	0.619	0.568	0.546	0.524	0.484	0.607
1974	0.868	0.621	0.556	0.523	0.505	0.475	0.591
1975	0.873	0.638	0.558	0.537	0.519	0.501	0.604
1976	0.885	0.640	0.540	0.515	0.491	0.470	0.590
1977	0.866	0.623	0.547	0.516	0.484	0.459	0.582
1978	0.900	0.639	0.551	0.503	0.480	0.453	0.588
1979	0.870	0.630	0.568	0.510	0.493	0.456	0.588
1980	0.903	0.634	0.557	0.510	0.477	0.439	0.587
1981	0.852	0.626	0.558	0.523	0.499	0.473	0.589
1982	0.868	0.647	0.560	0.512	0.489	0.438	0.586
1983	0.817	0.651	0.576	0.523	0.492	0.447	0.584
1984	0.782	0.694	0.603	0.554	0.513	0.481	0.605
1985	0.756	0.612	0.553	0.514	0.494	0.480	0.568
1986	0.756	0.623	0.542	0.506	0.471	0.447	0.557
1987	0.855	0.633	0.547	0.505	0.483	0.467	0.582
1988	0.898	0.630	0.536	0.501	0.473	0.452	0.582
1989	0.906	0.631	0.548	0.496	0.469	0.442	0.582
1990	0.892	0.655	0.596	0.528	0.502	0.472	0.608
1991	0.855	0.696	0.608	0.559	0.495	0.467	0.613
1992	0.903	0.653	0.610	0.546	0.512	0.435	0.610
1993	0.906	0.658	0.603	0.554	0.534	0.469	0.621
1994	0.741	0.677	0.617	0.564	0.519	0.485	0.600
1995	0.765	0.665	0.620	0.567	0.523	0.486	0.604
1996	0.859	0.665	0.590	0.538	0.499	0.447	0.600
1997	0.718	0.647	0.590	0.542	0.496	0.456	0.575
1998	0.760	0.645	0.581	0.540	0.512	0.454	0.582
1999	0.731	0.609	0.556	0.514	0.489	0.463	0.560
2000	0.704	0.601	0.561	0.520	0.487	0.455	0.555
2001	0.684	0.612	0.569	0.521	0.478	0.445	0.552
2002	0.660	0.602	0.561	0.508	0.474	0.440	0.541
2003	0.704	0.613	0.564	0.511	0.476	0.442	0.552
2004	0.721	0.653	0.577	0.528	0.495	0.455	0.572
2005	0.859	0.623	0.574	0.525	0.487	0.450	0.586
2006	0.906	0.641	0.587	0.536	0.488	0.449	0.601
2007	0.794	0.655	0.589	0.541	0.483	0.446	0.585
2008	1.140	0.647	0.587	0.544	0.506	0.454	0.646
2009	0.792	0.630	0.579	0.542	0.501	0.459	0.584
2010	0.765	0.633	0.580	0.548	0.509	0.479	0.586
2011	0.840	0.625	0.568	0.538	0.513	0.491	0.596
2012	0.751	0.624	0.572	0.537	0.507	0.479	0.578
Mean	0.825	0.638	0.573	0.529	0.496	0.461	0.587
Min	0.660	0.601	0.536	0.496	0.469	0.435	0.435
Max	1.140	0.696	0.620	0.567	0.534	0.501	1.140

Table 9: Age dependent estimates of instantaneous rates of natural mortality for Georges Bank yellowtail flounder based on Chen and Wantanabe (1989).

