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Re-evaluation of Georges Bank Yellowtail Flounder Natural Mortality Based on Life History Approaches

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ABSTRACT

In this study, we investigated several life-history based approaches to estimating natural mortality (M) for Georges Bank Yellowtail Flounder *Limanda ferruginea*. In previous Georges Bank Yellowtail Flounder stock assessments, an age and time invariant value of M = 0.2 is assumed based on historical tagging studies and the relationship between total mortality to effort in the late 1950s. Using both fishery dependent and independent data sources through 2013, Georges Bank Yellowtail Flounder natural mortality was re-evaluated based on maximum age, growth, maturity and fish reproductive potential. Further, we explored a size-dependent approach by relating mean age of Georges Bank Yellowtail Flounder to fish size using an exponential functional form. The size dependent approach was explored as an alternative to the maximum age approach based on the premise of limited sample sizes often encountered using the observed maximum age in the population and the potential for M to be underestimated. Results from our analyses indicated that M may be 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 the retrospective problems for Georges Bank Yellowtail Flounder.

RÉSUMÉ

Dans le cadre de cette étude, nous avons étudié plusieurs approches fondées sur le cycle biologique pour estimer la mortalité naturelle (M) de la limande à queue jaune du banc de Georges (*Limanda ferruginea*). Dans les évaluations précédentes du stock de limande à queue jaune du banc de Georges, on suppose une valeur invariable d'âge et de temps de M = 0,2 selon les études historiques de marquage ainsi que la relation entre la mortalité totale et l'effort à la fin des années 1950. À l'aide de sources de données dépendantes et indépendantes de la pêche en 2013, la mortalité naturelle de la limande à queue jaune du banc de Georges a été réévaluée en fonction de l'âge maximal, de la croissance, de la maturité et du potentiel reproducteur des poissons. De plus, nous avons étudié une approche fondée sur la taille en établissant un lien entre l'âge moyen des limandes à queue jaune du banc de Georges et la taille des poissons au moyen d'une formule de fonction exponentielle. L'approche fondée sur la taille a été étudiée comme solution de rechange de l'approche fondée sur l'âge maximal selon la prémisse de la taille souvent limitée des échantillons utilisant l'âge maximal observé dans la population et la possibilité que la valeur de M soit sous-estimée. Les résultats de nos analyses démontrent que la valeur de M pourrait être supérieure à 0,2 et qu'elle est probablement de 0,3 à 0,5. Bien que la valeur de M semble plus élevée que l'hypothèse actuelle dans l'évaluation du stock, nous ne croyons pas que les résultats de cette étude changeront la perception du stock ou résoudront les problèmes rétrospectifs liés à la limande à queue jaune du banc de Georges.

INTRODUCTION

Georges Bank Yellowtail Flounder currently assumes a constant rate of natural mortality of M = 0.2 (Legault et al. 2012). This assumption is based on historical tagging studies (Lux 1969) and changes in total mortality to effort in the late 1950s (Brown and Hennemuth 1971). Hoenig's commonly used approach also known as "the rule of thumb" (Hoenig 1983) also suggests that natural mortality for Georges Bank Yellowtail Flounder is approximately 0.2 based on the observed maximum age of 14 from historical U.S. Northeast Fisheries Science Center (NEFSC) surveys. However, Hewitt and Hoenig's (2005) reformulation of Hoenig's (1983) linear regression model suggest that M for Yellowtail Flounder is approximately 0.3. While these longevity approaches to estimating natural mortality are fairly similar in estimate, observations at the oldest ages tend to be very limited in sample size and beg the question about the representativeness of these M estimates relative to the average longevity of the population. In this paper, we evaluated the sufficiency of the current M assumption for Georges Bank Yellowtail Flounder using updated 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. Following the Gunderson and Dygert (1988) approach for relating reproductive effort to natural mortality, a Gonadosomatic Index (GSI) dependent M estimate was derived for Georges Bank Yellowtail Flounder based on selective histological analyses of ovarian development. Finally, we explored a size-dependent approach to estimating natural mortality by modeling the relationship between estimated mean age and length of the population using both U.S. commercial fishery and survey-independent 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 NEFSC spring and autumn research bottom trawl surveys, the NEFSC Northeast Fishery Observer Program (NEFOP) and the NEFSC commercial fisheries database (CFDBS). Retrieval of age samples from the databases was based on survey strata and commercial fishery statistical areas 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 (ALKs) were then generated for each of the age sample datasets and further disaggregated to account for sexual dimorphism to allow for sex-specific analyses. Ages derived from the survey were converted to decimal ages to account 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 ALKs. For analytical consistency, survey decimal ages were also applied to observer and landings ALKs for datasets aggregated by half year.

