UPDATED ESTIMATE OF THE GROWTH CURVE OF WESTERN ATLANTIC BLUEFIN TUNA

by

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Summary

The curve currently used by ICCAT to represent the growth of western Atlantic bluefin tuna was estimated using tagging information and modal sizes that corresponded primarily to very young fish (ages 1-3, primarily). The estimated maximum average size from this curve is very large (382 cm), which could be a result of the scarcity of large bluefin in the data used. Recently, scientists have developed techniques for reading ages from bluefin ear bones (otoliths); the accuracy of and the age readings have has been validated with bomb radio-carbon signals. These age-length readings are primarily for large bluefin (ages 5 and older), where they suggest slower growth and older ages than was previously assumed. However, aAnalyses of these data have resulted in growth curves that predicted very small mean sizes for the youngest age group, which could be a result of the lack of small fish in the data used. In this study, we combine the otolith-based age-length readings with the size frequency distributions of small (ages 1-3) bluefin caught by purse seiners in the 1970s where the age classes are distinctly visible to the eye. We analyzed the two datasets jointly using a maximum likelihood approach and assumed that variability in length at age increases with age. The resulting growth curve predicts sizes at young and old ages that are very consistent with observed data such as the maximum sizes observed in the catch, or the modal sizes for very young bluefin. The resulting curve is also very similar to the curve used by ICCAT for eastern Atlantic and Mediterranean bluefin. We recommend that ICCAT adopt this new growth curve for the assessments of western Atlantic bluefin tuna.

INTRODUCTION

The Atlantic bluefin tuna (*Thunnus thynnus*) is the largest tuna species with a wide spatial distribution and transatlantic migratory behavior. It is one of the most highly-valued marine fish and as a consequence it has been under great fishing pressure. The North Atlantic bluefin tuna stock is assessed and managed by the International Commission for the Conservation of Atlantic Tunas (ICCAT) under a two-management unit/stock scenarios (western Atlantic and Eastern Atlantic-Mediterranean units). The last assessment indicated that both stocks are currently overfished and undergoing overfishing (Anonymous, 2008). As the result of the depleted condition of these stocks, accurate assessments and projections of future stock status are of high importance. Although a rebuilding plan for the western stock has been in place since 1998, the stock has shown little signs of recovery. During the last assessment of the western stock, ICCAT scientists identified the growth of this species as one of the three major sources of uncertainty associated to the assessment results (Anonymous, 2008). Furthermore, Porch et al. (2008) showed that the results of the virtual population analysis for the western stock were tentatively sensitive to the use of an alternative bluefin tuna growth curve developed by Secor et al. (2008).

The current western Atlantic bluefin tuna growth function adopted by ICCAT was developed by Turner and Restrepo (1994) using age-length information derived from tagging and modal analyses with the majority of the samples corresponding to fish in the age range 1-3 yrs. Recently, Secor et al. (2008) and Neilson and

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Campana (2008) developed growth curves for the western stock of North Atlantic bluefin tuna using age data derived from otolith readings of mostly larger fish. Their analyses call into question some of the parameter estimates obtained by Turner and Restrepo (1994), especially the asymptotic length (L_∞), which is considerably larger than that estimated by Secor et al. (2008) and Neislon and Campana (2008) (see Table 1). On the other hand, the growth curves estimated by the latter authors are based on mostly large bluefin, and they do not predict accurately the observed size distributions of age 1-3 fish (see Anonymous, 2008).

The problem of multiple growth curves becomes problematic for assessments that rely heavily upon an assumed growth function. This is particularly true when different data types are used to estimate different growth curves. Typically growth curves are estimated from hard parts for which annual increments can be identified, length increments derived from tag-recapture studies (Fabens 1965) or modal progression where the growth of identifiable cohorts can be followed (Macdonald and Pitcher, 1979). Generally, each of the methods obtain data from fishery dependent sources, from which it may be difficult to obtain representative samples from the entire age range of the population and samples unaffected by processes of fishery selectivity. Further, each of these methods has specific peculiarities or biases which may complicate comparison of growth curves obtained from different data source. One potential solution for reconciling differences in growth curves obtained from different information sources is to construct integrated models that use each piece of information in a combined likelihood (Eveson et al. 2004). Operating under the hypothesis that each data set provides valuable, and perhaps unique, information on the overall growth pattern, such integrated models may provide a holistic view of growth.

In this paper, we attempt to reconcile the differences between different growth models by estimating a combined growth curve for western Atlantic bluefin tuna using both direct age-length observations from otoliths and modal progression data. When combined, the two datasets cover most of the size range observed for this species.

MATERIALS AND METHODS

We used two types of data to estimate a western Atlantic bluefin tuna growth curve, as follows:

> Data Type 1: Age-length observations derived from otolith readings of bluefin tuna. Two data sets were used: Those from Secor et al. (2008) of confirmed western origin (n=121), and those Neilson and Campana (2008) (n=25). Both studies used the same approach for reading the ages. Neilson and Campana (2008) used data on deposition of bomb radiocarbon to validate the ages. Details on the ageing and sampling methods used are described in those articles. However, the coauthors of Secor et al. (2008) noted the possibility of a small under-ageing bias in the older fish sampled (>10 years), but this should have a very small effect, if any, on the analyses presented here.
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> Data Type 2: Annual catch-at-size data (40 cm < FL<110 cm) available from ICCAT from purse seine fisheries for the years 1970-1976. These years and size ranges were chosen because the size frequency distributions for ages 1 to 3 are visibly distinct. At that time, purse seine fisheries operating off North America targeted small bluefin tuna. Details on how the catch-at-size data were assembled are available from Miyake (1985).

