

AN INITIAL APPLICATION OF THE SPATIAL STRUCTURE FRAMEWORK FOR NORTH ATLANTIC BLUEFIN DEVELOPED AT THE SEPTEMBER 2001 BLUEFIN MIXING WORKSHOP USING SIMPLE AGE-AGGREGATED MODELS

A.E. Punt¹ and D.S. Butterworth²

SUMMARY

The September 2001 ICCAT workshop on bluefin mixing identified a spatial structure (the six strata in Fig. 3 of the report of that meeting) as a starting point for preliminary model development towards incorporating greater biological realism in future assessments. A simple age-aggregated (production) model approach with inter-stratum mixing (overlap) is applied to provide some insight into the implications of the different catch histories in the six strata defined. Nine scenarios were considered, for different values of 1998 depletion in the western (strata 1-3) and eastern (strata 4-6) Atlantic each ranging from 0.2 to 0.4. Results for these scenarios suggest that with or without mixing, the 1997 catch levels of bluefin in the western Atlantic are sustainable; however, those in the east for 1997 are well above sustainable levels and need substantial reduction. Even at relatively modest levels of mixing, the fishery in the west will be adversely impacted unless this reduction in the east takes place. This conclusion is robust over quite a wide range of options for resource productivity and overlap parameter values.

RÉSUMÉ

L'Atelier ICCAT de septembre 2001 sur les échanges du thon rouge a identifié une structure spatiale (les six strates de la Fig.3 du rapport de cette réunion) comme point de départ pour le développement préliminaire d'un modèle en vue d'incorporer davantage de réalisme biologique dans les évaluations futures. Une approche du modèle simple (de production) regroupé par âge avec un mélange inter-strates (superposition) est appliquée pour découvrir les implications des différentes captures historiques dans les six strates définies. Neuf scénarios ont été examinés, pour différentes valeurs de la raréfaction de 1998 dans l'Atlantique ouest (strates 1-3) et est (strates 4-6) dans une fourchette allant de 0,2 à 0,4. Les résultats de ces scénarios suggèrent qu'avec ou sans mélange, les niveaux de capture du thon rouge de 1997 dans l'Atlantique ouest sont soutenable ; toutefois, ceux dans l'est pour 1997 sont bien en-dessus des niveaux soutenable et doivent être considérablement réduits. Même à des niveaux de mélange relativement modestes, la pêcherie dans l'ouest sera négativement affectée sauf s'il y a réduction dans l'est. Cette conclusion est robuste sur une gamme assez vaste d'options de productivité des ressources et se superpose aux valeurs du paramètre.

RESUMEN

Las Jornadas de Trabajo ICCAT de septiembre de 2001 sobre mezcla de atún rojo identificaron una estructura espacial (el estrato seis en la figura 3 del informe de dicha reunión) como punto de partida para el desarrollo del modelo preliminar encaminado a la incorporación de un mayor realismo biológico en futuras evaluaciones. Se aplica un enfoque de modelo de producción agregado por edad simple con mezcla entre estratos (superposición) para proporcionar una visión de las implicaciones de los diferentes historiales de capturas en el estrato seis que se ha definido. Se consideraron nueve escenarios, para diferentes valores de merma de 1998 en el Atlántico oeste (estrato 1-3) y este (estrato 4-6), oscilando cada uno entre 0,2 y 0,4. Los resultados para estos escenarios sugieren que con o sin mezcla, los niveles de captura de atún rojo de 1997 en el Atlántico oeste son sostenibles, sin embargo, los del este

¹ School of Aquatic and Fishery Sciences, University of Washington, Box 355020, Seattle, WA 98195-5020, USA. Email: aepunt@u.washington.edu

² MARAM (Marine Resource Assessment and Management Group), University of Cape Town, Department of Mathematics and Applied Mathematics, Rondebosch, 7701, South Africa.

para 1997 están muy por encima de los niveles sostenibles y necesitan una reducción sustancial. Incluso en niveles relativamente modestos de mezcla, la pesquería del Oeste se verá negativamente afectada a menos que se produzca dicha reducción en el Este. Esta conclusión es robusta en una amplia gama de opciones para la productividad del recurso y se superpone a los valores de los parámetros.

KEYWORDS

Bluefin tuna; Migrations; Population numbers; Yield predictions

1. INTRODUCTION

The ICCAT workshop on bluefin tuna mixing, that took place in September 2001 (ICCAT, 2001) specified six spatial strata (regions) for the Atlantic, Gulf of Mexico and Mediterranean Sea to serve as a basis for incorporating greater biological realism in future bluefin assessment models. A breakdown of historical catches in these regions from 1950 to 1997 was also provided.

This paper develops a simple dynamic Schaefer model approach, incorporating partial overlap of stocks of western and eastern origin, to identify what qualitative conclusions might be drawn from these catch histories. The population dynamics methodology and mixing / overlap assumptions are specified first, and then applied to the catch history data over a range of assumptions for input parameters. Qualitative conclusions are then drawn from the results obtained.

2. METHODOLOGY

This analysis considers two reproductive units in the Gulf of Mexico (western stock) and Mediterranean Sea (eastern stock), which each spread into the Atlantic each year with time-invariant distribution patterns, and with differing degrees of overlap.