Growth parameters were estimated from a von Bertalanffy growth model fitted to the NEFSC bottom trawl survey by sex, season, and the aggregate data for Georges Bank Yellowtail Flounder. Maturity parameter estimates were derived from O'Brien (1993) and stock mean weights-at-age were obtained from the most recent Georges Bank Yellowtail Flounder TRAC assessment (Legault et al. 2012; Tables 3 and 4).

For the Gunderson (1997) approach, gonadosomatic index (GSI) estimates were based on fish sampled primarily from commercial vessels participating in the NEFSC-Northeast Cooperative Research program (NEFSC-NCRP) Study Fleet. Supplemental samples were obtained from other vessels participating in NEFSC-NCRP field research studies. Samples of Yellowtail Flounder were obtained in the months leading up to and during spawning and were processed in the laboratory for body and individual organ masses.

Following the Gunderson approach described in both Gunderson and Dygert (1988) and Gunderson (1997), GSI analysis was limited to fish with fully developed gonads, prior to hydration and commencement of spawning. Egg size or gonad histology was used when available, as a criterion for inclusion in the analysis. For our analysis, we only 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 2 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 GSI was calculated as:

GSI = GW / (BM-GW)

Where GW is the gonad weight and 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 in the following equation:

GSIES = GW / (BM-GW-ES)

Where ES is the estimated weight of the stomach contents expressed in grams. Mean stomach contents (MS) from Southern New England Yellowtail Flounder was used as a proxy for measured ES mass, and was estimated to be 0.524% (excluding the empty stomachs) of the total body mass determined from 289 fish (SE = 0.034) over months consistent with GSI analyses for Georges Bank fish (March-June), sampled during the study. The ES for each fish used in the GSI analysis was calculated as the product of MS and BM. An upper bound of the over estimation of BM was then determined by excluding stomach mass from the calculation. The traditional calculation of GSI = (GW / (BM-GW) provides the lower bound.

ESTIMATING NATURAL MORTALITY

Age Independent Methods

Five age-independent methods were explored to estimate natural mortality for Georges Bank Yellowtail Flounder (Table 5). Estimated growth rate (k) parameter from the von Bertalanffy growth model and age at 50% maturity (t_{mat}) derived from O'Brien et al. (1993) were applied to Jensen (1996) to derive both growth and maturity estimates of natural mortality. The GSI estimates from NEFSC-NCRP study fleet program were applied to Gunderson's (1997) regression. Using the observed maximum age (t_{max}) from both fishery dependent and fishery independent data sources, M estimates were derived from the relationships described by both Hoenig (1983) and Hewitt and Hoenig (2005). In the case of the size-dependent approach, mean age at a length were derived from the ALK's developed from both fishery dependent and fishery independent data sources. A power function that relates fish size to mean age was then used to predict the corresponding average maximum age for Georges Bank Yellowtail Flounder as shown in the following relationship:

$$Mean\ Age = \alpha e^{\beta Length}$$

Where α and β are constants from the predicted relationship. The average maximum age for Georges Bank Yellowtail Flounder was predicted based on the observed maximum length and then applied to both Hoenig (1983) and Hewitt and Hoenig (2005) as a proxy to estimate natural mortality (Table 6 and Figure 3). Variance estimates for the predicted mean age were also calculated. However, after inspection of data density at the larger size classes that resulted in very small age sample sizes, an ad hoc criterion for minimum sample size of five was used to define bounds around the mean average age for Georges Bank yellowtail (Table 6).

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. Average catch weights-at-age of Georges Bank Yellowtail Flounder from 1973-2012 (Legault 2012), were back-calculated to January 1 stock 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 estimates, probably due to inter-species variation that is not accounted for in the ocean ecosystem model parameters, the Lorenzen (1996) M values were rescaled to allow for some consistency with Georges Bank Yellowtail Flounder life history. For the purpose of this exercise, 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 as having a U-shape curve also known as the "bathtub curve." The model uses two functions, one describing mortality decreasing early in life and a second describing mortality increasing towards the end of life. Chen and Wantanabe's (1989) two function model is based on K and t0 parameters of the von Bertalanffy growth function. Using Georges Bank Yellowtail Flounder 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 7, Figure 4).

RESULTS AND SUMMARY

The use of multiple indirect relationships for estimating the rates of natural mortality resulted in an average M = 0.4 of all approaches considered in this exercise (Table 8 and Figure 5). Estimates from the age-independent approaches generally ranged between 0.27 – 0.55 with the exception of Jensen's K estimator which resulted in a higher M = 0.745. However, Jensen's estimate appears to be unusually high and is not consistent with the expected M for a stock with typical observations of age 6 fish, and sometimes older, in the survey and commercial data. M estimates from the Gunderson (1997) approach resulted in the lowest age-independent M estimates with 95% confidence limits of the mean GSI ranging from 0.22 to 0.33. It should be noted that these estimates are similar to M estimates used in the most recent SNEMA Yellowtail Flounder assessment (NEFSC, 2013).

