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ARE LIFE-HISTORY PARAMETERS FOR BLUEFIN TUNA ANOMALOUS?

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SUMMARY

The natural mortality rate, length at maturity, somatic growth rate that are assumed in current stock assessments and operating models for bluefin tunas are presented with reference to a range of fish species. In the context of the wider order of perciforms, Atlantic bluefin tuna parameters are consistent with many other species. When compared with the data for scombrids, bluefin tuna have similar ratios of natural mortality rate to somatic growth rate. Maturity schedules for Atlantic bluefin were not inconsistent with those that may be predicted according to basic life-history analysis. Compared to Atlantic bluefin life-history parameters, those for Pacific bluefin were more comparable to other taxonomically related species. Southern bluefin tuna length at 50% maturity relative to asymptotic length, was amongst the highest recorded for any fish in the various datasets. There was no conclusive evidence to suggest that the current set of parameters for Atlantic bluefin tuna are anomalous.

RÉSUMÉ

Le taux de mortalité naturelle, la taille à maturité, le taux de croissance somatique, postulés dans les évaluations de stocks actuelles et les modèles opérationnels pour le thon rouge, sont présentés avec une référence à une gamme d'espèces de poissons. Dans le contexte de l'ordre plus large des perciformes, les paramètres du thon rouge de l'Atlantique correspondent à ceux de nombreuses autres espèces. En comparaison avec les données concernant les scombridés, les ratios du taux de mortalité naturelle et du taux de croissance somatique du thon rouge sont similaires. Les calendriers de maturité du thon rouge de l'Atlantique étaient cohérents avec ceux que l'on pouvait prédire au moyen de l'analyse de base du cycle vital. Par rapport aux paramètres de cycle vital du thon rouge de l'Atlantique, ceux du thon rouge du Pacifique ressemblaient davantage à ceux d'autres espèces apparentées sur le plan taxonomique. La taille du thon rouge du Sud à 50% de maturité par rapport à la taille asymptotique était parmi les tailles les plus élevées enregistrées pour tous les poissons dans les différents jeux de données. Aucune preuve concluante ne permet de penser que le jeu actuel de paramètres pour le thon rouge de l'Atlantique est anormal.

RESUMEN

La tasa de mortalidad natural, la talla de madurez y la tasa de crecimiento somático que se asumen en las evaluaciones actuales del stock y los modelos operativos para el atún rojo se presentan con referencia a un rango de especies de peces. En el contexto de un orden más amplio de perciformes, los parámetros del atún rojo del Atlántico son coherentes con muchas otras especies. Al compararlos con los datos para los escómbridos, el atún rojo tiene ratios similares entre la tasa de mortalidad natural y la tasa de crecimiento somático. Los calendarios de madurez para el atún rojo del Atlántico eran coherentes con los que podrían predecirse con análisis básicos del ciclo vital. En comparación con los parámetros del ciclo vital del atún rojo del Atlántico, los del atún rojo del Pacífico eran más comparables con otras especies taxonómicamente relacionadas. La talla al 50 % de madurez del atún rojo del sur en relación con la talla asintótica se encuentra entre las más elevadas registradas para cualquier pez en los diversos conjuntos de datos. No hay ninguna evidencia concluyente para sugerir que el actual conjunto de parámetros del atún rojo del Atlántico es anómalo.

KEYWORDS

Life-history analysis, bluefin tuna, stock assessment, parameter

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Introduction

Stock assessments rely on a range of input parameters for life-history characteristics some of which are uncertain and poorly informed by assessment data and are also consequential for the estimates and predictions of stock assessments. In this paper we focus on three quantities that are fixed as inputs to Atlantic bluefin stock assessments: the natural mortality rate of mature fish, the length at maturity relative to asymptotic length and the somatic growth rate (von Bertalanffy κ). These quantities are compared with those from a dataset including a much wider range of fish species (the data of Then et al. 2015) in addition to values used in stock assessments of North Pacific bluefin tuna (ISC 2016) and Southern bluefin tuna (CCSBT 2017).

1. Methods

Bluefin case studies

The current range of scenarios for Atlantic bluefin growth, maturity and natural mortality rate are presented in **Table 1**. Also included are values from the most recent Pacific bluefin tuna and Southern bluefin tuna stock assessments. In all these cases the natural mortality rate is specified by age. The average natural mortality rate of mature fish $\bar{M}$, was calculated as the mean of the natural mortality rate at age M_a multiplied by maturity at age m_a, weighted by survival at age under unfished conditions s_a: $\bar{M} = \sum M_a m_a s_a / \sum m_a s_a$. These data are presented in Table 1. The natural mortality rate assumption for Southern bluefin tuna was the intermediate of three values. For Western bluefin tuna, where a Richards growth model is used, the closest fitting von Bertalanffy curve was used to calculate a comparable growth parameter value κ (**Figure 1**). In all cases the length at maturity relative to asymptotic length Lm, was the length at 50% maturity relative to von Bertalanffy L∞.

Reference datasets

von Bertalanffy growth rate and natural mortality rate were extracted from the Then et al. (2015) dataset. These species were cross-referenced with those of FishBase to extract age at maturity. Where age at maturity was available, the length at maturity relative to von Bertalanffy L∞ was calculated from the growth parameters of Then *et al.* (2015). These data are presented in **Table 2**.

FishBase was also interrogated for the life-history information of fish of the same family as bluefin tuna - *scombridae*. For each species of scombridae, $\bar{M}$ k and Lm were calculated as the mean of all recorded values (**Table 3**).

Calculating dissimilarity

The multivariate distance (3-D: growth rate, length at relative maturity, $\bar{M}$) of case studies from the cloud of points presented by Then *et al.* (2015) was calculated by Mahalanobis' equation. To ensure that the data were approximately multivariate normal, all parameters were presented and distances were calculated in log space.

