APPENDIX 3

SAW 47 Working Paper 7 (TOR 3) – Life History Parameters

Evaluation of summer flounder life history parameters from NEFSC trawl survey data, 1992 – 2006.

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Background

In 2000, summer flounder stocks were determined to be overfished. Management of the species entered a ten year rebuilding period in order to increase abundance to sufficient levels. Recent stock assessments indicate that, although fishing mortality has decreased substantially and biomass is at the highest level ever recorded, the stock is still only about 50% of the target biomass. As the end of the rebuilding period nears and quotas continue to drop despite the high biomass, there has been growing concern that the stock assessment and/or biological reference points for the species are flawed.

During the 2007 stock assessment update, it was noted that there have been changes in certain biological parameters of the stock over the last few years. Among these are size at age and sex ratio. Changes in these and other parameters could affect population dynamics and rebuilding rates. The purpose of this paper is to review data collected during National Marine Fisheries Service, Northeast Fishery Science Center seasonal trawl surveys in order to investigate key biological parameters and evaluate potential implications on stock rebuilding and management of the species.

Methods

Data were obtained from the NEFSC trawl survey database. Since 1992, NEFSC finfish trawl surveys have occurred three to four times per year, and have recorded lengths, weights, ages, and sex from at least a subsample of summer flounder captured in the survey.

Length and weight at age

Evaluation of sample size at age revealed that sample size at older ages was very low, particularly during early years of the analysis. Data were therefore subset to years and ages that had a sufficient sample size.

Trends of size at age over time were evaluated in two ways. First, sex specific mean size at age was calculated for each year with sufficient sample size. SAS Proc REG (SAS 1990) was used to conduct regressions of size at age over time.

Second, observed data were fit to a von Bertalanffy growth function

$$L_t = L_\infty * (1 - e^{-(k*(t-t_0))})$$

to develop annual sex specific predicted length at age estimates using SAS Proc NLIN (SAS 1989a). For each year, residuals were resampled with replacement to develop 500 bootstrap datasets (Barker 2005), each of which was also fit using the von Bertalanffy growth function. Summary statistics were calculated for the parameter estimates, as well as predicted size at age. SAS Proc REG was used to perform regression analysis of mean predicted length at age over time.

For both methods, slope parameters of length at age over time were evaluated at the $\alpha = 0.10$ level.

Length-weight analysis was also conducted with SAS Proc NLIN using an allometric growth function.

$$W = \alpha L^\beta$$

For each year, residuals between observed and predicted weight at length were calculated and resampled to develop 500 bootstrap datasets which were also fit to the growth function. Summary statistics were calculated for the parameter estimates, as well as predicted weight at length. SAS Proc REG was used to evaluate trends in mean weight at length over time.

Maximum age, sex ratio, and natural mortality

Maximum age by sex was found by analytical review of the raw data, as were overall sex ratios and sex ratios by age. Sex ratio (*i.e.* percent female) at size was analyzed using SAS Proc GENMOD (SAS 1989b) with a normal distribution and a logit link function (*i.e.* a logistic regression).

Natural mortality for each sex was estimated using the approximation of 3 / T_{MAX} (Hoenig 1983). Annual estimates of natural mortality for the stock were determined using a weighted average of sex-specific natural mortality and annual sex ratio.

Fecundity

Individual fecundity was estimated by applying the fecundity:length relationship of Morse (1981) to the mid-year length at age for females.

$$F = 0.0007975 * L^{3.402}$$

Number of mature females by age and year were determined by multiplying the VPA estimated abundance at age by sex ratios at age and the VPA input maturity schedule. These were multiplied by fecundity at age and summed across ages to estimate total theoretical fecundity of the stock.

Results

Length and weight at age

The number of fish observed on trawl surveys was low for some ages and years, particularly during early years of the analysis. Data were therefore subset to years and ages where sample size was generally greater than 50 fish per year (all surveys combined). Prorating ages to the season fish were captured (assuming a January 1 birthdate) as done in earlier drafts resulted in low sample size for some seasons, but fitting equations using ages pooled across surveys in a year resulted in poor or unconverged fits for some years. As a result, length at age calculations (mean and von Bertalanffy) were conducted using samples from the winter survey only. The subset data include years from 1999 to 2006 and ages 0 through 4 for males and 0 through 5 for females. Sample size for these years and ages are generally greater than 40 fish (Table 1).

Mean lengths for males age 1 to 4 show no long term trends between 1999 and 2006 (Table 2, Figure 1), and regression results indicate no significant changes over time (Table 3). Trends in mean length at age for females were similar to males for ages 0 to 4; however, female mean length at age 5 decreased significantly between 1999 and 2006.

Fitting bootstrap data to the von Bertalanffy growth function resulted in unrealistic parameter estimates for males in 2000 and 2006 (Table 4). Bootstrap average maximum length for these years was approximately 100,000 cm. Although the mean estimated parameter values produce unrealistic estimates of length at age, specific bootstrap replicates with large maximum size estimates had correspondingly lower estimates of the growth parameter *k*, such that mean predicted length at age was not erratic for fish less than 8 years old. Regression results for length at ages 0 to 10 (the approximate age range observed in survey data) showed no significant trends (Table 5, Figure 2).

Estimated von Bertalanffy parameters for females were also unrealistic in 2000, though much less so than for males (Table 6). Regression results indicate no significant trend in predicted length at age for ages 0 to 4; however, predicted length at ages five and older decreased significantly between 1999 and 2006 (Table 7, Figure 3). For both males and females, regression results using von Bertalanffy predicted length at age were consistent with results of mean length at age.

Length:weight analysis was conducted on the same subset of years and ages as age:length analysis. As before, sample size was generally above 40 fish (Table 8). No significant trends were observed for weight at length for males (Tables 9 and 10, Figure 4) or females (Tables 11 and 12, Figure 5).

Maximum age, sex ratio, and natural mortality

Between 1985 and 1995, maximum age for males generally varied between age 4 and 5, while female maximum age ranged from age 6 to 8 (Figure 6). By 2000, maximum age of males had increased to between 8 and 9, where it remained stable until 2007 when one 12 year old male was captured. Female maximum age has increased steadily since 1995, with a peak of 14 years in 2005.

From 1992 to 1997 overall sex ratio averaged approximately 54% female (Figure 7). From 1997 to 2000, females increased from 53 to 58% of the stock, where it remained stable for 3 years. In 2003, the ratio dropped to 51% female and has varied widely from 47 to 57% since then.

Natural mortality was estimated as a weighted average of sex ratio and sex-specific natural mortality. Using maximum ages of 12 and 15 for males and females, respectively, sex-specific natural mortality is estimated at 0.25 for males and 0.20 for females. Applying these to overall sex ratios, M has remained relatively stable around 0.223, with a range of 0.221 in 2000 to 0.226 in 2005 (Figure 7).

Sex ratios by age (Figure 8) show a general decrease in percent female at age since the mid 1990s for all ages, although the declines are more evident for ages 2 and above. For example, 3 year old fish have dropped from an average of 75% female during 1992 to 1994 to 56% female in 2004 to 2006. Four year old fish have dropped from 85% female to 62% female over the same time period.

Sex ratio at size data (discussed below) indicate that greater than 90% of fluke can be sexed by 25 cm. Von Bertalanffy estimates indicate that both males and females attain this size by age 1. By age 2 both males and females have recruited to the commercial fishery (36 cm, 14”), so age 1 is the only age where they are large enough to be sexed and experience no harvest pressure. Natural mortality for age 1 fish is generally stable between 0.225 and 0.23 from 1992 to 2002, but has increased to approximately 0.235 in recent years (Figure 9). Even though age 2 fish are exploited, the sex ratio averages approximately 50:50 up to 43 cm (17”, age 3), and both sexes are likely harvested in equal proportions. Natural mortality of age 2 fish shows a gradual increase from 0.216 to 0.23 from 1992 to 2005, before dropping sharply back to 0.224 in 2006. Average M for age 1 and 2 also shows a gradual increase over all years from 0.222 to approximately 0.23.

When data are combined across years, logistic regression of percent female at size shows a 50:50 sex ratio at around 38 cm (15”). Fish smaller than this size are predominantly male, while larger fish are predominantly female (Figure 10). Using annual data, the 50% inflection ranges from 33 cm in 1992 and 1995 to 43 cm in 2003 and 2005 (Figure 11).

Combined data show that greater than 90% of all animals 25 cm and larger can be sexed. Sex ratio for fish 25-35 cm (*i.e.* able to be sexed but less than minimum size) has decreased from an average of 34.5% females for 1992-94 to 29.4% for 2004-06 (Figure 12). Natural mortality for fish in this size range has increased from an average of 0.233 for 1992-94 to 0.235 for 2004-06 (Figure 13). From 35 cm to 43 cm, the sex ratio is approximately 50:50, and fish in this size range are likely exploited in similar proportions. The sex ratio for fish 25 to 43 cm shows a decline from 48.4% female in 1992-1994 to 37.2% in 2004-2006. *M* for this size range has increased from 0.226 to 0.231 over the same time period.

Fecundity

Because of the concerns with sample size for age:length data, fecundity could only be evaluated for the years 1999 to 2006. Theoretical fecundity of the stock increased steadily from approximately 22.3 x 10^{12} eggs in 1999 to a maximum of over 36.5 x 10^{12} eggs in 2004 (Figure 14). Fecundity has decreased in each of the last two years, to approximately 31.0 x 10^{12} eggs in 2006. During this time period, recruitment (VPA output) has remained relatively stable between 28 million and 38 million individuals, except for 2004 where recruitment was estimated at only 17 million. The relationship between fecundity and recruitment is slightly negative, although this appears to be driven primarily by the 2004 data point (highest fecundity and lowest recruitment.

Discussion

Summer flounder biomass has increased substantially during the rebuilding period, yet managers continue to cut annual quotas in an attempt to reach established biomass reference points. This has led many managers and industry stakeholders to question the accuracy of the reference point targets. In recent months, evidence has been presented that summer flounder stocks may be experiencing changes in life history parameters, such as size at age and sex ratios. In addition, there have been implications that management measures themselves are impeding stock rebuilding by selectively harvesting larger individuals which are primarily female. This paper was undertaken to evaluate certain life history parameters and the implications they have on stock rebuilding.

Dery 1988 found males reached a maximum age of 7 years and females 12 years. This is generally consistent with maximum ages observed in NEFSC trawl surveys from 1992 to 2000. Since then, maximum ages of both males and females captured in the NEFSC trawl surveys have approximately doubled, likely as a result of reduced fishing mortality allowing fish to survive to older ages. Trawl data indicate that maximum ages of 12 for males and 15 for females may be more appropriate. As maximum ages for both sexes were observed in recent years, additional years of reduced fishing pressure may result in even older maximum ages. In addition, maximum ages may be confounded with survey catchability at size.

As identified by Terceiro (pers. comm.) length and weight at age do appear to have decreased in recent years. For males, decreases in length at age are not yet statistically significant, but may become so if the trend continues. For females, significant decreases in length at age have been observed for ages 5 and older. Although length:weight relationships have not changed, decreased length at age results in lower weight at age, which may result in slower than anticipated rebuilding rates.

In recent months, many fishermen have expressed concern regarding the finding of the NEAMAP trawl survey that most fluke greater than 41 cm (16”) are female. These findings are not new (*e.g.* Murawski and Figley 1977, Morse 1981), but this sexual dimorphism has greater implications for management and stock rebuilding as minimum size limits increase in an effort to reduce harvest. There does appear to be a general decline in the ratio of females to males observed in the trawl survey. However, for many ages this decline has been observed over 15 years, much longer than states have required large minimum sizes.

Natural mortality for summer flounder is generally approximated as $M = 0.2$ based on longevity information. Because summer flounder males and females appear to have different maximum ages, the sex ratio of the population could affect the overall stock natural mortality rate. The shift in sex ratio towards more males in recent years has led to a slight increase in natural mortality for the stock, but the increase does not appear substantial enough to affect rebuilding. However, estimates based on current data indicate that $M = 0.22$ might be a more appropriate estimate of overall natural mortality. A higher natural mortality rate would result in a higher F_{Target} and lower $\text{SSB}_{\text{Target}}$ than currently estimated. Although this analysis provides evidence for a higher M, additional analyses should be conducted. The Hoenig (1983) approximation used in this paper is often criticized as being inadequate (*e.g.* Pascual and Iribarne 1993, Hewitt and Hoenig 2005). In addition, maximum ages captured by trawl in a stock that is undergoing rebuilding may be underestimated.

Morse (1981) found that length was the best indicator of fecundity in fluke. Changes in female length at age and management strategies directing effort to large females could affect fecundity of the stock. In general, however, increases in total abundance have outpaced any decreases in fecundity, resulting in theoretical stock fecundity increasing more than 50% from 1999 to 2004. Fecundity declined in 2005 and 2006, coincident with slower stock growth. However, additional years of data are necessary to determine if there is a causal relationship.

Conclusions

Review of NEFSC trawl survey data do indicate that certain life history parameters have changed since 1992. Length at age has decreased significantly for older females. Maximum ages have approximately doubled since 2000. Sex ratios have shifted towards higher proportions of males. Natural mortality based on longevity and sex ratio has increased slightly. Despite decreases in fecundity at age, overall theoretical stock fecundity was higher in 2006 than in 1999. The implications of these patterns in biological parameters should be reviewed and considered when evaluating potential management strategies for stock rebuilding.

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Table 1. Sample size by age and year from the winter survey. Cells in bold italics indicate the years and ages used in the age:length analysis. A) Males, B) Females

A)	**Age**							
Year	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8+**
1992	150	75	14	1				
1993	113	144	5		1			
1994	102	185	19	6				
1995	92	155	3	1				
1996	229	145	18	2				
1997	106	152	27	22	4			
1998	67	92	71	7	2			1
1999	***46***	***161***	***101***	***15***	6			
2000	***18***	***164***	***122***	***72***	13	5	1	2
2001	***70***	***186***	***160***	***81***	23	10		2
2002	***75***	***239***	***172***	***75***	17	6	1	1
2003	***127***	***161***	***117***	***45***	12	3	1	1
2004	***51***	***221***	***112***	***46***	17	7	3	3
2005	***76***	***127***	***77***	***38***	19	8	2	2
2006	***72***	***148***	***78***	***50***	22	9	5	5

B)	**Age**							
Year	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8+**
1992	138	175	17	3	1	3		
1993	88	242	30	5	1	2		
1994	67	285	63	22			1	
1995	145	195	28	3				
1996	221	263	51	10	2			
1997	140	247	69	23	12	4		
1998	46	133	140	62	16	2		
1999	***48***	***135***	***151***	***92***	***35***	9	5	3
2000	***24***	***155***	***176***	***169***	***86***	18	10	3
2001	***113***	***149***	***279***	***146***	***74***	43	12	10
2002	***101***	***273***	***201***	***148***	***94***	43	14	4
2003	***83***	***145***	***134***	***99***	***59***	28	24	15
2004	***55***	***201***	***166***	***110***	***51***	45	24	31
2005	***45***	***89***	***103***	***54***	***37***	21	13	25
2006	***46***	***179***	***102***	***89***	***72***	36	18	43

Table 2. Results of mean length (cm) at age.

			Year							
Sex	**Age**		**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
Males	1	**Mean**	27.15	27.67	28.20	28.91	29.83	28.53	27.66	29.75
Males	1	**Std Dev**	3.47	2.22	2.39	2.96	3.39	2.79	2.91	3.54
Males	2	**Mean**	36.36	34.37	36.18	36.85	37.64	36.62	36.42	34.99
Males	2	**Std Dev**	3.30	2.56	2.91	2.79	3.05	3.09	3.16	2.91
Males	3	**Mean**	42.27	39.98	41.11	42.94	44.01	42.59	42.14	39.86
Males	3	**Std Dev**	2.98	2.95	3.00	2.93	3.39	2.90	2.90	3.52
Males	4	**Mean**	47.47	45.74	46.99	48.19	48.51	47.72	45.82	44.36
Males	4	**Std Dev**	3.64	3.18	3.21	3.36	3.45	2.79	3.14	3.08
Females	1	**Mean**	28.98	28.29	28.27	30.00	31.27	28.84	28.09	29.83
Females	1	**Std Dev**	3.18	2.93	2.83	3.33	3.16	3.30	2.98	3.97
Females	2	**Mean**	38.78	37.51	38.79	40.24	41.12	40.32	39.02	38.94
Females	2	**Std Dev**	3.58	4.18	3.76	3.35	3.48	3.52	3.50	3.40
Females	3	**Mean**	46.97	44.23	46.19	48.10	48.94	47.49	46.27	43.34
Females	3	**Std Dev**	2.87	4.11	3.79	3.94	3.66	3.08	3.28	4.13
Females	4	**Mean**	53.10	52.41	54.47	54.61	55.58	53.75	52.09	49.52
Females	4	**Std Dev**	3.03	3.70	4.29	3.65	3.63	3.38	3.12	3.76
Females	5	**Mean**	60.49	57.98	59.49	60.30	58.59	57.65	56.95	53.32
Females	5	**Std Dev**	3.74	3.25	4.16	3.57	4.60	3.51	3.12	3.01

Table 3. Regression results for the slope of mean length at age over time. Rows in bold italics are significant at 0.05 level.

Sex	Age	RMSE	Estimate	Std Err	T value	P Value	Lo 95 CI	Up 95 CI
Male	1	0.8577	0.2388	0.1324	1.8041	0.1213	-0.0851	0.5626
Male	2	1.1190	0.0334	0.1727	0.1936	0.8529	-0.3891	0.4559
Male	3	1.5629	-0.0065	0.2412	-0.0270	0.9794	-0.5966	0.5836
Male	4	1.4199	-0.2242	0.2191	-1.0234	0.3456	-0.7603	0.3119
Female	1	1.1565	0.0936	0.1785	0.5247	0.6186	-0.3430	0.5303
Female	2	1.1513	0.1691	0.1776	0.9521	0.3778	-0.2656	0.6038
Female	3	2.0131	-0.1241	0.3106	-0.3995	0.7034	-0.8842	0.6360
Female	4	1.8421	-0.3315	0.2842	-1.1663	0.2878	-1.0270	0.3640
Female	***5***	***1.5172***	***-0.7445***	***0.2341***	***-3.1803***	***0.0191***	***-1.3174***	***-0.1717***

Table 4. Results of von Bertalanffy growth analysis using bootstrap data for males.
A) Parameter estimates, B) Predicted length at age. Lengths are in cm.