The dynamics of western stock animals are given by:

$$B_{y+1,A}^W = \begin{cases} \phi_1^W B_y^W + r B_y^W (1 - B_y^W / K^W) - C_y^1 & \text{if } A = 1 \\ \phi_j^W B_y^W - C_y^j \frac{B_{y,A}^W}{B_{y,A}^W + B_{y,A}^E} & \text{otherwise} \end{cases} \quad (1)$$

- where B_y^W is total biomass of the western stock at the start of year y ,
 $B_{y,A}^W$ is the biomass of the western stock in region A at the start of year y ,
 r is the intrinsic rate of growth (assumed common across stocks),
 K^W is the carrying capacity of the western stock,
 C_y^j is the catch (in mass) from region j in year y ,
 ϕ_j^W is the proportion of the western stock in region j , and
 $B_{y,A}^E$ is the biomass of the component of the eastern stock in region A at the start of year y .

The dynamics of eastern stock animals are given by:

$$B_{y+1,A}^E = \begin{cases} \phi_6^E B_y^E + r B_y^E (1 - B_y^E / K^E) - C_y^6 & \text{if } A = 6 \\ \phi_j^E B_y^E - C_y^j \frac{B_{y,A}^E}{B_{y,A}^E + B_{y,A}^W} & \text{otherwise} \end{cases} \quad (2)$$

where B_y^E is total biomass of the eastern stock at the start of year y ,
 K^E is the carrying capacity of the eastern stock, and
 ϕ_j^E is the proportion of the eastern stock in region j .

The six regions are those selected by the September ICCAT Workshop on Bluefin Mixing (ICCAT, 2001 – see Fig. 3 thereof), viz. 1: Gulf of Mexico, 2: West Atlantic, 3: Central Atlantic, 4: Northeastern Atlantic, 5: East Atlantic; 6: Mediterranean Sea.

For the analyses that include mixing of the two stocks, the parameters that determine their mixing are selected so that (approximately) density declines with distance from the known spawning grounds. For the western stock therefore, density declines from region 2 though regions 3, 4 and 5. For the eastern stock, the densities are based on the assumption that density declines from east to west but that density in regions 4 and 5 is the same (they are roughly equidistant from the Mediterranean Sea). For simplicity of parameterization, density is assumed to decline linearly with region number, i.e.:

$$\phi_i^W = A_i \delta_i^W / \sum_j A_j \delta_j^W \quad \phi_i^E = A_i \delta_i^E / \sum_j A_j \delta_j^E \quad (3)$$

where A_i is (approximately) the area of region i (determined by counting the number of 5×5^0 squares in Fig. 3 of ICCAT (2001) – 25, 51, 30, 22, 36 and 14 for regions 1-6 respectively),
 δ_i^W is the relative density of the western stock in region i :

$$\delta_i^W = \begin{cases} 1 & \text{if } i = 1 \\ 1 - \frac{i-2}{3}(1-p^W) & \text{if } 2 \leq i \leq 5 \\ 0 & \text{if } i = 6 \end{cases} \quad (4a)$$

δ_i^E is the relative density of the eastern stock in region i :

$$\delta_i^E = \begin{cases} 0 & \text{if } i = 1 \\ \frac{i-2}{3} - \frac{i-5}{3} p^E & \text{if } i = 2 \text{ or } i = 3 \\ \frac{5}{6} + \frac{1}{6} p^E & \text{if } i = 4 \text{ or } i = 5 \\ 1 & \text{if } i = 6 \end{cases} \quad (4b)$$

p^W is the density of the western stock in region 5 relative to that in region 2, and
 p^E is the density of the eastern stock in region 2 relative to that in region 6.

Note that $\phi_6^W = 0$ and $\phi_1^E = 0$, i.e. no western origin animals enter the Mediterranean Sea, and none of eastern origin enter the Gulf of Mexico.

The values used for catches by region and year are those given in Table 2 of ICCAT (2001) over 1950-97. Projections assume for illustrative purposes that catch levels by region for 1997 continue unchanged for the following 10 years.

The computations assume the western and eastern stocks to be at their carrying capacities in 1950, i.e. $B_{1950}^W = K^W$, $B_{1950}^E = K^E$. Clearly this is a simplification, as there were bluefin catches taken before this time and also environmentally induced variability could impact these relations. Possible future analyses of this nature could attempt to adjust for these factors.

For the baseline computations, the value of r is set to 0.3yr^{-1} , based upon similar estimates for dynamic Schaefer model fits to the southern bluefin tuna (SBT) resource (Butterworth and Johnston, 2001, and associated subsequent refinements). Note that this corresponds to an MSY fishing mortality of 0.15yr^{-1} , which is close to the value of $M=0.14\text{yr}^{-1}$ conventionally assumed for ADAPT assessments of the west Atlantic bluefin. Mixing (overlap) for this baseline sets $p^W = p^E = 0.05$. For comparative runs without mixing, the western origin animals are confined to regions 1, 2 and 3, and those from the east to regions 4, 5 and 6.

3. RESULTS AND DISCUSSION

With r and the overlap (ϕ) parameters specified, only two free population model parameters remain: K^W and K^E . These were fixed by specifying current (1998) abundance levels and solving for K^W and K^E by use of Equations (1) and (2). Current abundance levels are specified as “depletions” (fractions of pre-exploitation levels). Here, however, we work with depletions by area (west=regions 1-3; east=regions 4-6), rather than by stock, as available indices of abundance relate to the combined numbers (or biomass) of bluefin from both stocks in some region, rather than to stock numbers (or biomass). Thus \tilde{B}_y^W relates to the biomass of bluefin from either stock in the western area (regions 1-3) in year y , and \tilde{K}^W to the corresponding eastern area. \tilde{B}_y^E and \tilde{K}^E are defined similarly. The depletions specified to determine the stock-specific values for K^W and K^E are then $\tilde{B}_{1998}^W / \tilde{K}^W$ and $\tilde{B}_{1998}^E / \tilde{K}^E$.