Age	M
1	0.963
2	0.689
3	0.585
4	0.534
5	0.513
6	0.514
7	0.538
8	0.592
9	0.696
10	0.908
Mean	0.653

Figures

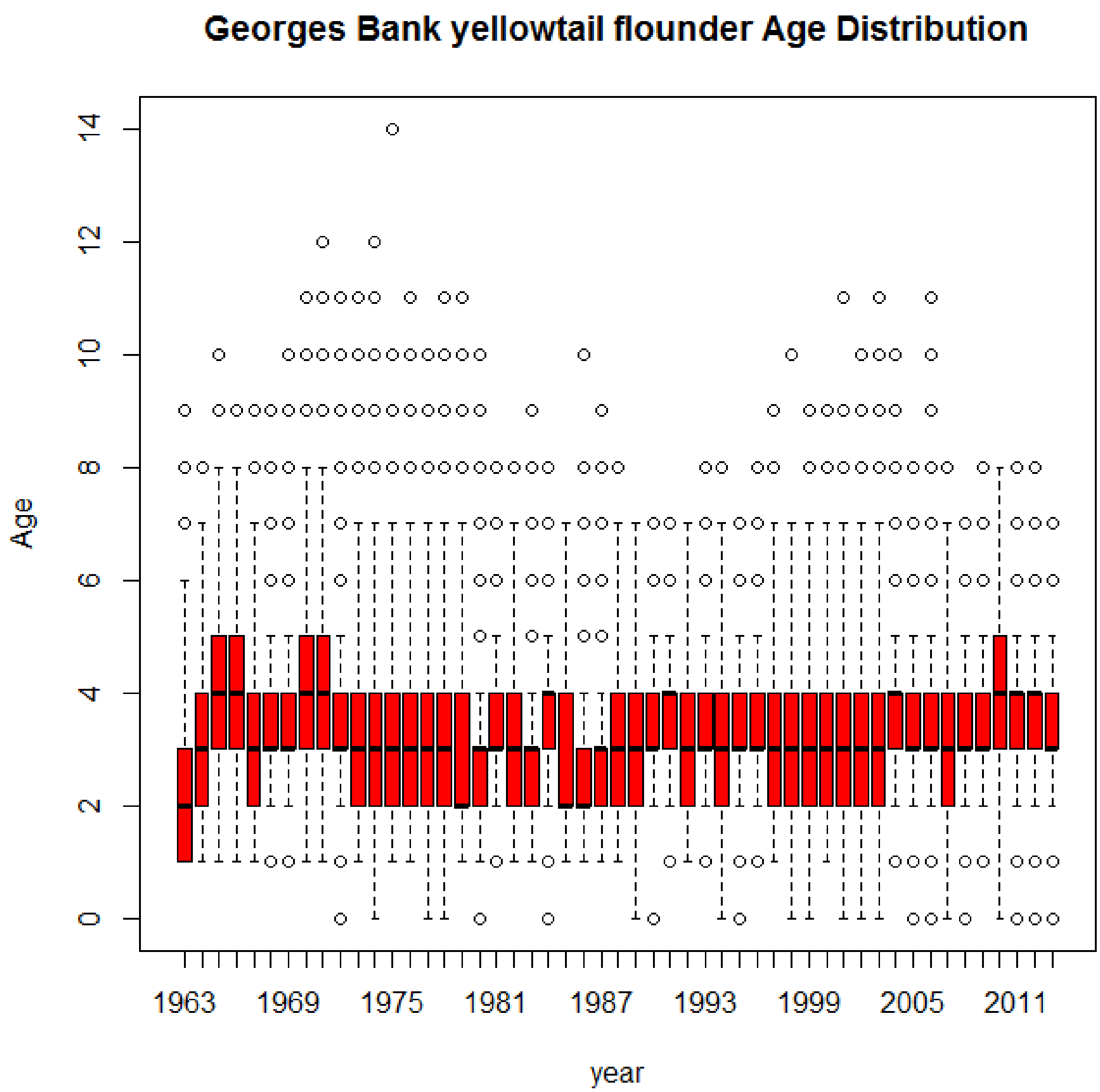

Figure 1: Age distribution of Georges Bank yellowtail based on aggregating age biological samples from U.S. Northeast Fisheries Science Center Spring and autumn survey, U.S. commercial landings and U.S. observer port samples. Observed maximum age of 14 resulted in natural mortality estimates ranging from (0.20-0.29) depending on estimation approach.