Results from the size dependent approach resulted in M estimates of approximately 0.31 for the Hoenig (1983) estimator and 0.43 for the Hewitt and Hoenig (2005) estimator. This was based on aggregating all data sources and assuming a maximum size of 58 cm with an average population age of approximately 10 years, ranging from 5-14 years of age. However, when our analyses were adjusted for sample sizes, with an assumed maximum size of 56 cm and an average population age of approximately 8.9 yrs (range: 6.3 – 11.3 years), the resulting M estimates increased slightly from 0.31 to 0.34 for the Hoenig (1983) estimator and from 0.43 to 0.47 for the Hewitt and Hoenig (2005) estimator.

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, with an average maximum age of 6.3 years, and 0.33-0.46 for females, with an average maximum age of 7.5 years. For M adjusted estimates for males, M = 0.48 with 95% confidence interval of 0.36 - 0.95 based on Hoenig (1983) and M = 0.67 (0.51 - 1.34) based on Hewitt and Hoenig (2005). In the case of females, the adjusted M estimate was approximately 0.40 (0.28 - 0.68) based on Hoenig (1983) and 0.56 (0.40 - 0.96) based on Hewitt and Hoenig (2005).

The age dependent M estimated by the 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+; Table 9, Figures 6 and 7). Evaluation of Lorenzen 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, likely due to change in selectivity associated with increased mesh sizes. The Chen and Wantanabe (1989) estimator also yielded high estimates of M 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 lack of biological justification for the increase in M for Yellowtail Flounder >10 years old, interpretation of the Chen and Wantanbe (1989) estimator should not be considered any further. For an overall summary of the age-independent M estimates explored in this study, see Table 8 and Figure 5 for details.

The results from this study suggest that M 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 likely 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, collected from the NEFSC research bottom trawl surveys (fall and spring), and U.S. commercial and observer 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. Commercial	1964-2012	84,396	78%
All	1963-2013	108,895	100%

Table2. Number of age samples by age group for Georges Bank Yellowtail Flounder collected from the NEFSC research bottom trawl surveys (fall and spring) , and U.S. commercial and observer biological sampling.

Age	NMFS Fall	NMFS Spring	U.S. Observer	U.S. Commercial	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	tmat	Year	Males= 1.3, Females = 1.8	O'Brien et al. 1993

Table 4. 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 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)	$M(t) = \begin{cases} \dfrac{k}{1-e^{-k(t-t_0)}}; t \le t_M \\ \dfrac{k}{a_0 + a_1(t-t_M) + a_2(t-t_M)^2}; t \ge t_M \end{cases}$ $\begin{cases} a_0 = 1-e^{-k(t_M-t_0)} \\ a_1 = ke^{-k(t_M-t_0)} \\ a_2 = -0.5k^2e^{-k(t_M-t_0)} \end{cases}$ $t_M = -\dfrac{1}{k}\ln\left[1-e^{kt_0}\right]+t_0$

Table 6. 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 age sample size ≥ 5. Sample size (n) is the number of age samples for a given length bin. Values in parenthesis are the observed range of ages at the maximum length or adjusted length. NA refers to ages with noranges available. Note that decimal ages were used as a proxy for seasonal growth progression based on the NEFSC spring and fall bottom trawl survey (April and September).

Data Source	n	Obs. Max Len (Cm)	Est.A Age (yrs)	nadj	Adj. Max Len (cm)	Adj. Est. Age (yrs)
NMFS Survey Male	1	58	14.75 (NA)	8	47	3.82 (3.75-4.30)
NMFS Survey Female	2	55	7.53 (6.30-8.75)	6	54	7.71 (6.75-9.30)
NMFS Survey All	1	58	14.75 (NA)	6	54	7.71(6.75-9.30)
U.S. Observer	1	56	7.30 (NA)	7	52	8.87 (8.30-10.30)
U.S. Commercial	1	58	5.3 (NA)	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 7. 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

Table 8. 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 3) 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)	NMFS Survey Males	0.303	-	-	0.477	0.361	0.950
	NMFS Survey Females	0.382	0.271	0.651	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. Commercial	0.315	-	-	0.344	0.227	0.604
	ALL	**0.309**	**-**	**-**	**0.337**	**0.245**	**0.540**
Hewitt and Hoenig (2005)	NMFS Survey Males	0.427	-	-	0.670	0.508	1.336
	NMFS Survey Females	0.538	0.381	0.916	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. Commercial	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 9. Lorenzen estimates of instantaneous rates of natural mortality (M) based on January stock 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