The growth parameters of the von Bertalanffy function were estimated using a joint likelihood function combining both data types as explained below. Individual variability in length-at-age was assumed based on the method suggested by Kirkwood and Somers (1984) with assumes that the asymptotic size is variable (see also Hampton, 1991).

Length-age observations

The age-length data were fitted assuming that length-at age is normally-distributed, with the variance increasing as a function of size. The negative log-likelihood for these observations is:

$$\varphi_1 = \sum_i \left[\frac{\ln\,(2\pi\sigma_i^2)}{2} + \frac{(l_i - \hat{l}_i)^2}{2\sigma_i^2} \right], \qquad \text{eq. (1)}$$

where the predicted length for each observation is given by the von Bertalanffy growth function with parameters L_∞, k and t_0:

$$\hat{l}_i = L_\infty(1 - \exp(-k(t_i - t_0))), \qquad \text{eq. (2)}$$

and the variance for each observation is given by:

$$\sigma_i^2 = \sigma_{L\infty}^2(1 - \exp(-k(t_i - t_0))^2. \qquad \text{eq. (3)}$$

The maximum likelihood estimate of the parameters L_∞, k and t_0 and $\sigma_{L\infty}^2$ would be obtained by finding the values that minimize φ_1.

Length frequency observations

Turner and Restrepo (1994) used catch-at-size data from the 1970s where the modal lengths for the youngest ages were visible. In this study we used essentially the same data but incorporated it more fully into the maximum likelihood estimation by using all of the data, and not just the modal lengths-at-age. Visual examination of the annual catch-at-size data from purse seine fisheries showed that three age classes were evident in the size range 40 cm to 110 cm in the years 1970-1976. After 1976, the three age groups were no longer obvious, as a result of the shifting of the purse seine fisheries to target larger bluefin.

The catch-at-size data for each year were reduced in proportion to the total in that year, with the maximum (for 1970) being set at 200 observations. This was done so that the number of observations (on the order of 10^5 in the original catch-at-size data) would not have an overwhelming weight in the likelihood function. The resulting length frequencies are shown in Table 2.

The length frequency data were assumed to follow a multinomial distribution. The negative log-likelihood for these observations is (Quinn and Deriso, 1999):

$$\varphi_2 = -\sum_y \sum_j \hat{F}_{yj} \ln(\hat{F}_{yj}/F_{yj}), \text{ where} \qquad \text{eq. (4)}$$

F_{yj} = observed length frequency for year y and size j,
$\hat{F}_{yj}$= predicted length frequency for year y and size j.

The predicted length frequencies in a given year are calculated on the basis of the length-at-age distributions for ages (a) 1-3 (which are calculated from the parameters L_∞, k and t_0 and $\sigma_{L\infty}^2$) and the proportions of fish of ages 1-3 each year. For a given year,

$$\hat{F}_{yj} = \sum_a \sum_j n_y f_{aj} \theta_{ay}, \text{ where} \qquad \text{eq. (5)}$$

n_y = total number of fish in the length frequency in year y,
θ_{ay}= estimated proportion of fish of age a in year y, and
f_{aj} = probability density function (PDF) of length j for each age group, a.

The PDF is calculated as:

$$f_{aj} = \frac{1}{\sqrt{2\pi}\sigma_a} exp\left[-\frac{1}{2\sigma_a^2}(j - \hat{l}_a)^2\right], \text{ with} \qquad \text{eq. (6)}$$

$$\sigma_a^2 = \sigma_{L\infty}^2(1 - \exp(-k(a - t_0))^2 \text{ and} \qquad \text{eq. (7)}$$

$$\hat{l}_a = L_\infty(1 - \exp(-k(a - t_0))). \qquad \text{eq. (8)}$$

Parameter estimation

A total of 25 parameters were estimated (L_∞, k and t_0 , $\sigma_{L\infty}^2$and 21 proportions, θ_{ay}) by minimizing the joint negative log-likelihood function:

$$\varphi = \varphi_1 + \varphi_2. \qquad \text{eq. (9)}$$

The minimization was done with the software AD Model Builder (http://admb-project.org/) which is particularly well suited for nonlinear estimation problems that involve many parameters.

A penalty term, P_y, for each year was added to the joint negative log-likelihood as suggested by Quinn and Deriso (1999) to ensure that the age proportions in a given year added up to 1.0:

$$P_y = 10^6(1 - \sum_a \theta_{ay})^2. \qquad \text{eq. (10)}$$

RESULTS AND DISCUSSION

Estimates of the parameters obtained in this study are presented in Table 3. The mean lengths and weights at age predicted from these parameters are given in Table 4.

The fit to the length-age observations is shown in Figure 1. Some of the oldest fish (age 30 or older) have sizes that fall below the predicted curve and this gives the impression of a biased fit. However, note that there are multiple observations in the 10-15 year age range that are of larger size than those corresponding to the older fish. Thus, the fit appears to be adequate.