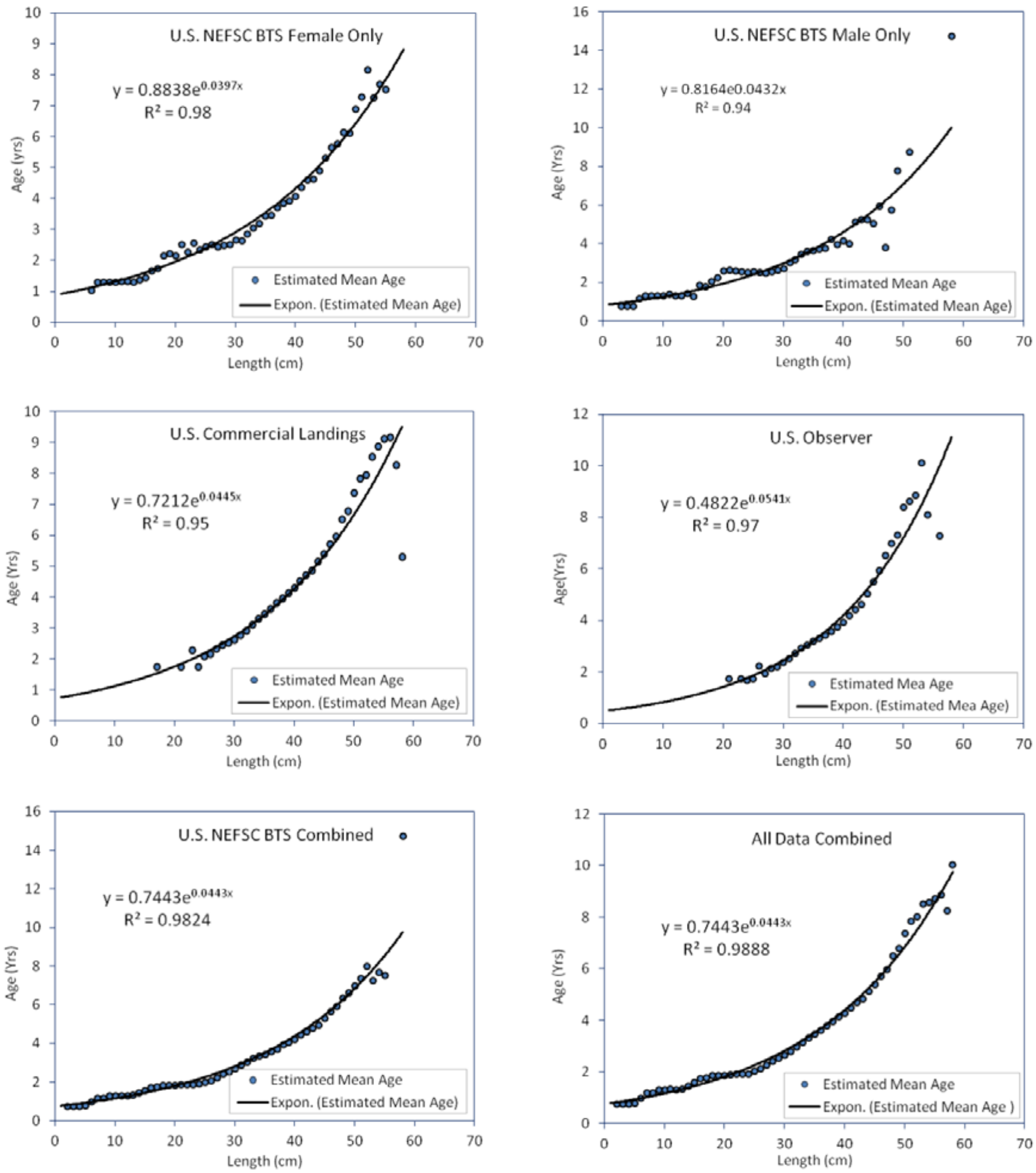

Figure 2: Weighted mean age at length for Georges Bank yellowtail flounder (blue circles) derived from the Northeast Fisheries Science Center spring and autumn bottom trawl survey, commercial and observed biological age and length samples. Relationship between length and mean age was modeled as a power function and fitted to a) NEFSC BTS female data b) NEFSC BTS male data c) U.S. commercial landings data d) U.S. observer data e) Aggregated