A)

		Year							
Param		**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
L_inf	**Mean**	57.69	105879.36	73.02	69.65	66.93	66.29	52.88	99089.26
L_inf	**Std Err**	0.24	15286.72	0.79	0.31	0.33	0.32	0.10	13789.90
k	**Mean**	0.37	0.07	0.19	0.22	0.25	0.25	0.43	0.08
k	**Std Err**	3.69E-03	2.59E-03	2.42E-03	2.02E-03	2.44E-03	2.51E-03	2.71E-03	2.87E-03
t0	**Mean**	-0.82	-2.87	-1.77	-1.51	-1.45	-1.40	-0.73	-3.67
t0	**Std Err**	1.15E-02	3.30E-02	1.67E-02	1.14E-02	1.22E-02	1.34E-02	7.46E-03	4.30E-02

B)

		Year							
Age		**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
0	**Mean**	14.17	21.13	19.74	19.15	19.62	18.49	14.06	23.98
0	**Std Err**	0.10	0.06	0.05	0.05	0.05	0.06	0.07	0.04
1	**Mean**	27.26	27.95	28.53	28.95	29.80	28.66	27.67	29.75
1	**Std Err**	0.02	0.02	0.02	0.01	0.01	0.02	0.02	0.02
2	**Mean**	36.26	34.27	35.74	36.79	37.70	36.56	36.45	35.03
2	**Std Err**	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
3	**Mean**	42.49	40.14	41.67	43.06	43.84	42.73	42.13	39.88
3	**Std Err**	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
4	**Mean**	46.83	45.61	46.56	48.09	48.64	47.56	45.82	44.35
4	**Std Err**	0.03	0.01	0.01	0.01	0.02	0.02	0.02	0.02
5	**Mean**	49.88	50.73	50.61	52.13	52.39	51.35	48.23	48.50
5	**Std Err**	0.06	0.04	0.03	0.03	0.04	0.04	0.03	0.04
6	**Mean**	52.04	55.53	53.97	55.39	55.34	54.34	49.80	52.35
6	**Std Err**	0.08	0.07	0.06	0.05	0.06	0.06	0.05	0.07
7	**Mean**	53.57	60.05	56.77	58.01	57.66	56.70	50.84	55.95
7	**Std Err**	0.11	0.11	0.09	0.07	0.09	0.08	0.06	0.11
8	**Mean**	54.66	64.31	59.10	60.14	59.49	58.57	51.52	59.32
8	**Std Err**	0.13	0.16	0.11	0.09	0.11	0.11	0.07	0.16
9	**Mean**	55.45	68.35	61.06	61.86	60.94	60.06	51.97	62.49
9	**Std Err**	0.15	0.21	0.14	0.12	0.13	0.13	0.08	0.21
10	**Mean**	56.03	72.18	62.70	63.26	62.09	61.24	52.27	65.48
10	**Std Err**	0.16	0.27	0.17	0.14	0.15	0.15	0.08	0.27

Table 5. Regression results for the slope of male predicted length at age over time.

Age	RMSE	Estimate	Std Err	T value	P Value	Lo 95 CI	Up 95 CI
0	3.4782	0.3580	0.5367	0.6671	0.5295	-0.9552	1.6713
1	0.8369	0.2059	0.1291	1.5940	0.1620	-0.1101	0.5219
2	1.1417	0.0678	0.1762	0.3851	0.7135	-0.3632	0.4989
3	1.4866	-0.0515	0.2294	-0.2243	0.8300	-0.6128	0.5099
4	1.4686	-0.1516	0.2266	-0.6691	0.5283	-0.7061	0.4029
5	1.5410	-0.2343	0.2378	-0.9851	0.3626	-0.8161	0.3476
6	2.0495	-0.3016	0.3162	-0.9538	0.3770	-1.0754	0.4722
7	2.9216	-0.3561	0.4508	-0.7900	0.4596	-1.4592	0.7469
8	3.9818	-0.4000	0.6144	-0.6511	0.5391	-1.9034	1.1033
9	5.1309	-0.4353	0.7917	-0.5498	0.6023	-2.3725	1.5020
10	6.3189	-0.4635	0.9750	-0.4753	0.6514	-2.8493	1.9223

Table 6. Results of von Bertalanffy growth analysis using bootstrap data for females.
A) Parameter estimates, B) Predicted length at age. Lengths are in cm.

A)

		Year							
Param		**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
L_inf	**Mean**	98.94	175.38	95.32	83.70	72.92	68.16	70.01	68.25
L_inf	**Std Err**	0.55	21.38	0.35	0.19	0.13	0.09	0.15	0.22
k	**Mean**	0.15	0.09	0.16	0.21	0.28	0.33	0.29	0.24
k	**Std Err**	1.39E-03	1.60E-03	1.07E-03	9.93E-04	1.31E-03	1.36E-03	1.58E-03	1.90E-03
t0	**Mean**	-1.40	-1.87	-1.22	-1.17	-0.98	-0.70	-0.82	-1.58
t0	**Std Err**	9.69E-03	1.71E-02	6.70E-03	5.92E-03	5.94E-03	5.43E-03	6.54E-03	1.37E-02

B)

		Year							
Age		**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
0	**Mean**	18.21	19.38	16.81	17.86	17.46	13.87	14.44	20.67
0	**Std Err**	0.05	0.07	0.04	0.04	0.05	0.06	0.06	0.07
1	**Mean**	29.22	28.68	28.42	30.13	31.08	29.11	28.31	30.55
1	**Std Err**	0.02	0.03	0.02	0.01	0.02	0.02	0.02	0.02
2	**Mean**	38.67	37.15	38.28	40.10	41.33	40.05	38.68	38.32
2	**Std Err**	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
3	**Mean**	46.79	44.85	46.66	48.19	49.05	47.90	46.44	44.44
3	**Std Err**	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
4	**Mean**	53.77	51.88	53.79	54.76	54.86	53.55	52.25	49.28
4	**Std Err**	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
5	**Mean**	59.78	58.29	59.85	60.11	59.25	57.61	56.62	53.10
5	**Std Err**	0.02	0.02	0.02	0.01	0.02	0.02	0.02	0.02
6	**Mean**	64.96	64.15	65.01	64.46	62.56	60.54	59.90	56.13
6	**Std Err**	0.04	0.04	0.03	0.02	0.03	0.03	0.04	0.03
7	**Mean**	69.42	69.52	69.40	68.00	65.07	62.64	62.36	58.54
7	**Std Err**	0.06	0.07	0.05	0.04	0.04	0.04	0.05	0.05
8	**Mean**	73.27	74.43	73.15	70.88	66.96	64.17	64.22	60.45
8	**Std Err**	0.09	0.10	0.07	0.05	0.05	0.05	0.06	0.06
9	**Mean**	76.60	78.94	76.34	73.22	68.39	65.26	65.62	61.98
9	**Std Err**	0.11	0.14	0.09	0.06	0.06	0.06	0.08	0.08
10	**Mean**	79.48	83.08	79.06	75.14	69.48	66.06	66.68	63.19
10	**Std Err**	0.14	0.18	0.11	0.08	0.07	0.06	0.09	0.10

Table 7. Regression results for the slope of female predicted length at age over time.
Rows in bold italics are significant at the 0.05 level.

Age	RMSE	Estimate	Std Err	T value	P Value	Lo 95 CI	Up 95 CI
0	2.4271	-0.1979	0.3745	-0.5284	0.6162	-1.1143	0.7185
1	1.0632	0.1244	0.1641	0.7584	0.4770	-0.2770	0.5258
2	1.3838	0.1393	0.2135	0.6525	0.5383	-0.3832	0.6618
3	1.7126	-0.0470	0.2643	-0.1778	0.8648	-0.6936	0.5997
4	1.7485	-0.3597	0.2698	-1.3330	0.2309	-1.0198	0.3005
5	***1.5973***	***-0.7464***	***0.2465***	***-3.0283***	***0.0232***	***-1.3494***	***-0.1433***
6	***1.4044***	***-1.1709***	***0.2167***	***-5.4032***	***0.0017***	***-1.7012***	***-0.6407***
7	***1.3408***	***-1.6087***	***0.2069***	***-7.7758***	***0.0002***	***-2.1149***	***-1.1025***
8	***1.5285***	***-2.0433***	***0.2359***	***-8.6636***	***0.0001***	***-2.6204***	***-1.4662***
9	***1.9350***	***-2.4642***	***0.2986***	***-8.2531***	***0.0002***	***-3.1948***	***-1.7336***
10	***2.4627***	***-2.8649***	***0.3800***	***-7.5389***	***0.0003***	***-3.7947***	***-1.9350***

Table 8. **Sample size of weights by age and year from the winter survey. Cells in bold italics indicate the years and ages used in the age:length analysis. A) Males, B) Females**

A)	**AGE**							
Year	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8+**
1992								
1993	113	144	5		1			0
1994	99	184	19	6				0
1995	92	155	3	1				0
1996	229	144	18	2				0
1997	106	151	26	22	4			0
1998	67	92	71	7	2			1
1999	***46***	***159***	***101***	***15***	6			0
2000	***18***	***164***	***122***	***72***	13	5	1	2
2001	***70***	***186***	***160***	***81***	23	10		2
2002	***75***	***239***	***172***	***75***	17	6	1	1
2003	***127***	***161***	***117***	***45***	12	3	1	1
2004	***51***	***221***	***112***	***46***	17	7	3	3
2005	***76***	***127***	***77***	***38***	19	8	2	2
2006	***72***	***148***	***78***	***50***	22	9	5	5

B)	**AGE**							
Year	**1**	**2**	**3**	**4**	**5**	**6**	**7**	**8+**
1992								
1993	88	242	30	5	1	2		0
1994	67	285	63	22			1	0
1995	141	191	28	3				0
1996	219	263	51	10	2			0
1997	140	246	69	23	12	4		0
1998	46	133	139	62	16	2		0
1999	***48***	***135***	***151***	***92***	***35***	9	5	3
2000	***24***	***155***	***176***	***169***	***86***	18	10	3
2001	***113***	***149***	***279***	***146***	***74***	43	12	10
2002	***101***	***272***	***201***	***148***	***94***	43	14	4
2003	***83***	***145***	***134***	***99***	***59***	28	24	15
2004	***55***	***201***	***166***	***110***	***51***	45	24	31
2005	***45***	***89***	***103***	***54***	***37***	21	13	25
2006	***46***	***179***	***102***	***89***	***72***	36	18	43

**Table 9. Results of length:weight analysis using bootstrap data for males.
A) Parameter estimates, B) Predicted length at age. Weights are in kg.**

A)

		Year							
Param		**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
a	**Mean**	5.27E-06	6.73E-06	3.61E-06	5.67E-06	4.10E-06	4.61E-06	3.25E-06	9.14E-06
a	**Std Err**	2.66E-08	2.98E-08	1.87E-08	2.09E-08	1.88E-08	2.46E-08	1.63E-08	4.81E-08
b	**Mean**	3.18	3.11	3.28	3.15	3.24	3.21	3.31	3.03
b	**Std Err**	1.35E-03	1.17E-03	1.38E-03	9.75E-04	1.20E-03	1.43E-03	1.35E-03	1.42E-03

B)

		Year							
Length (cm)		**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
10	**Mean**	0.01	0.01	0.01	0.01	0.01	0.01	0.01	0.01
10	**Std Err**	1.52E-05	1.49E-05	1.38E-05	1.17E-05	1.29E-05	1.55E-05	1.28E-05	1.93E-05
20	**Mean**	0.07	0.07	0.07	0.07	0.07	0.07	0.07	0.08
20	**Std Err**	7.17E-05	6.85E-05	7.12E-05	5.61E-05	6.59E-05	7.65E-05	6.68E-05	8.07E-05
30	**Mean**	0.26	0.26	0.25	0.25	0.25	0.25	0.25	0.27
30	**Std Err**	1.23E-04	1.20E-04	1.34E-04	1.03E-04	1.27E-04	1.39E-04	1.24E-04	1.26E-04
40	**Mean**	0.64	0.65	0.64	0.63	0.64	0.64	0.65	0.64
40	**Std Err**	1.11E-04	1.20E-04	1.37E-04	9.86E-05	1.35E-04	1.33E-04	1.27E-04	1.16E-04
50	**Mean**	1.30	1.30	1.32	1.27	1.31	1.31	1.35	1.26
50	**Std Err**	3.68E-04	3.07E-04	3.59E-04	1.95E-04	2.81E-04	3.62E-04	3.87E-04	4.26E-04
60	**Mean**	2.32	2.29	2.40	2.25	2.37	2.35	2.47	2.18
60	**Std Err**	1.17E-03	9.56E-04	1.17E-03	6.87E-04	9.26E-04	1.18E-03	1.24E-03	1.25E-03
70	**Mean**	3.78	3.69	3.98	3.66	3.91	3.85	4.12	3.48
70	**Std Err**	2.66E-03	2.17E-03	2.75E-03	1.64E-03	2.20E-03	2.75E-03	2.88E-03	2.73E-03
80	**Mean**	5.78	5.59	6.16	5.57	6.04	5.91	6.40	5.21
80	**Std Err**	5.09E-03	4.14E-03	5.36E-03	3.21E-03	4.33E-03	5.33E-03	5.60E-03	5.06E-03
90	**Mean**	8.40	8.07	9.07	8.07	8.84	8.63	9.46	7.44
90	**Std Err**	8.71E-03	7.06E-03	9.35E-03	5.56E-03	7.56E-03	9.22E-03	9.74E-03	8.46E-03

Table 10. Regression results for the slope of male predicted weight at length over time.

Length (cm)	RMSE	Estimate	Std Err	T value	P Value	Lo 95 CI	Up 95 CI
10	0.0011	4.00E-05	1.70E-04	0.2363	0.8211	-0.0004	0.0005
20	0.0049	1.40E-04	7.60E-04	0.1901	0.8555	-0.0017	0.0020
30	0.0077	2.10E-04	1.18E-03	0.1798	0.8633	-0.0027	0.0031
40	0.0067	1.40E-04	1.03E-03	0.1357	0.8965	-0.0024	0.0027
50	0.0328	-1.50E-04	5.06E-03	-0.0300	0.9771	-0.0125	0.0122
60	0.0985	-7.00E-04	1.52E-02	-0.0459	0.9649	-0.0379	0.0365
70	0.2176	-1.50E-03	3.36E-02	-0.0446	0.9659	-0.0837	0.0807
80	0.4086	-2.50E-03	6.31E-02	-0.0396	0.9697	-0.1568	0.1518
90	0.6919	-3.61E-03	1.07E-01	-0.0338	0.9741	-0.2649	0.2576

Table 11. **Results of length:weight analysis using bootstrap data for females. A) Parameter estimates, B) Predicted length at age. Weights are in kg.**

A)

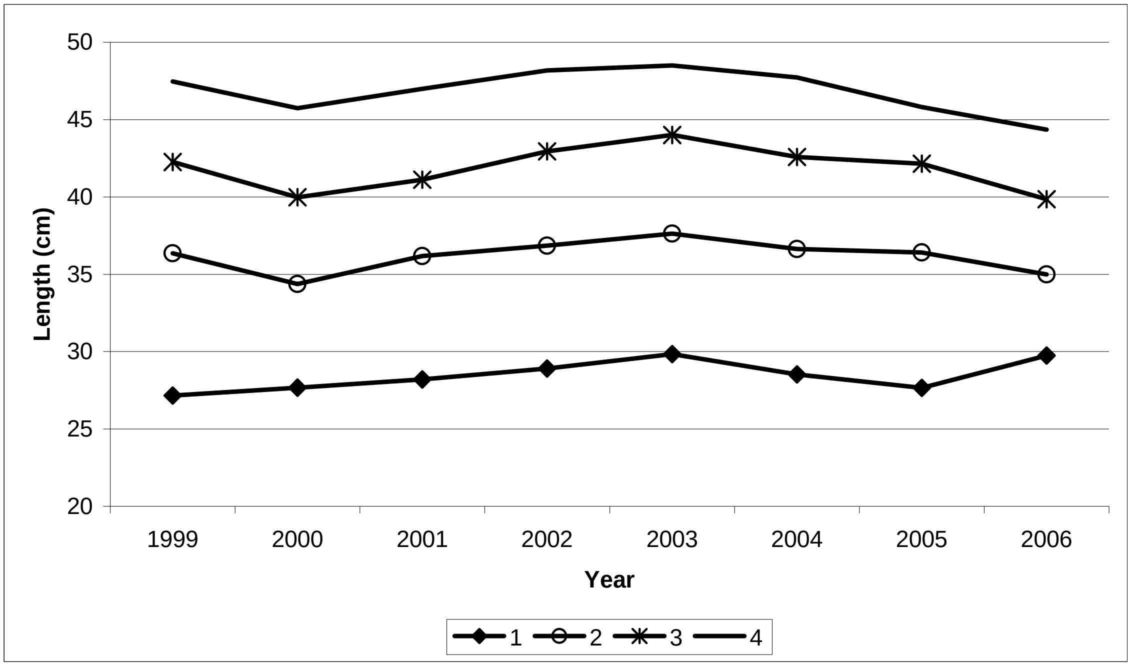
		Year							
Param		**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
a	**Mean**	2.65E-06	4.60E-06	2.84E-06	4.83E-06	4.00E-06	4.61E-06	3.24E-06	5.12E-06
a	**Std Err**	1.20E-08	2.20E-08	1.11E-08	1.80E-08	1.92E-08	2.17E-08	2.14E-08	3.85E-08
b	**Mean**	3.35	3.21	3.33	3.19	3.24	3.21	3.30	3.18
b	**Std Err**	1.14E-03	1.20E-03	9.68E-04	9.33E-04	1.20E-03	1.18E-03	1.67E-03	1.89E-03

B)