Nine scenarios have been considered: all combinations of western area depletion ($\tilde{B}_{1998}^W / \tilde{K}^W$) of 0.2, 0.4 and 0.6, and eastern area depletion ($\tilde{B}_{1998}^E / \tilde{K}^E$) of 0.2, 0.4 and 0.6. It seems reasonable to argue that these two ranges may cover the actual situation. Past exploitation of these resources is perceived to have been heavy, so that 1998 depletions above 0.6 seem improbable. At the other extreme, for depletions below 0.2, the form of model used can encounter difficulties in fitting, essentially because past catches in some region become greater than the biomass of bluefin which the overlap model allocates to that region in the year concerned.

The population trajectories corresponding to these nine scenarios are shown by area in Fig. 1 and by stock in Fig. 2, both for the baseline level of mixing / overlap, and for the situation where there is no overlap of the two stocks. For three of the scenarios, it is not possible (when there is mixing) to match the target depletions by area exactly (see Table 1c), but the “lack of fit” is appreciable only for the scenario that intended a western / eastern area depletion combination of 0.2 / 0.6.

These two Figures show that for both the eastern area and the eastern stock, results hardly differ with or without mixing. This is a reflection of the fact that for all nine scenarios, pre-exploitation abundance (K or \tilde{K}) in the east is much greater than that in the west. There are, however, appreciable differences for the western area, which tend to be larger for higher values of depletion. Whereas with no mixing / overlap, the trend for abundance in the western area since 1980 has been flat or increasing, when mixing is taken into account, this trend becomes decreasing or flat. This reason for this mixing result is that the eastern stock is being reduced by heavy exploitation in the east, and this in turn reduces the number of eastern origin bluefin to be found in the western area.

As far as the stocks are concerned (Fig. 2), all scenarios show a rapid decline in the abundance of the eastern stock over the 1990's. The western stock trend is either flat or increasing over this period. Western stock depletions when there is mixing are lower than when there is not, except for the three scenarios for which 1998 depletion by area is larger for the west than for the east.

The question arises of whether available abundance index data (CPUE series) can distinguish between these scenarios. Probably the most representative of these series in the context of this exercise are the Japanese oceanic longline series. Regressions of log CPUE against year for these series over

1980-97 give annual slopes of 0.047yr^{-1} (se 0.029) for the western area (series JLL NWAtl; Table 6 of ICCAT 1999) and -0.075 yr^{-1} (se 0.017) for the eastern area (series Japan LL E & Med; Table 5 of ICCAT 1999). For comparative purposes, the corresponding slopes for the estimated abundance trends in Fig. 1 are shown in Table 2 for each of the nine scenarios. At a 5% significance level, these CPUE data for the west cannot distinguish the scenarios. However, the series for the east is more informative in this context; only the scenarios with an eastern area depletion of 0.2 fall close to the 95% confidence interval for this eastern CPUE series, suggesting that the more pessimistic scenarios for eastern area (and stock) depletion are the more likely.

The projections under continuation of 1997 catch levels (western area 2527 tons; eastern area 46750 tons) show marked downward trends for both areas (Fig. 1), except for the western area if there is no mixing. Viewed by stock (Fig. 2), the indications for the east stock remain poor. For the west stock with mixing, for western area depletions of 0.4 or 0.6, trends are either upwards or above *MSY* level and downward (but with catches below *MSY* – see Table 1d); however, abundance drops in some instances for a western area depletion of 0.2.

Figs 3 and 4 show the consequences for the western area and stock respectively of changing the extent of mixing / overlap by modifying the values specified for the p^W and p^E parameters. Fitting problems arise as the scenarios with intended western area depletion of 0.2 or eastern area depletion of 0.6 cannot achieve these targets for the higher mixing rates. Even so, the general impression is one that the extent of mixing assumed makes little qualitative difference to results: only for the case of a western area depletion of 0.6, and 0.4 for the eastern area, is the magnitude of the difference appreciable when viewed by stock (Fig. 4). Thus it seems that it is more the presence of mixing, rather than its extent, which is the key factor in changing perceptions of status and trends for the western stock.

Fig. 5 shows the consequences of changing the value input for r , the intrinsic growth rate parameter, for the baseline scenario where both areas have a 1998 depletion of 0.4. The effects on trajectories are not large. Note that r was not increased beyond 0.35 because fitting difficulties arise at higher values.

Table 1 provides estimates of stock status and productivity for the nine baseline scenarios with mixing, and for the corresponding cases without overlap. Tables 1a and b show that both pre-exploitation (K, \tilde{K}) and current ($B_{1998}, \tilde{B}_{1998}$) abundance levels are greater for the east than the west - both by stock and by area. When mixing is taken into account, abundance in the west increases by area, but for most scenarios decreases by stock compared to the no mixing case. *MSY* estimates (Table 1d) mimic the patterns shown for K in Table 1a (as here $MSY = rK/4$ and r is fixed). The area-based estimates of *MSY* for the west are higher when there is allowance for mixing. [Note that in the presence of mixing, *MSY* and *RY* estimates are computed by apportioning *MSY* and *RY* estimates by stocks to regions in accordance with the ϕ values that apply.]