sex NEFSC BTS f) All data combined from a-e. Decimal ages (April = -0.30 and September = 0.75) were used as a proxy to allow for seasonal progression of growth.

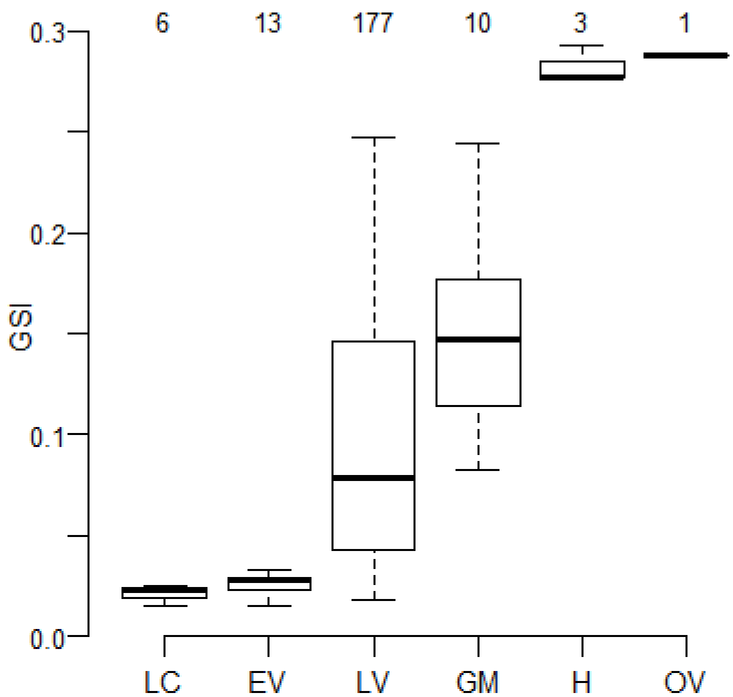

Figure 3: Gonadosomatic index (GSI) for mature (pre-spawning) yellowtail flounder females reported by most advanced oocyte stage. Fish were confirmed as pre-spawning by the lack of post-ovulatory follicles in the gonad histology sample. Numbers at top indicate sample sizes.