		Year							
Length (cm)		**1999**	**2000**	**2001**	**2002**	**2003**	**2004**	**2005**	**2006**
10	**Mean**	0.0060	0.0074	0.0061	0.0075	0.0069	0.0074	0.0064	0.0077
10	**Std Err**	1.14E-05	1.49E-05	1.01E-05	1.19E-05	1.42E-05	1.46E-05	1.77E-05	2.35E-05
20	**Mean**	0.0611	0.0682	0.0612	0.0680	0.0655	0.0681	0.0633	0.0696
20	**Std Err**	6.91E-05	8.15E-05	6.11E-05	6.48E-05	8.01E-05	7.91E-05	1.01E-04	1.21E-04
30	**Mean**	0.2381	0.2504	0.2361	0.2478	0.2437	0.2496	0.2413	0.2525
30	**Std Err**	1.62E-04	1.80E-04	1.44E-04	1.44E-04	1.81E-04	1.72E-04	2.23E-04	2.49E-04
40	**Mean**	0.6250	0.6299	0.6156	0.6203	0.6189	0.6278	0.6236	0.6304
40	**Std Err**	2.30E-04	2.44E-04	2.13E-04	2.01E-04	2.55E-04	2.30E-04	2.90E-04	2.99E-04
50	**Mean**	1.3212	1.2885	1.2948	1.2639	1.2756	1.2840	1.3027	1.2819
50	**Std Err**	2.33E-04	2.23E-04	2.19E-04	1.92E-04	2.44E-04	2.14E-04	2.58E-04	3.12E-04
60	**Mean**	2.4357	2.3124	2.3768	2.2609	2.3031	2.3037	2.3783	2.2896
60	**Std Err**	4.91E-04	4.46E-04	3.68E-04	3.26E-04	4.24E-04	4.85E-04	7.58E-04	9.96E-04
70	**Mean**	4.0852	3.7914	3.9723	3.6969	3.7957	3.7765	3.9564	3.7389
70	**Std Err**	1.39E-03	1.30E-03	1.04E-03	9.35E-04	1.24E-03	1.37E-03	2.17E-03	2.61E-03
80	**Mean**	6.3940	5.8186	6.1982	5.6602	5.8512	5.7948	6.1487	5.7181
80	**Std Err**	3.07E-03	2.86E-03	2.34E-03	2.08E-03	2.77E-03	2.95E-03	4.69E-03	5.36E-03
90	**Mean**	9.4927	8.4900	9.1770	8.2416	8.5711	8.4540	9.0718	8.3180
90	**Std Err**	5.77E-03	5.33E-03	4.46E-03	3.89E-03	5.22E-03	5.44E-03	8.66E-03	9.61E-03

Table 12. **Regression results for the slope of female predicted weight at length over time.**

Length (cm)	RMSE	Estimate	Std Err	T value	P Value	Lo 95 CI	Up 95 CI
10	0.0006	1.30E-04	1.00E-04	1.2622	0.2537	-0.0001	0.0004
20	0.0032	6.30E-04	5.00E-04	1.2579	0.2552	-0.0006	0.0019
30	0.0059	1.09E-03	9.00E-04	1.2101	0.2717	-0.0011	0.0033
40	0.0056	5.00E-04	8.70E-04	0.5741	0.5868	-0.0016	0.0026
50	0.0176	-2.67E-03	2.71E-03	-0.9873	0.3616	-0.0093	0.0040
60	0.0567	-1.04E-02	8.74E-03	-1.1845	0.2810	-0.0318	0.0110
70	0.1312	-2.49E-02	2.02E-02	-1.2280	0.2655	-0.0744	0.0247
80	0.2540	-4.88E-02	3.92E-02	-1.2453	0.2594	-0.1447	0.0471
90	0.4399	-8.52E-02	6.79E-02	-1.2546	0.2563	-0.2513	0.0809



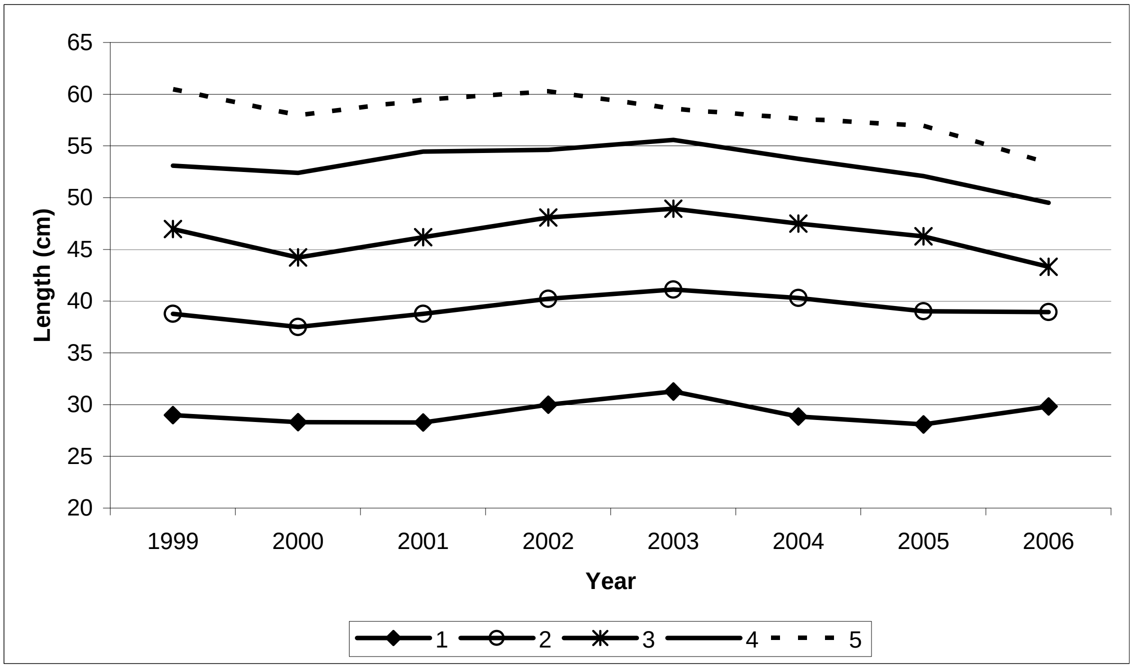


Figure 1. Mean length at age for males age 1 to 4 (top) and females age 1 to 5.

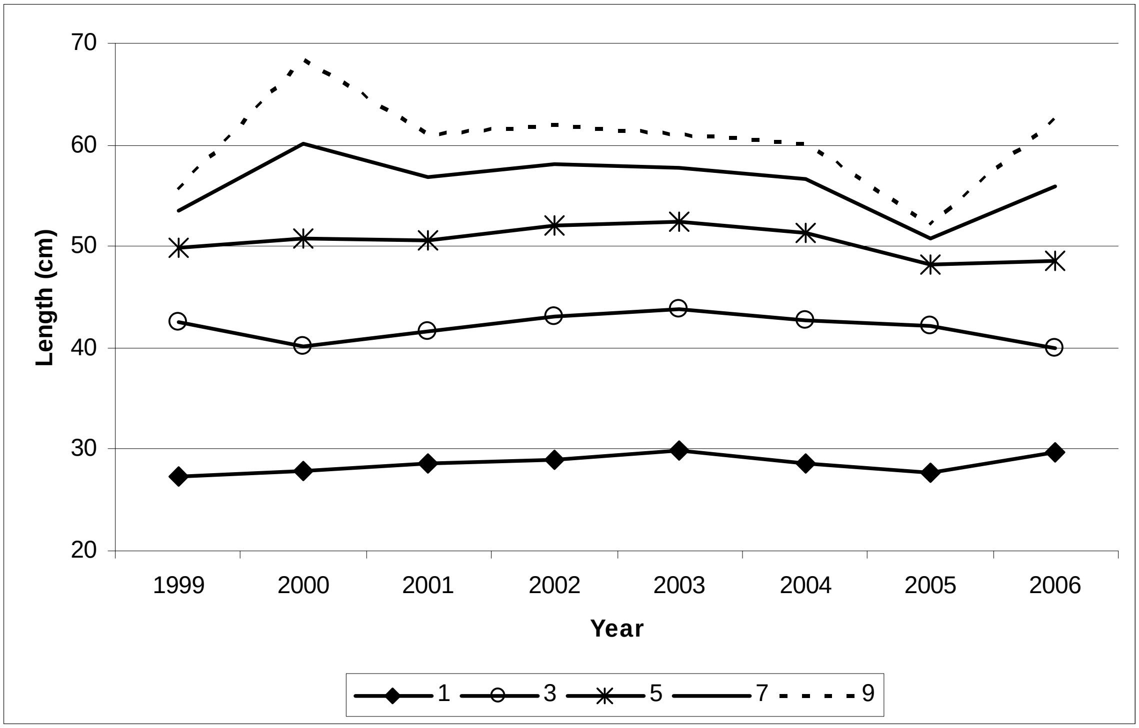


Figure 2. Mean predicted length at age for selected ages of males.

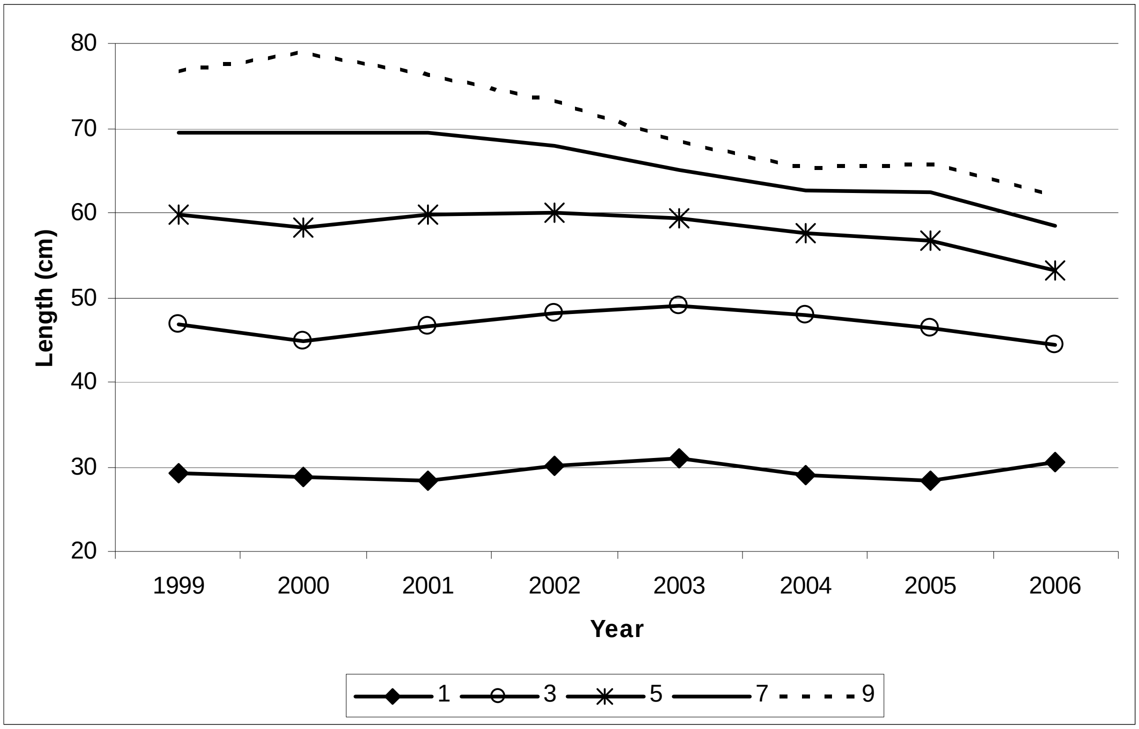


Figure 3. Mean predicted length at age for selected ages of females.

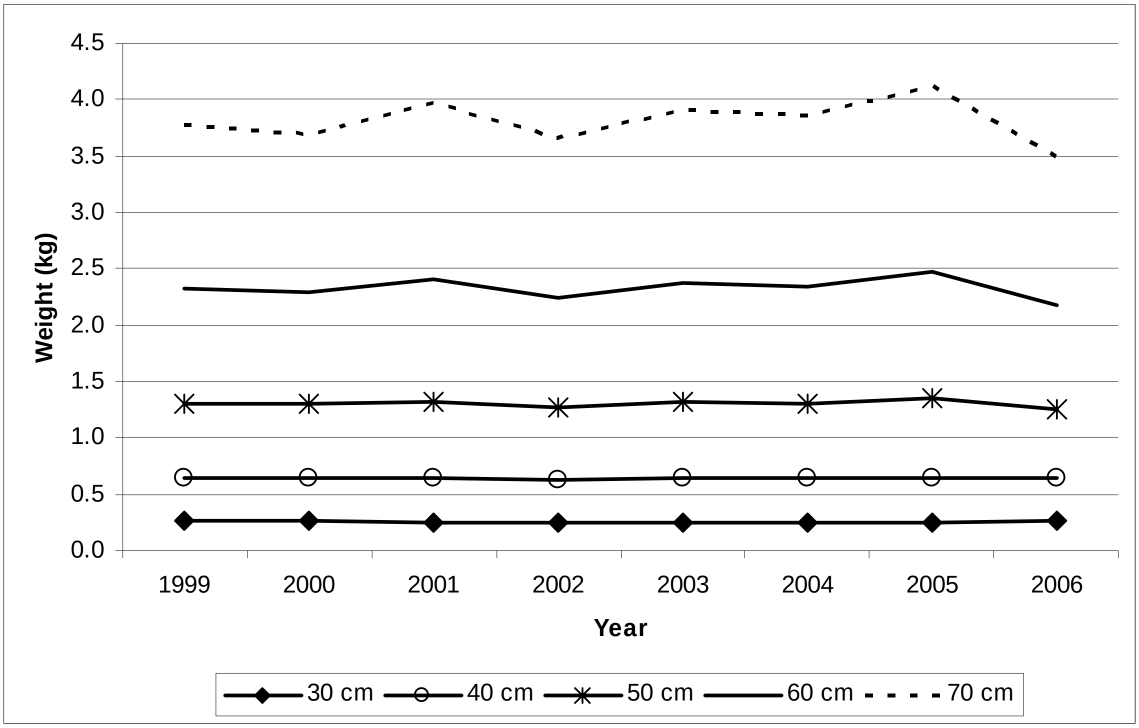


Figure 4. Mean predicted weight at length for selected lengths of males.

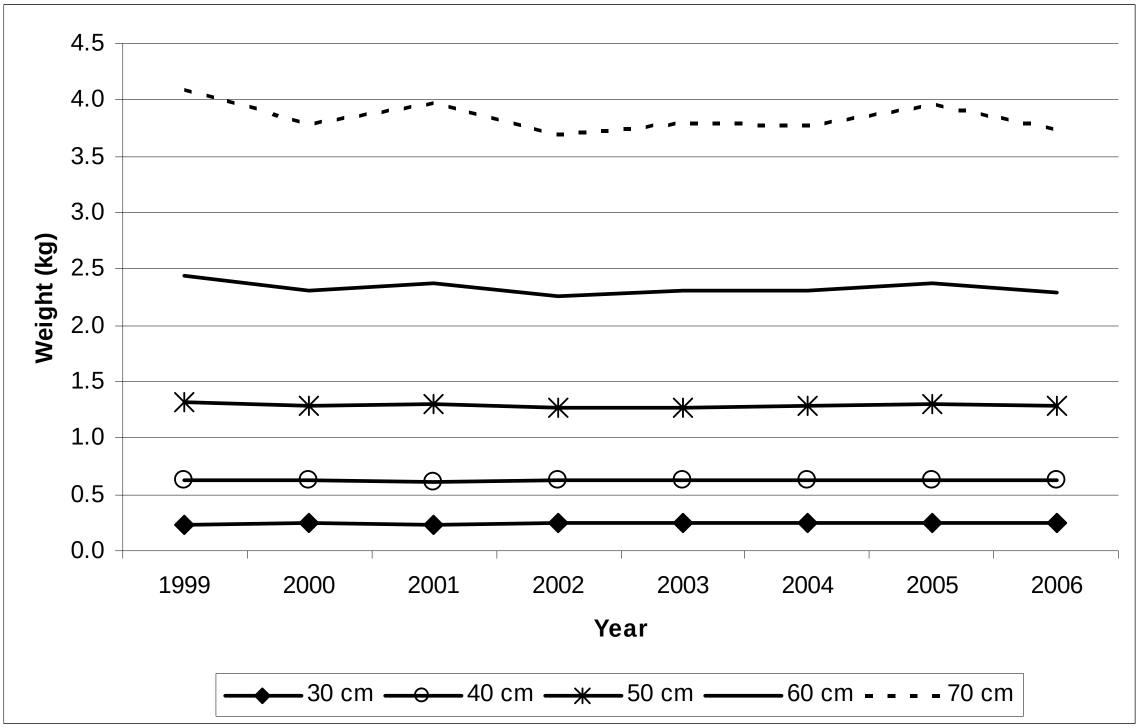


Figure 5. Mean predicted weight at length for selected lengths of females.

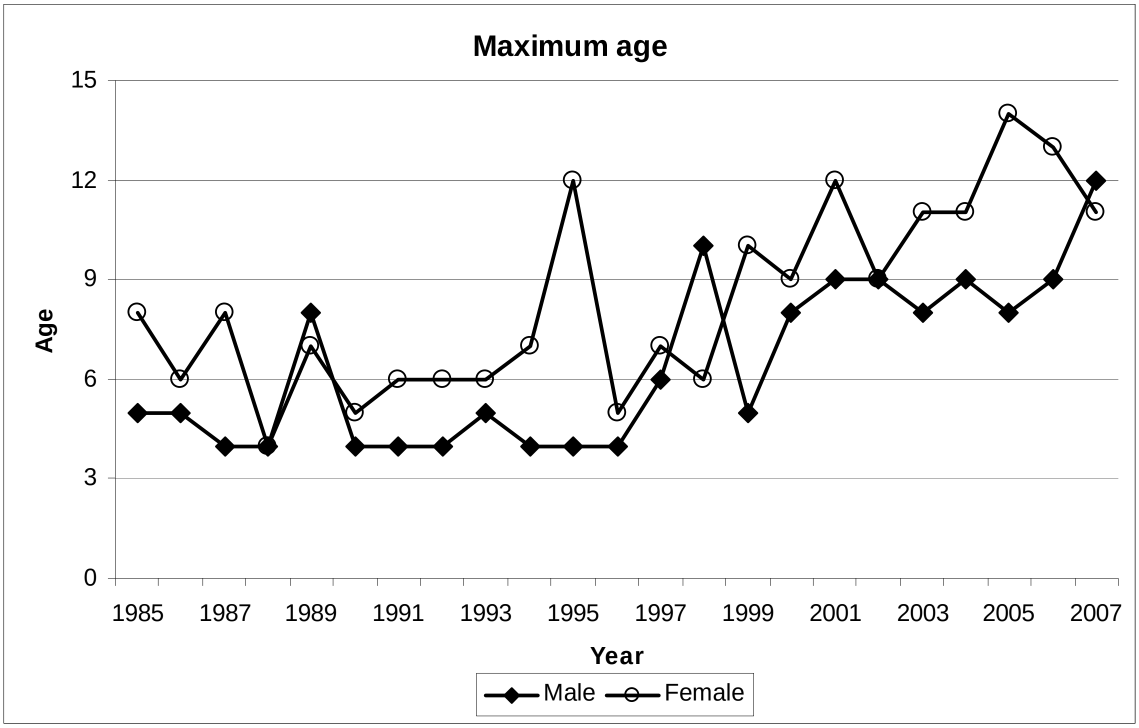


Figure 6. Observed maximum age by sex in NEFSC trawl surveys.