The current (1998) replacement yield (*RY*) estimates in Table 1e suggest that 1997 catch levels in the western area are certainly themselves sustainable (with or without mixing), over the range of scenarios considered but the latter conclusion can be reversed by the extent of catches in the east. The 1997 catch level in the east is certainly not sustainable for any of the scenarios considered and needs appreciable reduction (by more than 50% unless the current depletion level in the east area is in excess of 0.4).

4. CONCLUDING REMARKS

The relatively simple approach of this paper suggests that with or without mixing, the 1997 catch levels of bluefin in the western Atlantic are sustainable; however, those in the east for 1997 are well above sustainable levels and need substantial reduction. Even at relatively modest levels of mixing, the fishery in the west will be adversely impacted unless this reduction in the east takes place. This

conclusion is robust over quite a wide range of 1998 depletion levels for the western and eastern areas, of extents of mixing (overlap), and of values for the intrinsic growth rate parameter r .

The next steps in such an approach would likely be:

- i) exploring the implications of more complex implementations of mixing / overlap mechanisms within this age-aggregated framework;
- ii) extending to an age-structured population model framework so that information on catch-at-length can be incorporated in a formal parameter estimation procedure.

It should be noted that the framework used here does not make allowance for process error, as might be of consequence (for example) of periods of sustained above or below expected recruitment or inter-annual variability in movement rates. Such considerations could, however, be incorporated in extension ii) above.

REFERENCES

- BUTTERWORTH, D.S. and S.J. Johnston. 2001. Exploratory analyses of southern bluefin tuna dynamics using production models. CCSBT document CCSBT-SC\0108\24.
- ICCAT. 1999. Report of the ICCAT SCRS Bluefin Tuna Stock Assessment Session (Genoa, Italy – September 14 to 23, 1998). ICCAT Coll. Vol. Sci. Pap. 49(2); pp. 1-191.
- ICCAT. 2001. Report of the ICCAT Workshop on Bluefin Mixing (Madrid - 3-7 September, 2001).

Table 1. Estimates of five quantities of management interest. Results are shown for nine scenarios concerning the 1998 depletion of the populations in the west and east Atlantic, and whether or not allowance is made for mixing ($p^W = p^E = 0.05$). For the analyses that include mixing, the values for quantities are reported by stock (western and eastern) and area (regions 1-3 and regions 4-6). Biomass-related units are tons throughout. For the 'No mixing' results, the leftmost three values shown refer to western (not eastern) depletion levels.

(a) Carrying capacity, K

		West Atlantic (western stock / regions 1-3)			East Atlantic (eastern stock / regions 4-6)		
Western area depletion		Eastern area depletion					
		0.2	0.4	0.6	0.2	0.4	0.6
With Mixing (by stock)							
0.2		52864	47663	44609	321377	370494	410200
0.4		54490	47588	40497	313855	374993	479837
0.6		71306	52341	40361	302557	363061	492643
With Mixing (by area)							
0.2		104983	108979	113254	269258	309177	341554
0.4		105124	109710	121880	263221	312871	398455
0.6		118375	111905	124028	255488	303497	408975
No Mixing							
		71214	71374	71769	294452	346601	459577

(b) 1998 population size

		West Atlantic (western stock / regions 1-3)			East Atlantic (eastern stock / regions 4-6)		
Western area depletion		Eastern area depletion					
		0.2	0.4	0.6	0.2	0.4	0.6
With Mixing (by stock)							
0.2		5943	169	930	68905	140874	193909
0.4		28476	15815	2306	66218	153218	278083
0.6		60786	41969	22627	61337	146573	297175
With Mixing (by area)							
0.2		20997	26539	36111	53852	114505	158728
0.4		42050	43884	51749	52644	125148	228640
0.6		71025	67143	74417	51098	121399	245385
No Mixing							
		14243	28549	43061	58890	138640	275746

(Table 1 Continued)

(c) 1998 depletion (values indicated by asterisks are cases in which no solution for the given combination of current depletions exist)

		West Atlantic (western stock / regions 1-3)			East Atlantic (eastern stock / regions 4-6)		
Western area depletion		Eastern area depletion					
		0.2	0.4	0.6	0.2	0.4	0.6
		With Mixing (by stock)					
0.2		0.112	0.004	0.021	0.214	0.380	0.473
0.4		0.523	0.332	0.057	0.211	0.409	0.580
0.6		0.852	0.802	0.561	0.203	0.404	0.603
		With Mixing (by area)					
0.2		0.200	0.244*	0.319*	0.200	0.370*	0.465*
0.4		0.400	0.400	0.425*	0.200	0.400	0.574*
0.6		0.600	0.600	0.600	0.200	0.400	0.600
		No Mixing					
		0.200	0.400	0.600	0.200	0.400	0.600

(d) Maximum Sustainable Yield, *MSY*

		West Atlantic (western stock / regions 1-3)			East Atlantic (eastern stock / regions 4-6)		
Western area depletion		Eastern area depletion					
		0.2	0.4	0.6	0.2	0.4	0.6
		With Mixing (by stock)					
0.2		3965	3575	3346	24103	27787	30765
0.4		4087	3569	3037	23539	28124	35988
0.6		5348	3926	3027	22692	27230	36948
		With Mixing (by area)					
0.2		7874	8173	8494	20194	23188	25617
0.4		7884	8228	9141	19742	23465	29884
0.6		8878	8393	9302	19162	22762	30673
		No Mixing					
		5341	5353	5383	22084	25995	34468

(e) 1998 replacement yield (1997 catch by area: west = 2527; east = 46750)

		West Atlantic (western stock / regions 1-3)			East Atlantic (eastern stock / regions 4-6)		
Western area depletion		Eastern area depletion					
		0.2	0.4	0.6	0.2	0.4	0.6
		With Mixing (by stock)					
0.2		1583	50	273	16239	26193	30673
0.4		4078	3168	652	15674	27184	35077
0.6		2690	2495	2983	14671	26220	35373
		With Mixing (by area)					
0.2		4317	4693	5690	13505	21550	25256
0.4		6481	7697	6816	13271	22655	28914
0.6		5044	6916	8982	12317	21799	29374
		No Mixing					
		3418	5139	5167	14134	24955	33090

Table 2. Slopes of the logarithms of population size regressed against year (1980–97). Results are shown for nine scenarios concerning the 1998 depletion of the populations in the west and east Atlantic, and whether or not allowance is made for mixing ($p^W = p^E = 0.05$).