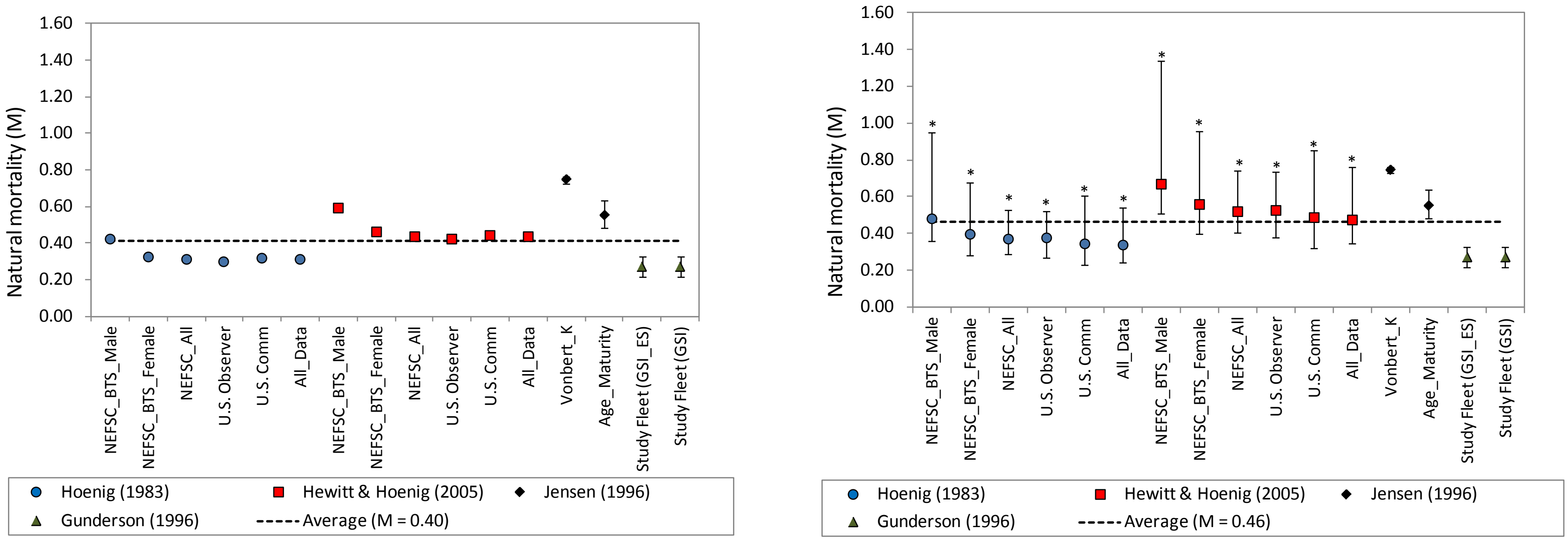

Figure 4: Summary estimates of age independent rates of natural mortality (M) for Georges Bank yellowtail flounder based on Hoenig (1983) = blue circles, Hewitt and Hoenig (2005) = red squares, Jensen (1996) = black diamonds and Gunderson (1997) = green triangles. The dash line represents the average M estimates among the methods applied to various data sources (survey, commercial and observer), life history parameters (growth and maturity) and Gonadosomatic index (GSI) estimates from Study Fleet data. The left plot reflects M estimates from Hoenig (1983) and Hewitt (2005) for which variance estimates were not available in some cases when sample sizes were low, while the right plot show M estimates adjusted for sample size (*) >=5.

Figure5: Lorenzen estimates of instantaneous rates of natural mortality for Georges Bank yellowtail flounder from 1973-2012 based total catch weights-at-age derived from the most recent TRAC assessment.

