A comparison between the hake cannibalism and inter-species predation models presented in Bergh *et al.* (2016) and Ross-Gillespie (2016)

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Outline of this document

This document compares the structure, assumptions and results of the Bergh *et al*. (2016) and Ross-Gillespie (2016) hake cannibalism and inter-species predation models. For ease of reference, the Bergh *et al.* (2016) model will be referred to as the OLRAC model and the Ross-Gillespie (2016) model as the MARAM model. The tabular below summarises the content of the document.

References

Bergh, M., Fourie, A. and Joselson, N. 2016. Modification of the prevailing species, sex, age and size disaggregated hake stock assessment model to incorporate hake cannibalism and inter-species predation. Document FISHERIES/2016/MAR/SWG-DEM/06.

Punt, A. E. and Leslie, R. W. 1995. The effects of future consumption by the Cape fur seal on catches and catch rates of the Cape hakes. 1 . Feeding and diet of the Cape hakes *Merluccius capensis* and *M . paradoxus*. *South African Journal of Marine Science*, 16(1), 37(55).

Rademeyer, R. A. and Butterworth, D. S. 2014b. Specifications of the South African hake 2014 Reference Case assessment. Document MARAM/IWS/DEC14/Hake/P2 reviewed at the International Stock Assessment Workshop, Cape Town, December 2014.

Ross-Gillespie, A. 2016. Modelling cannibalism and inter-species predation for the Cape hake species *Merluccius capensis* and *M. paradoxus. PhD thesis, University of Cape Town.*

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Table 1: Comparison between **model structure** assumptions for the OLRAC and MARAM hake predation models. Rows highlighted in grey indicate that the assumptions are identical.

Category		OLRAC	MARAM
General	Maximum age	15 years	15 years
	Disaggregation	Sex-disaggregated Species- and age-disaggregated No coast-disaggregation	Sex-aggregated Species- and age-disaggregated No coast-disaggregation
	Time-step	Biannual time-step	Monthly time-step
	Initial population setup	Estimate total natural mortality at pre-exploitation, calculate the initial population structure from this, and then the predation mortality rates at pre-exploitation. Pristine total mortality is estimated Basal mortality is the difference between total pristine mortality and pristine predation mortality, is age-dependent and time invariant	Calculate the predation mortality rate at pre-exploitation equilibrium but starting with the plus age group and moving iteratively to age zero. Total natural mortality at pre-exploitation is the sum of the basal mortality and the predation mortality. Pristine total mortality is the sum of the basal mortality and the predation mortality Basal mortality is fixed on input, age- and time-invariant
	Last year in model	2016	2013
Predation-specific	General	Hake ration and dietary percentages are fixed on input. Aim is to develop method to reflect the relationship between hake diet and prey availability. Diet data are not formally included in the likelihood. Aim is to develop methods for including the data in the likelihood function.	Hake ration and dietary percentages vary with predator and prey abundances. Diet data are formally included in the likelihood.
	Number of hake consumed	Hake consumed = ration x prop_hake x number_predators, where ration and prop_hake are fixed on input Hake consumed is calculated as the sum over all hake predator species, genders and ages and then distributed across these predator groups through a preference function.	Hake consumed = Holling Type II function of hake predator and prey numbers, other prey numbers and predator-prey preference
	Other (non-hake) prey of hake	No other prey component	Other prey component included
	Other (non-hake) predators of hake	No other predator component	No other predator component
	Preference function	Preference function is a beta function, informed by data in Butterworth and Harwood (1991) and BEP (1991) – fixed on input	Preference function is a gamma function by predator and prey age, informed by the DAFF 1999-2013 dataset – parameters estimated in the model
	Daily ration	Daily ration is modelled as a function of species and age with exponential functions from the Punt and Leslie (1995) results, converted to ration by **length** and re-fitted with polynomials. Daily ration is a fixed input into the model	Daily ration is a model output by predator species and age, with a lower bound of 0.1% of body mass and an upper bound of 4% of body mass, enforced through a penalty.
	Proportion of hake in the diet of hake predators	Year invariant. Fit polynomial to Punt and Leslie (1995) proportions by age, convert to length and fit logistic.	Year dependent. Model output by age which is converted to proportions by length and, fit to proportions estimated from the DAFF 1999-2013 data set
	Other		The MARAM model allows for the *M. capensis* preference for hake prey to shift from primarily *M. capensis* to primarily *M. paradoxus* prey as the predators grow larger. Further, this model incorporates a competition component that effectively limits the predation mortality rate at 0.06 per month or 0.72 per annum.

Table 2: Summary of the differences between the Rademeyer and Butterworth (2014) model and the predation-off variants of the MARAM and OLRAC models.

Rademeyer and Butterworth (2014)	**OLRAC**	**MARAM**
Sex-disaggregated	Sex-disaggregated	Sex-aggregated
Fits to age-length keys	Fits to age-length keys	Does not fit to age-length keys
Modified Ricker stock-recruitment relationship	Modified Ricker stock-recruitment relationship	Beverton-Holt stock-recruitment relationship
Pope's approximation for the catch equation	Pope's approximation for the catch equation	Baranov formulation of the catch equation
Annual time-step	Biannual time-step	Monthly time step

Table 3: Comparison between the **input data** for the OLRAC and MARAM hake predation models. Rows highlighted in grey indicate that the data are identical. Rows highlighted in blue indicate that the data are the same apart from the additional years of data included in the OLRAC model. Rows highlighted in yellow in either the OLRAC or the MARAM column indicate that the data are use in that model only. The remaining rows in white indicate that there are more substantial differences in the underlying data; in these cases the "Additional Comments" column provides extra information on the differences.

Type Description		Coast	Species	Gender	OLRAC	MARAM	Additional Comments
Catches			Both		1917-2016	1917-2013	
CPUE	ICSEAF	WC	Species combined	Sex-agg	1955-1977	1955-1977	
		SC	Species combined	Sex-agg	1969-1977	1969-1977	
	GLM	WC	Both	Sex-agg	1978-2015	1978-2012	GLM analyses have been updated, resulting in slightly different series
		SC	Both	Sex-agg	1978-2015	1978-2012	
Survey abundance	Summer	WC	Both	Sex-agg	1985-2016	1985-2012	
	Winter	WC	Both	Sex-agg	1985-1990	1985-1990	
	Spring	SC	Both	Sex-agg	1986-2008	1986-2008	
	Autumn	SC	Both	Sex-agg	1988-2016	1988-2011	
Commercial CAL	Offshore	WC	Species combined	Sex-agg	1981-2015	1981-2012	
	Offshore	SC	Species combined	Sex-agg	1975-2014	1975-1996	The OLRAC model takes a recent update into account, which adds 7 years' of data from 2008-2014.
	Inshore	SC	M. capensis	Sex-agg	1981-2015	1981-2012	
	Longline	WC	Species combined	Sex-agg	1994-1997	1994-1997	
		SC	M. capensis	Sex-agg	1994-1997	1994-1997	
	Longline	WC	Both	Sex-disagg	2000-2010	-	
		SC	Both	Sex-disagg	2001-2010	-	
Survey CAL	Summer	WC	Both	Sex-agg	1985-2005	1985-2012	For the MARAM model aggregates the sex-disaggregated CAL data for the years in which these are available. Furthermore, the CAL proportions for the MARAM model were calculated in a slightly different manner, taking stratum density into account, although it was found that this alternative way of calculating the CALs did not make a substantial difference to the assessment results.
	Winter	WC	Both	Sex-agg	1985-1990	1985-1990	
	Spring	SC	Both	Sex-agg	1986-2004	1986-2008	
	Autumn	SC	Both	Sex-agg	1988-2005	1988-2011	
	Summer	WC	Both	Sex-disagg	1993-2016	-	
	Spring	SC	Both	Sex-disagg	2006-2008	-	
	Autumn	SC	Both	Sex-disagg	1993-2016	-	
Age length keys			Both	Sex-agg	1988-2008	-	
Proportion of hake in diet			M. cap on M. cap	Sex-agg	Fixed on input from Punt and Leslie (1995)	Model fit to DAFF dataset averaged over years 1999-2013	
			M. cap on M. par	Sex-agg			
			M. par on M. par	Sex-agg			
Predator-prey preference			M. cap on M. cap	Sex-agg	Fixed on input from Punt and Leslie (1995)	Model fit to DAFF dataset averaged over years 1999-2013	
			M. cap on M. par	Sex-agg			
			M. par on M. par	Sex-agg			

Table 4: Comparison between the negative log-likelihood components for the OLRAC and MARAM models. Rows in grey indicate that the data are identical. Rows in blue indicate that the data are the same apart from the additional years of data included in the OLRAC model. Rows in yellow in either the OLRAC or the MARAM column indicate that the data are use in that model only. The remaining rows in white indicate that there are more substantial differences in the underlying data.