The fits to the length-frequency data are shown in Figure 2. For some years the fitted length distributions miss the central tendency of the observed length distributions for some age groups (e.g., age 3 in 1971 and 1973). This could be due to a number of different factors such as changes in the timing of the purse seine fisheries between years, or changes in selectivity. Nonetheless, the overall fit to the data as assessed from the aggregated distributions seems adequate.

The standard errors of the estimated von Bertalanffy parameters are given in Table 3. The estimates are rather precise, with coefficients of variation ranging between 1.8% and 3.1%. Figure 3 presents likelihood profiles for L_∞, k and t_0 , with approximate 95% confidence intervals.

The predicted length-at-age distributions can be obtained from equations (6) to (8). These are shown in Figure 4. According to these predictions, only the first three (or four) age groups can be distinguished from each other, which coincides with what is observed from the catch-at-size data. Thereafter, as the mean lengths get closer to the asymptotic size and the variance of the distributions increases, it becomes progressively more difficult to distinguish age groups. This may have important implications in stock assessment applications in terms of setting the oldest age that is modeled explicitly (known as the "plus group").

ICCAT currently uses a method called "age-slicing" to convert catch-at-size data into a catch-at-age matrix. Age slicing is a deterministic approach that tends to smear year class effects (Lassen, 1988). The length-at-age distributions as estimated in this study could be used as a substitute approach that would take variability into account. For a given dataset (e.g. a year's size frequency distribution) the approach would consist of estimating the proportions at age, θ_a, conditional on the estimates of L_∞, k and t_0 and $\sigma^2_{L\infty}$, by minimizing equation (4). A related probabilistic approach to assigning ages from length frequencies has been proposed by Goodyear (1996)

Figure 5 shows the largest sizes of bluefin tuna caught, as reported to ICCAT, in the period 1970-2007, together with the values of L_∞ estimated in this and previous studies. If L_∞ is taken as the largest size that fish achieve on average (as opposed to the largest size that fish will ever achieve in theory), a comparison between maximum observed sizes and asymptotic length estimates can be used as a "reality check". Of course, this comparison assumes that the largest fish are available to fishing and that they have not disappeared from the population for causes such as overfishing. The figure shows that the estimated L_∞ from this study matches the observed maximum sizes quite well. On the other hand, the L_∞ value from Turner and Restrepo (1994) is above all observed maximum sizes, and the L_∞values from Secor et al. (2008) and Neilson and Campana (2008) are below.

The growth curve used by ICCAT for the stock in the eastern Atlantic and Mediterranean, estimated by Cort (1991), differs considerably from that used for the western stock (Turner and Restrepo, 1994). The difference between the two growth curves is difficult to reconcile in light of the behavior of bluefin from both stocks which includes considerable mixing. Figure 6 compares the two growth curves adopted by ICCAT and the growth curve estimated in this study. This latter curve is much closer to the Cort (1991) curve for the eastern stock than it is to the Turner and Restrepo (1994) curve for the western stock. The curves from Neilson and Campana (2008) and Secor et al. (2008) estimated for the West are also shown in Figure 6. They predict very small mean sizes for the youngest ages.

There is increasing interest in assessing the two stocks of Atlantic bluefin with models that incorporate mixing explicitly. Understanding differences in productivity between the two stocks becomes of immediate concern in such situations. If the two growth patterns are similar as suggested in this study, then the productivity of the two stocks should be more similar than it is currently thought.

We conclude that the growth curve for western Atlantic bluefin tuna presented in this study is an improvement over the estimate of Turner and Restrepo (1994), based on several reasons:

a- Turner and Restrepo (1994) used primarily tagging data that were subject to several sources of uncertainty. In many cases the data were not obtained in scientific campaigns. The initial sizes were not always measured and there were often doubts about reported lengths (fork length vs total length). The primary source of information in the present study was age-length readings made by trained scientists and using validated techniques.

b- Over 95% of the tagging data in Turner and Restrepo (1994) were for fish whose initial size was between 50 and 100 cm, and the modal lengths used in their analysis were also within this size range. The present study included fish ranging from 40 cm to 110 cm (length frequency data), and from 117 cm to 293 cm (age-length readings), thus covering a much broader range of sizes.

c- Turner and Restrepo (1994) incorporated the length frequency information into the estimation procedure only partially, by including the modal lengths at age into the objective function. In this study, we incorporated the observed size-frequency distributions more fully into the maximum likelihood estimation procedure.

In addition, we believe that the curves estimated by Secor et al. (2008) and Neilson and Campana (2008) suffer from a limitation similar to (a), above, in that their samples were limited to medium and larger fish. The resulting curves do not follow closely the observed size distributions for young bluefin.

For the reasons stated above, we recommend that ICCAT adopt the growth estimates presented in this study for the assessments of western Atlantic bluefin tuna.

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Table 1: Von Bertalanffy growth model parameters for western Atlantic bluefin tuna estimated by Turner and Restrepo (1994), Secor et al. (2008), and Neilson and Campana (2008).

	L_∞ (FL cm)	K	t_0	Sample size
Turner and Restrepo (1994)	382	0.079	-0.707	?
Secor et al. (2008)	257	0.200	0.830	121
Neilson and Campana (2008)	289	0.116	-0.089	25

Table 2. Length-frequency data from western Atlantic purse seine fisheries for 1970-1976. The original catch-at-size data were truncated at 110 cm and scaled to a maximum of 200 observations.