Evaluating life-history strategies

Life-history theory suggests that fitness is maximized when fish mature at or before the age that cohort biomass is maximized. The relative size or age where cohort biomass is maximized is determined by the ratio M/κ, and empirical evidence demonstrates that the M/κ is typically correlated with relative length at maturity (Beverton 1992; Prince *et al.* 2015). The M/κ and relative length at maturity of the eight parameter sets for Atlantic bluefin (**Table 1**) were compared to those found in the Then *et al.* (2015) dataset (**Figure 4**). Relative biomass at age was plotted for a single cohort using the eights sets of assumed parameters (**Table 1**), and the age where the cohort reaches maturity (defined here from age where probability of maturity ≥ 0.5 to the first age where the entire cohort is mature), was superimposed on the plot (**Figure 5**). Simulated populations that reach maturity well after the age of maximum cohort biomass may indicate parameter combinations that are sub-optimal in terms of maximizing population fitness and unlikely to be observed in nature.

2. Results

In the context of the wider order of *perciforms*, Atlantic bluefin tuna parameters were consistent with many other species (**Figure 2**). None of the combinations of Atlantic bluefin tuna parameters were more distant than the 95th percentile of data (**Figure 2 d;e**).

When compared with the Fish Base data for *scombrids*, bluefin tuna have substantially lower values for natural mortality rate and somatic growth rate (**Figure 3a**), and for this reason fell outside the cloud of points for scombrids (**Figure 3d**). Importantly however, the various parameter combinations for Atlantic bluefin tuna had a similar ratio of these parameters to other *scombrids* (**Figure 4**).

The maturity schedule for Atlantic bluefin was not inconsistent with that predicted according to basic life-history analysis (maturity ranges were near the maximum cohort biomass, **Figure 5**).

Compared to Atlantic bluefin life-history parameters, those for Pacific bluefin were more comparable to other taxonomically related species (**Figures 2 and 3**). Southern bluefin tuna length at 50% maturity relative to asymptotic length was amongst the highest recorded in the various datasets (**Figures 2b and 3b**).

3. Discussion

This cursory investigation of life-history parameters confirms how difficult it is to draw conclusions by meta-analysis of taxonomically related species. The only way in which Atlantic bluefin tuna parameters could be considered anomalous is in their absolute values of somatic growth and natural mortality rate in comparison to the values for *scombrids* recorded in FishBase. However absolute differences are to be expected since bluefin tuna have a unique physiology and ecology that is certainly not comparable to other fast growing tropical fishes such as yellowfin tuna and skipjack tuna. Importantly however, the ratio of natural mortality rate to somatic growth was comparable. The additional life-history analysis also could find no conclusive evidence to suggest that the current range of parameter values for bluefin tuna might be considered anomalous. Interestingly this may not necessarily be the case for Southern bluefin tuna for which 50% maturity was assumed to occur at around 90% of their asymptotic length, an extremely high value for any fish species. It should be noted however that in the case of Southern Bluefin tuna, the maturity ogives are derived by close-kin genetics analysis and are subsequently uncharacteristically ‘flat’ maintaining fraction of mature individuals to much lower lengths than would be expected from the length at 50% maturity used in this analysis. This also highlights a problem with comparing maturity data: it is difficult to ensure apples with apples comparisons. For example, FishBase often records the fraction mature as the proportion of fish that have reached sexual maturity. The maturity ogive for Southern Bluefin tuna is not comparable and instead models maturity as the proportion of maximum reproductive capacity at length. The latter is consistent with how maturity curves are interpreted in assessments, and accounts for phenomenon such as more frequent spawning events per year and higher juvenile survival from larvae produced by larger mature individuals.

4. Acknowledgements

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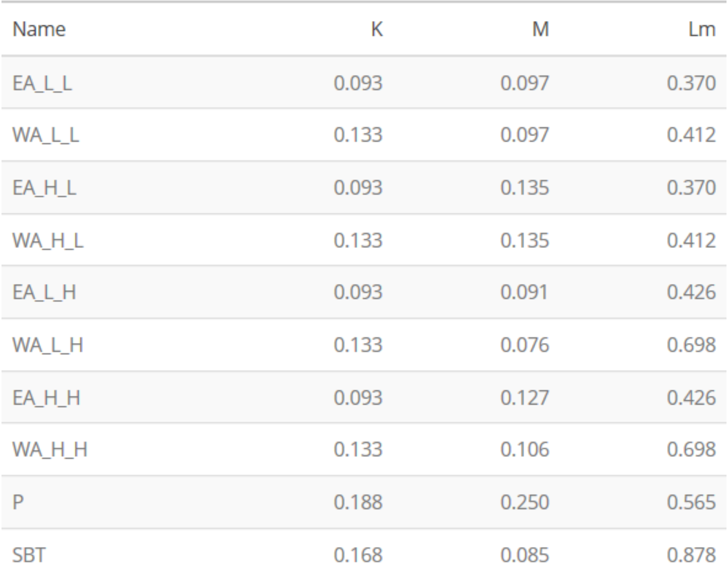
Table 1. Parameter values assumed by recent assessments and Bluefin tuna operating models. K is the von Bertalanffy growth parameter κ, M is the average natural mortality rate of mature fish under unfished conditions, Lm is the length at 50% maturity relative to asymptotic length. For the western stock that is modelled with a Richards growth curve, the closest fitting von Bertalanffy K value was assumed (**Figure 1**). The rows are named by bluefin model assumptions. EA refers to the East Atlantic stock. WA refers to the West Atlantic stock. The first extension refers to low/high natural mortality rate, the second extension low/high age at maturity. Hence WA_L_H refers to the low natural mortality rate, high age at maturity scenario for Western Atlantic bluefin tuna. P is the North Pacific bluefin stock (ISC 2016) and SBT is the southern bluefin tuna stock (SBT). The SBT natural mortality rate used here is the intermediate value for age 10+ individuals (maturity is assumed to be 100% after age 8, SBT 2017). For Western bluefin tuna, where a Richards growth model is used, the closest fitting von Bertlanffy curve was used to calculate a comparable growth parameter value κ (**Figure 1**).