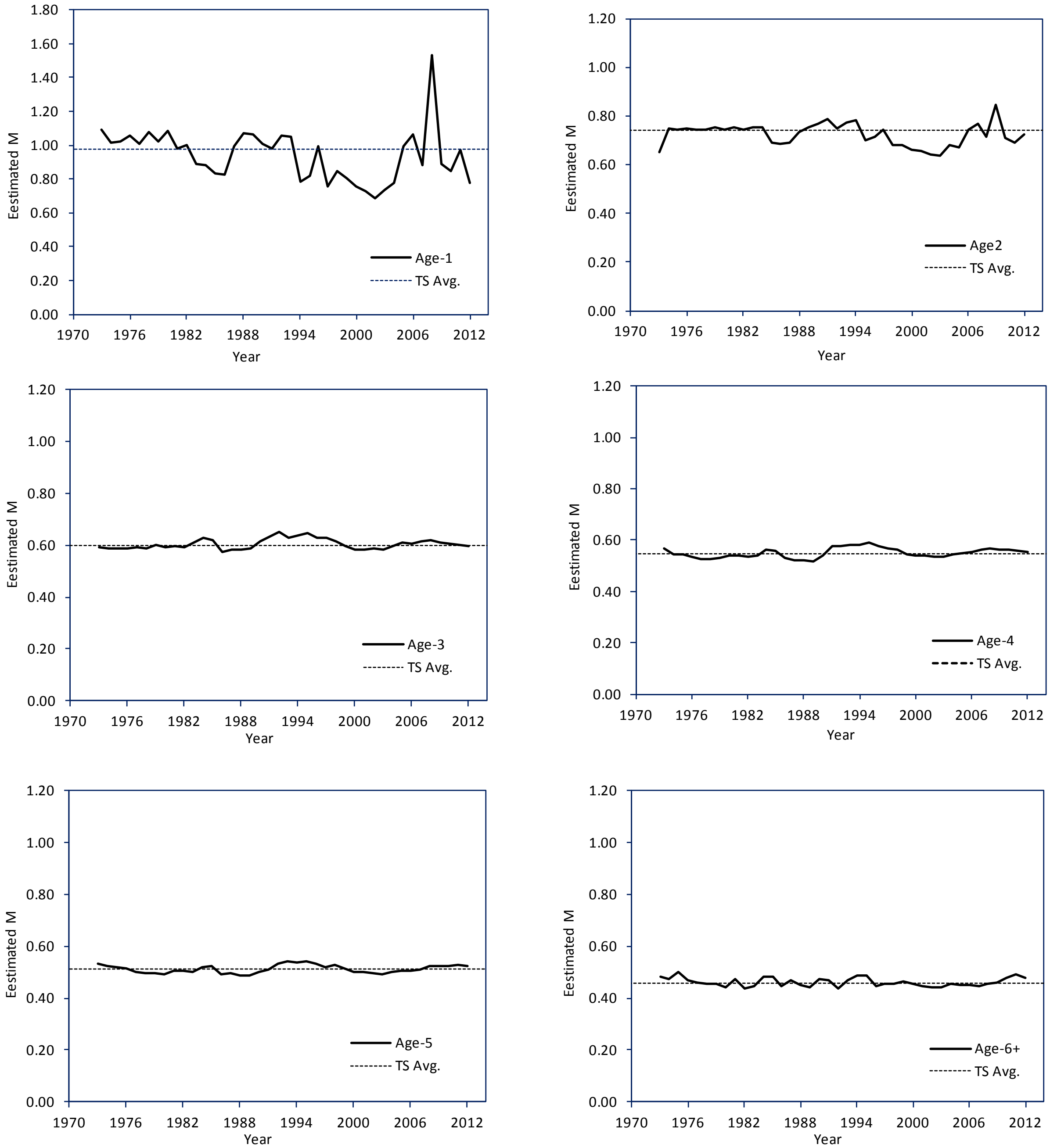

Figure5: Lorenzen estimates of instantaneous rates of natural mortality for Georges Bank yellowtail flounder from 1973-2012 based total catch weights-at-age derived from the most recent TRAC assessment.