Length	1970	1971	1972	1973	1974	1975	1976	1977
40	0.024	0.000	0.000	0.000	0.000	0.000	0.000	0.000
41	0.024	0.000	0.000	0.000	0.000	0.000	0.000	0.000
42	0.000	0.000	0.000	0.000	0.000	0.000	0.000	0.000
43	0.017	0.000	0.000	0.000	0.000	0.000	0.000	0.000
44	0.024	0.000	0.000	0.000	0.000	0.000	0.000	0.003
45	0.041	0.000	0.000	0.000	0.000	0.000	0.000	0.003
46	0.143	0.025	0.000	0.000	0.000	0.000	0.000	0.003
47	0.194	0.025	0.000	0.000	0.012	0.000	0.000	0.000
48	0.644	0.126	0.000	0.000	0.067	0.000	0.000	0.000
49	0.661	0.200	0.010	0.000	0.138	0.000	0.000	0.000
50	3.392	1.455	0.010	0.009	0.403	0.020	0.012	0.001
51	3.494	1.714	0.010	0.033	0.593	0.033	0.012	0.001
52	7.140	5.531	0.113	0.082	1.707	0.168	0.054	0.001
53	7.462	5.939	0.184	0.131	2.432	0.333	0.080	0.000
54	6.075	5.790	0.049	0.246	2.192	1.160	0.325	0.011
55	5.770	6.013	0.612	0.446	1.859	1.731	0.508	0.011
56	2.484	2.871	0.331	0.794	1.072	3.386	0.666	0.052
57	2.433	2.611	1.282	0.431	0.799	4.514	0.527	0.041
58	0.574	0.883	2.629	0.425	0.789	3.804	0.265	0.101
59	0.557	0.772	4.214	0.206	0.694	2.955	0.213	0.061
60	0.231	0.421	5.460	0.193	0.787	1.622	0.035	0.094
61	0.164	0.236	6.135	0.099	0.645	0.710	0.018	0.034
62	0.135	0.298	3.648	0.084	0.261	0.167	0.009	0.046
63	0.202	0.372	1.756	0.121	0.166	0.065	0.009	0.013
64	0.197	0.596	1.583	0.047	0.047	0.045	0.006	0.021
65	0.147	1.078	0.326	0.099	0.012	0.033	0.006	0.008
66	0.313	1.901	0.194	0.135	0.002	0.080	0.000	0.015
67	0.398	2.679	0.297	0.197	0.002	0.118	0.000	0.007
68	1.024	3.313	0.940	0.135	0.003	0.284	0.019	0.009
69	1.551	2.905	0.807	0.247	0.003	0.652	0.019	0.001
70	3.347	6.384	0.867	0.490	0.086	2.189	0.051	0.007
71	3.840	5.865	1.358	1.375	0.098	3.723	0.105	0.005
72	6.404	9.827	2.438	2.117	0.189	8.554	0.120	0.118
73	6.811	10.384	1.538	3.169	0.284	11.203	0.178	0.113
74	7.715	10.279	1.616	4.299	0.551	15.186	0.620	0.463
75	8.751	10.205	1.943	5.778	0.682	15.617	0.937	0.350
76	5.279	9.081	4.396	6.667	0.820	13.730	1.822	1.355
77	5.075	9.155	5.316	6.533	0.891	12.145	1.967	1.005
78	4.038	6.856	5.640	6.396	1.220	6.948	1.934	2.276
79	3.427	5.336	7.348	5.164	1.041	4.957	1.630	1.271
80	2.458	3.048	8.599	3.286	0.904	2.707	0.979	2.022
81	2.135	1.527	7.403	1.498	0.631	1.553	0.766	0.751
82	1.837	0.756	3.876	0.754	0.666	0.618	0.257	1.213
83	2.143	0.496	2.189	0.493	0.666	0.453	0.258	0.462
84	1.730	0.482	2.636	0.274	0.547	0.302	0.192	0.625
85	1.526	0.111	2.196	0.076	0.559	0.226	0.182	0.163
86	1.354	0.136	1.063	0.123	0.535	0.063	0.091	0.210
87	1.728	0.099	0.306	0.073	0.345	0.038	0.072	0.047
88	1.860	0.000	0.132	0.024	0.556	0.025	0.174	0.073
89	2.285	0.037	0.224	0.048	0.378	0.000	0.288	0.025
90	3.213	0.199	0.215	0.024	0.634	0.013	0.753	0.031
91	3.095	0.236	0.419	0.048	0.658	0.013	1.052	0.005
92	4.551	0.322	1.042	0.099	0.903	0.013	1.820	0.015
93	5.570	0.285	1.236	0.144	1.010	0.051	3.013	0.010
94	6.122	0.581	1.552	0.191	1.020	0.076	4.790	0.026
95	7.361	0.581	0.785	0.367	0.960	0.051	5.420	0.016
96	7.765	0.929	1.457	0.284	0.885	0.089	6.364	0.036
97	8.971	0.633	0.884	0.699	0.838	0.165	6.969	0.020
98	9.035	1.425	1.113	0.816	0.650	0.273	5.669	0.078
99	6.828	1.832	2.299	1.904	0.614	0.286	4.002	0.058
100	6.041	3.424	1.569	2.146	0.787	0.177	2.406	0.198
101	3.970	2.090	1.232	2.472	0.514	0.139	1.576	0.140
102	2.925	2.056	2.054	3.072	0.441	0.172	0.678	0.305
103	2.620	1.685	1.185	2.488	0.239	0.261	0.360	0.165
104	1.208	2.325	0.672	1.593	0.287	0.304	0.125	0.333
105	0.580	1.991	1.276	1.337	0.192	0.317	0.096	0.167
106	0.216	1.797	1.096	0.914	0.083	0.357	0.044	0.265
107	0.199	1.759	0.319	0.543	0.142	0.382	0.037	0.098
108	0.109	1.425	0.203	0.423	0.000	0.337	0.045	0.172
109	0.058	1.462	0.398	0.170	0.047	0.299	0.035	0.074
110	0.306	1.695	0.087	0.076	0.012	0.406	0.015	0.125
TOT:	**200.0**	**166.5**	**112.8**	**72.6**	**37.3**	**126.3**	**60.7**	**15.4**