	West Atlantic (regions 1-3)			East Atlantic (regions 4-6)		
	Eastern area depletion					
Western area depletion	0.2	0.4	0.6	0.2	0.4	0.6
	With Mixing					
0.2	-0.023	-0.024	-0.019	-0.038	-0.026	-0.021
0.4	0.007	-0.006	-0.013	-0.038	-0.024	-0.015
0.6	0.004	0.013	0.002	-0.037	-0.024	-0.014
	No Mixing					
	0.009	0.042	0.060	-0.036	-0.024	-0.014

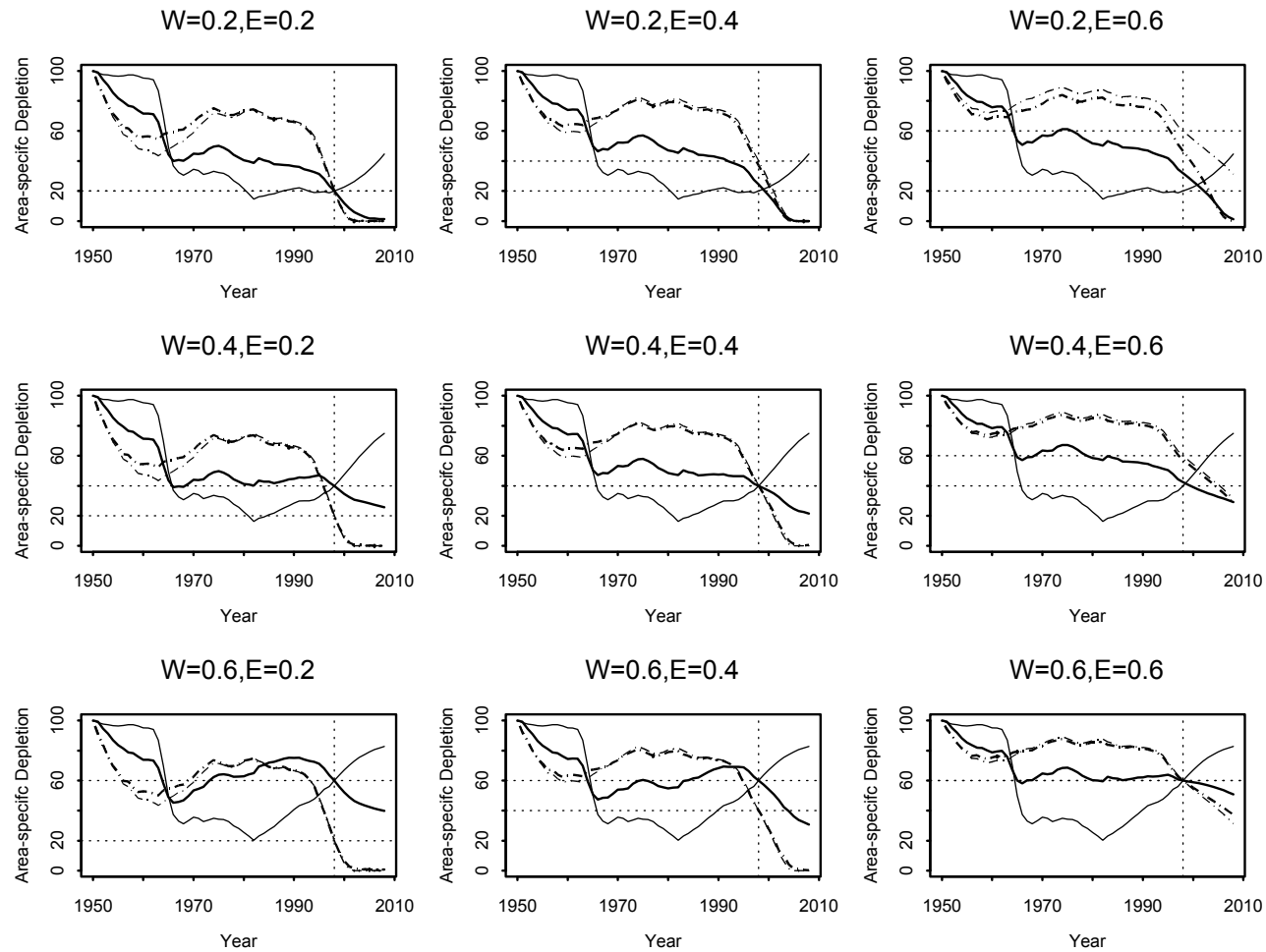


Figure 1. Time-trajectories of population size by *area* (eastern area: dashed lines; western area: solid lines). Results are shown for the baseline analyses that allow for mixing ($p^W = p^E = 0.05$; thicker lines) and that ignore mixing (thinner lines), for nine combinations for the “target” depletion of the western and eastern areas (“W” and “E” respectively). The horizontal and vertical dotted lines indicate the “target” depletions for the western and eastern areas.