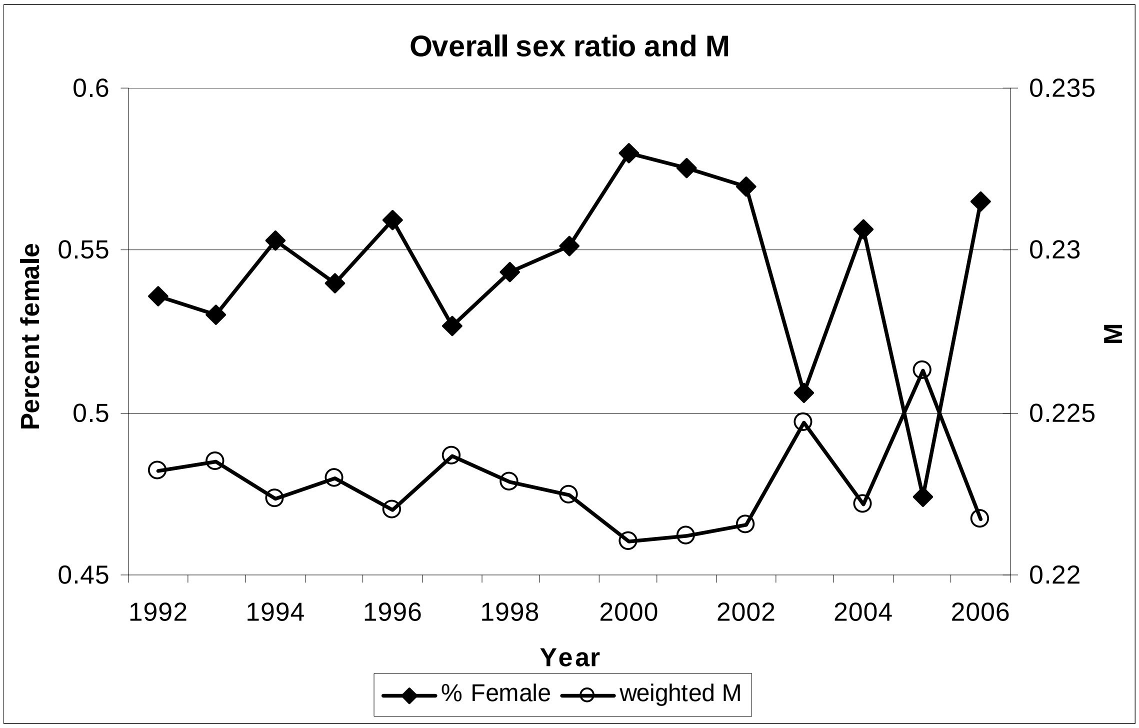


Figure 7. Sex ratio and natural mortality estimate by year across all ages.

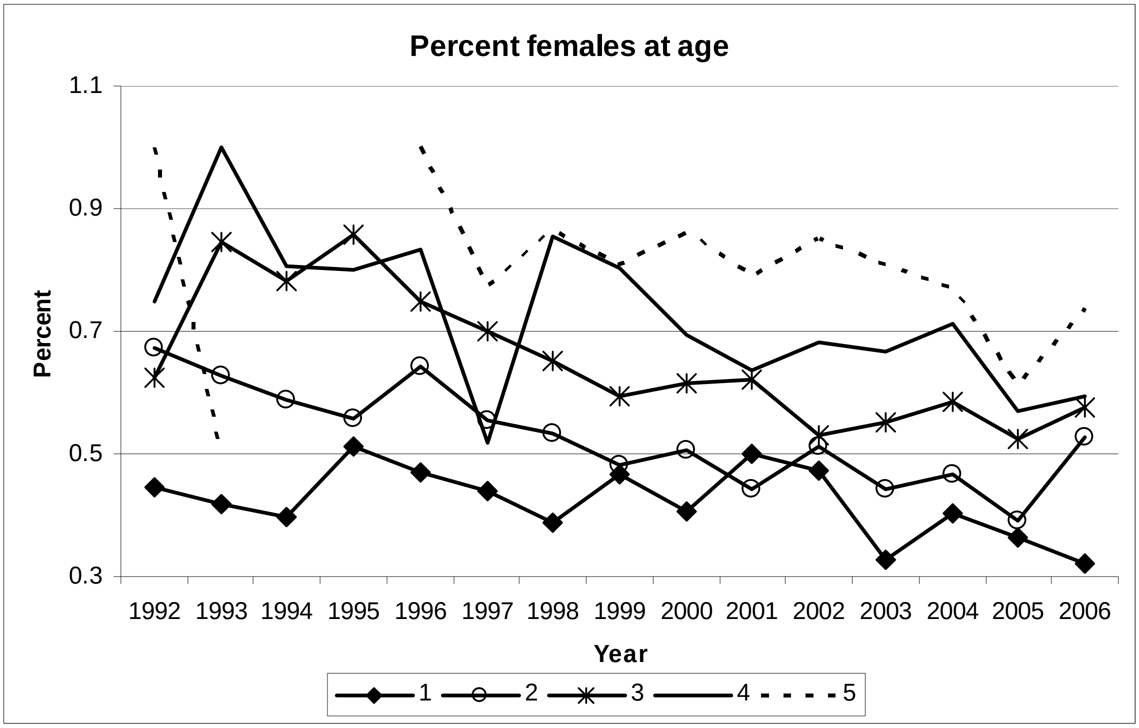


Figure 8. Percent female at age for selected ages.

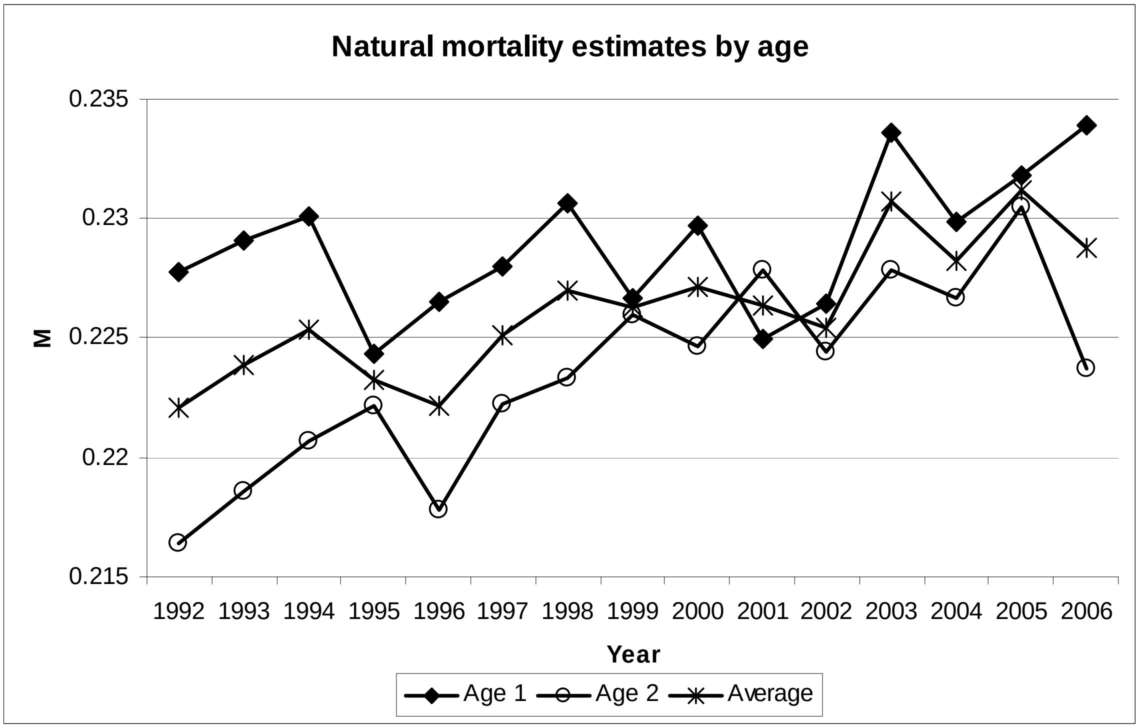


Figure 9. Natural mortality estimates by age for 1 and 2 year old fish

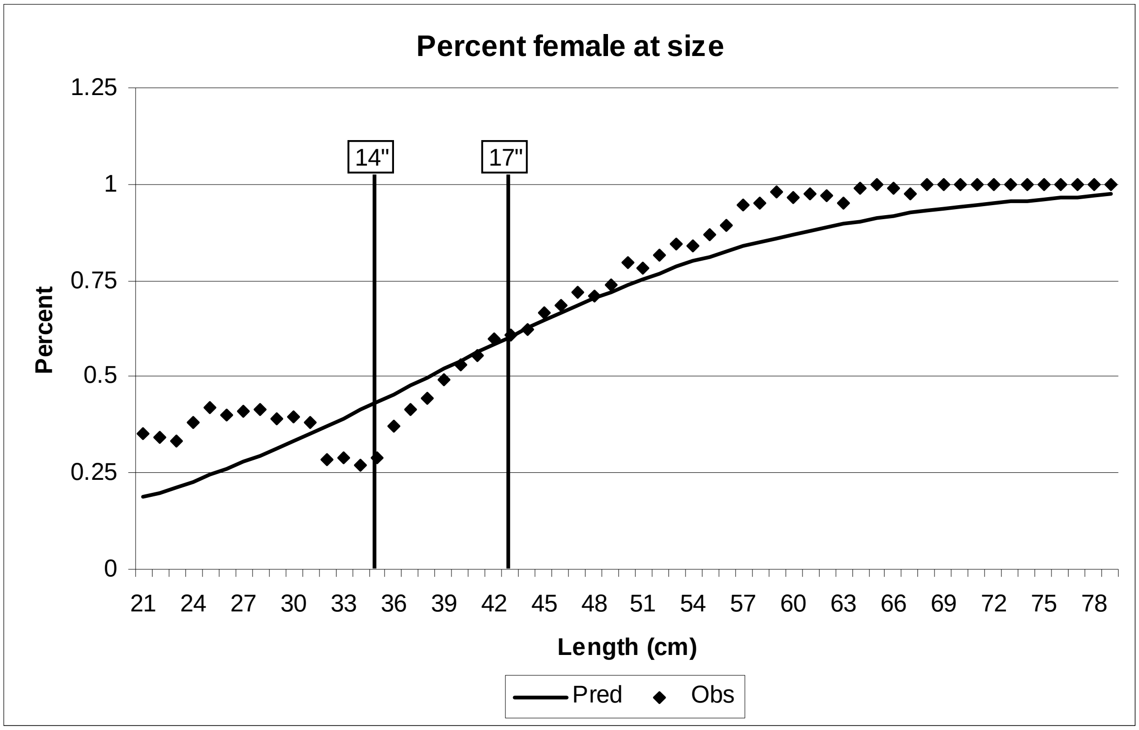


Figure 10. Logistic regression of percent female at size for all years combined.

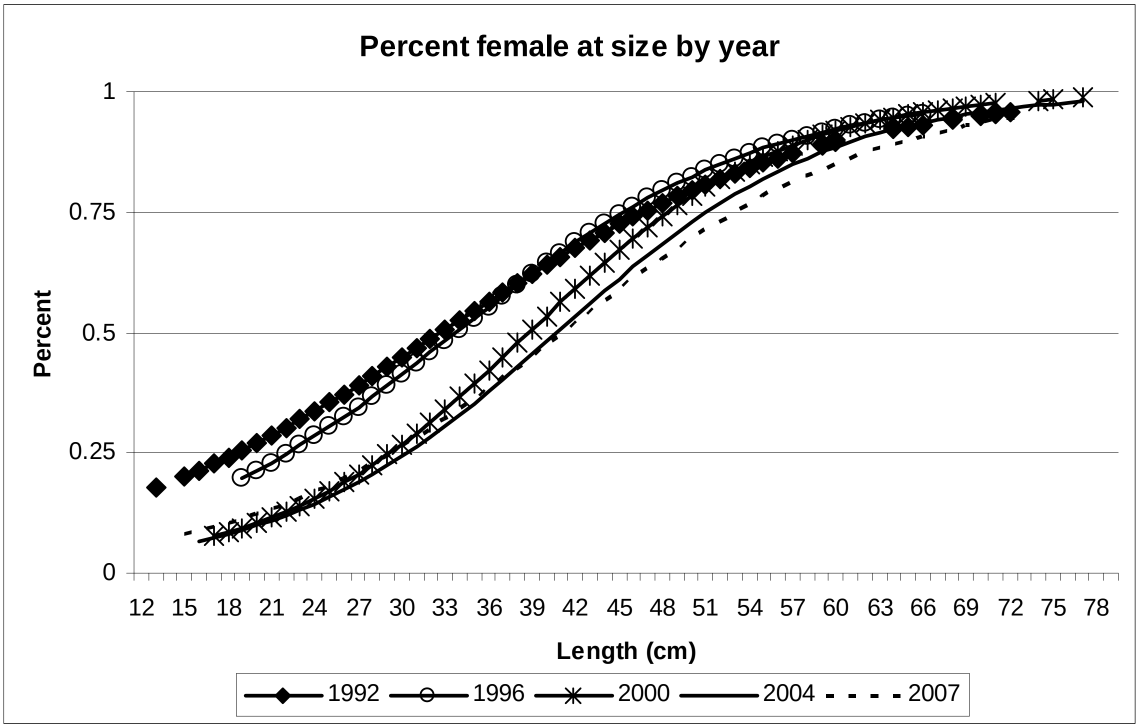


Figure 11. Logistic regression of percent female at size by year for selected years.

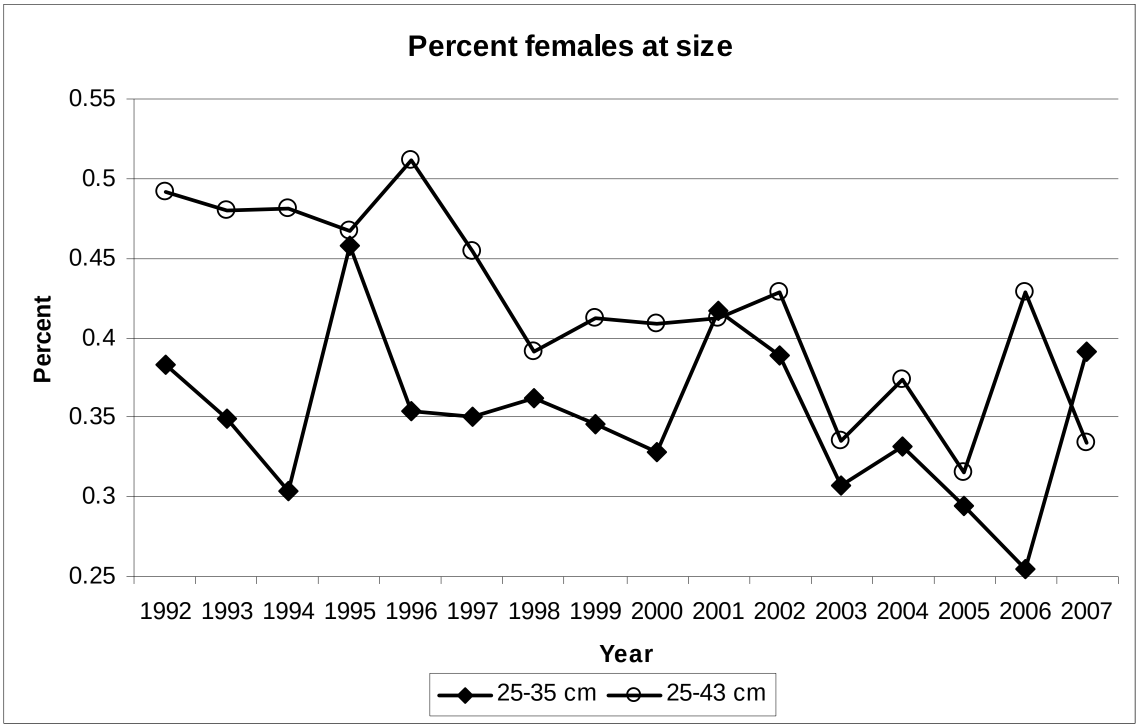


Figure 12. Percent female by year for two different size classes.

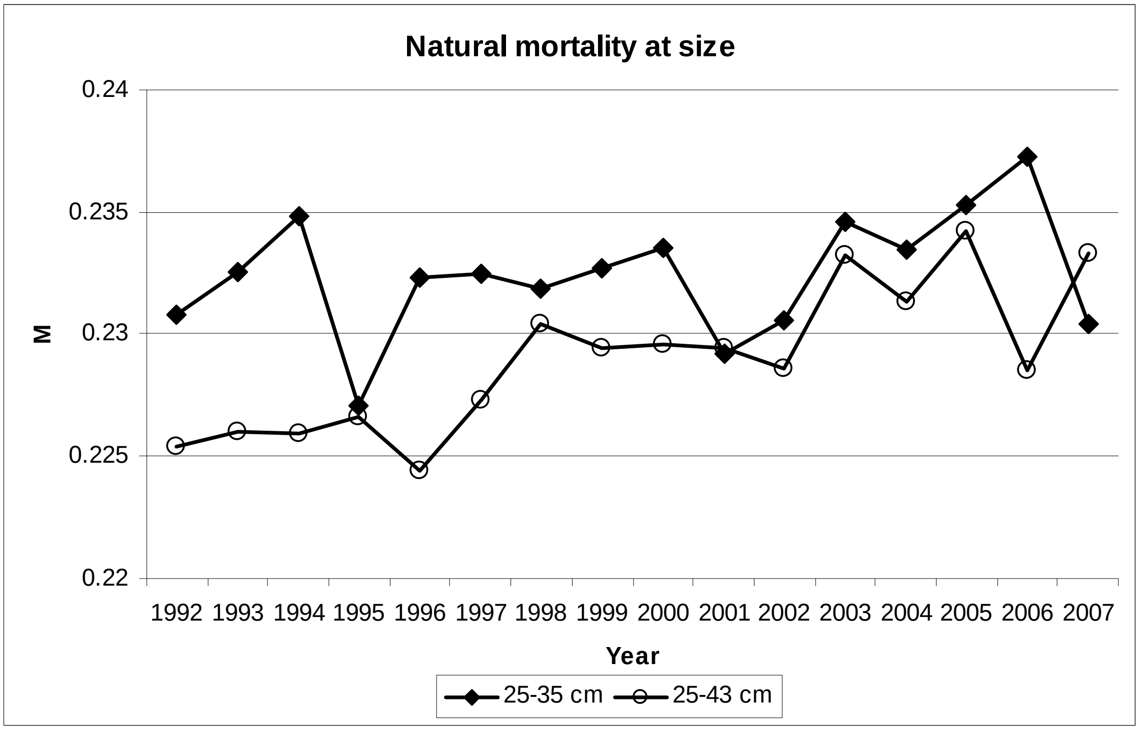


Figure 13. Natural mortality estimates for two different size groups.