Table 3a. Estimates of the von Bertalanffy growth parameters and the individual variability parameter obtained in this study. The table shows also the standard errors and correlations between the parameters.

			Correlations			
Parameter	Value	S.E.	L_∞	k	t_0	$\sigma^2_{L\infty}$
L_∞	314.90	5.772	1			
k	0.089	0.0027	-0.946	1		
t_0	-1.13	0.035	-0.570	0.794	1	
$\sigma^2_{L\infty}$	19.43	0.594	0.577	-0.559	-0.333	1

Table 3b. Estimates of the proportions by age and year, θ_{ay}, estimated from the length-frequency data.

Year/age	**1**	**2**	**3**
1970	0.210	0.352	0.439
1971	0.212	0.614	0.174
1972	0.225	0.576	0.199
1973	0.043	0.680	0.277
1974	0.392	0.265	0.343
1975	0.162	0.805	0.033
1976	0.045	0.189	0.766
1977	0.026	0.811	0.163

Table 4. Estimated lengths and weights at age, and their corresponding standard deviations, obtained in this study. Lengths (FL) are in cm and weights are in kg.

Age	**Length**	**Sdev**	**Age**	**Length**	**Sdev**
0	30.2	1.87	18	257.7	15.90
1	54.5	3.36	19	262.6	16.20
2	76.8	4.74	20	267.1	16.48
3	97.1	5.99	21	271.2	16.73
4	115.7	7.14	22	274.9	16.96
5	132.7	8.19	23	278.3	17.17
6	148.2	9.15	24	281.4	17.37
7	162.4	10.02	25	284.3	17.54
8	175.5	10.83	26	286.9	17.70
9	187.4	11.56	27	289.3	17.85
10	198.2	12.23	28	291.5	17.98
11	208.2	12.85	29	293.5	18.11
12	217.3	13.41	30	295.3	18.22
13	225.6	13.92	31	297.0	18.32
14	233.2	14.39	32	298.5	18.42
15	240.2	14.82	33	299.9	18.50
16	246.6	15.22	34	301.2	18.58
17	252.4	15.57	35	302.4	18.66

Age	**Weight**	**Sdev**	**Age**	**Weight**	**Sdev**
0	0.6	0.11	18	330.3	59.69
1	3.5	0.63	19	348.9	63.06
2	9.5	1.72	20	366.6	66.25
3	18.9	3.42	21	383.2	69.26
4	31.6	5.71	22	398.9	72.09
5	47.2	8.53	23	413.6	74.74
6	65.3	11.81	24	427.3	77.23
7	85.4	15.44	25	440.1	79.54
8	107.1	19.35	26	452.1	81.70
9	129.8	23.45	27	463.2	83.71
10	153.1	27.67	28	473.5	85.58
11	176.7	31.94	29	483.1	87.31
12	200.3	36.21	30	492.0	88.91
13	223.7	40.42	31	500.2	90.39
14	246.5	44.55	32	507.8	91.77

15	268.7	48.56	33	514.8	93.03
16	290.1	52.44	34	521.2	94.20
17	310.7	56.15	35	527.2	95.27