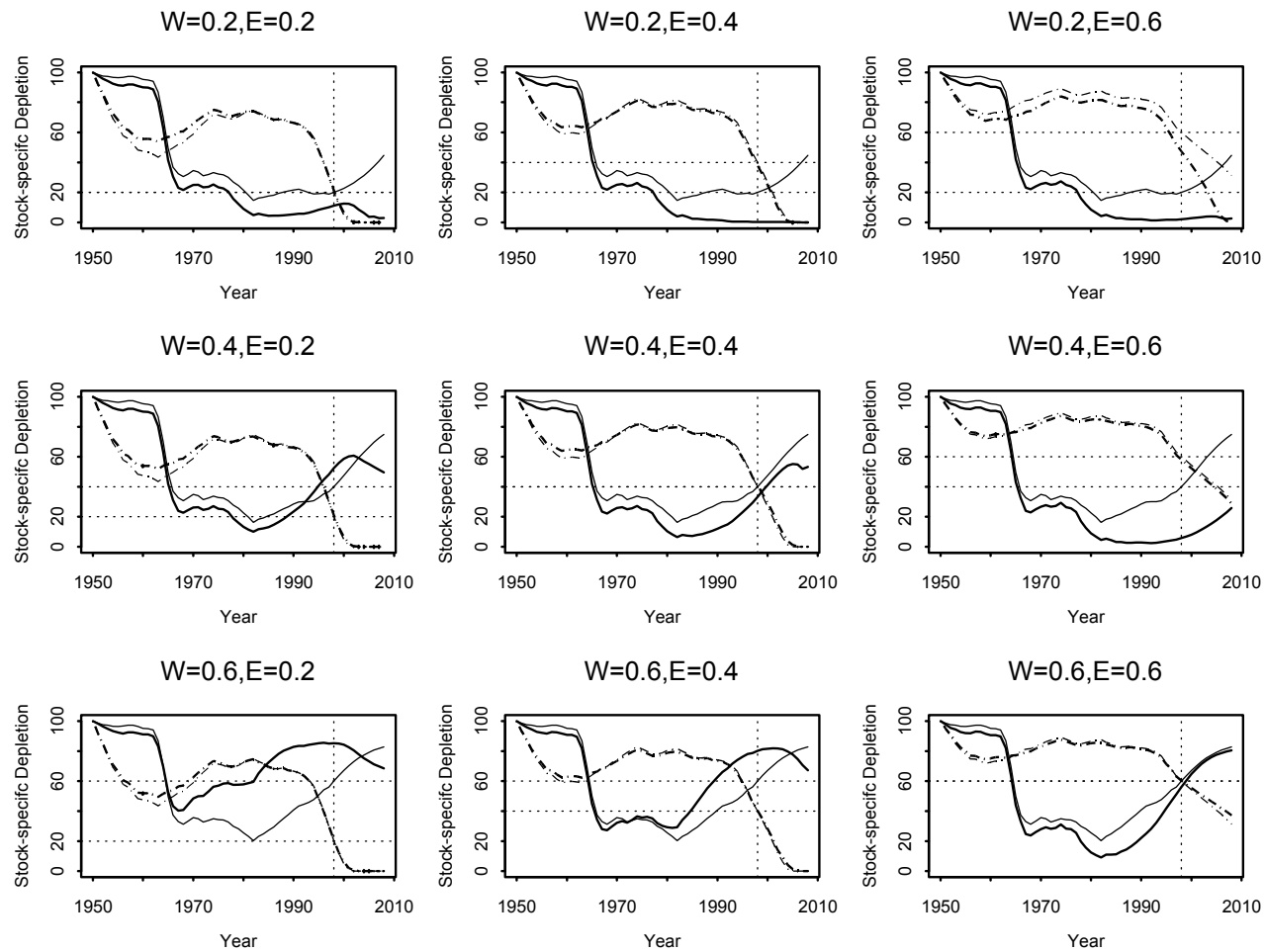


Figure 2. Time-trajectories of population size by *stock* (eastern stock: dashed lines; western stock: solid lines). Results are shown for the baseline analyses that allow for mixing ($p^W = p^E = 0.05$; thicker lines) and that ignore mixing (thinner lines), for nine combinations for the “target” depletion of the western and eastern areas (“W” and “E” respectively). The horizontal and vertical dotted lines indicate the “target” depletions for the western and eastern areas.