		Predation off						**Predation on**					
		OLRAC			**MARAM**			**OLRAC**			**MARAM**		
	No. of Fitted Parameters		**259**			**232**			**267**			**259**	
	Hake	**Par**	**Comb**	**Cap**	**Par**	**Comb**	**Cap**	**Par**	**Comb**	**Cap**	**Par**	**Comb**	**Cap**
CPUE	ICSEAF WC		-29.8			-29.7			-29.4			-26.0	
	ICSEAF SC		-10.0			-9.7			-8.1			-4.9	
	GLM WC	-60.5		-45.9	-33.7		-38.6	-63.5		-48.8	-31.1		-36.9
	GLM SC	-56.0		-32.3	-44.7		-62.0	-56.8		-33.6	-53.7		-56.8
Survey abundance	Summer	-13.3		-2.6	-13.3		-3.2	-13.4		-3.6	-13.4		-3.6
	Winter	-3.0		-0.5	-3.6		0.6	-2.9		0.3	-3.3		0.9
	Spring	0.9		-6.9	2.0		-5.7	1.6		-7.2	1.9		-6.0
	Autumn	5.8		-16.8	5.2		-13.2	5.0		-18.0	6.1		-13.4
Stock-recruitment	SR Residuals		7.6			19.9			6.5			8.6	
Commercial CAL, sex-aggregated	Trawl Off WC Both Species		-22.3			-18.3			-20.8			-16.2	
	Trawl Off SC Both Species		-10.8			-4.3			-10.6			3.3	
	Trawl Inshore SC			-22.8			-21.3			-23.8			-19.1
	Longline WC Both Species		-14.1			-11.7			-14.0			-11.7	
	Longline SC			-6.8			-6.5			-6.2			-6.4
Commercial CAL, sex-disaggregated	Longline WC	-26.0		-21.7				-27.5		-21.7	-		-
	Longline SC	-0.1		-20.7				-0.5		-20.2	-		-
Survey CAL, sex-aggregated	Summer WC	-0.1		14.6	2.5		58.8	-0.1		14.6	0.8		58.7
	Winter WC	-0.8		8.3	-1.2		9.4	-1.2		8.8	-1.6		9.3
	Spring SC	5.1		-1.6	7.9		-7.4	4.8		-0.9	7.1		-8.1
	Autumn SC	5.1		-2.0	10.2		-29.4	4.9		-5.1	8.9		-26.4
Survey CAL, sex-disaggregated	Summer WC	-4.1		31.3	-		-	-4.9		30.2	-		-
	Spring SC	3.5		-4.3	-		-	3.5		-3.4	-		-
	Autumn SC	19.5		-3.1	-		-	19.3		1.1	-		-
Age-Length Keys	ALK	49.1		70.9	-		-	49.4		72.9	-		-
Predation	Proportion of hake in diet		-			-			-			68.0	
	Preference		-			-			-			41.4	
Totals	-lnL (strictly comparable)		-53.0			-37.7			-51.2			-40.4	
	-lnL (roughly comparable)		-81.3			-70.8			-82.8			-66.2	
	-lnL (non-comparable)		-134.0			-132.6			-141.9			-126.3	
	-lnL (unique)		51.6			-			52.3			109.4	
	Penalties		0.04			10.0			5.10			7.7	
	Total –lnL (excl. penalties)		**-217**			**-241**			**-224**			**-124**	

Table 5a: Selected parameter estimates and key model outputs for the OLRAC and MARAM predation-off and predation-on models.

	(a) OLRAC				(b) MARAM			
	Predation-off		Predation-on		Predation-off		Predation-on	
	M. par	M. cap	M. par	M. cap	M. par	M. cap	M. par	M. cap
Ksp	675	269	290	96	1453	723	481	285
h	1.1	1.8	1.0	0.5	0.9*	0.9*	0.9*	0.9*
gamma	0.3	0.1	0.3	2.4	-	-		
Max(Bsp(y)/Ksp)	1.0	1.0	1.4	1.0	1.0	1.0	1.3	1.0
Bsp(2013)	155	174	146	68	220	455	70	213
Bsp(2013)/Ksp	0.23	0.65	0.50	0.71	0.2	0.40	0.15	0.75

Table 5b: Summary of key features in the results for the OLRAC and MARAM predation-on models.

OLRAC	MARAM
Spawning biomass	
Pristine spawning biomass is lower than for the conventional stock assessment model (the Rademeyer and Butterworth 2014 K^{sp} estimates are 1504 for *M. paradoxus*, and 491 for *M. capensis*).	
M. paradoxus K^{sp}: 290 *M. capensis* K^{sp}: 96	*M. paradoxus* K^{sp}: 481 *M. capensis* K^{sp}: 285
M. paradoxus exhibits competitive release	
Depletion	
Bsp/Ksp for *M. paradoxus*	
Max: 1.38* (1958*) 2013: ~50% predation off: 23%	Max: 1.34 (1956) 2013: 14% predation off ~15%
Natural mortality	
Natural mortality is higher than for the conventional stock assessment model	
M. paradoxus (pristine): 1.0 at age 0 to 0.2 at age >9 *M. capensis* (pristine): 0.9 at age 0 to 0.3 at age >9	*M. paradoxus* (pristine): 0.92 at age 0 to 0.2 at age >11 *M. capensis* (pristine): 0.92 at age 0 to 0.2 at age >11
Daily ration	
Fixed on input 0.12%-0.95% for *M. paradoxus*, and 1.47%-2.28% for *M. capensis*	Model output 0.1%-0.7% for *M. paradoxus*, 0.5%-4.0% for *M. capensis*
Proportion of hake in the diet	
Fixed on input par on par: 0.03-0.50 par on par: 0 throughout cap on par: 0.00-0.23 cap on cap: 0.00-0.14	Model output par on par: 0.00-0.51 par on par: 0 throughout cap on par: 0.00-0.21 cap on cap: 0.02-0.10
Preference	
Preference function parameters fixed on input Optimum prey/predator length 51-57% Maximum prey/predator length 75-80%	Preference function parameters fit in model Optimum prey/predator length 39%-50% Maximum prey/predator length 65-70%