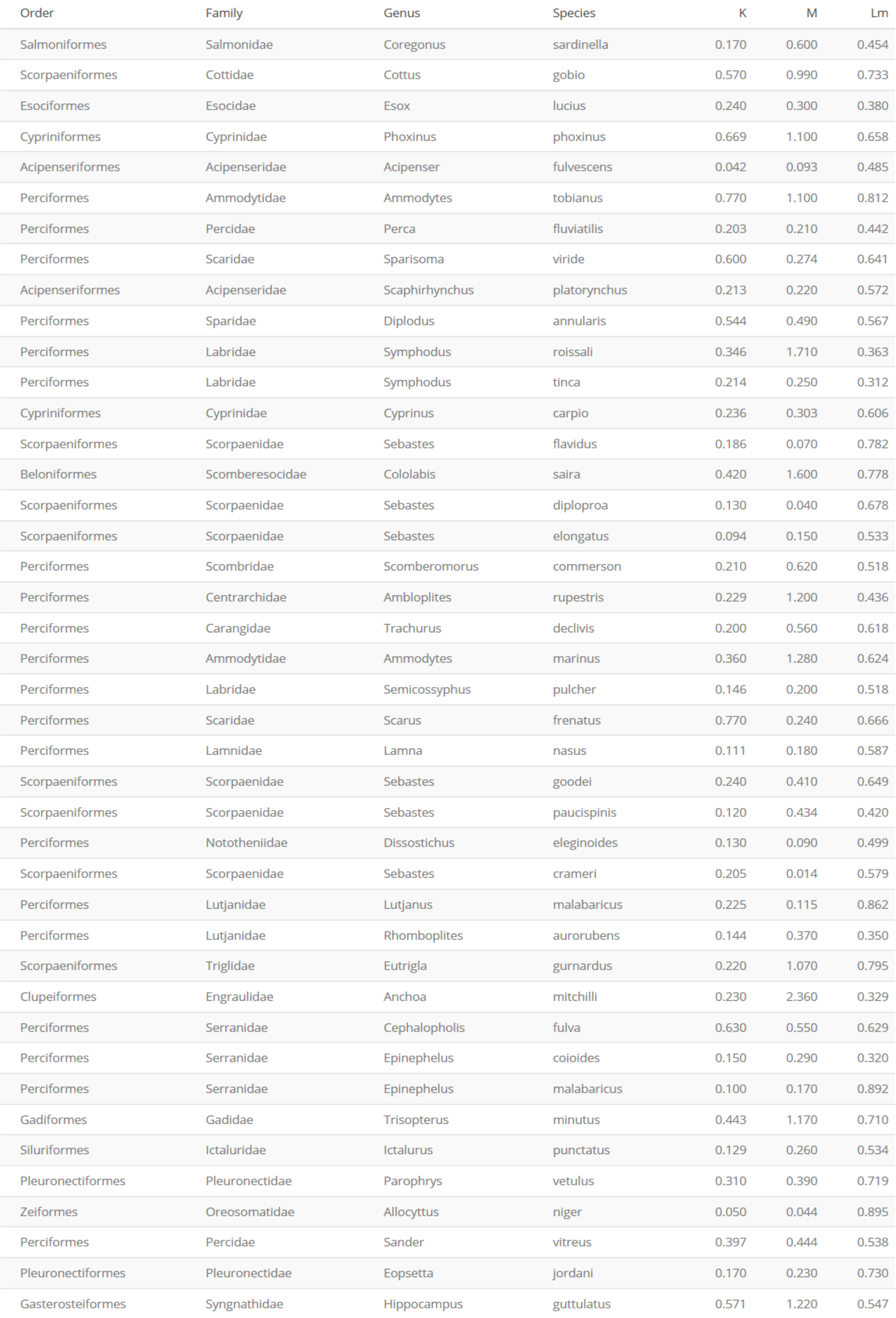


Name	K	M	Lm
EA_L_L	0.093	0.097	0.370
WA_L_L	0.133	0.097	0.412
EA_H_L	0.093	0.135	0.370
WA_H_L	0.133	0.135	0.412
EA_L_H	0.093	0.091	0.426
WA_L_H	0.133	0.076	0.698
EA_H_H	0.093	0.127	0.426
WA_H_H	0.133	0.106	0.698
P	0.188	0.250	0.565
SBT	0.168	0.085	0.878

Table 2. Life history parameters for the species of Then *et al.* 2015 for which there was also covariate maturity data available in FishBase.