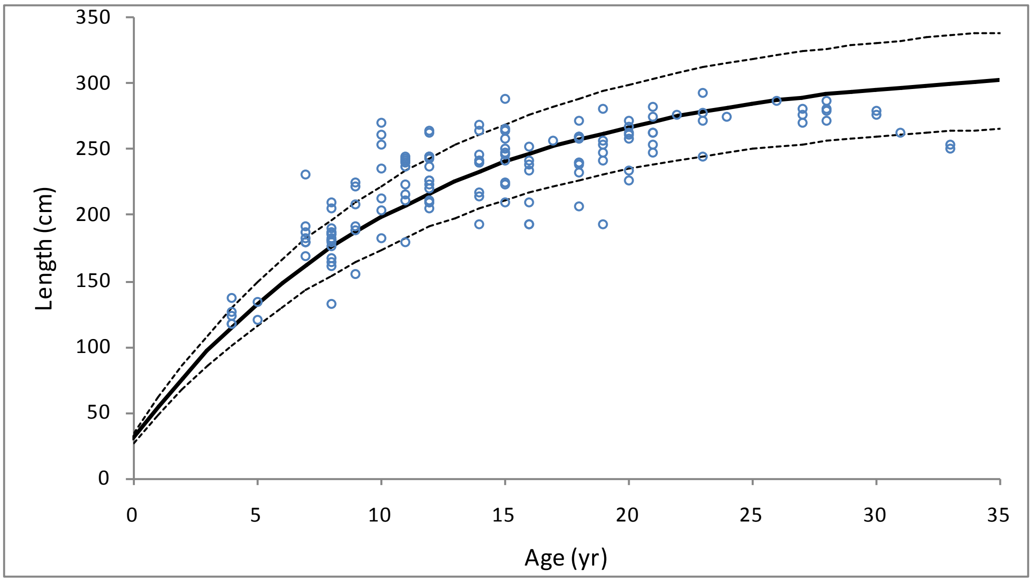

Figure 1. Observed length-age observations used in this study (circles), and the estimated growth curve (solid line) with 95% confidence intervals for the length-at-age distributions (dashed lines).

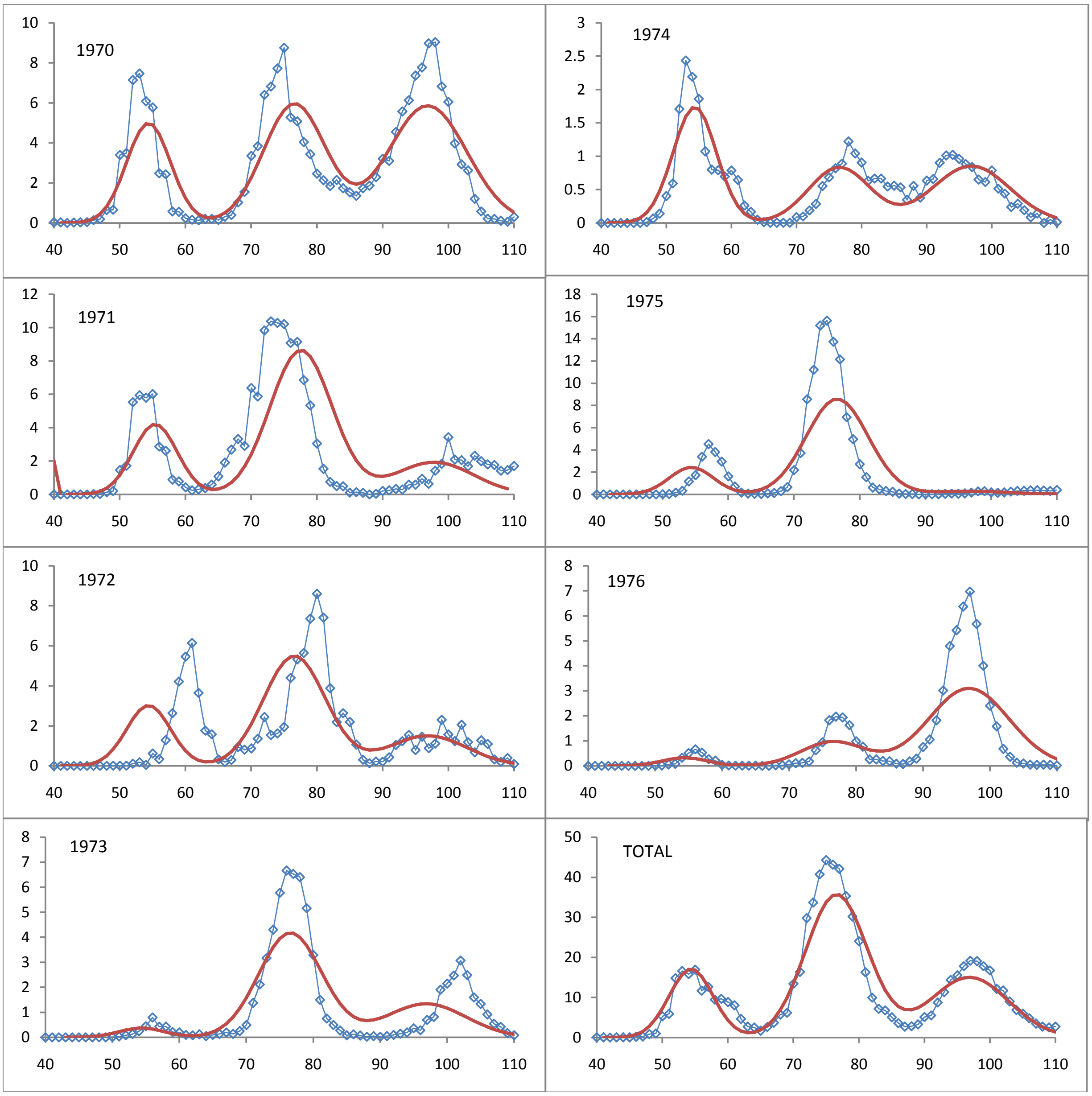

Figure 2. Observed (lines with symbols) and predicted (solid lines) length frequencies from this study. The panel on the right at the bottom shows the aggregated data for 1970-1976. The visible age groups are ages 1, 2 and 3.