FIGURES

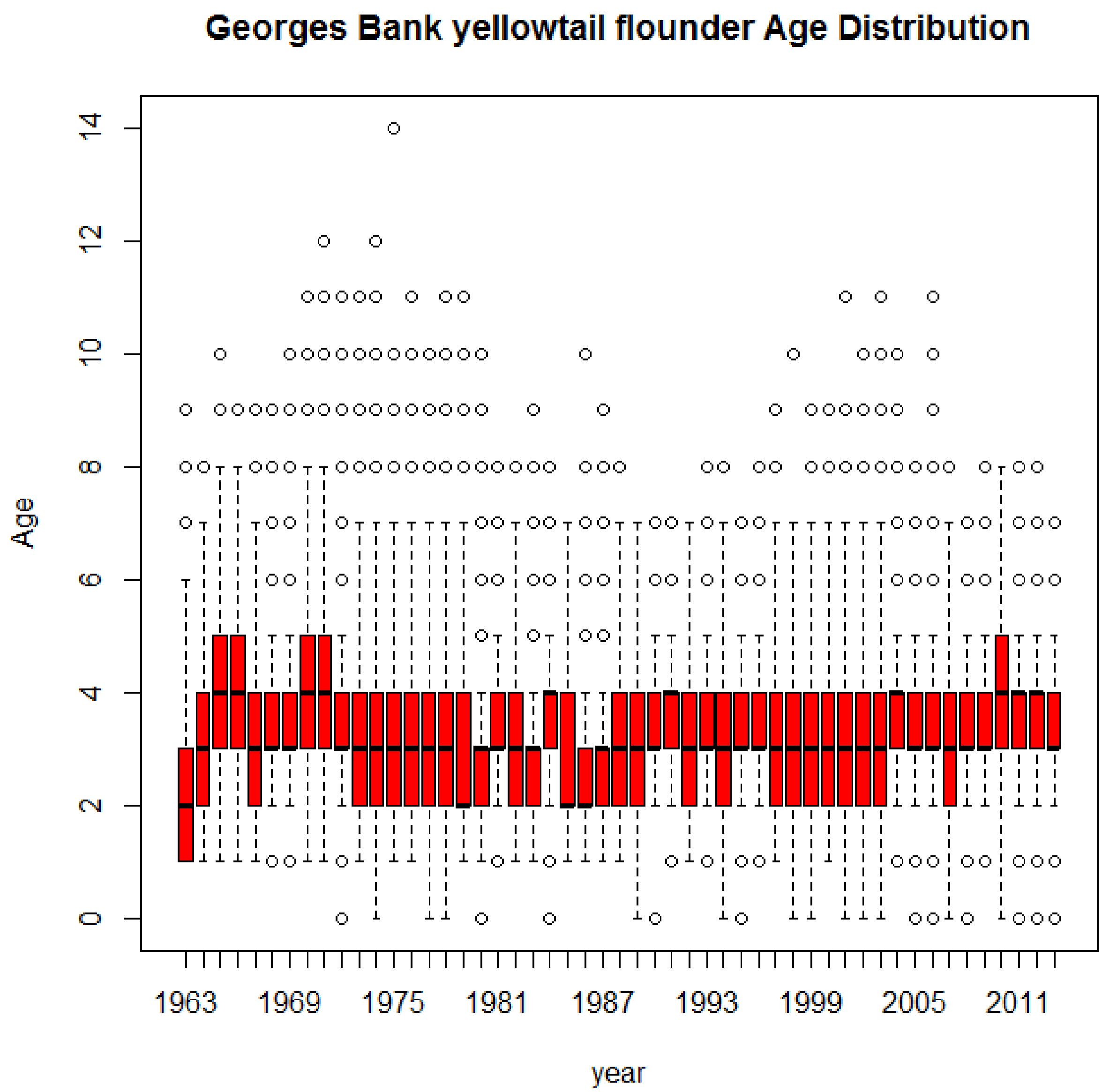


Figure 1. Age distribution of Georges Bank yellowtail based on aggregated age samples from the Northeast Fisheries Science Center trawl surveys (spring and autumn), the U.S. commercial landings and the observer biological samples (1963-2013). Observed maximum age of 14 resulted in natural mortality estimates ranging from (0.20-0.29) depending on the application of the Hoenig's (1983) or the Hewitt and Hoenig (2005) estimator.