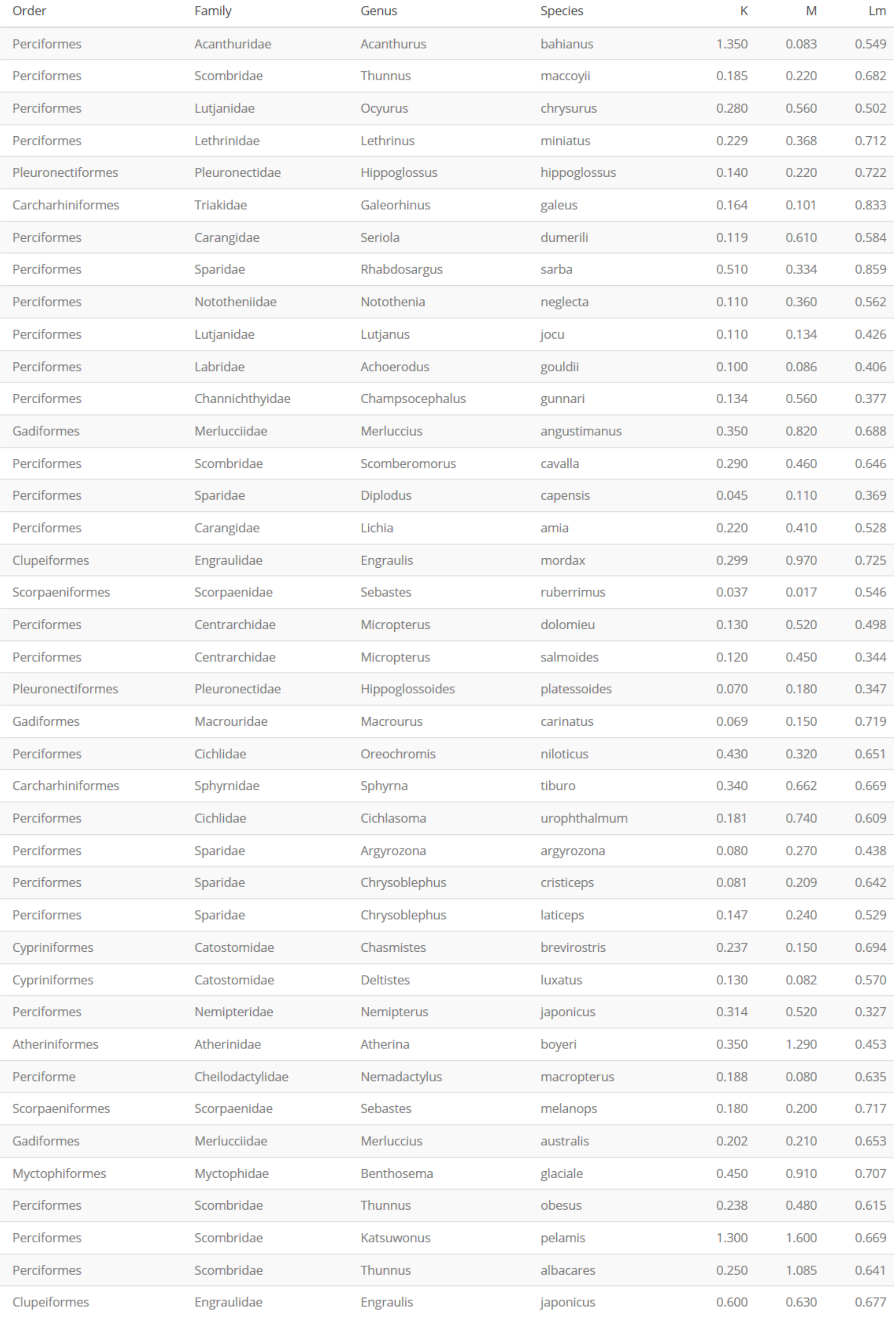
	Order	Family	Genus	Species	K	M	Lm
1	Perciformes	Sparidae	Pterogymnus	laniarius	0.130	0.360	0.659
4	Beloniformes	Hemiramphidae	Hyporhamphus	melanochir	0.524	0.550	0.663
6	Perciformes	Carangidae	Trachurus	novaezelandiae	0.230	0.180	0.743
7	Gasterosteiformes	Gasterosteidae	Gasterosteus	aculeatus	1.160	1.060	0.827
8	Perciformes	Sciaenidae	Protonibea	diacanthus	0.315	0.855	0.696
9	Scorpaeniformes	Scorpaenidae	Sebastes	alutus	0.126	0.048	0.766
11	Scorpaeniformes	Scorpaenidae	Sebastes	pinniger	0.139	0.038	0.711
15	Clupeiformes	Engraulidae	Engraulis	anchoita	0.713	0.900	0.525
17	Perciformes	Sparidae	Pagrus	pagrus	0.096	0.440	0.308
18	Gadiformes	Macrouridae	Hymenocephalus	italicus	0.196	0.645	0.613
19	Gadiformes	Macrouridae	Nezumia	aequalis	0.122	0.940	0.365
21	Perciformes	Acanthuridae	Acanthurus	nigrofuscus	0.568	0.174	0.789
24	Perciformes	Lutjanidae	Lutjanus	vitta	0.853	0.342	0.792
25	Perciformes	Serranidae	Plectropomus	leopardus	0.098	0.147	0.546
26	Perciformes	Serranidae	Plectropomus	maculatus	0.206	0.390	0.900
30	Clupeiformes	Clupeidae	Brevoortia	tyrannus	0.391	0.370	0.715
31	Clupeiformes	Engraulidae	Engraulis	ringens	1.400	1.100	0.667
32	Perciformes	Kyphosidae	Girella	tricuspidata	0.240	0.380	0.709
33	Carcharhiniformes	Carcharhinidae	Carcharhinus	sorrah	0.490	0.050	0.910
34	Carcharhiniformes	Carcharhinidae	Rhizoprionodon	taylori	1.175	0.630	0.722
36	Perciformes	Sciaenidae	Sciaenops	ocellatus	0.190	0.040	0.490
37	Perciformes	Arripidae	Arripis	trutta	0.380	0.800	0.630
39	Perciformes	Lutjanidae	Lutjanus	analis	0.160	0.130	0.415
40	Perciformes	Serranidae	Mycteroperca	bonaci	0.169	0.160	0.486
41	Scorpaeniformes	Cottidae	Hemilepidotus	jordani	0.218	0.180	0.749
44	Perciformes	Carangidae	Trachurus	japonicus	0.350	0.990	0.492
48	Perciformes	Serranidae	Plectropomus	areolatus	0.090	0.400	0.537
51	Gadiformes	Gadidae	Trisopterus	esmarkii	0.490	1.490	0.630
52	Gadiformes	Gadidae	Gadus	morhua	0.190	0.170	0.489
56	Acipenseriformes	Acipenseridae	Acipenser	transmontanus	0.023	0.180	0.378
59	Perciformes	Lethrinidae	Lethrinus	nebulosus	0.282	0.146	0.648
60	Pleuronectiformes	Pleuronectidae	Limanda	ferruginea	0.160	0.256	0.644
61	Perciformes	Lutjanidae	Lutjanus	adetii	0.150	0.240	0.943
62	Perciformes	Lutjanidae	Lutjanus	erythropterus	0.392	0.150	0.855
64	Perciformes	Serranidae	Cromileptes	altivelis	0.350	0.260	0.678
67	Pleuronectiformes	Pleuronectidae	Atheresthes	stomias	0.077	0.190	0.463
68	Clupeiformes	Clupeidae	Brevoortia	patronus	0.475	1.090	0.732
72	Perciformes	Lutjanidae	Lutjanus	griseus	0.170	0.350	0.312
73	Beryciformes	Berycidae	Beryx	splendens	0.141	0.570	0.604
74	Perciformes	Channichthyidae	Chaenodraco	wilsoni	0.780	2.260	0.707
79	Perciformes	Lutjanidae	Lutjanus	argentimaculatus	0.177	0.130	0.834