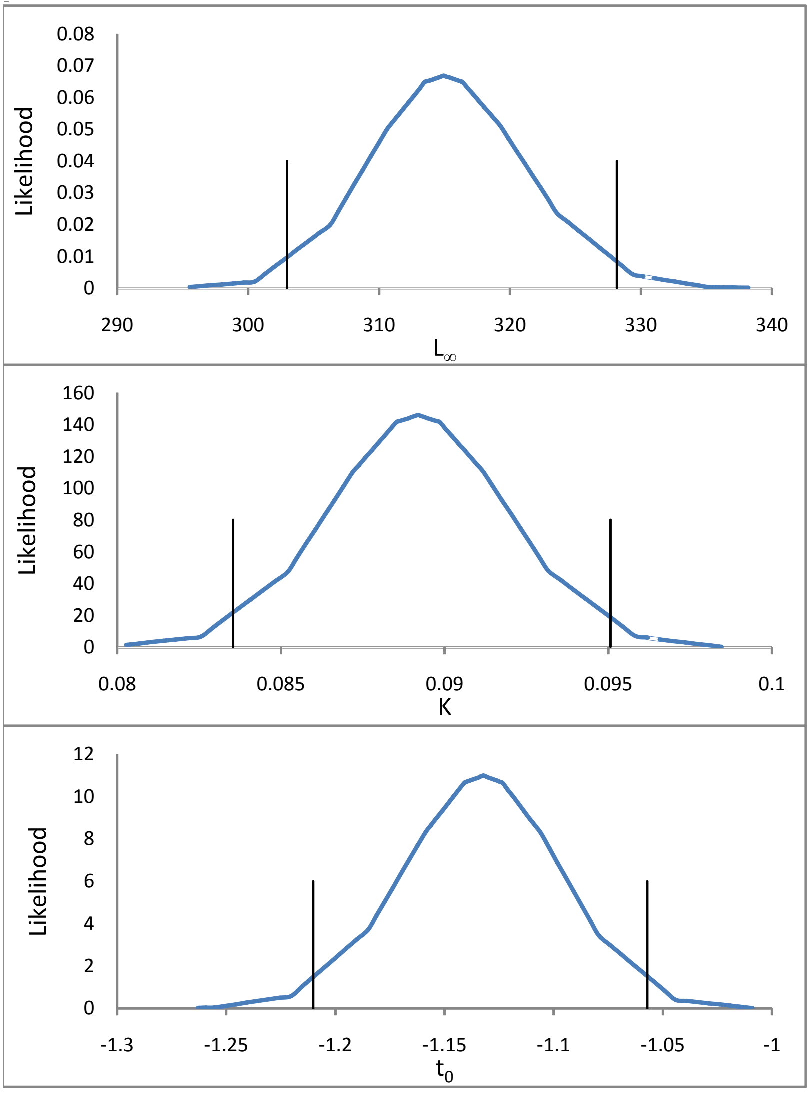

Figure 3. Likelihood profiles for the parameters L_∞, k and t_0 , with approximate 95% confidence intervals (denoted by the vertical lines).

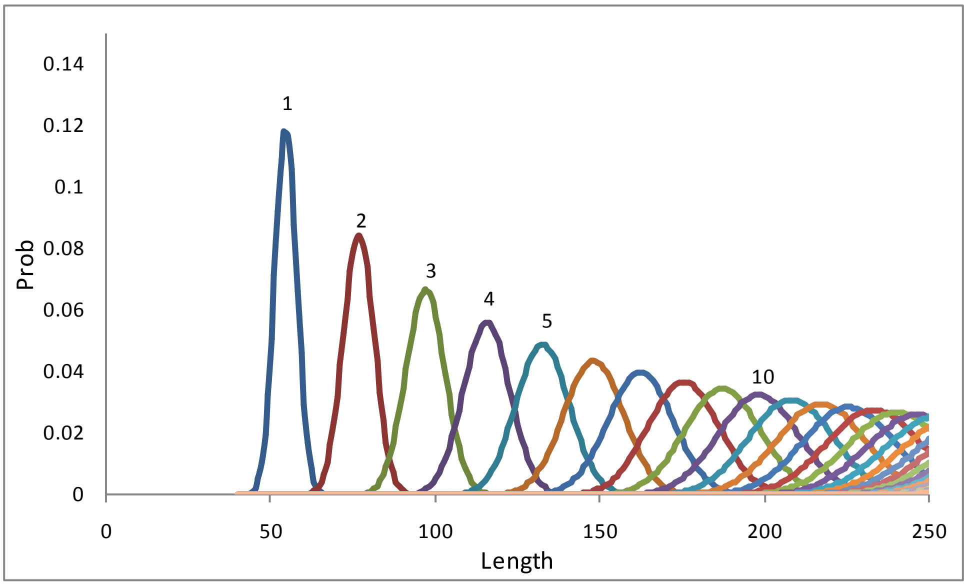

Figure 4. Predicted length-at-age distributions for western Atlantic bluefin tuna. The numbers above distributions denote the corresponding age group.