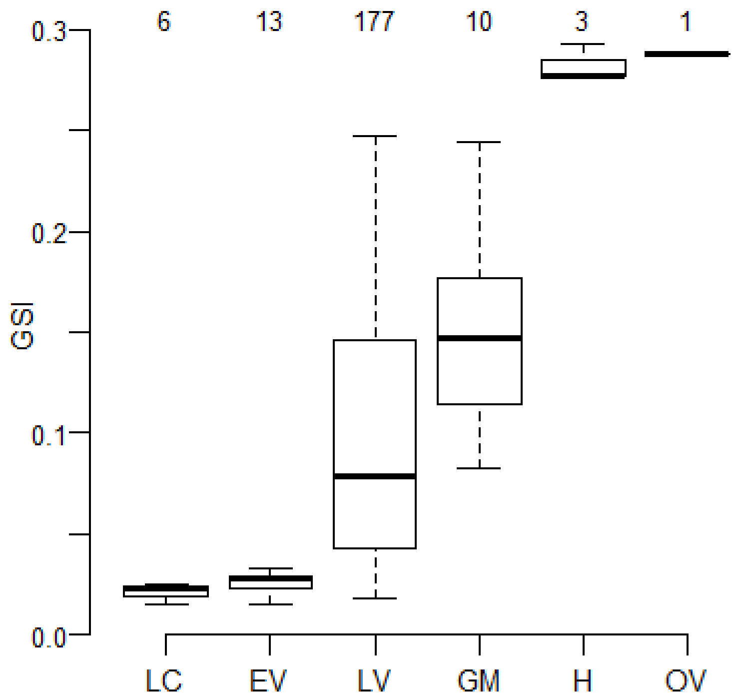


Figure 2. Gonadosomatic index (GSI) for mature (pre-spawning) Georges Bank Yellowtail Flounder females based on the most advanced oocyte stage. Fish were confirmed as pre-spawning by the lack of post-ovulatory follicles in the gonad histology sample. Numbers at top indicate sample sizes. LC = Late Cortical Alveolar; EV = Early Vitellogenic ; LV = Late Vitellogenic; GM = Germinal Vesicle migration; H = Hydration; OV = Ovulated.

