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UPDATED SEAPODYM REFERENCE MODELS FOR FOUR PACIFIC TUNA SPECIES

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1 Executive Summary

The Pacific Community (SPC) maintains SEAPODYM reference models – spatially explicit, environmentally driven, age-structured population models parametrised from fisheries and other observations by adjoint-based maximum likelihood estimation – for the four principal tuna species of the Western and Central Pacific Ocean: skipjack, bigeye, yellowfin and South Pacific albacore. This Information Paper reports progress in updating these reference models with new ocean forcings simulated by coupled NEMO–PISCES models with the JRA55 and ERA5 reanalyses at 1° monthly resolution, an extended SEAPODYM framework, and additional observations, including tagging and early-life-stage data which were not used previously. Catch and length-frequency data are fitted for all four species, tagging for the three tropical tunas, and early-life-stage data for all except bigeye.

The paper's main focus is the question of whether the updated models improve on the previous reference models. Compared over the common 1986–2010 period, all four updated models improve their statistical validation scores across the data types to which they were fitted, with the improvement being uniform for skipjack and bigeye, and partial for yellowfin and albacore, for which some of the metrics are unchanged or slightly poorer. For skipjack, bigeye and yellowfin, part of this improvement is demonstrated on independent, out-of-sample data, since the first decade of the comparison window lies outside their fitting period whereas albacore is compared over a shared estimation period. The improvement is largest for bigeye and smallest for skipjack, whose previous reference was already the most advanced of the four. Two of the models, skipjack and bigeye, are well advanced, while yellowfin and albacore remain under active development.

Once finalised, the updated models will be used to project the impacts of climate change on tuna population dynamics and to evaluate the consequent economic impacts on regional tuna fisheries. The parameter-estimation method and the underlying convergence and sensitivity analyses are described in the companion methodology paper (Senina *et al.*, 2026) and the results of these analyses will be reported once the models are finalised.

1.1 Acknowledgments

The continued development and application of the SEAPODYM model to the work of the WCPFC Scientific Committee is facilitated through Project 62. The project affiliates the independently funded work on SEAPODYM into the SC's work programme. It is conducted in collaboration with the Oceanic Fisheries Programme (OFP) of the Secretariat of the Pacific Community. This work under Project 62 was supported by a Climate Change and Tuna Project coordinated by the Oceanic Fisheries Programme at SPC, FAO ABNJ2 Tuna Project funded by the Global Environmental Fund, and by the GCF Regional Tuna Programme, Component B, Activity 3.1.

2 Introduction

The Spatial Ecosystem and Population Dynamics Model (SEAPODYM) is a spatially explicit, age-structured model of tropical tuna populations in which movement, reproduction and mortality are driven by the physical and biogeochemical ocean environment, and whose parameters are estimated from fisheries and other observations by adjoint-based maximum likelihood (SEAPODYM Reference Manual, 2022; Senina *et al.*, 2020a). The Pacific Community (SPC) maintains SEAPODYM reference models for the four principal tuna species of the Western and Central Pacific Ocean (WCPO) – skipjack, bigeye, yellowfin and South Pacific albacore – and uses them to advise the WCPFC Scientific Committee on the spatial population dynamics of these stocks under environmental variability and climate change.

This update is undertaken under Output 1.2.1 of the FAO–GEF project "Sustainable Management of Tuna Fisheries and Biodiversity Conservation in the Areas Beyond National Jurisdiction", whose objectives include updating the reference SEAPODYM models with available ocean and fisheries data and evaluating the impacts of current and future climate regimes on Pacific tuna population dynamics. Three developments motivate the present update: (i) a new version of the SEAPODYM framework (v5.1) with extended data-assimilation and estimation capabilities; (ii) new coupled NEMO–PISCES physical–biogeochemical ocean simulations, forced by the JRA55 and ERA5 atmospheric reanalyses, that provide long (1959–2022) and internally consistent time series of temperature, currents, dissolved oxygen and primary production at 1° monthly resolution; and (iii) extended observational datasets, including tagging and early-life-stage data.

This Information Paper reports on progress in that update. Two of the four models require a resolution refinement, while the other two are well advanced in their development but remain a work in progress; here we address a single question – whether the updated models improve compared to the previous reference models – by comparing their statistical validation scores for the fit to both the estimation data and the independent validation data, over the common 1986–2010 period for which the previous reference models are available. The methodological basis of all reference models – the parameter-estimation method, convergence and sensitivity analyses – is described in the companion paper (Senina *et al.*, 2026) and the results of all these analyses will be reported once all four models are finalised. The models will then be used to project the impacts of climate change on tuna population dynamics and to evaluate the consequent economic impacts on regional tuna fisheries.

3 Updating reference models with an enhanced SEAPODYM framework

3.1 SEAPODYM v5.1

Since the development of the previous reference models, the SEAPODYM code has undergone several improvements and major changes, significantly impacting the workflow and enabling quantitatively better models. The current reference models use an updated version of SEAPODYM (v5.1). The main code changes and model improvements are

outlined below by three development axes.