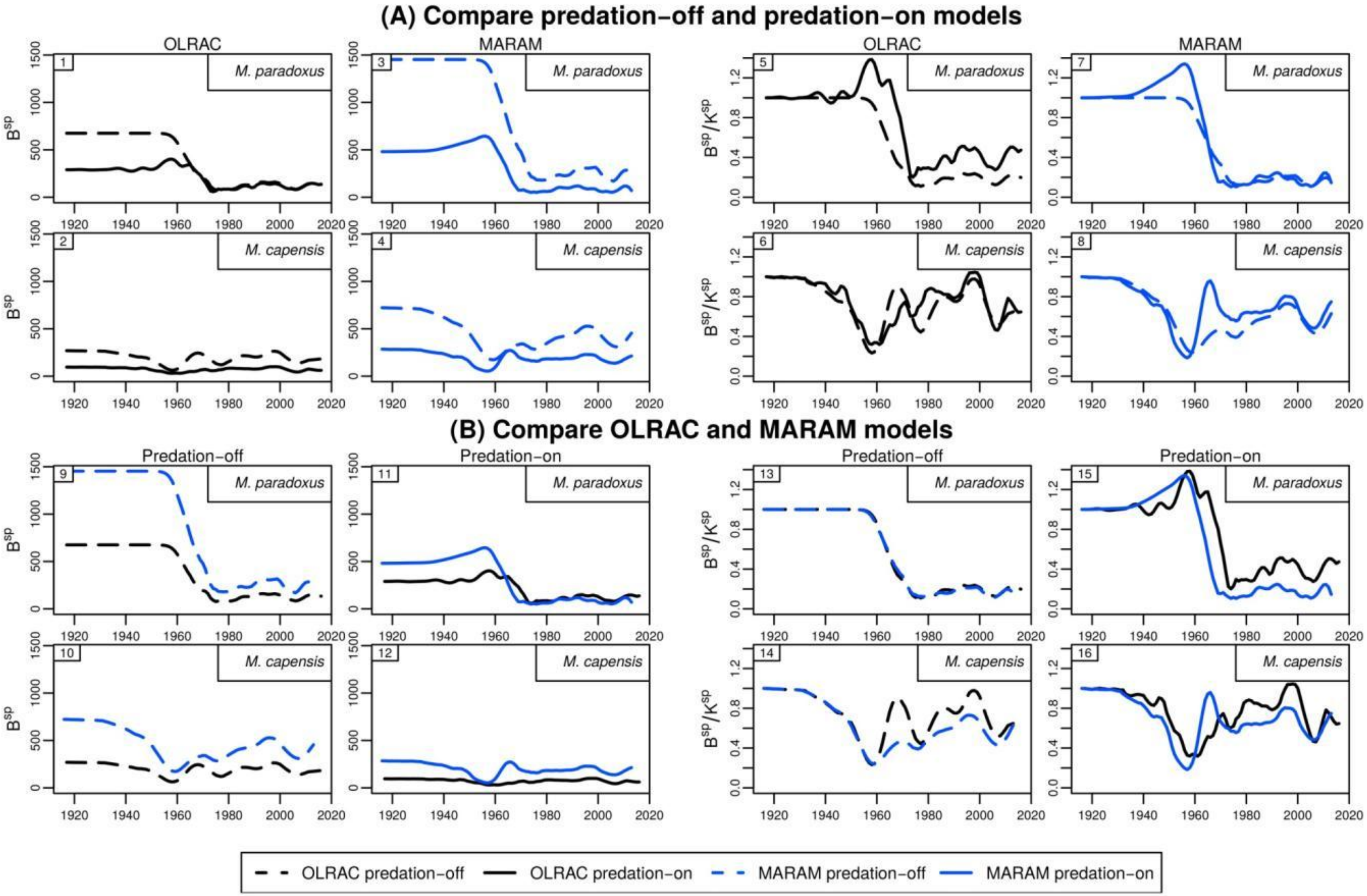

Figure 1. Spawning biomass trajectories are shown in two ways: (A) the trajectories are compared across the predation-off and predation-on variants for each of the OLRAC and MARAM models (plot no. 1-8) and (B) the trajectories are compared across the OLRAC and MARAM models for each of the predation-off and predation-in variants (plot no. 9-16). In all cases the OLRAC model is shown in black, while the MARAM model is shown in blue. The predation-off variant is shown with dashed lines and the predation-on variant with solid lines. The two left-hand columns show the spawning biomass trajectory in 1000 tons and the two right-hand columns show the biomass relative to pre-exploitation equilibrium.

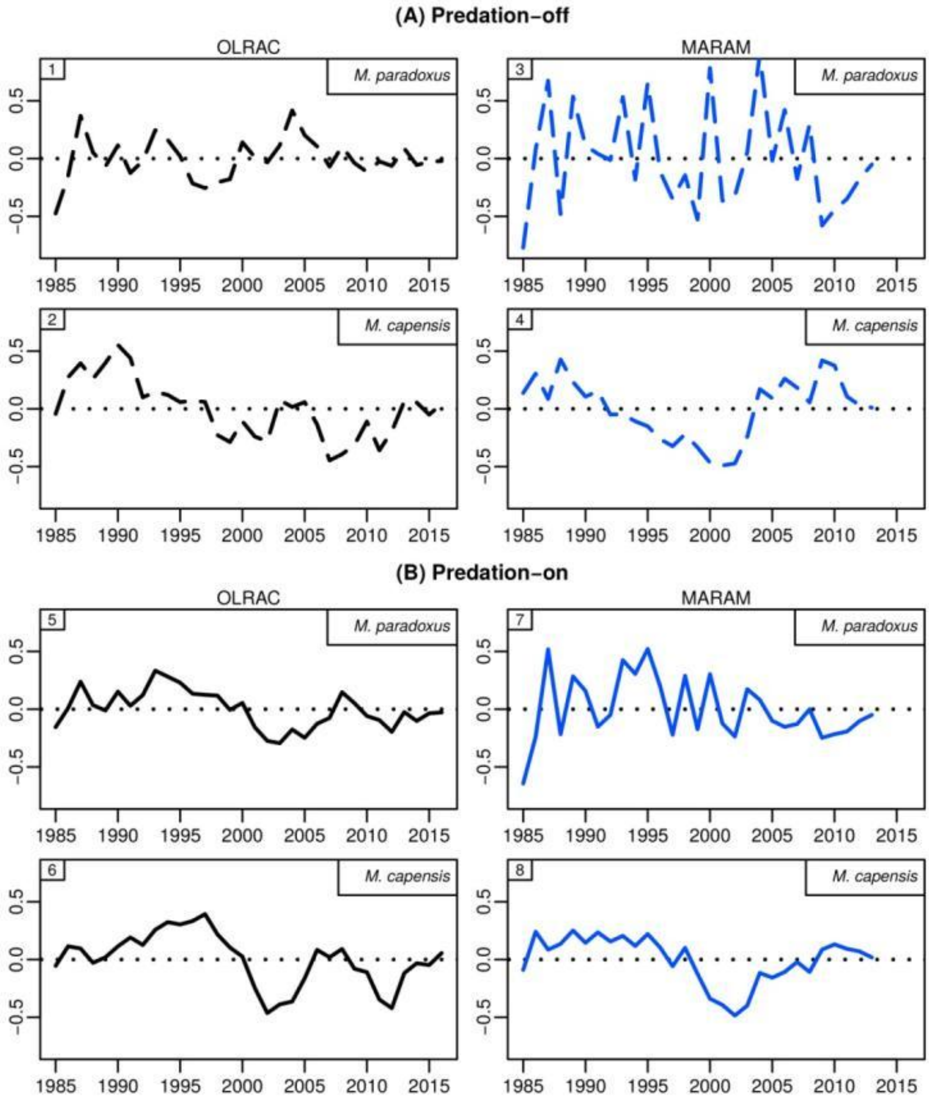

Figure 2. Stock recruitment residuals are shown for (A) the predation-off variant (plot no. 1-4) and (B) the predation-on variant. (plot no. 5-8). In all cases the OLRAC model is shown in black and the MARAM model in blue.