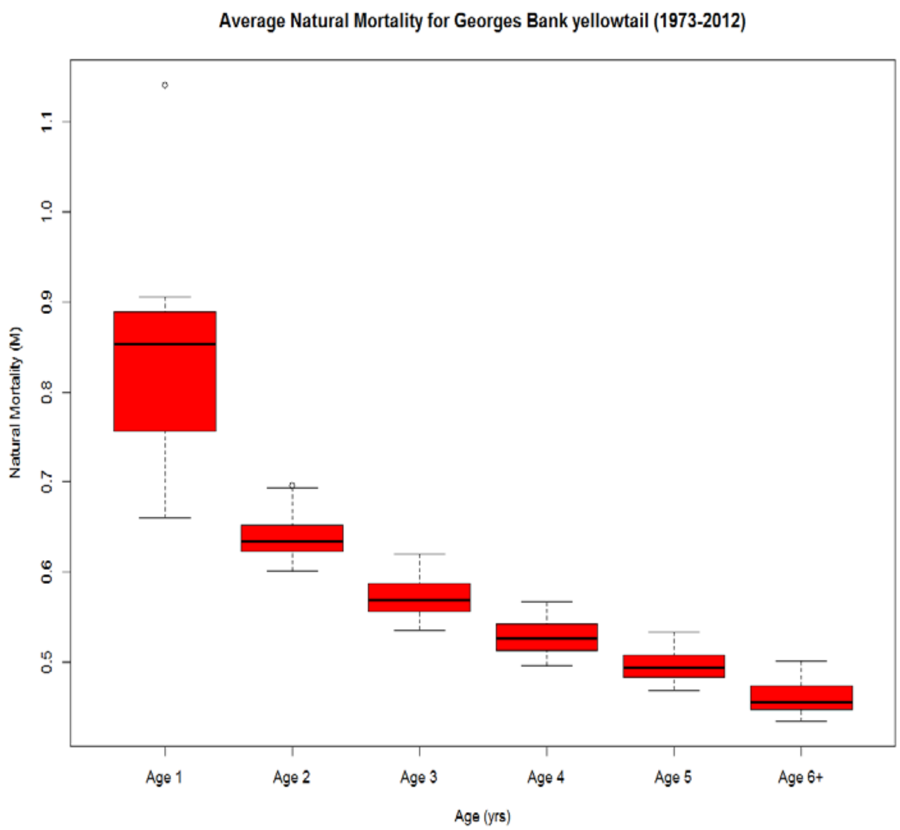

Figure 6: Lorenzen time series median at age from 1973-2012 and associated inter-quartile estimates of natural mortality for Georges Bank yellowtail flounder.

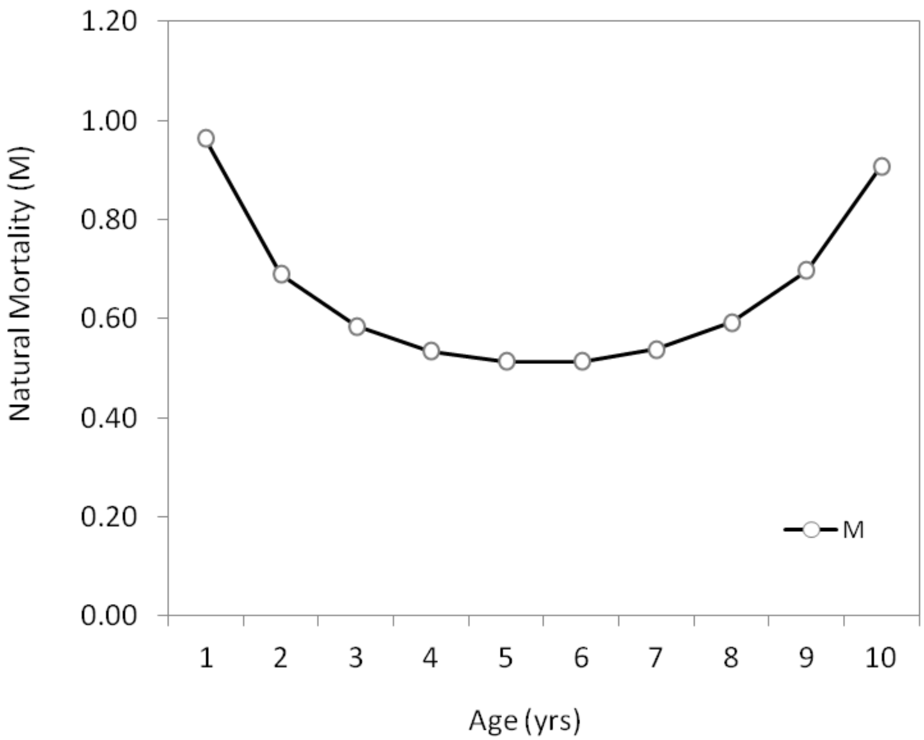

Figure 7: Instantaneous rates of natural mortality at age for Georges Bank yellowtail flounder based on Chen and Wantanabe (1989). Note that estimates were attempted for ages > 10, but were deemed infeasible.