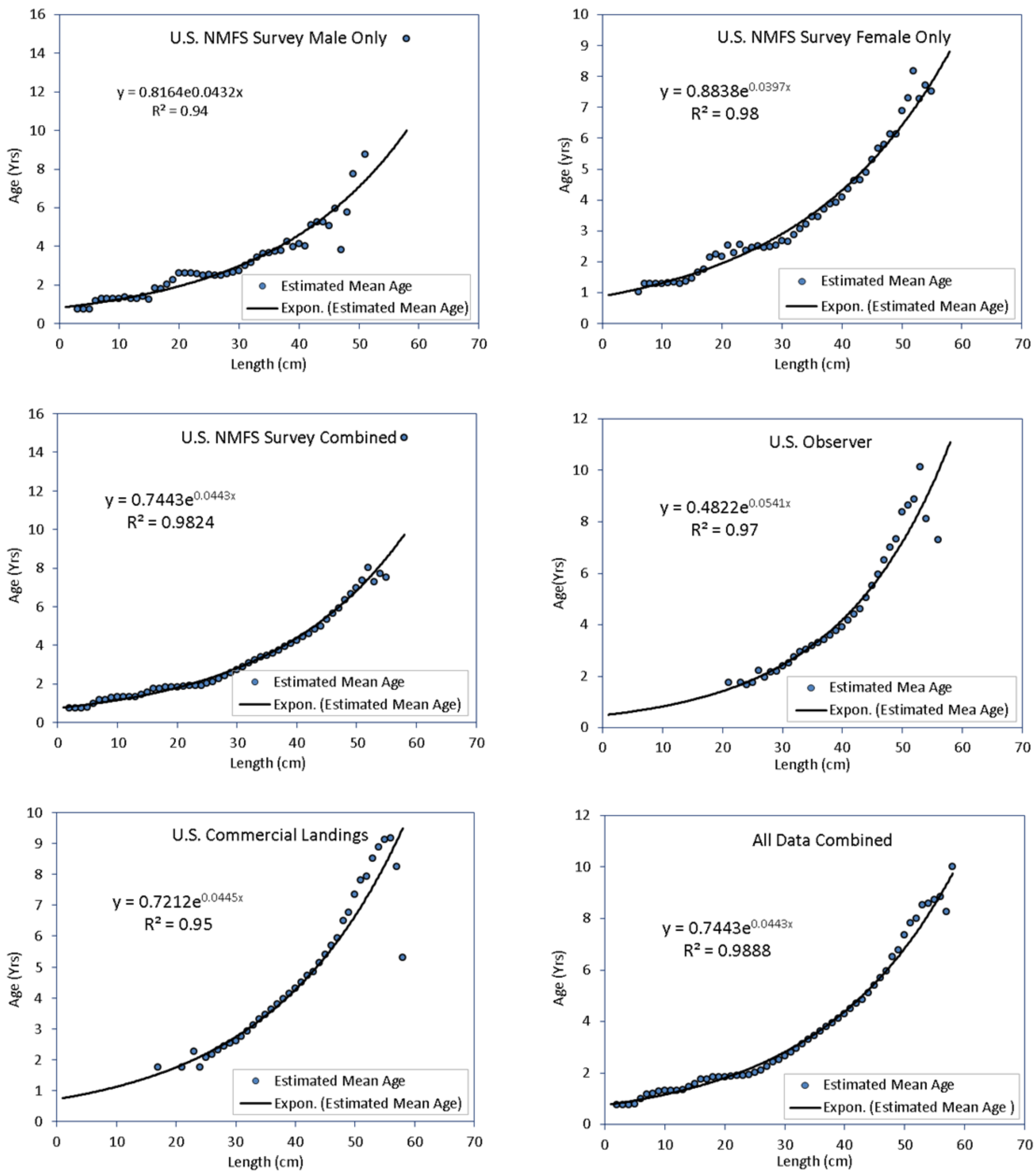


Figure 3. Weighted mean age at length for Georges Bank Yellowtail Flounder (blue circles) derived from the Northeast Fisheries Science Center spring and autumn bottom trawl survey and commercial and observed biological age and length samples. The relationship between length and mean age was modeled as 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, and 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.

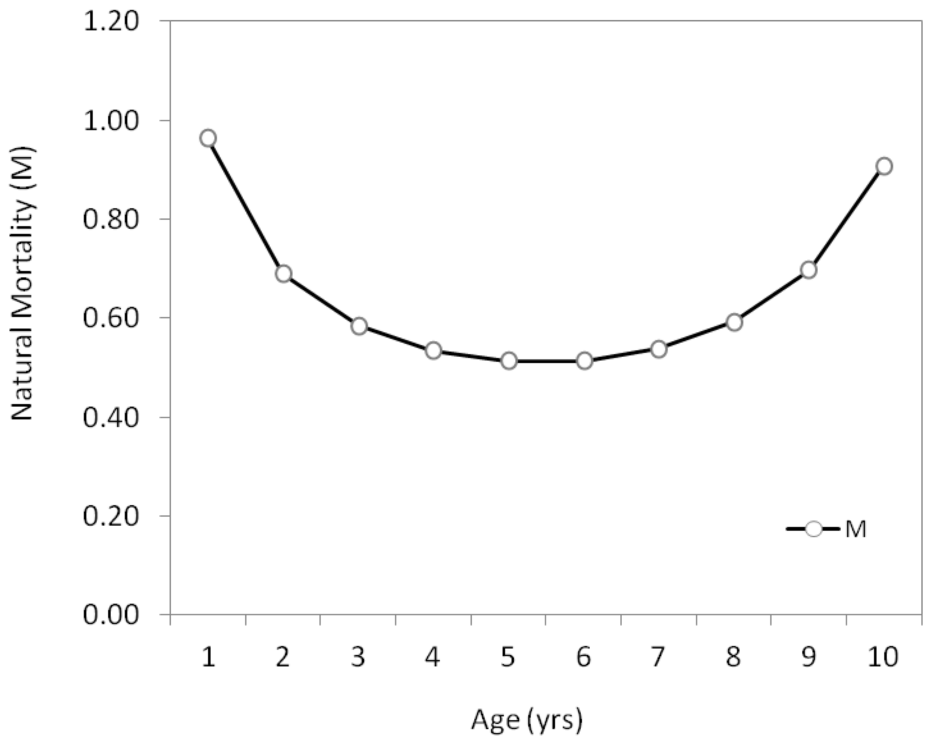
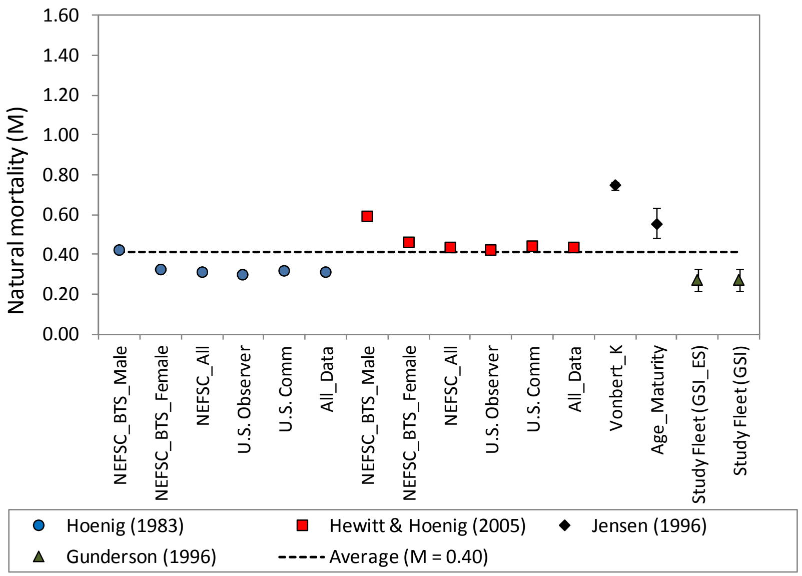


Figure 4. Instantaneous rate of natural mortality at age for Georges Bank Yellowtail Flounder based on Chen and Wantanabe (1989). Note that estimates were attempted for ages > 10, but were deemed infeasible.