Table 2 continued.



Order	Family	Genus	Species	K	M	Lm
Salmoniformes	Salmonidae	Coregonus	sardinella	0.170	0.600	0.454
Scorpaeniformes	Cottidae	Cottus	gobio	0.570	0.990	0.733
Esociformes	Esocidae	Esox	lucius	0.240	0.300	0.380
Cypriniformes	Cyprinidae	Phoxinus	phoxinus	0.669	1.100	0.658
Acipenseriformes	Acipenseridae	Acipenser	fulvescens	0.042	0.093	0.485
Perciformes	Ammodytidae	Ammodytes	tobianus	0.770	1.100	0.812
Perciformes	Percidae	Perca	fluviatilis	0.203	0.210	0.442
Perciformes	Scaridae	Sparisoma	viride	0.600	0.274	0.641
Acipenseriformes	Acipenseridae	Scaphirhynchus	platorynchus	0.213	0.220	0.572
Perciformes	Sparidae	Diplodus	annularis	0.544	0.490	0.567
Perciformes	Labridae	Symphodus	roissali	0.346	1.710	0.363
Perciformes	Labridae	Symphodus	tinca	0.214	0.250	0.312
Cypriniformes	Cyprinidae	Cyprinus	carpio	0.236	0.303	0.606
Scorpaeniformes	Scorpaenidae	Sebastes	flavidus	0.186	0.070	0.782
Beloniformes	Scomberesocidae	Cololabis	saira	0.420	1.600	0.778
Scorpaeniformes	Scorpaenidae	Sebastes	diploproa	0.130	0.040	0.678
Scorpaeniformes	Scorpaenidae	Sebastes	elongatus	0.094	0.150	0.533
Perciformes	Scombridae	Scomberomorus	commerson	0.210	0.620	0.518
Perciformes	Centrarchidae	Ambloplites	rupestris	0.229	1.200	0.436
Perciformes	Carangidae	Trachurus	declivis	0.200	0.560	0.618
Perciformes	Ammodytidae	Ammodytes	marinus	0.360	1.280	0.624
Perciformes	Labridae	Semicossyphus	pulcher	0.146	0.200	0.518
Perciformes	Scaridae	Scarus	frenatus	0.770	0.240	0.666
Perciformes	Lamnidae	Lamna	nasus	0.111	0.180	0.587
Scorpaeniformes	Scorpaenidae	Sebastes	goodei	0.240	0.410	0.649
Scorpaeniformes	Scorpaenidae	Sebastes	paucispinis	0.120	0.434	0.420
Perciformes	Nototheniidae	Dissostichus	eleginoides	0.130	0.090	0.499
Scorpaeniformes	Scorpaenidae	Sebastes	crameri	0.205	0.014	0.579
Perciformes	Lutjanidae	Lutjanus	malabaricus	0.225	0.115	0.862
Perciformes	Lutjanidae	Rhomboplites	aurorubens	0.144	0.370	0.350
Scorpaeniformes	Triglidae	Eutrigla	gurnardus	0.220	1.070	0.795
Clupeiformes	Engraulidae	Anchoa	mitchilli	0.230	2.360	0.329
Perciformes	Serranidae	Cephalopholis	fulva	0.630	0.550	0.629
Perciformes	Serranidae	Epinephelus	coioides	0.150	0.290	0.320
Perciformes	Serranidae	Epinephelus	malabaricus	0.100	0.170	0.892
Gadiformes	Gadidae	Trisopterus	minutus	0.443	1.170	0.710
Siluriformes	Ictaluridae	Ictalurus	punctatus	0.129	0.260	0.534
Pleuronectiformes	Pleuronectidae	Parophrys	vetulus	0.310	0.390	0.719
Zeiformes	Oreosomatidae	Allocyttus	niger	0.050	0.044	0.895
Perciformes	Percidae	Sander	vitreus	0.397	0.444	0.538
Pleuronectiformes	Pleuronectidae	Eopsetta	jordani	0.170	0.230	0.730
Gasterosteiformes	Syngnathidae	Hippocampus	guttulatus	0.571	1.220	0.547

Table 2 continued.