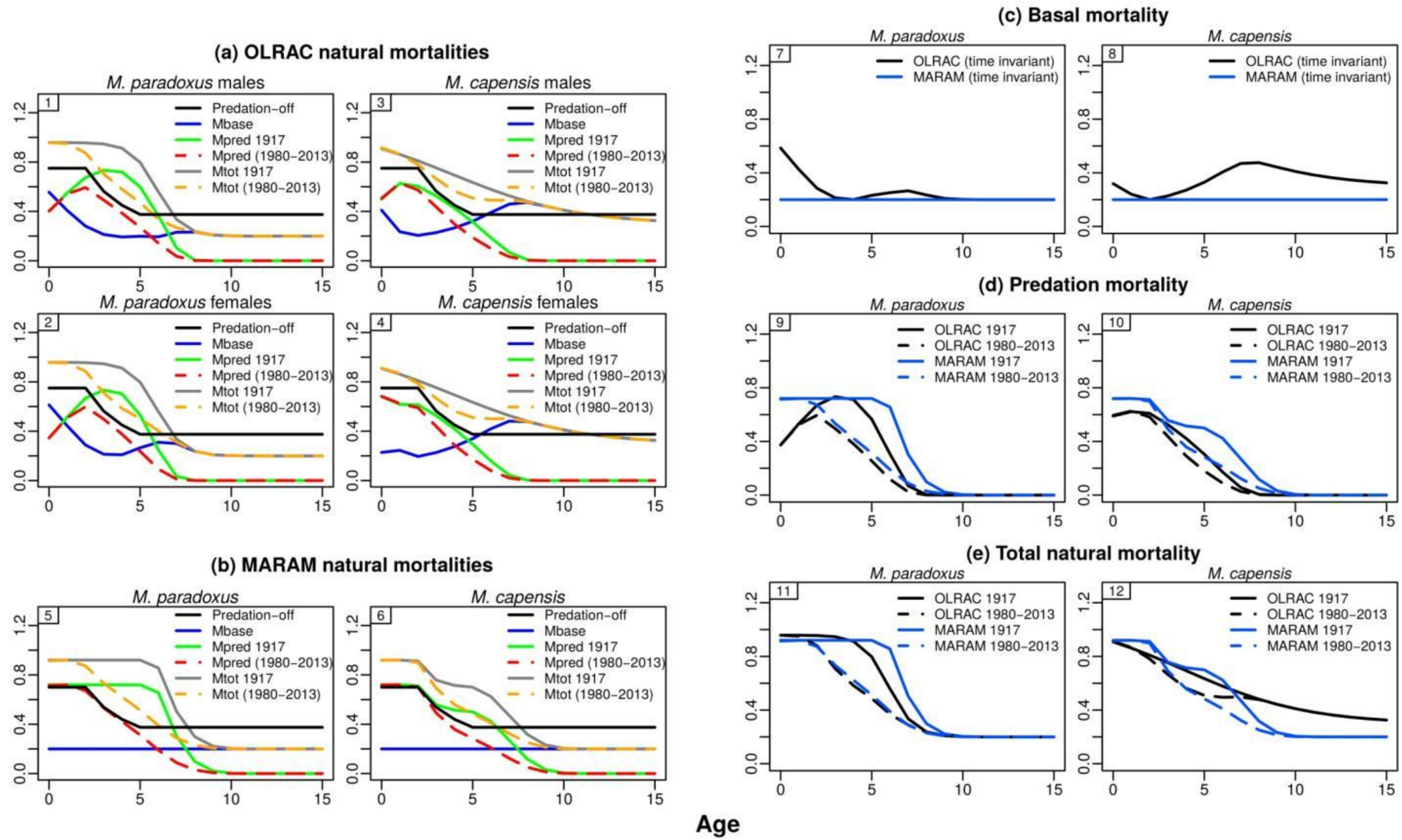

Figure 3: The natural mortality components for the two models. The two columns on the left-hand side (plot no. 1-6) overlay all the different mortality components on top of one another. In the legend, Mbase = Basal mortality, Mpred = Predation mortality and Mtot = Total natural mortality. Mortality rates are reported for the 1917 pre-exploitation equilibrium and as an average over 1980-2013. Mbase is the same for all years. The two right-hand columns (plot no. 7-12) provide a break-down of the individual mortality components. Note that the OLRAC sex-disaggregated mortality rates have been averaged for the plots on the right.

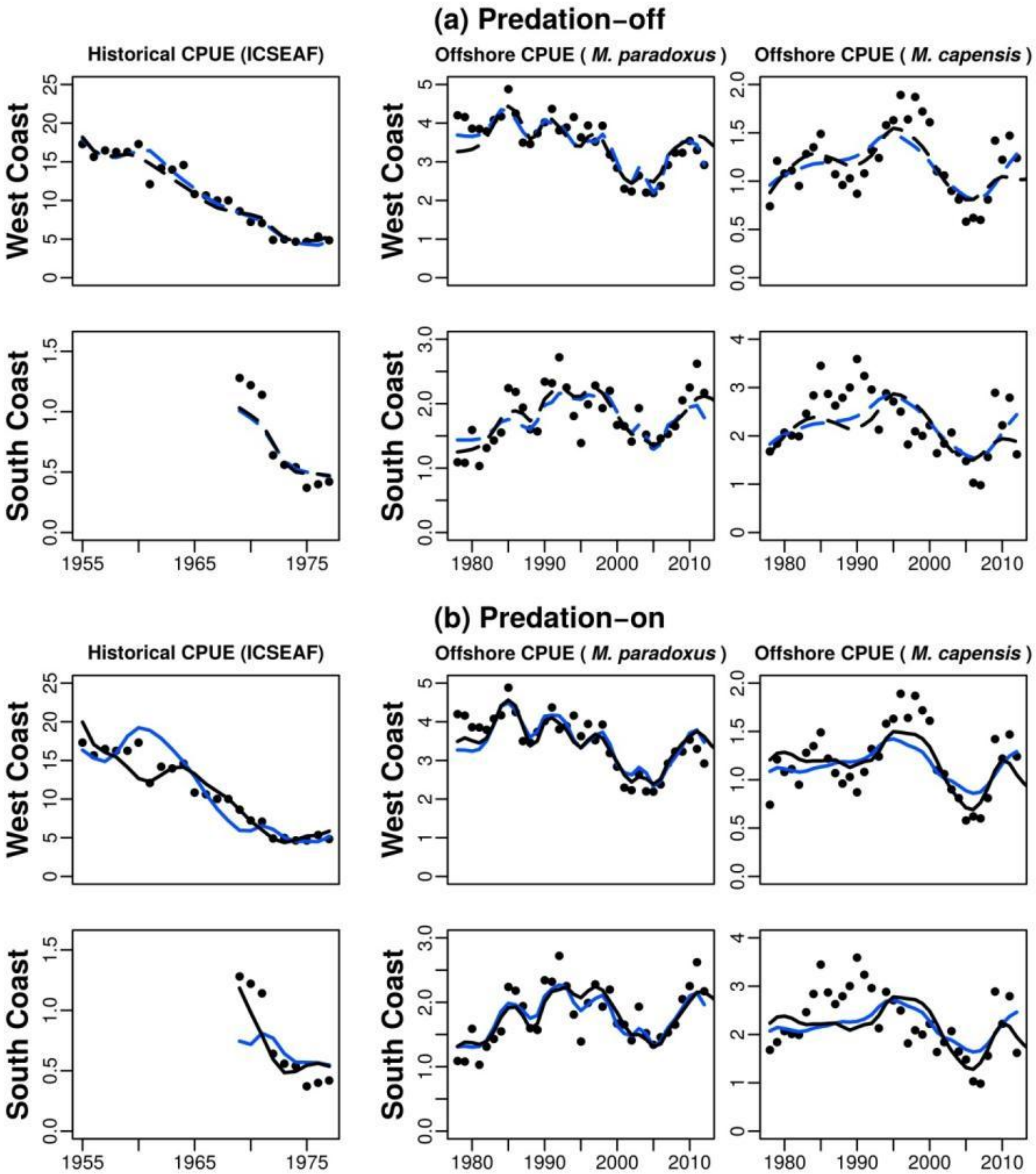

Figure 4. ICSEAF and GLM CPUE plots (observed and modelled) for M. paradoxus and M. capensis are shown for (a) the predation-off variant (top two rows) and (b) the predation-on variant (bottom two rows). The OLRAC model is shown in black and the MARAM model in blue.