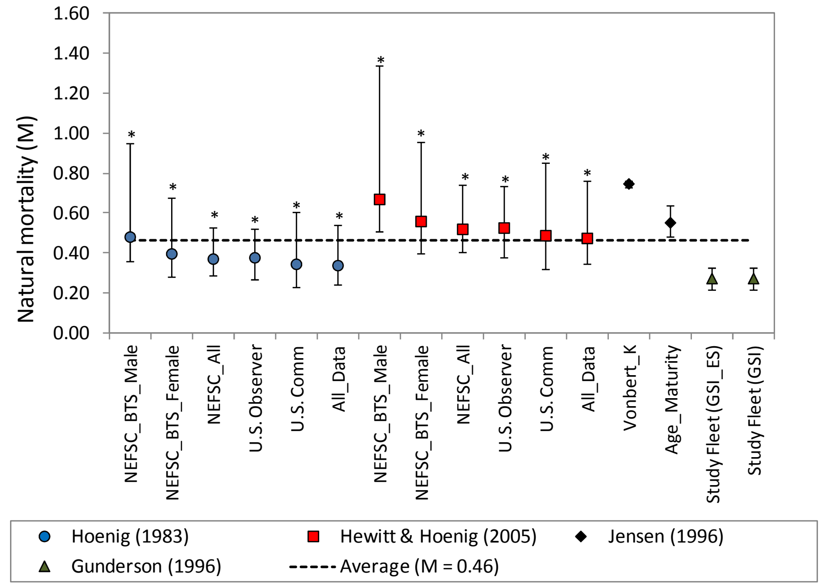


Figure 5. Summary estimates of age independent rates of natural mortality (M) for Georges Bank Yellowtail Flounder based on Hoenig (1983) = blue circles, Hewitt and Hoenig (2005) = red squares, Jensen (1996) = black diamonds and Gunderson (1997) = green triangles. The dash line represents the average M 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 shows M estimates adjusted for sample size (*) ≥5.