Order	Family	Genus	Species	K	M	Lm
Perciformes	Acanthuridae	Acanthurus	bahianus	1.350	0.083	0.549
Perciformes	Scombridae	Thunnus	maccoyii	0.185	0.220	0.682
Perciformes	Lutjanidae	Ocyurus	chrysurus	0.280	0.560	0.502
Perciformes	Lethrinidae	Lethrinus	miniatus	0.229	0.368	0.712
Pleuronectiformes	Pleuronectidae	Hippoglossus	hippoglossus	0.140	0.220	0.722
Carcharhiniformes	Triakidae	Galeorhinus	galeus	0.164	0.101	0.833
Perciformes	Carangidae	Seriola	dumerili	0.119	0.610	0.584
Perciformes	Sparidae	Rhabdosargus	sarba	0.510	0.334	0.859
Perciformes	Nototheniidae	Notothenia	neglecta	0.110	0.360	0.562
Perciformes	Lutjanidae	Lutjanus	jocu	0.110	0.134	0.426
Perciformes	Labridae	Achoerodus	gouldii	0.100	0.086	0.406
Perciformes	Channichthyidae	Champsocephalus	gunnari	0.134	0.560	0.377
Gadiformes	Merlucciidae	Merluccius	angustimanus	0.350	0.820	0.688
Perciformes	Scombridae	Scomberomorus	cavalla	0.290	0.460	0.646
Perciformes	Sparidae	Diplodus	capensis	0.045	0.110	0.369
Perciformes	Carangidae	Lichia	amia	0.220	0.410	0.528
Clupeiformes	Engraulidae	Engraulis	mordax	0.299	0.970	0.725
Scorpaeniformes	Scorpaenidae	Sebastes	ruberrimus	0.037	0.017	0.546
Perciformes	Centrarchidae	Micropterus	dolomieu	0.130	0.520	0.498
Perciformes	Centrarchidae	Micropterus	salmoides	0.120	0.450	0.344
Pleuronectiformes	Pleuronectidae	Hippoglossoides	platessoides	0.070	0.180	0.347
Gadiformes	Macrouridae	Macrourus	carinatus	0.069	0.150	0.719
Perciformes	Cichlidae	Oreochromis	niloticus	0.430	0.320	0.651
Carcharhiniformes	Sphyrnidae	Sphyrna	tiburo	0.340	0.662	0.669
Perciformes	Cichlidae	Cichlasoma	urophthalmum	0.181	0.740	0.609
Perciformes	Sparidae	Argyrozona	argyrozona	0.080	0.270	0.438
Perciformes	Sparidae	Chrysoblephus	cristiceps	0.081	0.209	0.642
Perciformes	Sparidae	Chrysoblephus	laticeps	0.147	0.240	0.529
Cypriniformes	Catostomidae	Chasmistes	brevirostris	0.237	0.150	0.694
Cypriniformes	Catostomidae	Deltistes	luxatus	0.130	0.082	0.570
Perciformes	Nemipteridae	Nemipterus	japonicus	0.314	0.520	0.327
Atheriniformes	Atherinidae	Atherina	boyeri	0.350	1.290	0.453
Perciforme	Cheilodactylidae	Nemadactylus	macropterus	0.188	0.080	0.635
Scorpaeniformes	Scorpaenidae	Sebastes	melanops	0.180	0.200	0.717
Gadiformes	Merlucciidae	Merluccius	australis	0.202	0.210	0.653
Myctophiformes	Myctophidae	Benthosema	glaciale	0.450	0.910	0.707
Perciformes	Scombridae	Thunnus	obesus	0.238	0.480	0.615
Perciformes	Scombridae	Katsuwonus	pelamis	1.300	1.600	0.669
Perciformes	Scombridae	Thunnus	albacares	0.250	1.085	0.641
Clupeiformes	Engraulidae	Engraulis	japonicus	0.600	0.630	0.677

Table 3. Life history parameters of FishBase recorded for other *scombridae*. Values are the averages of all reported values for each species.

Species	K	M	Lm
Auxis rochei	0.513	1.440	0.731
Auxis thazard	0.787	1.410	0.639
Euthynnus affinis	0.745	1.534	0.641
Euthynnus alletteratus	0.251	0.440	0.489
Katsuwonus pelamis	0.602	1.188	0.508
Rastrelliger kanagurta	1.248	2.481	0.660
Sarda sarda	0.529	0.870	0.527
Scomber japonicus	0.307	0.550	0.806
Scomber scombrus	0.344	0.193	0.728
Scomberomorus cavalla	0.172	0.297	0.542
Scomberomorus commerson	0.451	0.920	0.483
Scomberomorus guttatus	0.565	1.063	0.544
Scomberomorus maculatus	0.303	0.300	0.444
Scomberomorus tritor	0.318	0.870	0.412
Thunnus alalunga	0.199	0.213	0.676
Thunnus albacares	0.400	0.456	0.578
Thunnus atlanticus	0.392	0.670	0.589
Thunnus obesus	0.216	0.390	0.486

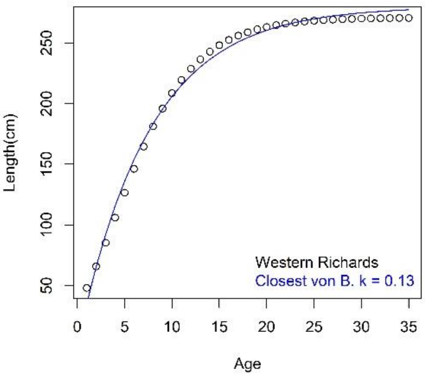


Figure 1. The Richards growth curve used in Western Atlantic assessments and the closest fitting von Bertalanffy growth curve.