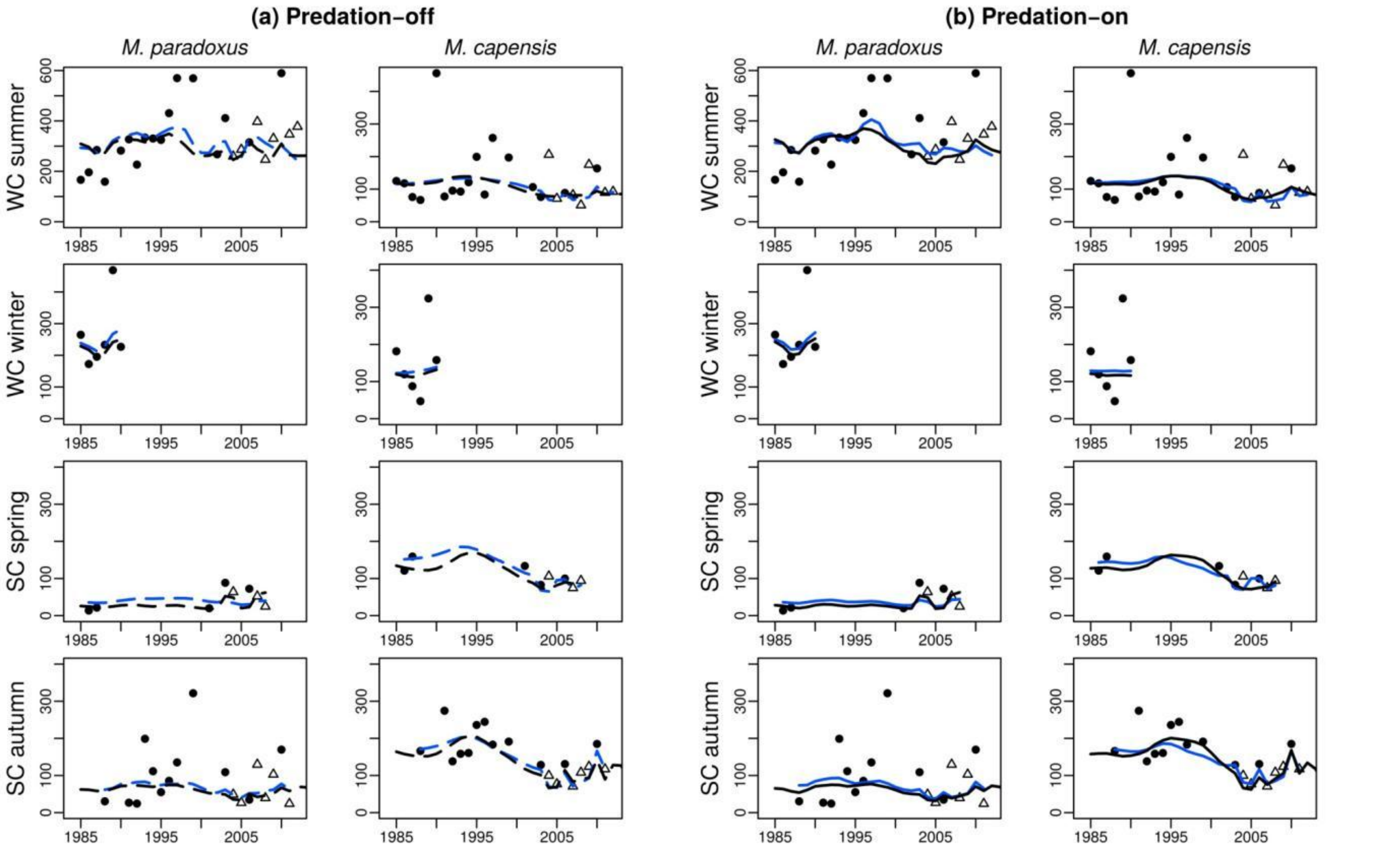

Figure 5. Survey abundance estimates plots (observed and modelled) for M. paradoxus and M. capensis are shown for (a) the predation-off variant (two left-hand columns) and for (b) the predation-on variant (two right-hand columns). The OLRAC model is shown in black and the MARAM model in blue. The data points are shown with black filled circles for years corresponding to old gear and with open triangles for years corresponding to new gear.

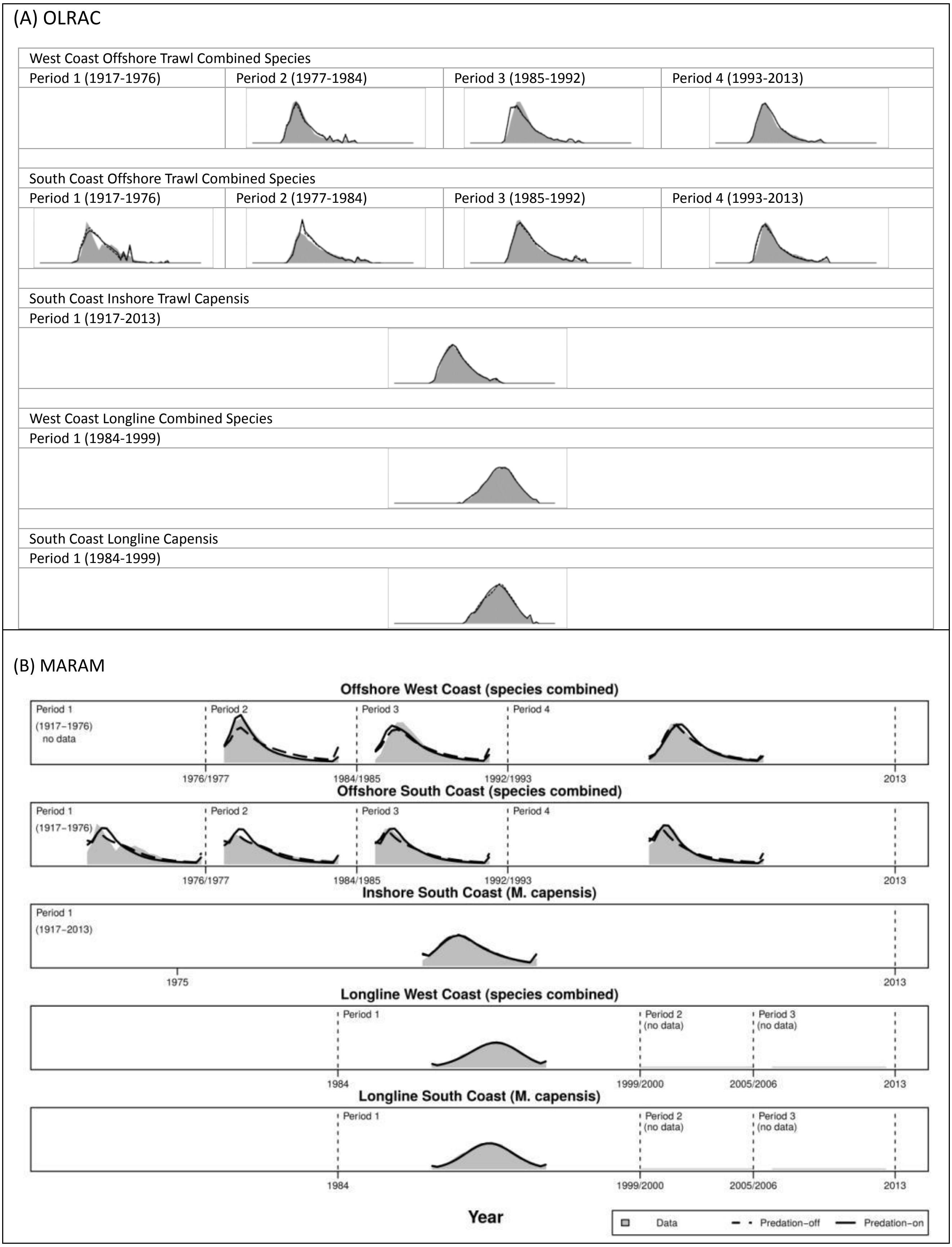

Figure 6a. Fits to commercial sex-aggregated catches-at-length are shown for (A) the OLRAC model and (B) the MARAM model. For each model, the predation-off (dashed lines) and predation-on (solid lines) fits are shown. These plots have been set up to illustrate the periods for which different selectivities are estimated. Each individual distribution is with respect to length.

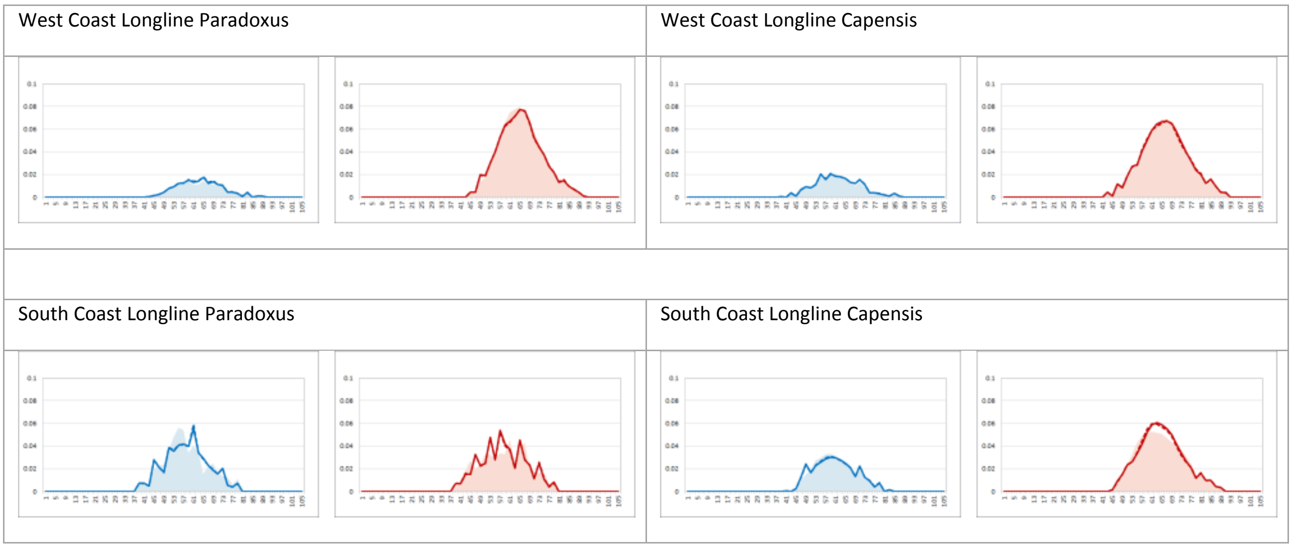

Figure 6b. Commercial sex-disaggregated CAL plots for the OLRAC assessment and cannibalism models. (shaded area = observed, dashed line = modelled assessment, solid line = modelled cannibalism)