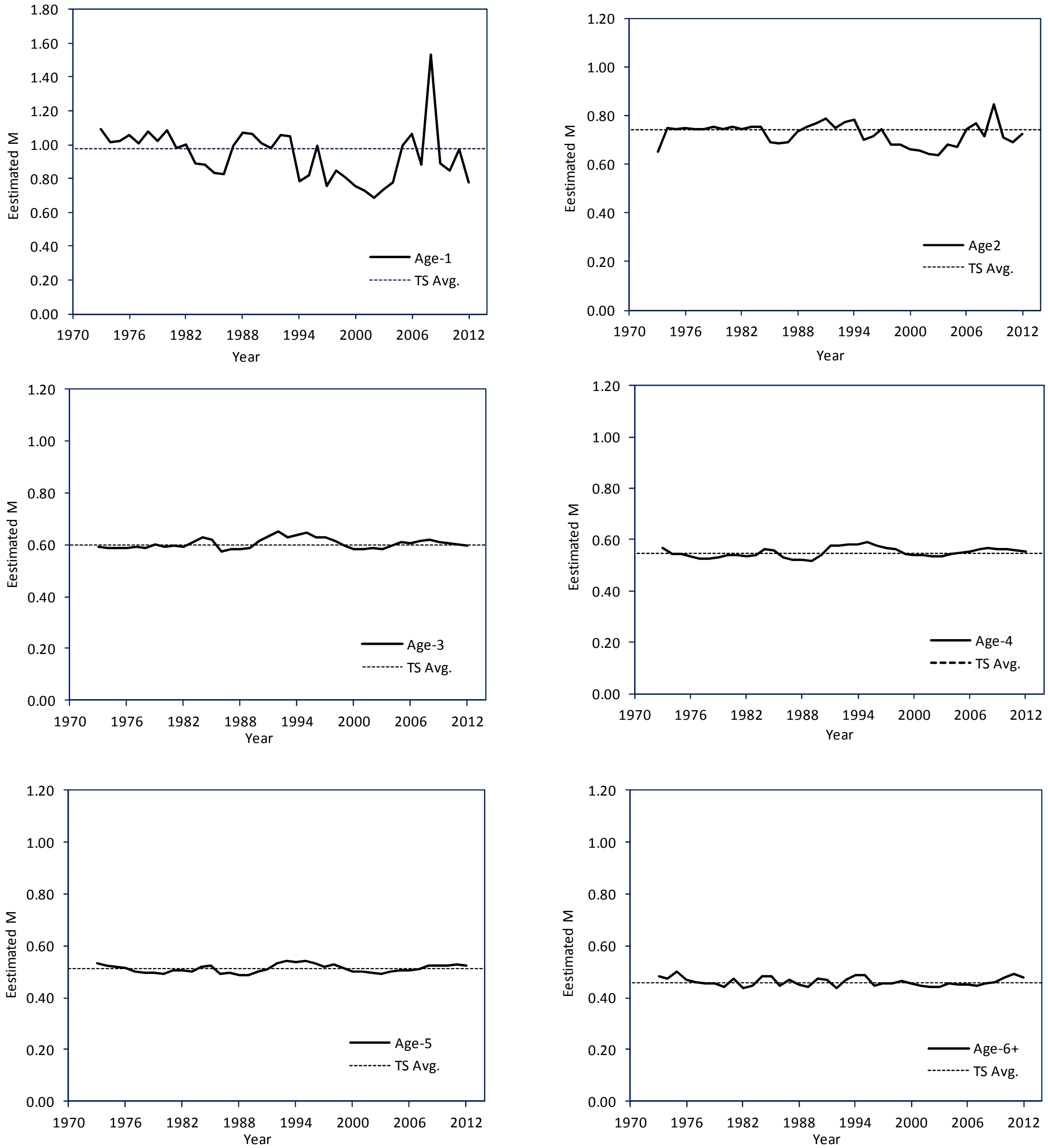


Figure 6. Lorenzen (1996) estimates of instantaneous rates of natural mortality for Georges Bank Yellowtail Flounder based on total stock weights-at-age derived from the most recent catch weights (Legault 2012), during 1973-2012.

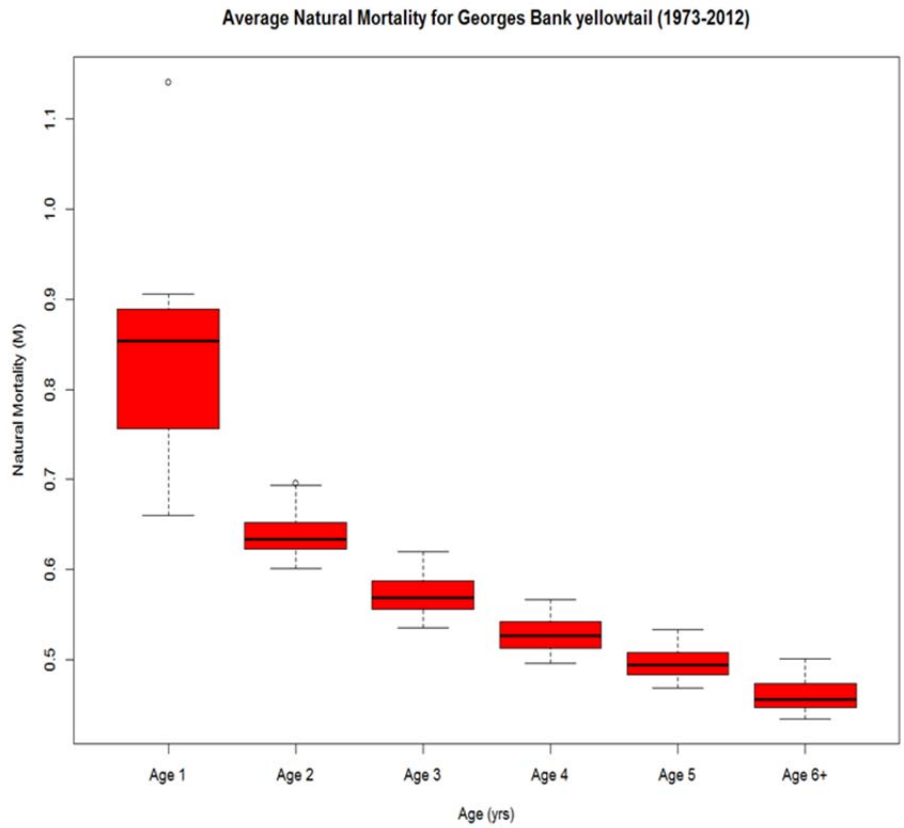


Figure 7. Instantaneous rate of natural mortality at age for Georges Bank Yellowtail Flounder based on Lorenzen (1996) during 1973-2012. Solid black line is median M at age with associated inter-quartile estimates.