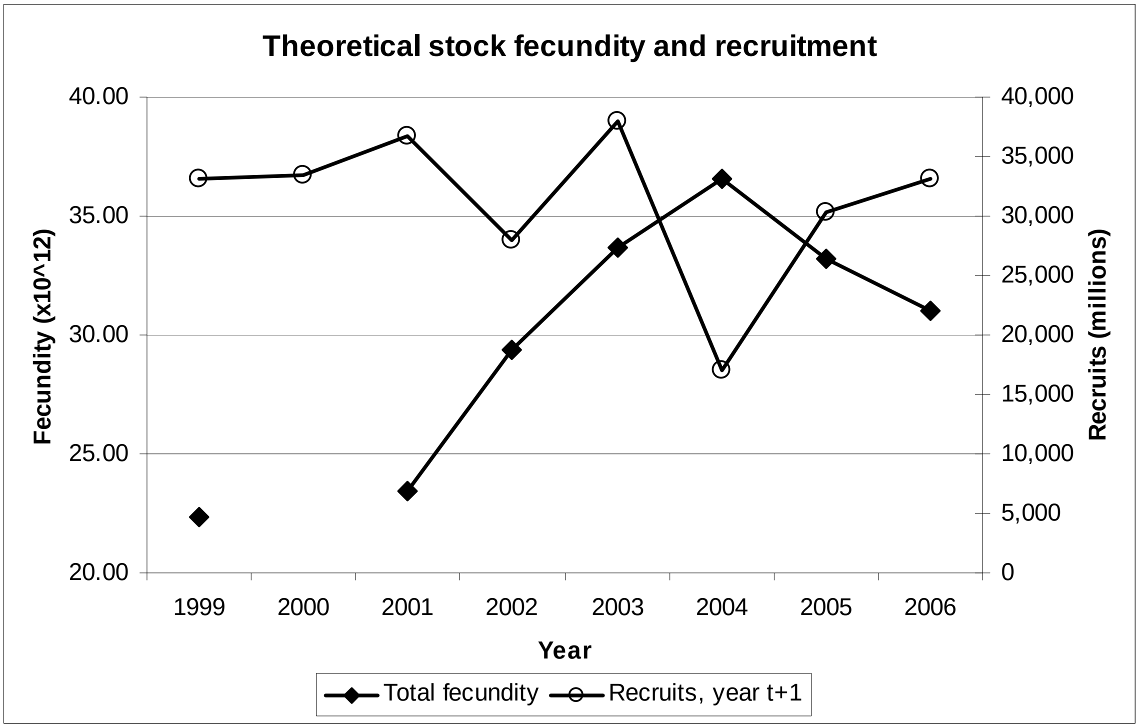


Figure 14. Overall fecundity and recruitment.

SAW 47 Working Paper 8 (TOR 3) – Natural Mortality
A Review of Natural Mortality of Summer Flounder
Rich Wong

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.

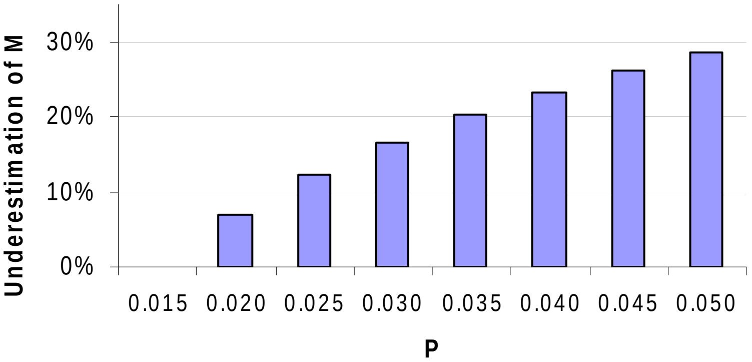


Figure 1. Underestimation of M relative to P = 1.5%.

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).

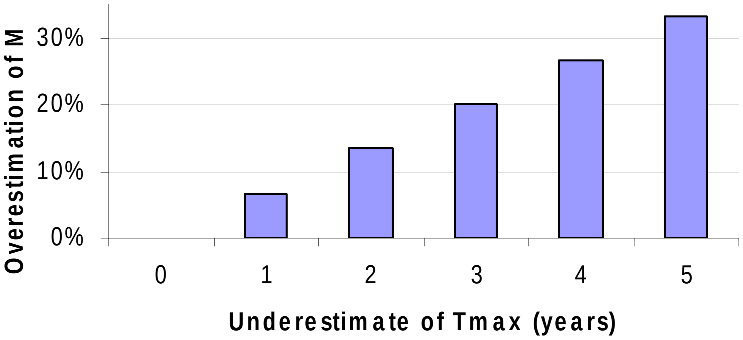


Figure 2. Effect of underestimating longevity by up to 5 years for summer flounder.

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).

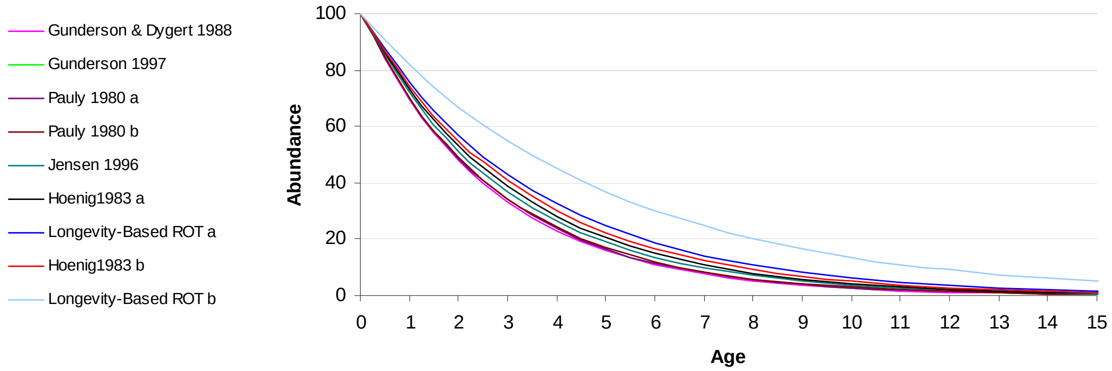


Figure 3. Survival curves from constant M estimates.

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(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).

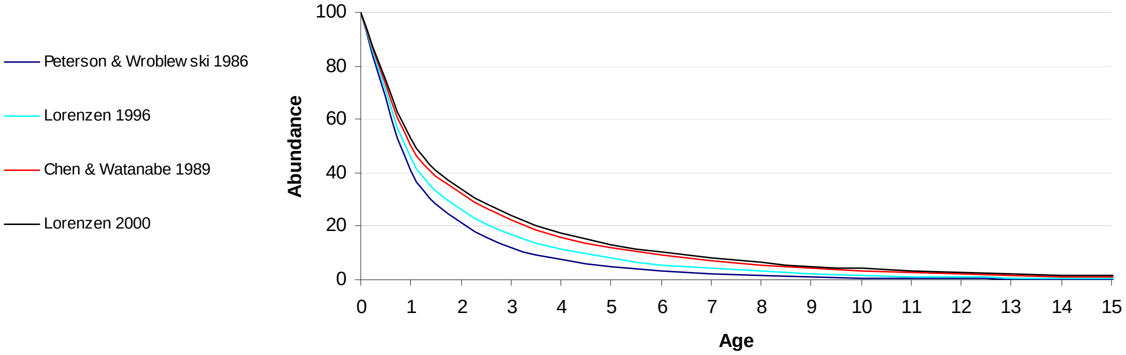


Figure 4. Survival curves from age-specific M estimates.

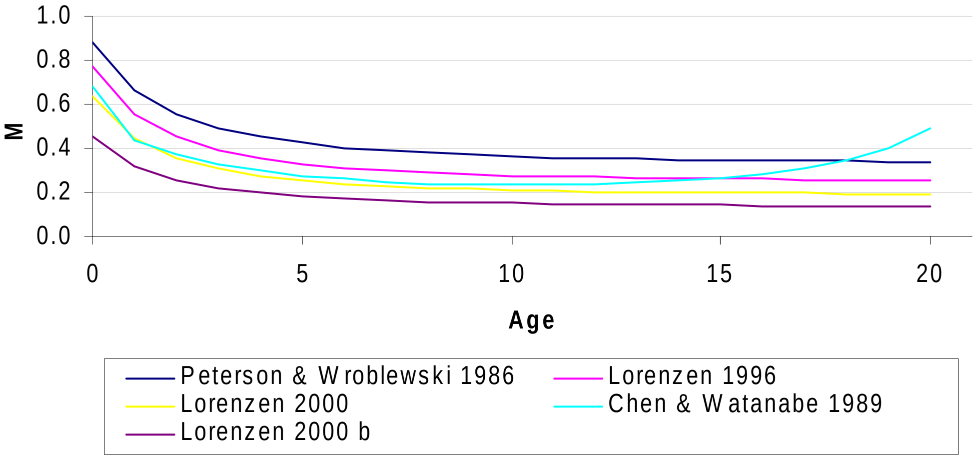


Figure 5. Age-specific M rates. Lorenzen 2000 is based on the 1.5% ROT, Lorenzen 2000 b is based on the 5% ROT.

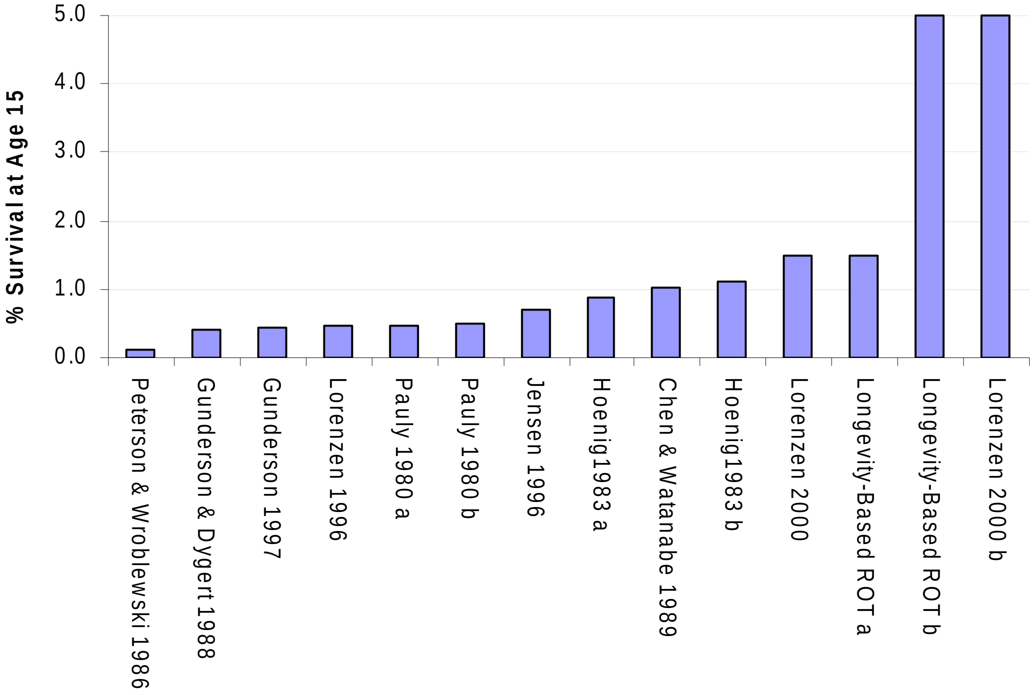


Figure 6. Percent survival at age = 15y.

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).

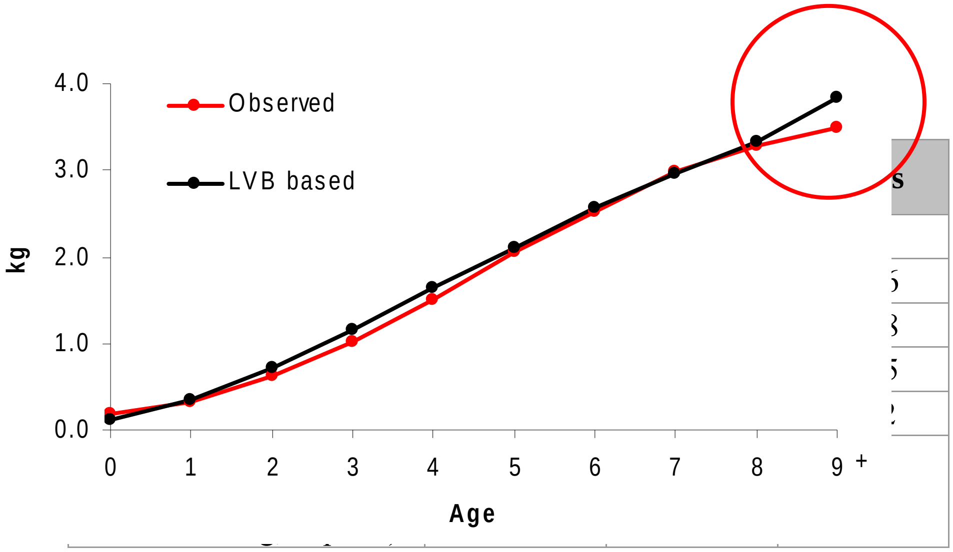


Figure 7. Observed mean weight-at-age from the NMFS trawl survey versus weight-at-age based on LVB length-at-age and L:W relationship.

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 *(10^ -3) * W^-0.25
K	0.207	0.259	0.268	Chen & Watanabe 1989	M1 = K/(1-EXP(-K*(t-t0))); early life stages
L_inf	76.95	73.97	61.15		M2 = K /(a0+a_1*(t-tm)+a_2*(t-tm)^2); senescence
T0	-1.24	-0.92	-1.32	Lorenzen 1996	M = 3.00*W^(-2.88)
L:W Parameter a	4.08E-06	3.68E-06	4.51E-06	Lorenzen 2000	M = Mr * (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.

	Lorenzen 2000			Lorenzen 1996			Chen & Watanabe 1989			Peterson & Wroblewski 1986		
Age	**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					

SAW 47 Working Paper 9 (TOR 3) – Analysis of Sex Ratios

Analysis of Trends in Sex Ratio, Implications for Natural Mortality, and Variation in Age-Length Keys in Summer Flounder

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Introduction

The analyses described herein use the biological database for summer flounder. The goals of these analyses are to answer the following questions to the extent permitted by this database.

1. Does information exist in the sex-ratio data that would support the need to construct a sex-explicit model for summer flounder?
2. Does information exist in the sex-ratio data that would support the need to utilize regionally-specific sex-at-age keys?
3. Does information exist in the sex-ratio data that would support a differential natural mortality rate for male and female summer flounder or a nonlinear whole-stock natural mortality rate?
4. Does variation exist in the relationship of size and age that would support the need to utilize regionally-specific age-length keys?

Sex Ratio as a Function of Age

Methods and Results

Sex ratio data for young-of-the-year are not available prior to 1982; consequently analyses of sex ratio focus on 1982-2007. Due to data limitations, and regional variability in sex ratios as discussed in a subsequent section, we exclude data from southern New England north and also from Cape Hatteras south in this set of analyses. We also exclude all age-year combinations where the number of sexed summer flounder is less than 20. For some analyses, we have collected the data into six year groups with the central four being half-decadal. Year group 1 contains data from 1982-1985 and year group six for 2006-2007.

Table 1 shows the sex ratio by year and age for summer flounder. The year-group averages are in Table 2. Perusal of Table 1 elucidates two general trends.

First, the young-of-the-year are dominantly male. A female-biased sex ratio for young-of-the-year summer flounder occurs only thrice in 26 years, a frequency significantly different than the expected 50:50 split (binomial test, $P < 0.0005$). Furthermore, the fraction male for young-of-the-year fish frequently exceeds 0.6; in fact a sex ratio at least this divergent from 50:50

occurs in 17 of 26 years. The average number of age-0 fish sexed per year is 51.5. Given this average, a 50:50 male:female ratio by chance when measured would return a ratio of 60:40 or greater 7.56% of the time. The occurrence rate observed, 17 in 26, would not be expected to occur by chance (binomial test, $P < 0.0001$). Thus, young-of-the-year summer flounder are consistently over-represented by male fish.

Table 1. The fraction of summer flounder that are male at age for ages and years where the total number of summer flounder sexed was ≥20.

Year	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age8
1982	0.707	0.519	0.369	0.133					
1983	0.583	0.466	0.361	0.296					
1984	0.576	0.589	0.304	0.250					
1985	0.674	0.484	0.378	0.263					
1986	0.645	0.590	0.500	0.056					
1987	0.714	0.622	0.474						
1988	0.714	0.783	0.357						
1989	0.574	0.586	0.227						
1990	0.662	0.548							
1991	0.739	0.617	0.476						
1992	0.614	0.534	0.291	0.200					
1993	0.750	0.578	0.348	0.103					
1994	0.436	0.580	0.412	0.135					
1995	0.622	0.451	0.401	0.115					
1996	0.579	0.528	0.302	0.250					
1997	0.667	0.563	0.440	0.281	0.167				
1998	0.574	0.602	0.477	0.303	0.102	0.083			
1999	0.720	0.524	0.502	0.396	0.171	0.045			
2000	0.543	0.571	0.485	0.381	0.297	0.123	0.083		
2001	0.682	0.484	0.529	0.350	0.291	0.171	0.194		
2002	0.737	0.523	0.492	0.474	0.284	0.128	0.069		
2003	0.633	0.644	0.569	0.422	0.331	0.190	0.040	0.062	
2004	0.655	0.582	0.562	0.440	0.260	0.193	0.103	0.059	
2005	0.808	0.635	0.638	0.454	0.397	0.341	0.190		
2006	0.429	0.683	0.515	0.426	0.305	0.197	0.108	0.125	0.062
2007	0.286	0.581	0.666	0.441	0.250	0.196	0.250	0.067	

The second observation is a consistent change in sex ratio with age (Figure 1), such that male frequencies over 0.5 occur only 8 times in 25 cases in age-2 fish and ratios above 0.3 occur only 6 times in age-4 fish. In fact, of the sex ratios accumulated by year-group in Table 2, only one age and year-group pair was characterized by a sex ratio not significantly different from 50:50 male-to-female. Thus, summer flounder are consistently characterized by biased sex ratios regardless of age or half-decadal period within the time series and the direction of bias changes with age.