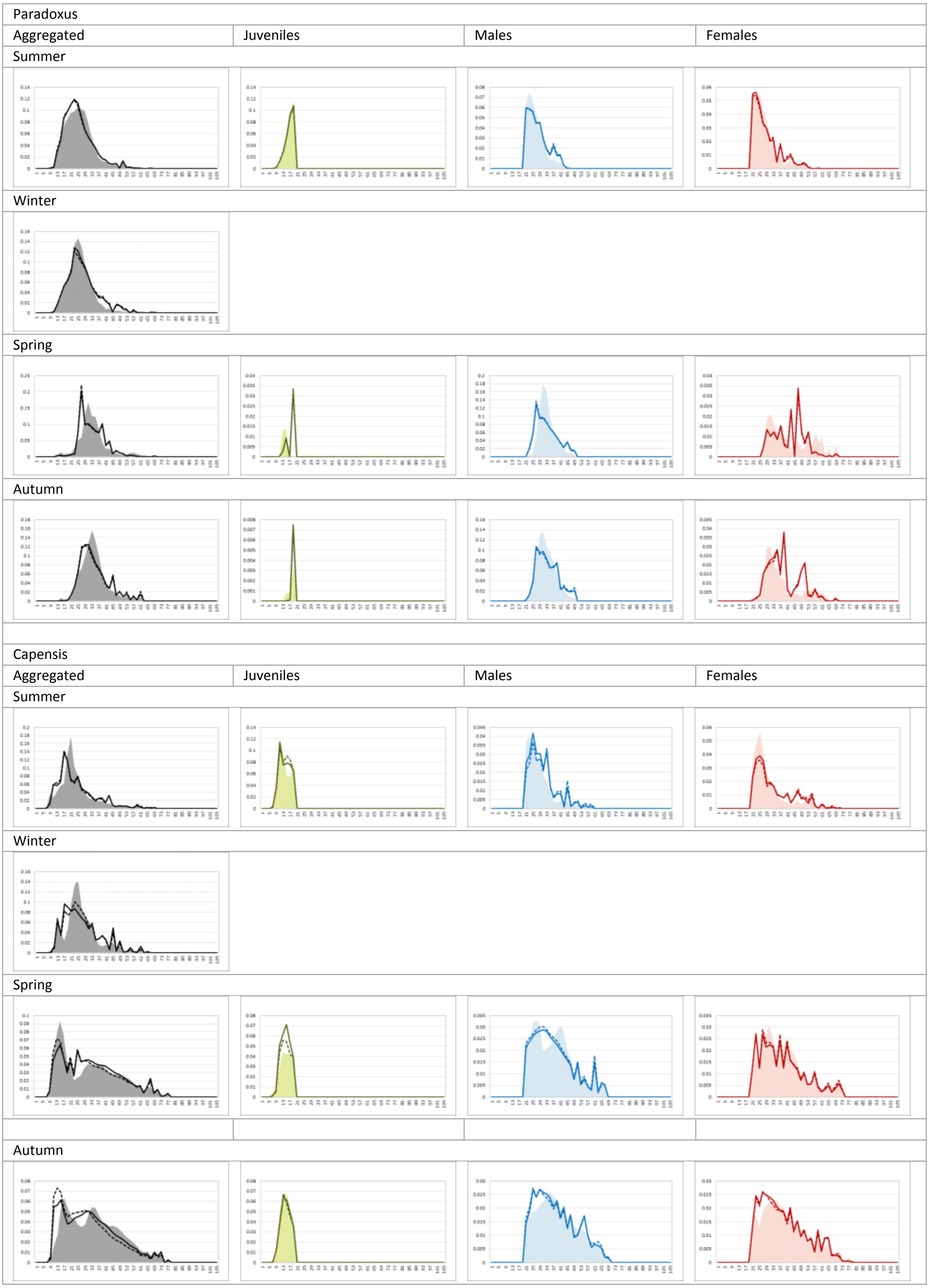

Figure 7a. Survey sex-aggregated and sex-disaggregated CAL plots for the OLRAC assessment and cannibalism models. (shaded area = observed, dashed line = modelled assessment, solid line = modelled cannibalism)

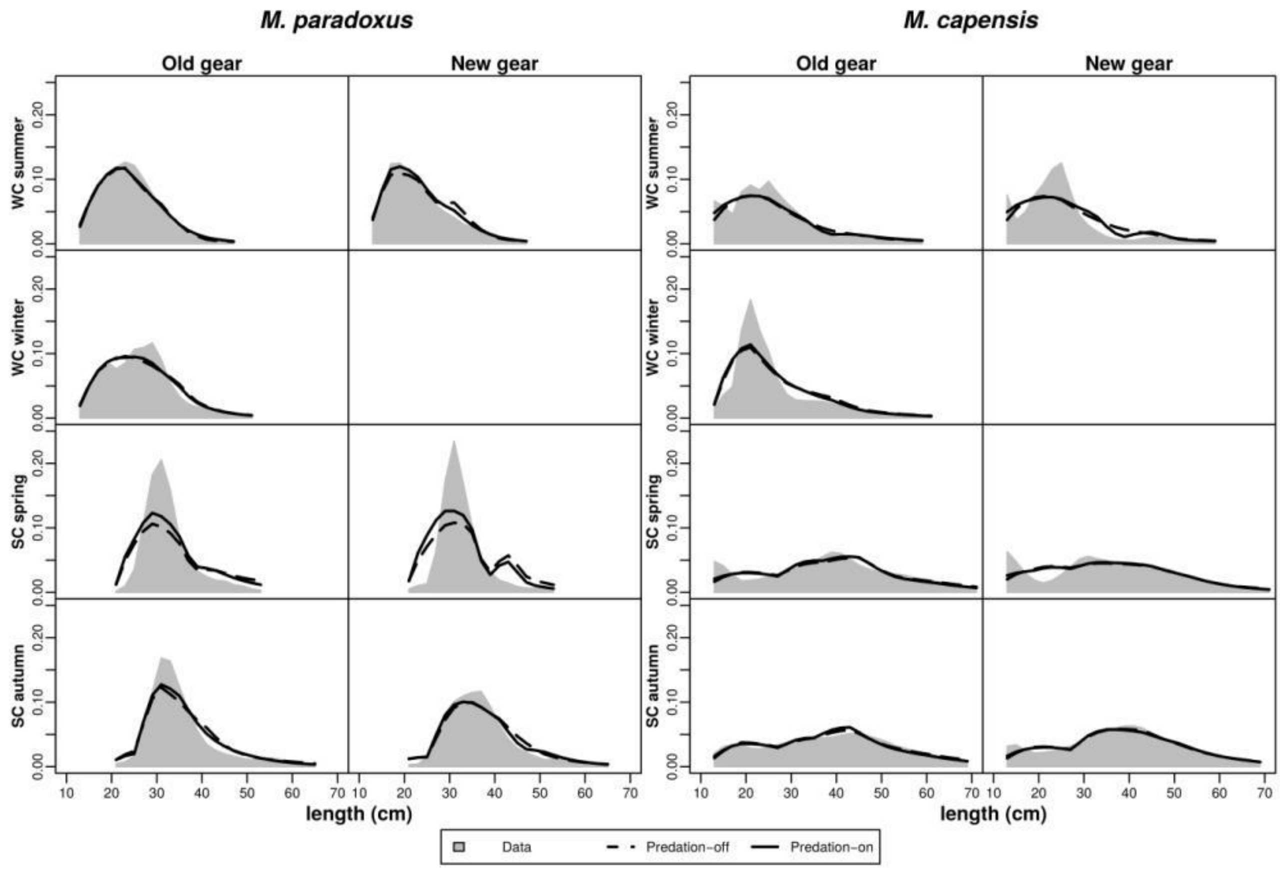

Figure 7b. The fits to the survey catch-at-length proportions for the MARAM model. Note that these proportions have been aggregated across gender for the years in which sex-disaggregated data are available. Furthermore, the CAL proportions for the MARAM model were calculated in a slightly different manner to those used in the OLRAC model, taking stratum density into account, although it was found that this alternative way of calculating the CALs did not make a substantial difference to the assessment results.