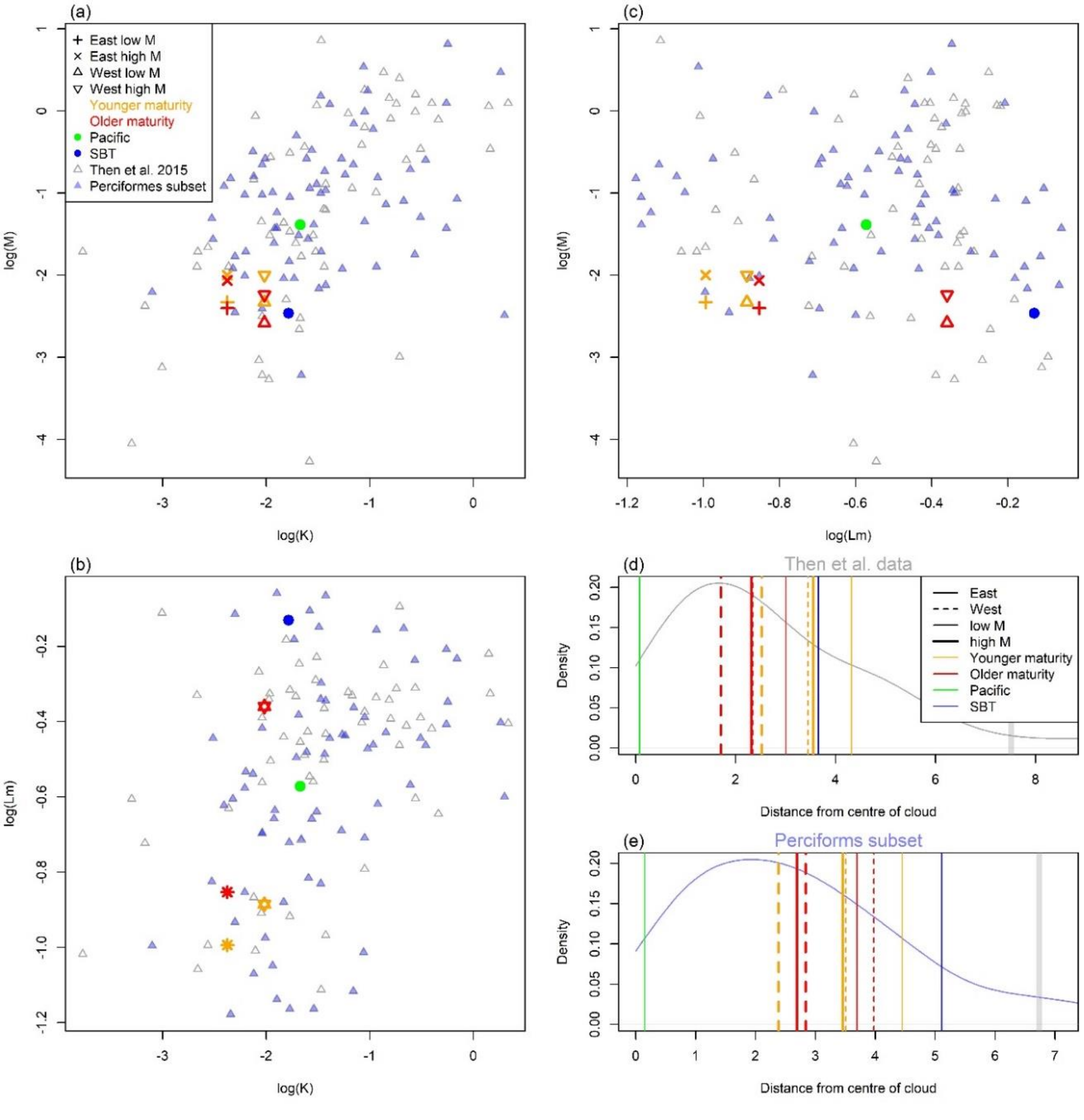


Figure 2. The similarity among assumed bluefin tuna life-history parameters (M=natural mortality rate, K = von Bertalanffy κ, Lm = length at maturity relative to asymptotic length) and those published by Then et al. 2015 (the 'Perciforms subset' are fish of that order in the Then *et al.* 2015 dataset). The bottom right panels (d and e) show the Mahalanobis distance (multivariate distance) of these values from the centre of the multivariate cloud of points. The vertical grey lines in panels d and e represent the 95th percentile of distances.