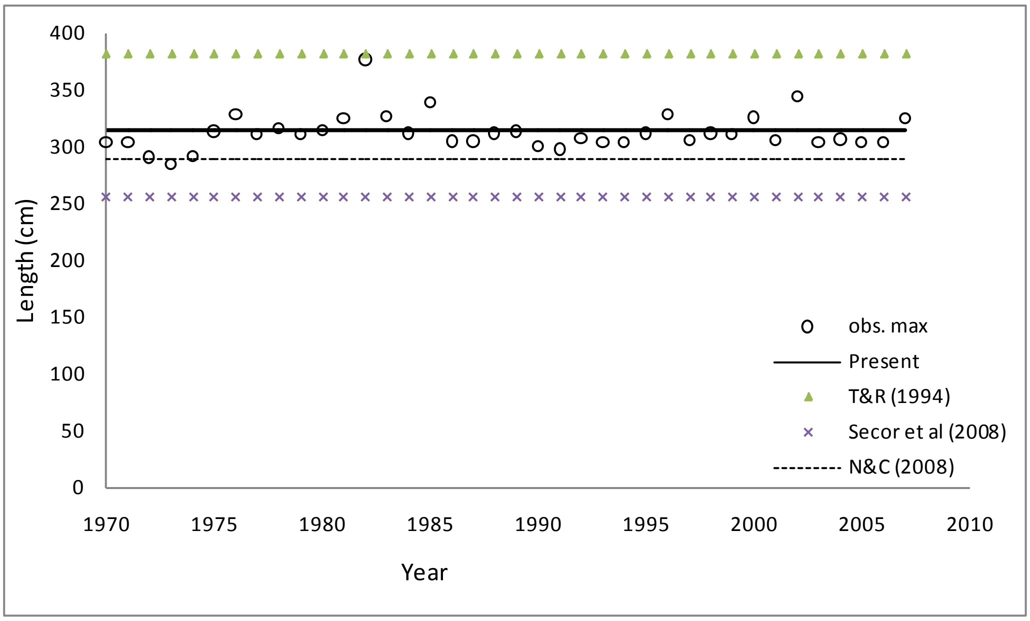

Figure 5. Observed maximum sizes (1970-2007) in the ICCAT catch-at-size database, and the estimates of L_∞ from the present study, Turner and Restrepo (1994), Secor et al. (2008), and Neilson and Campana (2008).

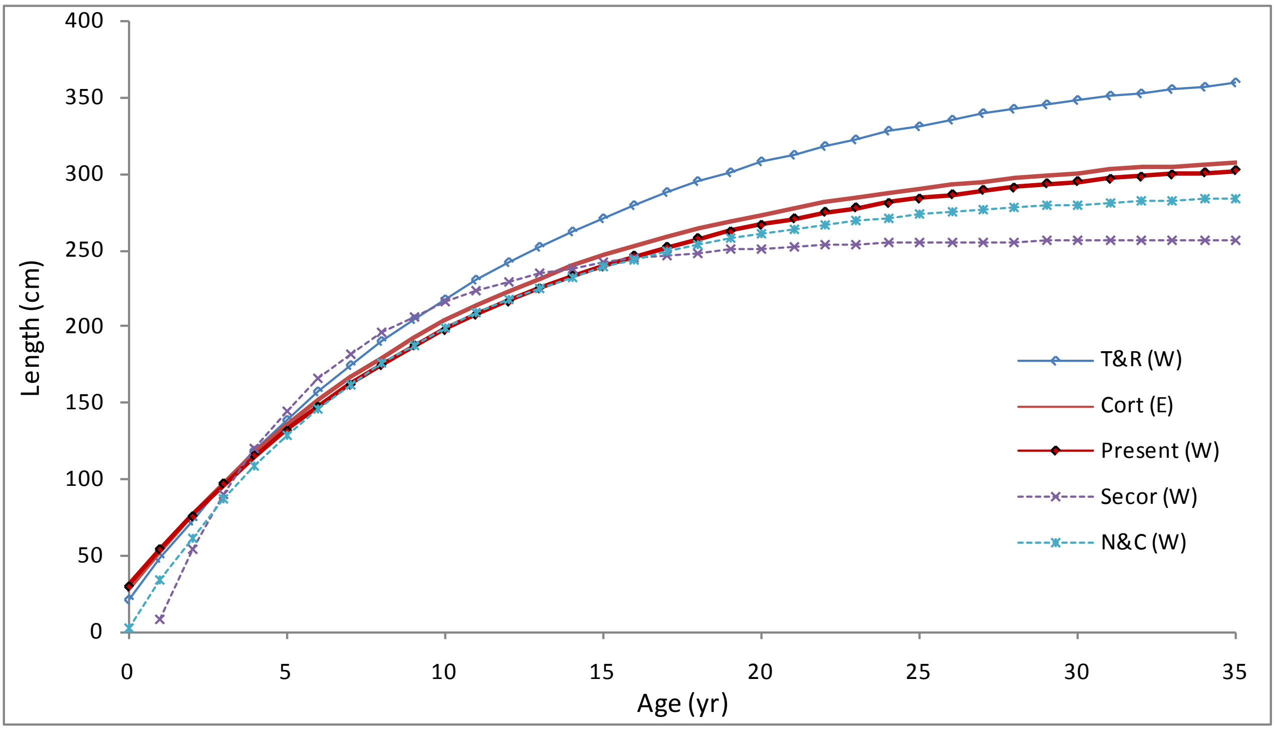

Figure 6. Estimated growth curves for western Atlantic bluefin from Turner and Restrepo (1994), Secor et al. (2008), Neilson and Campana (2008) and from the present study. Also shown is the curve for eastern Atlantic and Mediterranean bluefin from Cort (1991).