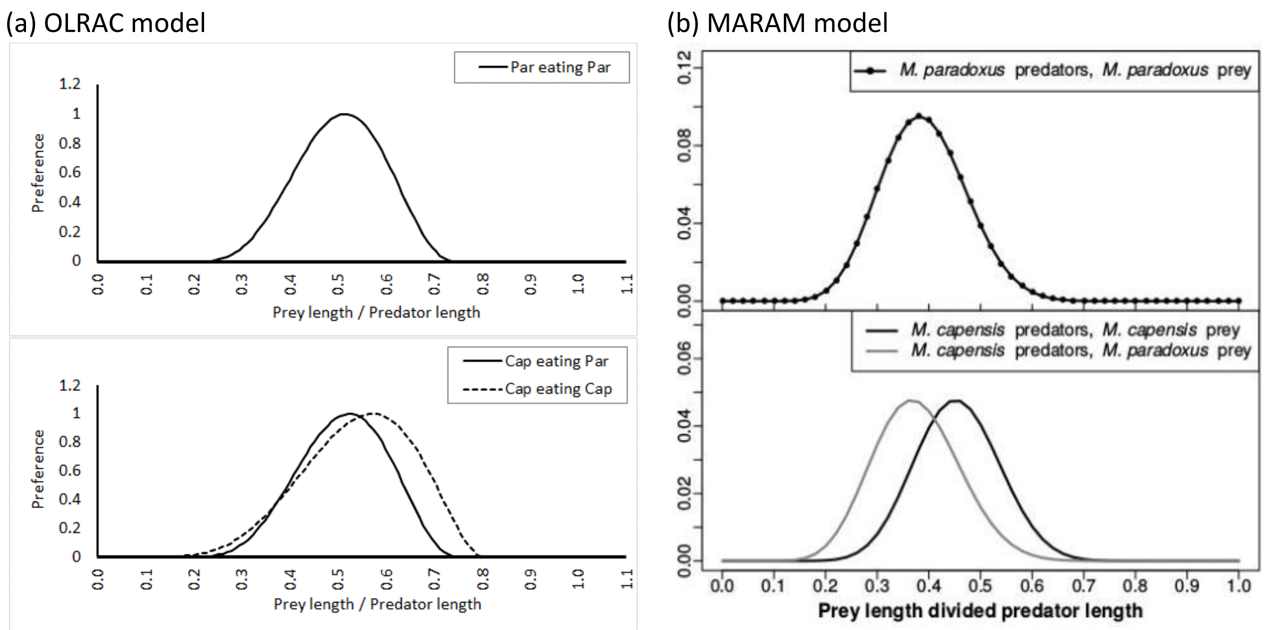

Figure 8. Predator-prey preference. The plots show the preference function evaluated in terms of the ratio of prey length to predator length.

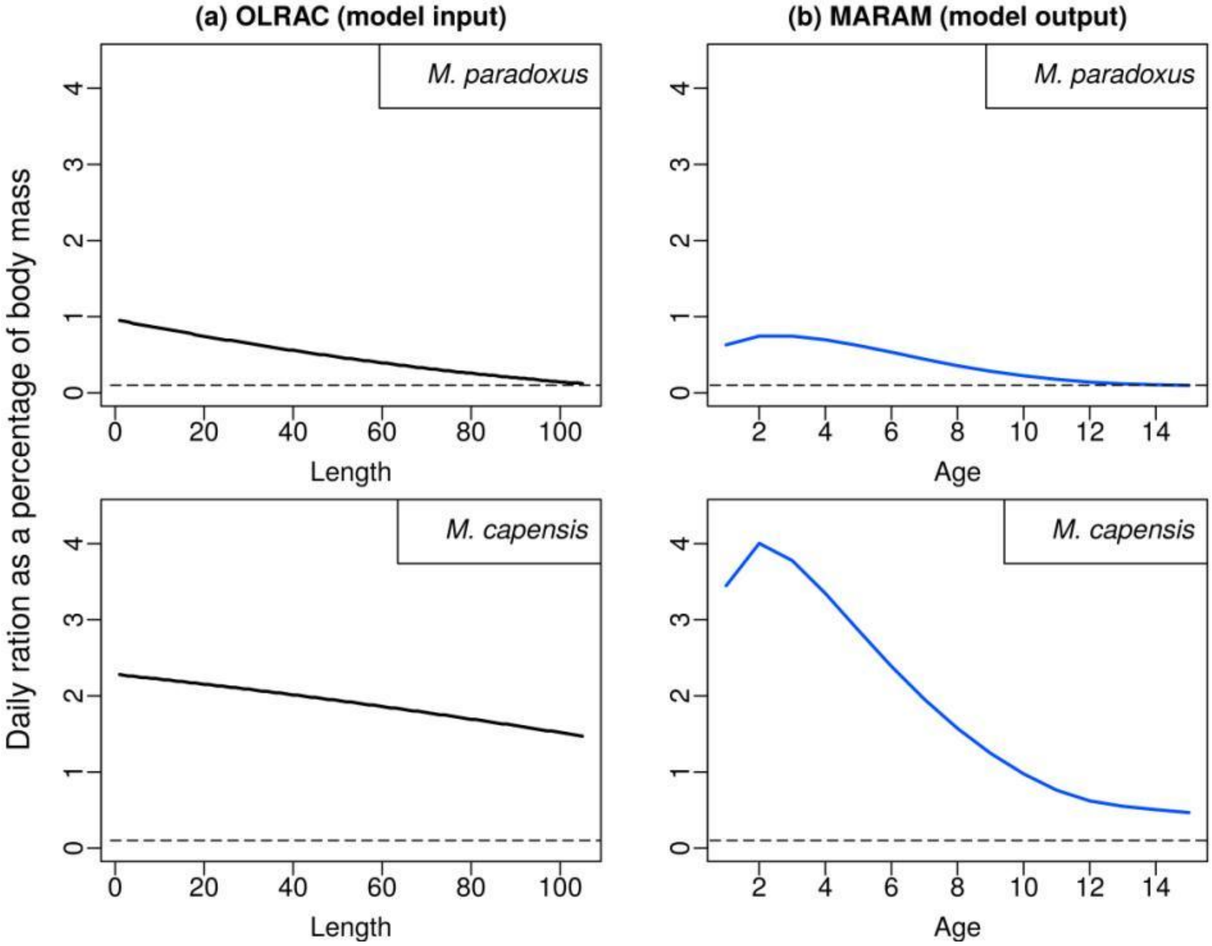

Figure 9: Plots of daily ration of hake predators as a percentage of body mass. The two left panels show the OLRAC daily rations as a function of predator length. These rations are taken from Punt and Leslie (1995) and are fixed on input The two right panels show the MARAM daily rations as a function of predator age, which are estimated in the model. The MARAM model enforces a lower bound of 0.1% on the daily ration; the dashed horizontal lines indicate this 0.1% mark. Furthermore, the MARAM model enforces a penalty so that the slope of daily ration with predator age is relatively close to -1/3.