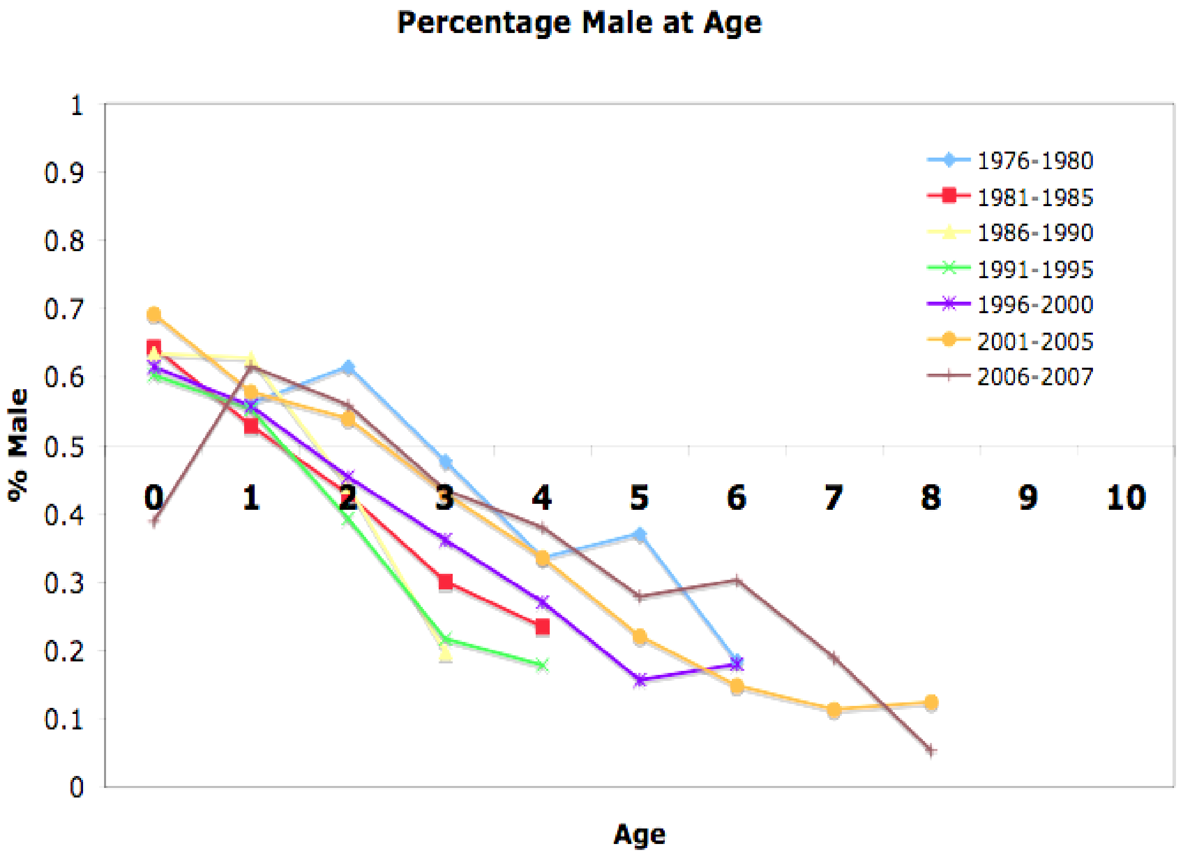


Figure 1. The percentage of the stock that is male by age, summarized by year-group.

Two additional observations are worthy of note. First, the three years where females predominate in age-0 fish include the last two years. This is unexpected from the time series record. However, the sex ratio for age-1 fish from the 2006 cohort conforms with typical age-1 sex ratios in being biased in favor of males. Thus, the aberrant 2006 young-of-the-year ratio is likely a sampling artifact. Second, the fraction of fish that are male at older age has increased over time, although remaining well below 0.5. This is particularly apparent for age-3 fish (Table 2). One explanation is that male fish are moderately more susceptible to the fishery at high fishing mortality rates, but two other explanations should first be considered. The same outcome would be obtained either if a reduction in natural mortality rate had occurred of if the originating sex ratio was biased to a greater degree in favor of males. Evidence in Table 1 does not strongly support the latter alternative. Evidence in a subsequent section does not support the penultimate option. The dispersion of males and females as the cohort ages, discussed in a subsequent section, might be interpreted to support the first alternative.

Table 2. The fraction of summer flounder that are male at age for ages and year groups where the total number of summer flounder sexed was ≥20. Parentheses indicate ratios not significantly different from an expected 50:50 split (binomial test, α = 0.05).

Year Group	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7	Age 8
1982-1985	0.644	(0.518)	0.357	0.222	0.167				
1986-1990	0.641	0.630	0.397	0.140					
1991-1995	0.601	0.543	0.370	0.133	0.074				
1996-2000	0.605	0.544	0.438	0.344	0.227	0.126	0.100		
2001-2005	0.690	0.568	0.550	0.423	0.302	0.192	0.117	0.071	0.158
2006-2007	0.386	0.621	0.588	0.436	0.277	0.197	0.164	0.097	0.042

Interpretation: Age-dependent Bias in Sex Ratio

A number of potential reasons exist for the male-dominated sex ratios seen in young-of-the-year summer flounder.

Females mature later than males. The observed females may under-represent the total number. The biological database records undifferentiated fish. Assigning all of these fish to the female sex, however, does not markedly change the data summarized in Table 2. Thus, maturity schedule cannot explain the male-dominated sex ratios observed for age-0 fish.

Young males may be more available to the survey. While this possibility cannot be excluded, the fact that females grow faster than males and that the male-biased sex ratios clearly are retained into age 2, albeit at diminishing intensity, suggest that availability is not an adequate explanation.

Protandry would produce the observed age-dependent sequence of sex ratios. Protandry, however, is not reported in flatfish, and would almost assuredly have been observed, were it to exist.

Biased sex ratios have been observed by others in summer flounder, however. Morse (1981) and Smith and Daiber (1977) found that younger, smaller fish were much more likely to be male and that this trend quickly reversed with increasing age. Morse (1981) offers that an initially male-dominated sex ratio is necessary to offset an apparently higher natural mortality rate in males, thus promoting a more nearly 1:1 sex ratio in the spawning stock.

The most viable explanation for biased sex ratios in young-of-the-year summer flounder is temperature-dependent sex determination. Temperature has been shown to influence sex ratios at the point of sexual differentiation in flatfish, not afterwards, and this influence of temperature seems to be a frequent characteristic of flounder species. For example, when barfin flounder, *Verasper moseri*, were reared at high temperatures (18°C for this species), all fish developed as males, whereas at 14°C, the sex ratio was close to 1:1 (Goto et al. 1999). Marbled sole, *Limanda yokohamae*, also show temperature-dependent sex determination; when the larvae were kept in 25°C water, the sex ratio was again strongly skewed towards males (Goto et al. 2000). Southern flounder, *Paralichthys lethostigma*, likewise develop a sex ratio skewed towards males when raised at higher (28°C) or lower (18°C) than optimal temperature, 23°C, which produces a 1:1 ratio (Luckenbach et al. 2003). Although little is known of the genetic determinants of sex, *Paralichthys olivaceus* uses an XX female/XY male system of genetic sex determination, yet high water temperatures (25-27.5°C) produce physiological males possessing an XX genotype.

Genetically determined males (XY) were never observed to develop into physiological females (Yamamoto 1999).

Among the flatfishes have been shown to exhibit temperature-dependent sex determination are two species of the same genus as summer flounder, the Japanese flounder or hirame, *Paralichthys olivaceus*,and the southern flounder, *Paralichthys lethostigma* (Yamamoto 1999; Luckenbach, et al.2003). Furthermore, in both cases, extreme temperatures result in a higher fraction of the young being male. This could potentially explain why a higher fraction of young-of-the-year summer flounder are found at the northern and southern edges of their range, as described subsequently.

Sex Ratio as a Function of Region and Depth

Methods and Results

For this analysis, we allocated strata to three depth zones (<25 fm; 25-50 fm; >50 fm). This division allocated sex-ratio data into approximately equivalent groups by data richness. Insufficient data were present to achieve a finer division of deeper-water strata. Strata were allocated to five regions: southern New England (we included Georges Bank strata in this grouping), the northern Mid-Atlantic Bight, Delmarva, and the strata south of Cape Hatteras. Finally, data were allocated to half-decadal year-groups: 1976-1980, 1981-1985, 1986-1990, 1991-1995, 1996-2000, 2001-2005, 2006-2007. We excluded all occurrences of age-year group, age-region, and age-depth combinations with sex ratios supported by a total count of males and females less than 30. ANOVAs were run by age using depth, year-group, and region as main effects. All interaction terms were included. Sex was implemented as a dependent variable by assigning a 0 to males and a 1 to females. Means, accordingly, were equivalent to the fraction female.

Table 3. Results of ANOVAs examining the impact of depth, region, and year-group on sex ratios at age. Blank cells indicate insufficient data. NS, non-significant at $\alpha = 0.05$. ×, an interaction term.

Age	Region	Depth	Year Group	Depth × Region	Depth × Year Group	Year Group × Region	Year Group × Depth × Region
0	NS		≤.001			NS	
1	NS	NS	NS	≤.001	NS	NS	0.01
2	0.05	≤.001	≤.001	≤.001	NS	≤.001	0.005
3	NS	0.002	≤.001	NS	NS	NS	0.005
4	≤.001	NS	0.01	NS	0.03	NS	NS
5	≤.001	NS	0.006	NS	NS	NS	NS
6	NS	NS	NS	NS	NS	NS	NS
7	NS	NS	NS	NS	NS	NS	NS

Depth significantly influenced sex ratio in summer flounder, ages 2 and 3 (Table 3). The catch of age-0 fish was insufficient in the deeper depth zones to analyze. Whereas depth was only significant for ages 2 and 3 in the ANOVA, Tukey's studentized range tests identified depth differences in sex ratios for ages 1 through 4. The presence of significant interaction terms, however, limits the interpretation of this *a posteriori* test. For these younger fish, exclusive of age 1, a tendency exists for the sex ratios to be more nearly 50:50 offshore (Figure 2). Age-1 males are distinctly proportionately more common offshore. At ages 5 and older, depth no longer impacts sex ratios significantly in summer flounder.

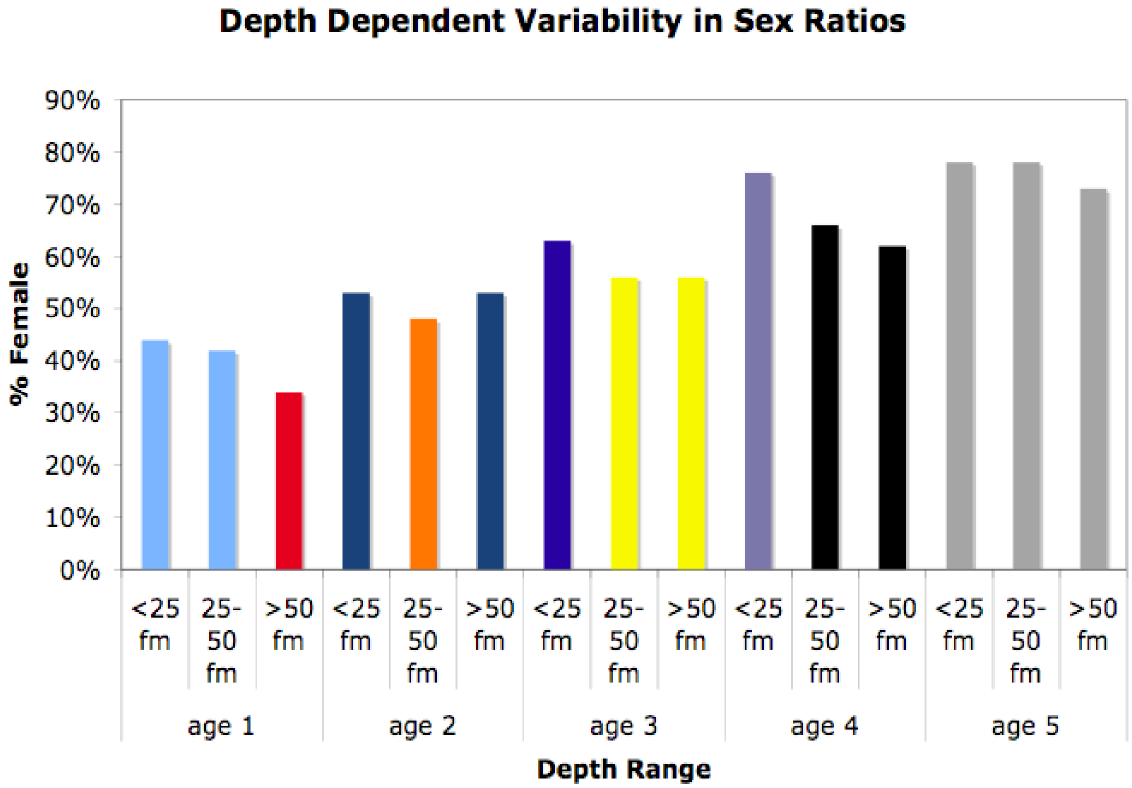


Figure 2. Mean percent female at age by depth. Bars within an age group with the same color were not significantly different in an *a posteriori* Tukey's test. ANOVA results are in Table 3

Sex ratios were significantly affected by region at age 2, but much more so for ages 4 and 5 (Table 3). The switch between depth and region as the dominant main effect between ages 3 and 4 is dramatic and suggests a differential segregation of the stock spatially as the fish age. Interaction terms were routinely significant between main effects for younger ages, but rarely significant after age 3. The change in significant main effect with age and the frequency of significant interaction terms including depth suggests that regionality in summer flounder sex ratios is not facilely explained simply in terms of depth and latitude. Tukey's studentized range tests document the tendency for the northern Mid-Atlantic and Delmarva regions to group together, while one of either the south Atlantic or southern New England regions differed significantly from the central region group (Figure 3). For the cases in which region was a significant main effect, a significantly lower fraction of females occurred in southern New England strata when compared to the Delmarva and northern Mid-Atlantic regions.

Year-group was highly significant for ages 0, 2, 3, 4, and 5. Tukey's studentized range tests clearly indicated a pattern for early years (1976-1980) and later years (2001-2007) to group together and for middle years (1981-1996) to group together (Figure 4). These groupings can be correlated with periods of low and high abundance. Furthermore, periods of lower abundance routinely had higher male ratios than periods of high abundance.

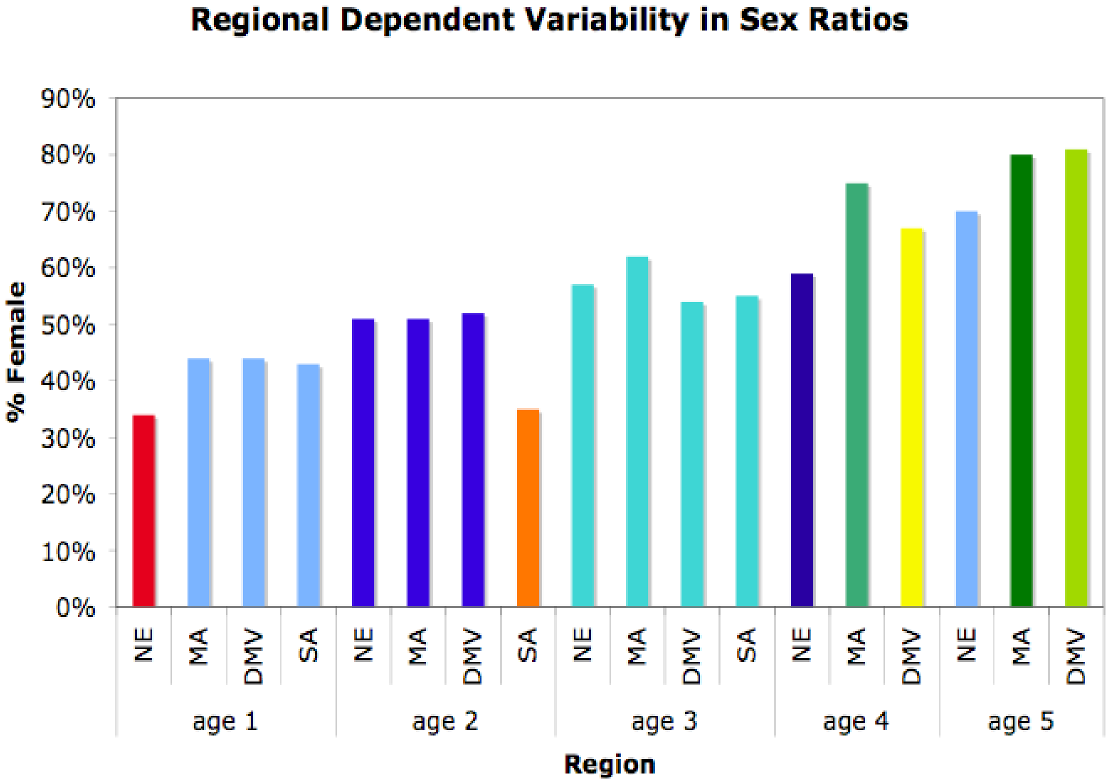


Figure 3. Mean percent female at age by region. Bars within an age group with the same color were not significantly different in an *a posteriori* Tukey's test. ANOVA results are in Table 3. NE, southern New England; MA, northern Mid-Atlantic; DMV, Delmarva; SA, south Atlantic.

Interpretation: Spatial Divergence in Sex Ratio

Examining the regional results for overall trends, it seems that the northern Mid-Atlantic and Delmarva regions have similar sex ratios regardless of age. In addition, the south Atlantic and southern New England regions have a tendency to be different from the Mid-Atlantic/Delmarva grouping, depending on age. When different, the southern New England and south Atlantic regions routinely have a higher fraction of males. This is precisely what would be expected from the temperature-dependent determination of sex that produces an increase in fraction male at the temperature extremes; however, sex determination in the first year of life militates against this explanation as the main effect of region is observed only later. Thus, alternative biological explanations or determinants from differential fishing mortality must be sought. The depth and year-group effects are, as yet, unexplained.