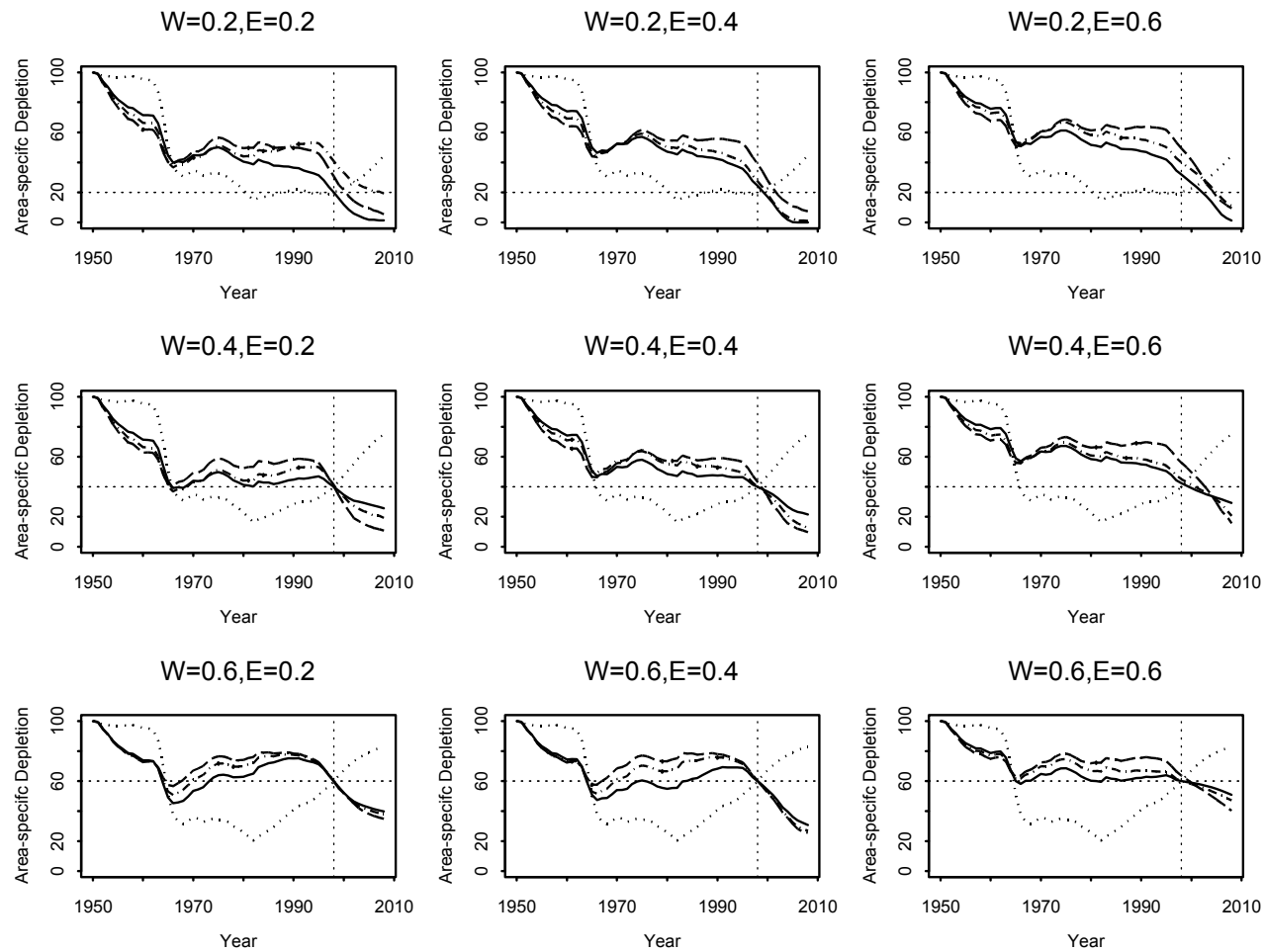


Figure 3. Time-trajectories of population size for the *western area* for nine combinations for the “target” depletion of the western and eastern areas (“W” and “E” respectively). Results are shown for an analysis that ignores mixing (dotted lines) and for three analyses that allow for mixing ($p^W = p^E = 0.05$ - solid lines; $p^W = p^E = 0.1$ - dashed lines; $p^W = p^E = 0.2$ - dash-dot lines). The horizontal and vertical dotted lines indicate the “target” depletion for the western area.