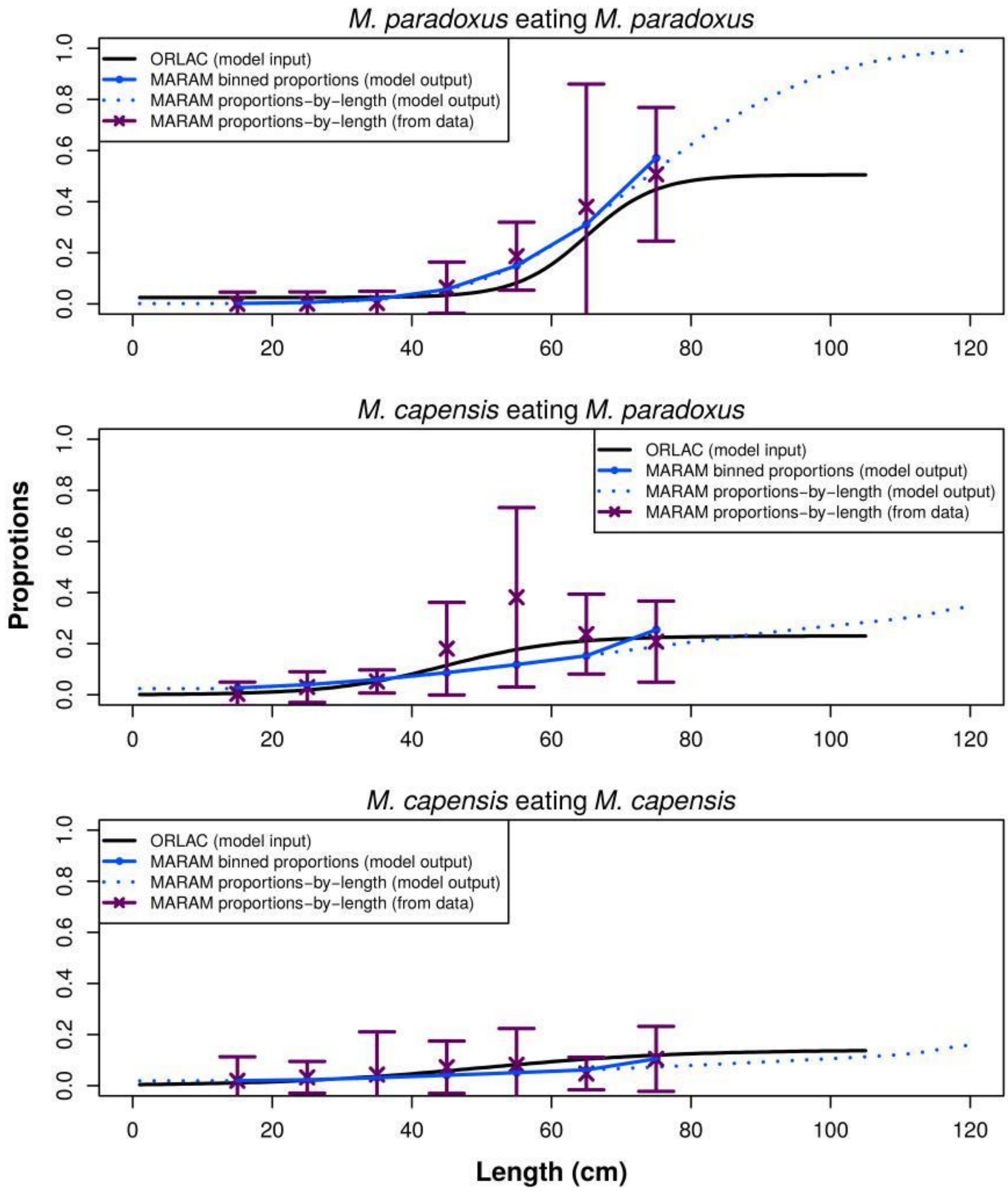

Figure 10: Plots of the proportion of hake in the diet of hake predators. The three panels show the proportions of hake in the diet of hake predators for the OLRAC model (black) and the MARAM model (blue). The OLRAC proportions are taken from Punt and Leslie (1995) and are fixed on input. The MARAM proportions are model outputs, fit to estimates from the 1999-2013 DAFF stomach content data – these estimates from the data are shown with purple crosses along with their 95% confidence intervals. The MARAM proportions are averaged over the years 1999-2013, the years for which stomach content data are available.

Note that for the MARAM model, the model and observed proportions were binned before calculating the likelihood. The binning was done by calculating the total amount of hake consumed in a given length class and dividing by the total ration. Since the daily ration decreases with predator age, the proportions at greater predator lengths will contribute less to the binned proportions. This is why, for example, the proportion of *M. paradoxus* eating *M. paradoxus* can go up to 1 at length 120, but the 70cm plus group proportion is at 0.6.

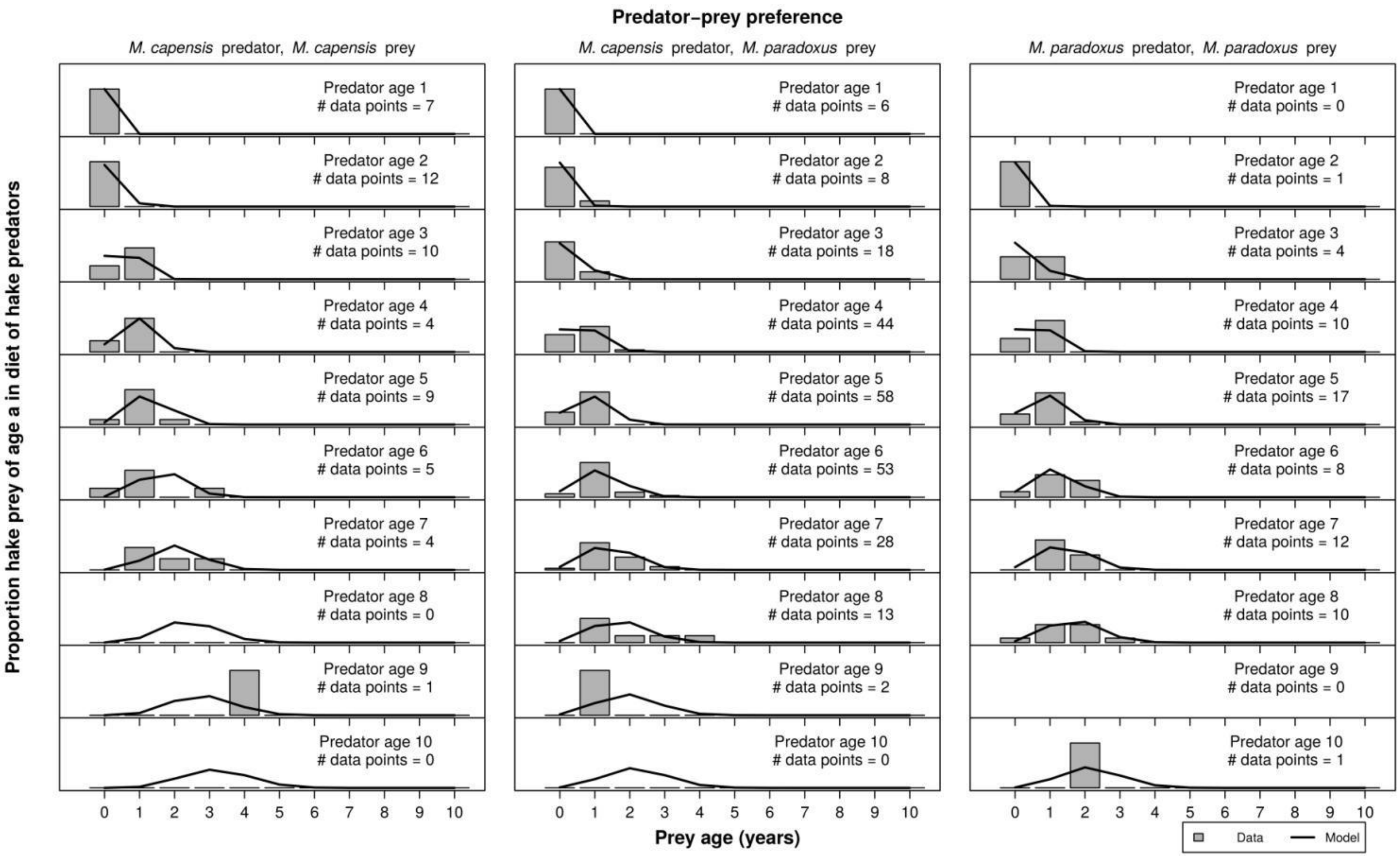

Figure 11: Fits of the MARAM model to the preference data. These data are derived from the DAFF 1999-2013 dataset, converting the counts per predator and prey length group age groups using the expected age-at-length from the von Bertalanffy growth curve. The counts have been accumulated over the years 1999-2013 and are fit to the model-predicted preference counts for the same period.