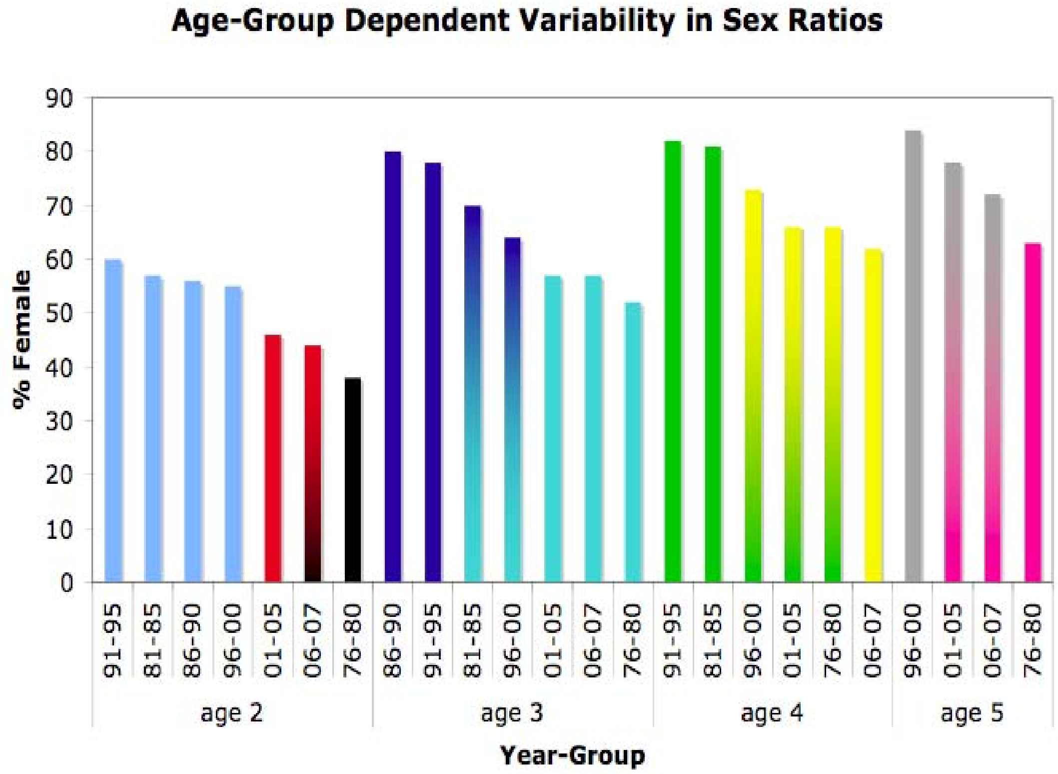


Figure 4. Mean percent female at age by year-group. Bars within an age group with the same color were not significantly different in an *a posteriori* Tukey's test. ANOVA results are in Table 3.

Sex Ratio-imposed Requirement on Relative Mortality Rate

Methods and Results

The gradual shift in sex ratio from male-dominated to female-dominated with increasing age might accrue from differential mortality or differential availability. The latter would seem unlikely, as the trends in sex ratio are consistent across a wide range of age groups.

The differential rate of natural mortality can be directly calculated from the information provided in Table 2. The calculation is based on the following governing equation:

$$N_{1_m} + N_{1_f} = N_{0_m} e^{-Z_m t} + N_{0_f} e^{-Z_f t} \tag{1}$$

where N is abundance of males m or females f, Z is total mortality rate, t is time, and numerals designate consecutive time periods. The equation can be converted to ratio form by dividing through by N_1:

$$1 = \frac{N_{0_m}}{N_1} e^{-Z_m t} + \frac{N_{0_f}}{N_1} e^{-Z_f t} \tag{2}$$

Equation (2) can be solved iteratively under the conditions that the sum of the two terms on the right-hand side closely approximate 1, that $N_{1_m} \le N_{0_m}$, and that $N_{1_f} \le N_{0_f}$.

Table 4. Relative natural mortality rates of male and female summer flounder calculated from the changes in sex ratios with age, by year-group, Delmarva and northern Mid-Atlantic region only, from equation (2).

Year Group	Male (Z_m)	Female (Z_f)
1976-1980	0.46	0.12
1981-1985	0.82	0.42
1986-1990	0.51	0.13
1991-1995	0.53	0.30
1996-2000	0.25	0.22
2001-2005	0.53	0.22
All years	0.62	0.22

Table 4 demonstrates that the change in sex ratio over the lifespan of a cohort requires a differential natural mortality rate, whereby males die at a much faster rate than females. The calculation is robust in measuring the relative mortality rate. The mortality rate for males is often twice that of females. Considering the entire dataset, all years combined, the natural mortality rate for males is about three times the female rate (Table 4). The calculation is less robust in measuring absolute natural mortality rate as any mortality process distributed evenly among the sexes would not impact an estimate based on varying sex ratios. Nevertheless, the female natural mortality rate of 0.22 for all years is remarkably similar to the assumed female natural mortality rate derived from estimates of female lifespan.

Interpretation: Sex-specific Natural Mortality Rate

The change in sex ratio with age requires that male and female summer flounder be modeled separately as far as natural mortality rate. In lieu of a sex-explicit model, a whole stock mortality rate might be employed, although this is less satisfactory. The natural mortality rate, derived thusly, is not linear, however (Table 5). We calculated this age-dependent rate using the equation:

$$Z_{m+f} = -\log\left(\frac{N_{0_m}}{N_{0_{m+f}}} e^{-Z_m t} + \frac{N_{0_f}}{N_{0_{m+f}}} e^{-Z_f t}\right) \tag{3}$$

Equation (3) was employed using age-independent mortality rates for males and females from Table 4, based on the observation of relatively constant mortality with age within sex inferred from Figure 5. Whole-stock natural mortality rates derived thusly vary from 0.45 for young-of-the-year summer flounder to 0.25 for fish age 7 and older (Table 5).

Table 5. Whole-stock mortality rate based on the age-dependency in sex ratio from 1976-2007 and the male and female natural mortality rates reported in Table 4.

Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6	Age 7
0.447	0.424	0.394	0.362	0.316	0.286	0.262	0.245

A higher natural mortality rate in males could potentially be explained by some type of biological refuge for females. Female summer flounder are known to grow at a faster rate than males and may therefore be less prone to predation (Poole 1961). However, male and female growth rates are similar until age 2, so such an explanation would not be warranted when considering the apparent differential natural mortality in fish younger than age 2.

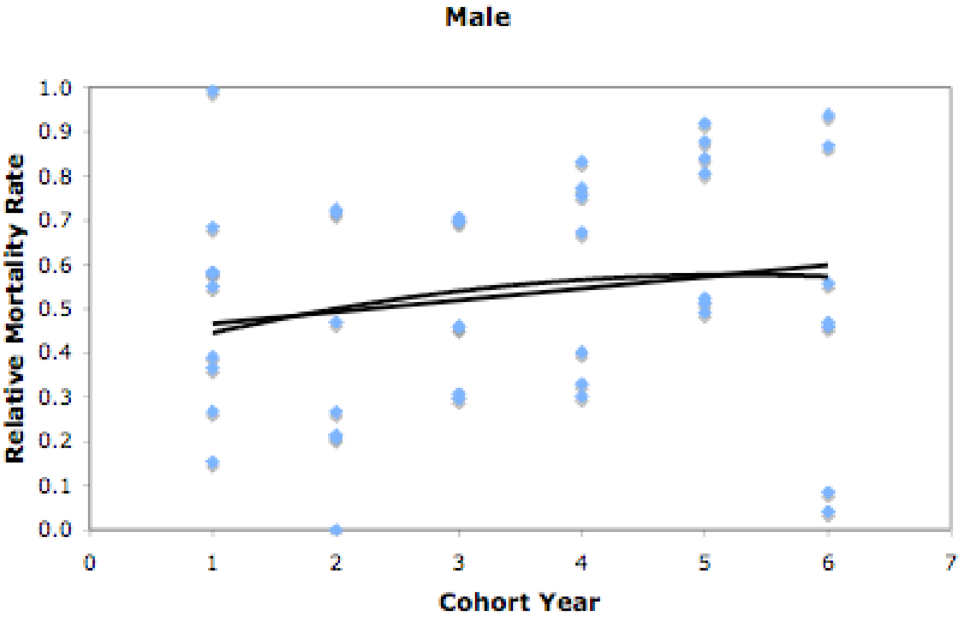
Some precedent exists for higher morality rates in male relative to female flatfish. Morse (1981) already proposed a higher natural mortality rate for males in summer flounder. Santos (1994) computed natural mortality rates for the four-spot megrim (*Lepidorhombus boscii*) by sex. The natural mortality rate for males was 0.41, and for females 0.34. Pearson and McNally (2005) also calculated mortality rates, using three different methods, for the sand sole, *Psettyichthys melanostictus*. The natural mortality rate for females ranged between 0.35 and 0.45, whereas the mortality rate for males was estimated to fall between 0.40 to 0.60.

Comparison of Age-Length Keys: Relationship of Length at Age with Region and Depth

Methods and Results

Tables 6 and 7 show the results of ANOVAs examining the relationship of depth, region, and year-group on length at age. For these analyses, the dependent variable, length, was ranked. Thus, the analysis is nonparametric. Depth significantly impacted length-at-age for males and females, ages 1 through 3 and age 4 for females. At age 0, summer flounder are only present in shallow waters, and at age 5 and older, depth no longer influences length-at-age, for the most part. Tukey's studentized range tests show that fish in deeper water are larger at a given age than fish in shallower water (Figure 6).

Length at age varied significantly with region for male and female summer flounder, ages 0-4, but not at older ages. Whereas Tukey's Studentized Range tests identified a tendency for some regions to group together at some ages, overall, fish are smaller in the south and get progressively larger at all ages, 0-4, northward (Figure 7). When regions did group together they did so in a north-central, south-central trend. In other words, the southern New England region never grouped with the south Atlantic or Delmarva regions, and the south Atlantic never grouped with the northern Mid-Atlantic and southern New England regions.



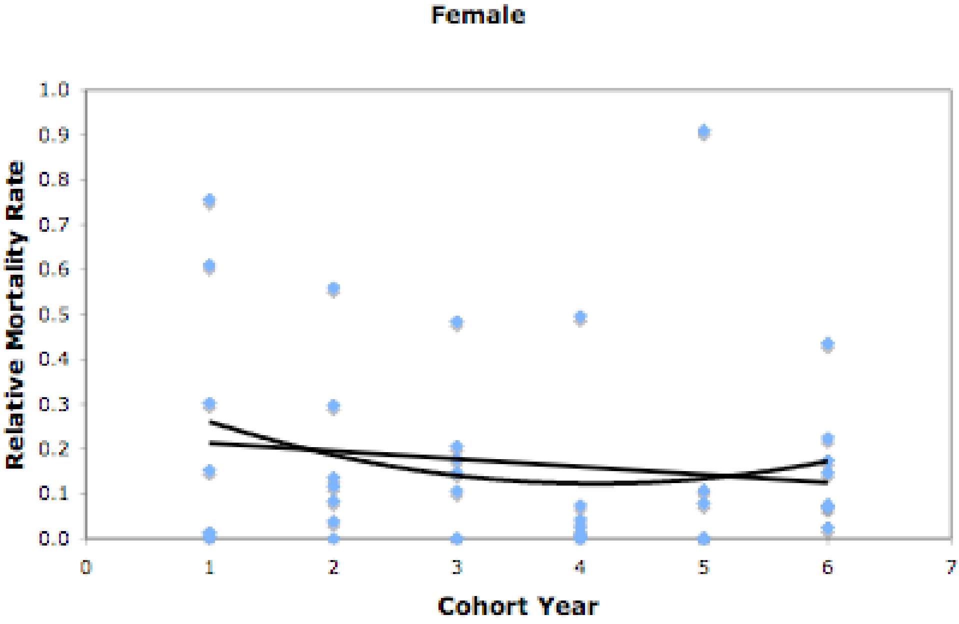


Figure 5. Trends in natural mortality rate by age for male and female summer flounder. Points are values from each of the years from 1976-2006 where sufficient data density permitted the estimate of within-cohort natural mortality rate at age. Neither polynomial nor linear curve fits transit a slope significantly at variance to zero.

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Length at age varied significantly with region for male and female summer flounder, ages 0-4, but not at older ages. Whereas Tukey's Studentized Range tests identified a tendency for some regions to group together at some ages, overall, fish are smaller in the south and get progressively larger at all ages, 0-4, northward (Figure 7). When regions did group together they did so in a north-central, south-central trend. In other words, the southern New England region never grouped with the south Atlantic or Delmarva regions, and the south Atlantic never grouped with the northern Mid-Atlantic and southern New England regions.

Disregarding the influence of fishing mortality on age-at-length, these trends indicate that summer flounder either grow at faster rates in deeper water and northern latitudes or that larger fish at age preferentially aggregate in these regions. Alternatively, in shallow waters and at southern latitudes larger fish may be more accessible to the fishery. While the fishery may not keep younger fish due to minimum size restrictions, younger fish may still be removed by the fishery as discard mortality. Whether it be a biological reason (e.g., differential growth rates) or a fishery-related reason (bigger fish at any age are more accessible in shallow/southern water), it seems clear that the average size of fish at age is larger in deeper/northern water than in shallow/southern water.

However, significant interaction terms also occur commonly in fish 4 years or less in age and these involve both depth and region with relatively equal frequency and intensity. The frequency of significant interaction terms including depth and region suggests that regionality in the trends in age at length for summer flounder cannot facilely be explained simply in terms of depth and latitude. A more complex mixture of biology and, perhaps, relative fishing impact is likely to be required. These trends are remarkably reminiscent of those observed earlier for sex ratio (Table 3).

Table 6. Results of ANOVAs examining the impact of depth, region, and year-group on male length for summer flounder. All regional data were included. Blank cells indicate insufficient data. NS, non-significant at $\alpha = 0.05$. ×, an interaction term.

Age	Region	Depth	Year Group	Depth × Region	Depth × Year Group	Year Group × Region	Year Group × Depth × Region
0	≤.001		≤.001			NS	
1	≤.001	≤.001	≤.001	≤.001	0.006	≤.001	NS
2	≤.001	≤.001	≤.001	NS	≤.001	≤.001	
3	≤.001	≤.001	≤.001	≤.001	NS	NS	NS
4	0.02	NS	≤.001	≤.001	NS	NS	NS
5	NS	NS	≤.001	NS	NS	NS	NS
6	NS	NS	NS	NS	NS	NS	NS
7	NS	NS	NS	NS	NS	NS	

Table 7. Results of ANOVAs examining the impact of depth, region, and year-group on female length for summer flounder. All regional data were included. Blank cells indicate insufficient data. NS, non-significant at $\alpha = 0.05$. ×, an interaction term.

Age	Region	Depth	Year Group	Depth × Region	Depth × Year Group	Year Group × Region	Year Group × Depth × Region
0	≤.001		≤.001			NS	
1	≤ .001	≤.001	≤.001	≤.001	NS	≤.001	0.003
2	≤.001	≤.001	≤.001	≤.001	≤.001	0.02	NS
3	≤.001	≤.001	≤.001	≤.001	0.03	0.02	NS
4	≤.001	0.008	≤.001	NS	≤.001	NS	0.02
5	NS	NS	≤.001	NS	NS	NS	NS
6	NS	0.01	≤.001	NS	NS	NS	NS
7	NS	NS	0.006	NS	NS	NS	

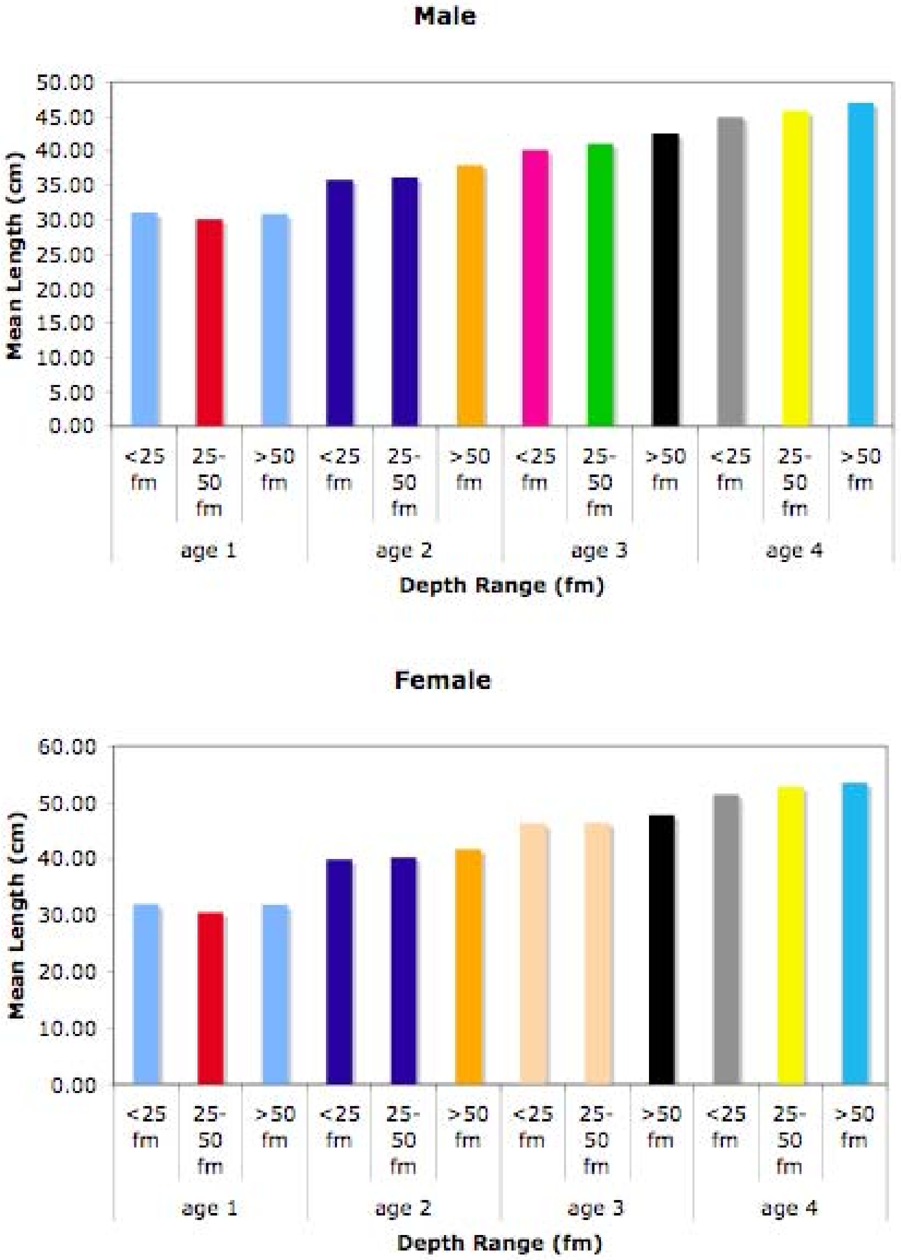

Figure 6. Mean length at age for male and female summer flounder. Bars within an age group with the same color were not significantly different in an *a posteriori* Tukey's test. ANOVA results are in Tables 6 and 7.