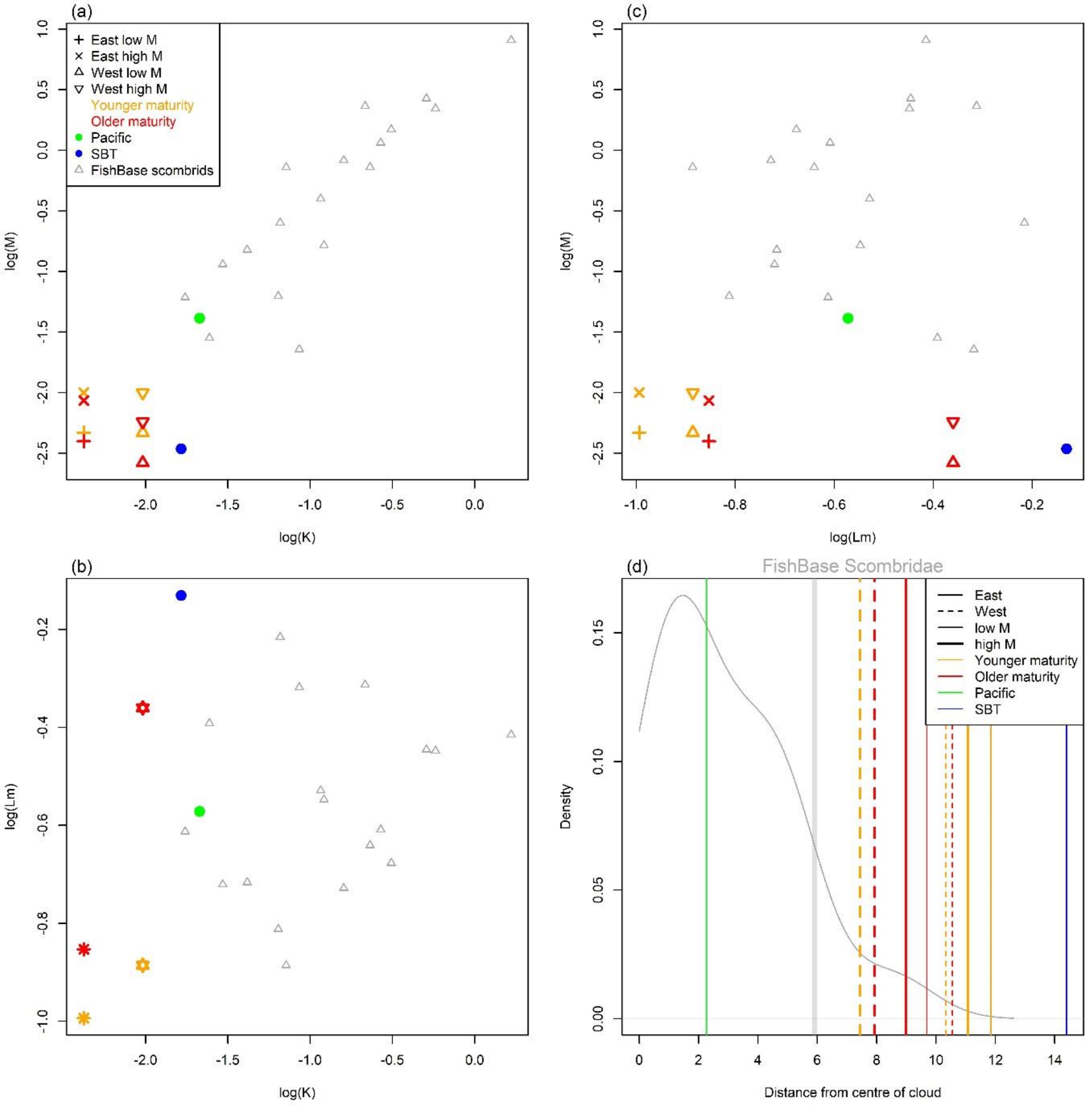


Figure 3. As **Figure 2** but comparison between case study bluefin parameters and scombrid species of FishBase for which all parameters are available.

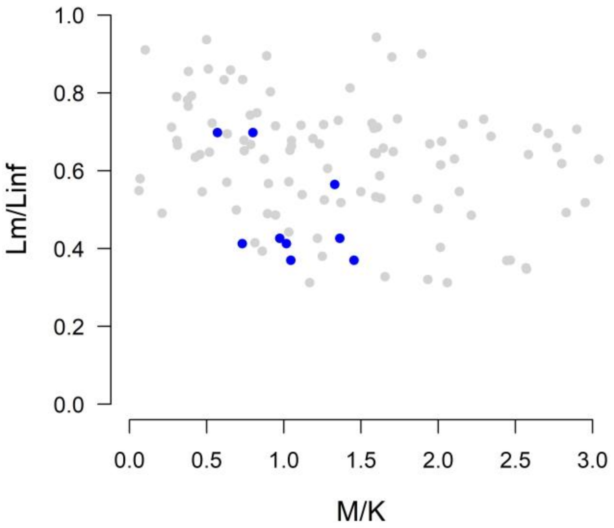


Figure 4. The ratio of M/K and relative size of maturity (Lm/Linf) for the 8 parameter sets for Atlantic bluefin (blue dots) and the 124 records from the Then *et al.* (2015) dataset.

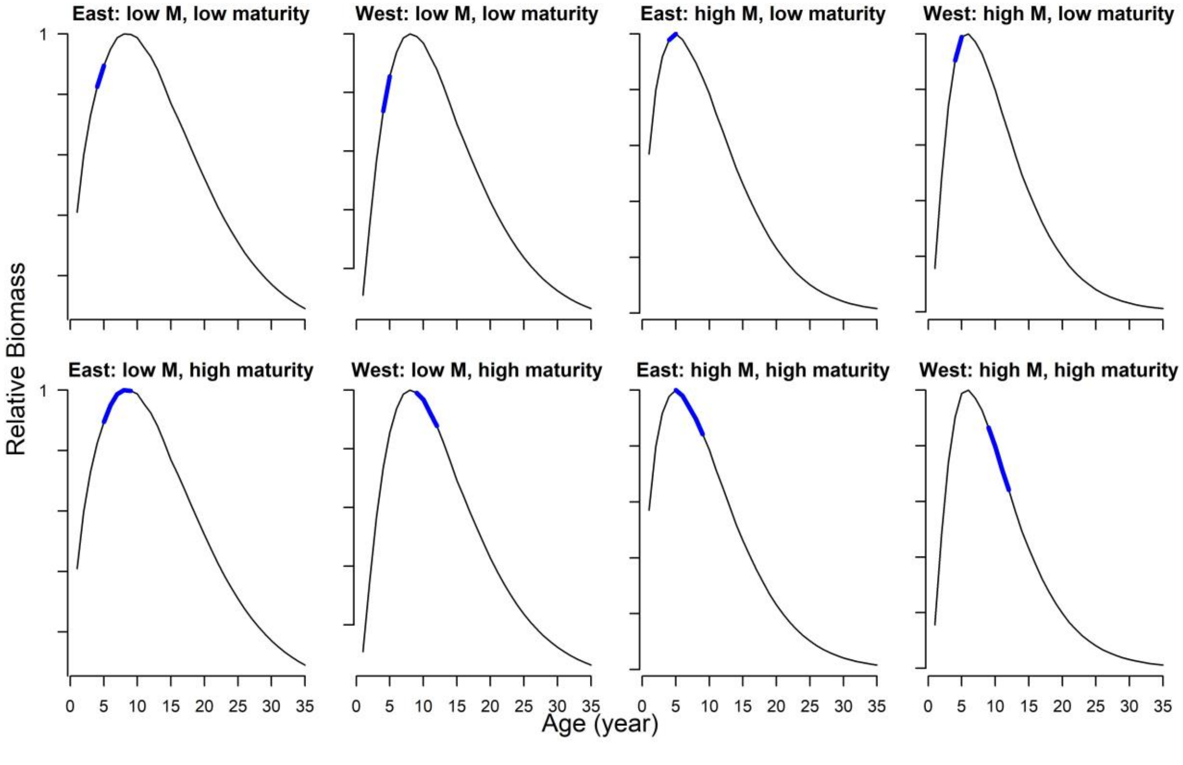


Figure 5. Cohort biomass at age for the 8 parameter sets for Atlantic Bluefin with different assumptions on natural mortality rate and maturity. The blue solid line indicates the age class where the cohort reaches maturity.