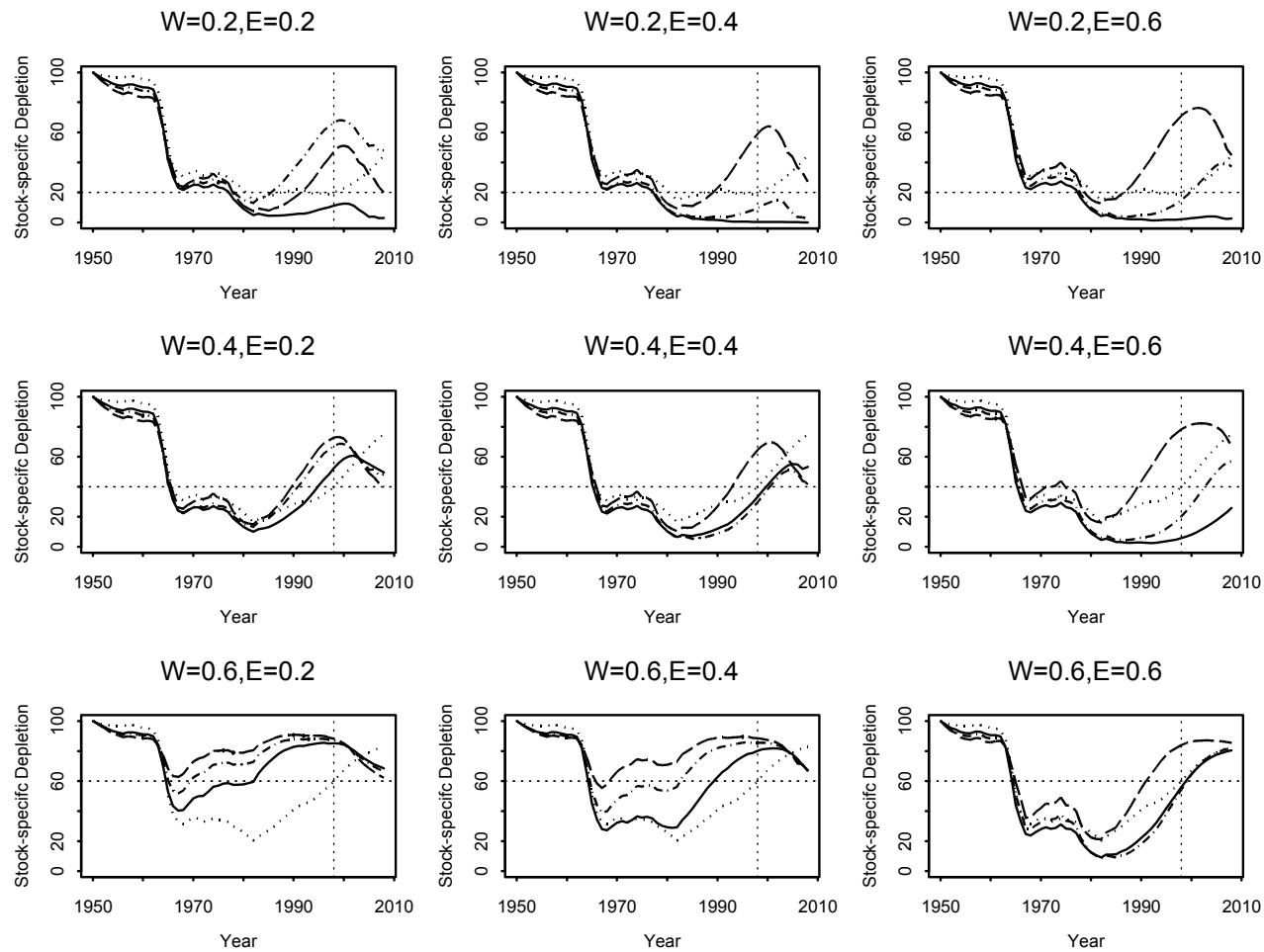


Figure 4. Time-trajectories of population size for the *western stock* for nine combinations for the “target” depletion of the western and eastern areas (“W” and “E” respectively). Results are shown for an analysis that ignores mixing (dotted lines) and for three analyses that allow for mixing ($p^W = p^E = 0.05$ - solid lines; $p^W = p^E = 0.1$ - dashed lines; $p^W = p^E = 0.2$ - dash-dot lines). The horizontal and vertical dotted lines indicate the “target” depletion for the western area.

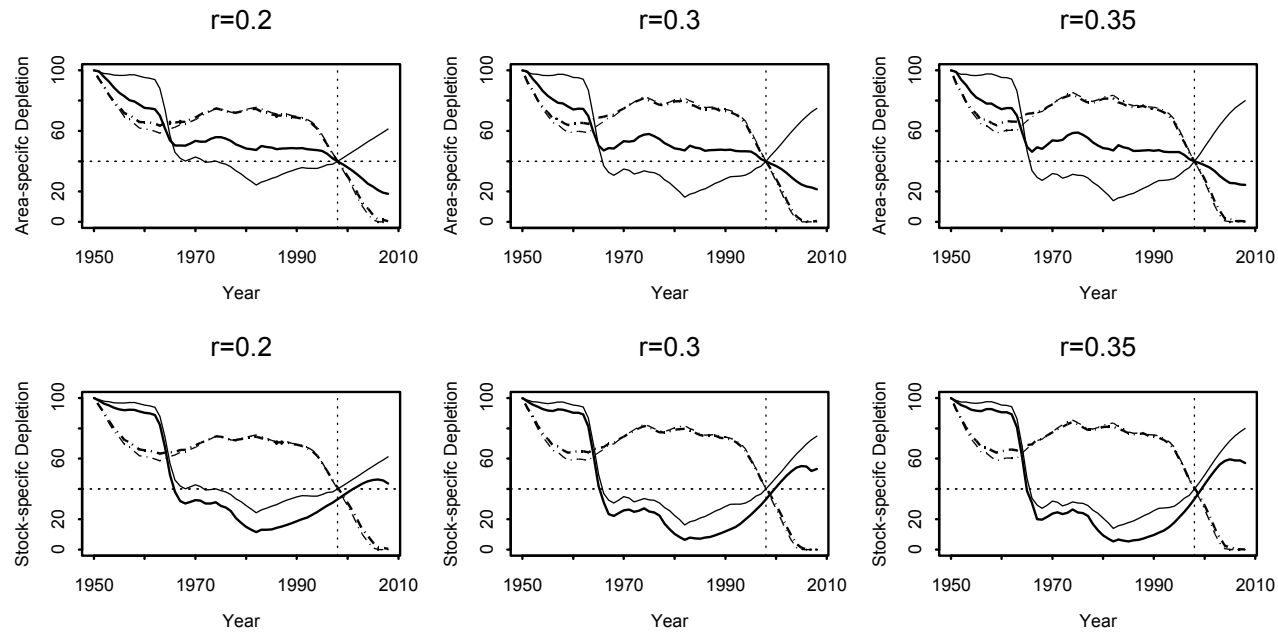


Figure 5. Time-trajectories of population size by area (upper panels; east - dashed lines; west - solid lines) and stock (lower panels) for three values for the intrinsic rate of growth, r (in yr^{-1}). The results in this figure pertain to the choice of a depletion of 0.4 for both the western and eastern areas. Results are shown for analyses that allow for mixing ($p^W = p^E = 0.05$; thicker lines) and that ignore mixing (thinner lines). The dotted horizontal and vertical lines indicate the “target” depletions for the western and eastern areas.