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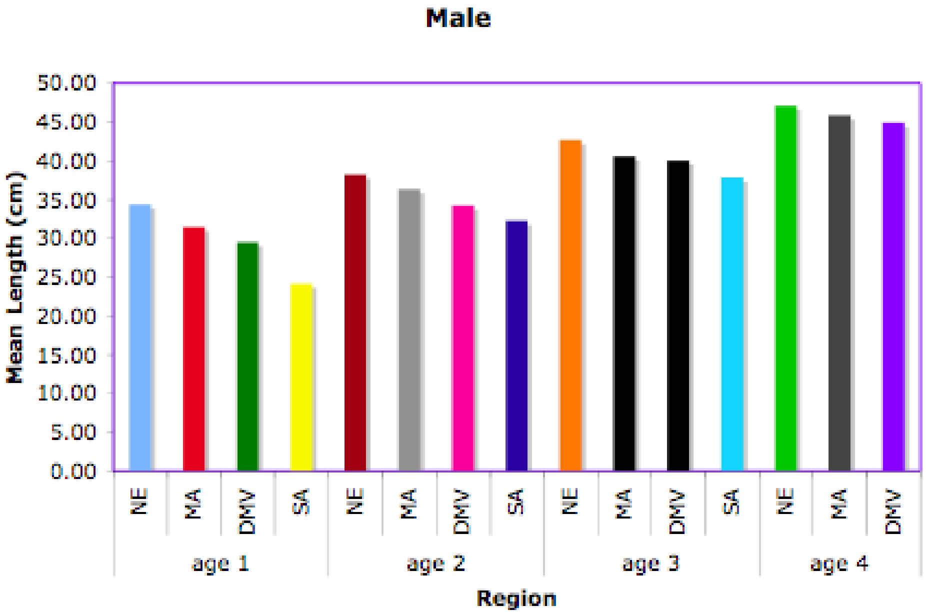

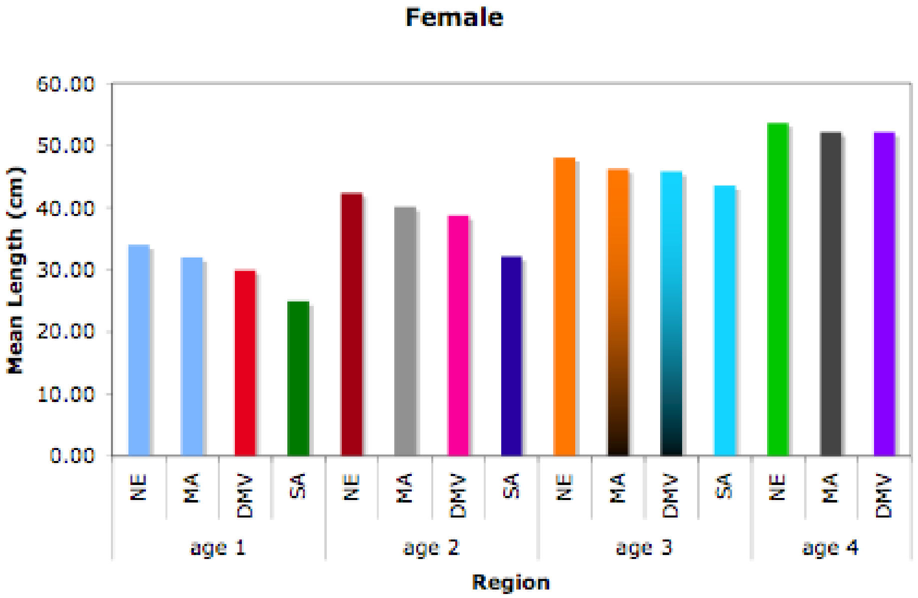

Figure 7. Mean length at age for male and female summer flounder. Bars within an age group with the same color were not significantly different in an *a posteriori* Tukey's test. ANOVA results are in Tables 6 and 7. NE, southern New England; MA, northern Mid-Atlantic; DMV, Delmarva; SA, south Atlantic

Disregarding the influence of fishing mortality on age-at-length, these trends indicate that summer flounder either grow at faster rates in deeper water and northern latitudes or that larger fish at age preferentially aggregate in these regions. Alternatively, in shallow waters and at southern latitudes larger fish may be more accessible to the fishery. While the fishery may not keep younger fish due to minimum size restrictions, younger fish may still be removed by the fishery as discard mortality. Whether it be a biological reason (e.g., differential growth rates) or a fishery-related reason (bigger fish at any age are more accessible in shallow/southern water), it seems clear that the average size of fish at age is larger in deeper/northern water than in shallow/southern water.

However, significant interaction terms also occur commonly in fish 4 years or less in age and these involve both depth and region with relatively equal frequency and intensity. The frequency of significant interaction terms including depth and region suggests that regionality in the trends in age at length for summer flounder cannot facilely be explained simply in terms of depth and latitude. A more complex mixture of biology and, perhaps, relative fishing impact is likely to be required. These trends are remarkably reminiscent of those observed earlier for sex ratio (Table 3).

Year-group consistently affected length at age for male and female summer flounder until age 6. Year-group no longer impacted length at age for male summer flounder at age 6 and older, but continued to do so for female fish. A few trends are clear in both males and females. First, summer flounder averaged much smaller at all ages in the period from 1976-1980 than any other year group. Additionally, year groups including years 1981-1985 and 2006-2007, generally group together as periods where size was smaller at age. Other year-groups are not consistently associated with small or large size-at-age groups. The former groupings are interesting because these periods are associated with relatively high abundance in comparison to the intermediate years. Additionally, a similar trend was noted in the sex ratio analyses.

Tables 8 and 9 repeat the ANOVAs of Tables 6 and 7, but restrict regional coverage to the two central regions, Delmarva and northern Mid-Atlantic. The frequency of significant main effects is much reduced in these ANOVAs relative to the earlier ones, although depth effects in particular continue to be present. Even for depth, significant main effects are less common, as are significant interaction terms, indicating that the central component of the stock offers a more spatially coherent picture than those portions near the northern and southern range limits.

Table 8. Results of ANOVAs examining the impact of depth, region, and year-group on male summer flounder length. Only the Mid-Atlantic and Delmarva regions were included. Blank cells indicate insufficient data. NS, non-significant at α = 0.05. ×, an interaction term.

Age	Region	Depth	Year Group	Depth × Region	Depth × Year Group	Year Group × Region	Year Group × Depth × Region
0	≤.001		≤.001			NS	
1	NS	≤.001	≤.001	≤.001	≤.001	NS	NS
2	NS	≤.001	≤.001	NS	≤.001	NS	NS
3	NS	NS	≤.001	0.04	NS	NS	NS
4	NS	NS	≤.001	NS	NS	NS	NS
5	NS	NS	0.002	NS	NS	NS	NS
6	NS	NS	NS	NS	NS	NS	
7	NS	NS	NS				

Interpretation: Spatial Variation in Length-at-age

The ANOVAS of Tables 6-9 suggest that a single age-length key is not likely to be representative across all regions and in different depths. Furthermore, the differential with region and depth suggests that differential fishing pressure cannot be excluded as the mechanism generating these differences.

Table 9. Results of ANOVAs examining the impact of depth, region, and year-group on female summer flounder length. Only the Mid-Atlantic and Delmarva regions were included. Blank cells indicate insufficient data. NS, non-significant at α = 0.05. ×, an interaction term.

Age	Region	Depth	Year Group	Depth × Region	Depth × Year Group	Year Group × Region	Year Group × Depth × Region
0	≤.001		≤.001			NS	
1	NS	≤.001	≤.001	≤.001	NS	0.005	≤.001
2	NS	≤.001	≤.001	NS	≤.001	NS	NS
3	NS	≤.001	≤.001	NS	0.01	NS	NS
4	NS	NS	≤.001	NS	0.004	NS	NS
5	NS	NS	≤.001	NS	NS	NS	NS
6	NS	NS	≤.001	NS	NS	NS	NS
7	NS	NS	0.04	NS	NS	NS	NS

Comparison of Age-Length Keys: Comparison of Key Structure Across Region and Depth

Methods and Results

These analyses focused on the age-length keys for the Delmarva and northern Mid-Atlantic region and, independently, on the three depth zones previously described, as these two regions were most similar in length at age. To compare keys efficiently, lengths were combined into 12 units, the central 10 being 5 cm intervals. Size 12 included fish ≥70 cm and size 1 included fish <20 cm. This yielded three age-length keys for the three depth zones and two for the two regions. Each of these returned a significant result from a by-region or by-depth chi-square test, and from a Cochran-Mantel-Haenszel test controlling for depth or region. Tests were conducted on doubly standardized arrays (columns and rows). These results are anticipated since the ages are not independently distributed with respect to lengths in these keys.

The commonest age at length translates a diagonal from the northwestern to the southeastern corner of the age-length array (age in columns, length in rows). This trend is consistent across keys. A same cell-to-same cell mapping evaluated by a Spearman's rank correlation test on doubly standardized arrays returned a significance level of $P < 0.0005$ or better for each pair-wise comparison (e.g., Delmarva vs northern Mid-Atlantic). This also is expected from the anticipated structure of the keys.

These two standard statistics are described because these approaches, plus the afore-described ANOVAs (Tables 6-9) represent typical statistical treatments of age-length data. None of them answer the query concerning equivalency of the age-length relationship documented by the distribution of ages at length in the two-dimensional array of the key.

To directly compare two keys, we used Geary's C and Moran's I statistics on the set of residuals obtained by calculating the expected key structure in one array from the observed key structure in the other. Each row was standardized, but a column standardization was not performed. Residuals were calculated for each array cell as $\exp ected_{i,j} - observed_{i,j}$ where the expected values were obtained from the first of two paired arrays. The null hypothesis is that the residuals will be randomly distributed in x-y space. A statistical test revealing a non-random pattern in the residuals indicates that some portion of the two arrays under examination differ in the distribution of values among cells; that is, that the age-length relationship differs.

The test statistics were calculated following Cliff and Ord (1973) where:

$$Moran's\ I = \left(\frac{n}{W}\right) \frac{\sum_{i=1}^{n} \sum_{\substack{j=1 \\ i \neq j}}^{n} w_{ij} z_i z_j}{\sum_{i=1}^{n} z_i^2}\ ; \tag{4}$$

$$Geary's\ C = \left(\frac{n-1}{2W}\right) \frac{\sum_{i=1}^{n} \sum_{\substack{j=1 \\ i \neq j}}^{n} w_{ij} (x_i - x_j)^2}{\sum_{i=1}^{n} z_i^2} \tag{5}$$

and

$$W = \sum_{\substack{i=1 \\ i \neq j}}^{n} \sum_{j=1}^{n} w_{ij}\ ; \tag{6}$$

$$z_i = x_i - \bar{x}; \tag{7}$$

$n =$ number of samples; $x_i =$ datum of each sample i; and $w_{ij} =$ a weighting measure as described subsequently. Significance levels were calculated under the assumption of randomization (Jumars et al., 1977).

Calculation of Moran's I or Geary's C is contingent on the mathematical representation of the spatial relationship of the cell values (w_{ij}). We employed a King's moves weighting such that any two cells i and j located in the array at position k,l for i and at positions $k,l+1,\ k,l-1,\ k-1,\ l,$ and $k+1,l$ for j were given $w_{ij} = 1.0$. For the remainder, $w_{ij} = 0$.

Moran's I is sensitive to the location of extreme departures from the mean ($x_i - \bar{x}$). The expected value of I for spatially randomly distributed samples is $-(n-1)^{-1}$, a number close to zero at high n (Cliff and Ord, 1973). High values of I occur if x_i and x_j are both, much above or much below the mean. Geary's C is sensitive to sample-to-sample variation ($x_i - x_j$). Values above 1.0 indicate negative spatial autocorrelation (i.e., neighboring values less similar than expected by chance), an even distribution. Values below 1.0 indicate positive spatial autocorrelation (i.e., neighboring values more similar than expected by chance), a patchy distribution.

Both statistics are provided; however the question at hand is the relationship of nearest neighbors in the array and thus a strong preference is given to Geary's C as the statistic best evaluating similarity between two age-length arrays.

An important question concerns the incorporation of zeros. The northeastern and southwestern corners of the arrays routinely contain zeros. These paired zeros increase the number of cells and thus bias the statistic in proportion to their importance, as they are a guaranteed characteristic of the array if formulated correctly. An additional concern is singleton zeros, as the residual obtained is less constrained than for cases with paired non-zero values. In our opinion, the most valid approach is to discount paired-zeros only. Results of comparison of three age-length keys for the three depths and two geographic regions are provided in Tables 10 and 11. These comparisons are based on the exclusion of paired-zero cells.

Table 10. Values of Geary's C and Moran's I and significance for the cases in which array cells characterized by paired zeros were excluded. Age-length keys compared were for males only. The first array in each array pair as listed is the parent array used to generate the expected values for the second array. Residuals were calculated for the second array. Significance values are Moran's I over Geary's C $\left(\frac{Moran's\ I}{Geary's\ C}\right)$. NS, not significant. For region, Delmarva was used as the parent array.

Array Pair	Moran's I	Geary's C	Significance
Depth 1 vs. 2	0.182	2.175	$\frac{P < 0.05}{P < 0.005}$
Depth 1 vs. 3	-0.005	2.281	$\frac{NS}{P < 0.005}$
Depth 2 vs. 3	0.164	0.932	$\frac{P < 0.005}{NS}$
Region	-0.090	2.353	$\frac{NS}{P < 0.005}$

Table 11. Values of Geary's C and Moran's I and significance for the cases in which array cells characterized by paired zeros were excluded. Age-length keys compared were for females only. The first array in each array pair as listed is the parent array used to generate the expected values for the second array. Residuals were calculated for the second array. Significance values are Moran's I over Geary's C $\left(\frac{Moran's\ I}{Geary's\ C}\right)$.

NS, not significant. For region, Delmarva was used as the parent array.

Array Pair	Moran's I	Geary's C	Significance
Depth 1 vs. 2	0.056	1.645	$\frac{NS}{P < 0.01}$
Depth 1 vs. 3	0.174	1.392	$\frac{P < 0.05}{P < 0.10}$
Depth 2 vs. 3	0.026	0.890	$\frac{NS}{NS}$
Region	-0.013	1.573	$\frac{NS}{P < 0.05}$

The trend with depth is exemplified by Table 12 in which is compared via residuals the arrays for depths 1 (<25 fm) and 3 (>50 fm). A negative residual indicates a higher value in the second array (>50 fm). Consistently, across size groups, the negative residuals occur at older ages indicating that male fish of a given size tend to be older at deeper depths. This is consistent with ANOVA results described earlier in Tables 6-9. Table 13 compares the male arrays for the two regions. In this case, the residual pattern is more complex; however, negative values tend to occur at younger ages for a given size, indicating that males tend to be older at size in the southern portion of the Mid-Atlantic Bight. This is also consistent with ANOVA results.

Table 12. Residual pattern for the comparison of and example age-length relationship in summer flounder males between arrays representing depths 1 and 3.

Length (cm)	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
<20	54.43	-60.76	6.33				
20-<25	30.01	-40.91	10.90				
25-<30	23.04	-35.13	12.62	-0.60	0.07		
30-<35	6.92	14.68	-15.40	-5.69	-0.51		
35-<40	0.33	42.35	-31.37	-10.17	-0.69	-0.46	
40-<45		10.06	30.03	-28.95	-9.65	-1.49	
45-<50		1.00	18.93	12.20	-22.38	-7.77	-1.99
50-<55			4.42	18.67	-9.67	-2.05	-11.37
55-<60			1.91	-4.88	3.29	11.77	-12.09

Table 13. Residual pattern for the comparison of and example age-length relationship in summer flounder males between arrays representing Delmarva and the northern Mid-Atlantic Bight.

Length (cm)	Age 0	Age 1	Age 2	Age 3	Age 4	Age 5	Age 6
<20	17.5540	-24.7482	7.1942				
20-<25	20.0380	-25.6052	5.5672				
25-<30	9.2232	-16.8604	7.6844	-0.2277	0.1805		
30-<35	0.4179	-2.9349	0.8727	1.4069	0.2375		
35-<40	-0.0198	-14.4489	7.3256	5.8648	1.2466	0.0317	
40-<45		-1.8036	-17.6687	12.4069	7.1451	-0.0799	
45-<50		-0.4988	-8.7182	-3.3502	12.3292	0.4147	-0.1767
50-<55		-1.6949	-2.6635	3.8740	6.7192	-6.2349	
55-<60		-4.0000	16.6667	13.3333	-31.3333	5.3333	

Interpretation

The male age-length relationships are more variable over depth and region than the female ones. Probably, this accrues from the higher natural mortality rates for the males which are also probably more variable spatially. The analyses suggest that a single age-length key may not be adequate, particularly for the males. However, comparison of model runs using different age-length keys would be needed to determine whether the observed variations are substantive for stock modeling. Regardless, the analyses again focus on the need to differentiate the two sexes and to investigate a spatially explicit model.

Conclusions and Recommendations

1. Young-of-the-year summer flounder are dominantly male. Sex ratio changes gradually with age such that male frequencies over 0.5 occur infrequently by age 2 and rarely exceed 0.3 by age 4. The biased sex ratio at birth is likely the result of temperature-dependent sex determination (TSD).
2. The age-dependency of sex ratio indicates the need to implement a sex-explicit model for summer flounder. Spatial variation in sex ratio suggests that a single sex-at-age key is not likely to be representative across all regions and in different depths.
3. The change in sex ratio with age also requires that separate natural mortality rates be used for male and female summer flounder stock assessment models. In lieu of a sex-explicit model, a whole stock mortality rate might be employed, although this is less satisfactory. The natural mortality rate, derived thusly, is not linear, but varies from 0.45 for age-0 fish to 0.25 for fish age 7 and older.
4. Higher natural mortality rate in male summer flounder is supported by published information on summer flounder and other flatfish.
5. Spatial variation in length-at-age suggests that a single age-length key is not likely to be representative across all regions and in different depths. The differential with region

and depth suggests that differential fishing pressure cannot be excluded as the mechanism generating these differences.

6. The male age-length relationships are move variable over depth and region than the female ones, but each varies significantly. The analyses suggest that a single age-length key may not adequately describe the stock, particularly for the males.

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