- **Code performance**
  - A cleaner and better structured public codebase on GitHub (https://github.com/PacificCommunity/seapodym-codebase.git), working branch 'development', which compiles into five different binaries *seapodym* for simulation runs, *seapodym_clte* for simulation and estimation, *seapodym_densities* with estimation model for unexploited stocks, *seapodym_habitats* for habitat models with parameter estimation, and *seapodym_fluxes* to compute regional connectivity in the population dynamics model with or without fishing.
  - A decrease of the RAM needs for the adjoint code and hence for the estimation by about 55%.
- **Model structure**
  - A new observation model for early larvae observed in larval net sampling.
  - Alternative models for reproduction: two formulations of the Beverton–Holt function, both with optional Allee effect, and a more mechanistic representation of reproduction (adult-density function at age 0, H_s-dependent survival during the first month of life).
  - Normalisation of the parametric prey function of the spawning habitat to enable unbiased reproduction rate estimation.
  - Three types of thermal function in spawning habitat: Gaussian, asymmetric Gaussian and logistic thresholds.
  - Several alternative models for environmental dependence of diffusion rate.
  - Accounting for the species' lethal thermal limits in the thermal habitat accessibility.
  - Default asymmetric Gaussian thermal function in the feeding habitat's accessibility formulation.
  - Support for an arbitrary number of forage groups in the estimation model.
- **Estimation framework**
  - Integration of early-life history data, including eggs hatching success as a result of laboratory studies, larval density from broad scale larval surveys, and spawning seasonality from adult gonad sampling studies.
  - Implementing multiple choices for larval data integration and likelihood types.
  - Implementing alternative observation models for observed larval quantities, CPUEs and/or presence probabilities.
  - More flexible set-up of tagging data to inform movement parameters, including minimal density threshold for the inclusion of tag recapture groups, selection of tags by time at liberty, choice of likelihood formulation and weights.
  - A Taylor derivative test for analytical gradient verification.

- Estimation of a catchability trend parameter.
- Stock likelihood term as the penalty.
- Optional addition of parametric penalty to the likelihood.
- More flexible set-up of local and global sensitivity analyses.
- Convergence and parameter-uncertainty diagnostics computed from the Hessian at the solution: a scale-invariant Newton decrement as the convergence criterion, a positive-definiteness check, and parameter standard errors, correlations and least-identified directions, all implemented now in the codebase.

3.2 Environmental forcing

The four reference models are driven by ocean fields from coupled NEMO–PISCES physical–biogeochemical simulations forced by the JRA55 and/or ERA5 atmospheric reanalyses, providing consistent, long time series of temperature, currents, dissolved oxygen and primary production, together with mid-trophic (micronekton) biomass from the SEAPODYM–LMTL sub-model (SEAPODYM Reference Manual, 2022), on a 1° grid, degraded for parameter estimation to 2°.

3.3 Model configurations

The model PDE equations and methodology are fully described in SEAPODYM Reference Manual (2022) and companion paper (Senina *et al.*, 2026). Here we detail the configuration of the four reference models – age structure, growth and maturity models and estimation, Maximum Likelihood Estimation (MLE) and validation time periods, the use of fisheries, tagging and early-life datasets in the joint likelihood. This information is also summarised in Table 1.

3.3.1 Skipjack model

Six different life stages are considered: eggs (result of adults' spawning), early larvae (0–7 days old), larvae (7 days to 1 month old), small juveniles (1–3 months old), juveniles (older than 3 months but not yet reached age of 50% maturity, which is set to 11 months), and adults, including only a mature part of the population (> 11 months old corresponding to fork length > 43.7cm). The age between 0 and $a_{max} = 3$ years is discretized into monthly age classes and 2 more years are modelled as a single A+ class, thus resulting for skipjack in 37 age classes covering five years of life span. The estimates of length-at-age, weight-at-age and maturity-at-age relationships were taken from the 2016 MULTIFAN-CL assessment report (McKechnie *et al.*, 2016) and interpolated to the model age structure.

The fisheries data used in MLE were structured into eight pole-and-line, eight purse-seine, one longline fishery and one small-scale fishery combining other gears (see Table 2 of Senina *et al.* (2025)). Fishing mortality was computed using both methods: using fishing effort according to the continuous Gordon-Schaefer model, or using catch removal method (SEAPODYM Reference Manual, 2022), applied to the fisheries according to

their data quality and target species properties. As in the previous reference model, all purse-seine fleets were kept as catch-removal fisheries.

The early larvae likelihood integrated in SEAPODYM v5 (Bonnin and Senina, 2024) to enable direct comparison of model predictions with the larval survey observations was computed over the 1995–2000 period.

Optimisations were run over the 1991–2012 time window, with the predictions of the first four years of simulation excluded from the likelihood to reduce the effect of the initial conditions on the MLE solution.

3.3.2 Yellowfin model

Four different life stages are considered: larvae (age 0–1mo), small juveniles (age 1–3mo), juveniles and immature sub-adult (age 4–24mo) and adults. The age between 0 and 6.7 years are discretized into monthly age classes, and 6.7 more years are modelled as a single A+ class, thus resulting in 83 age classes covering 13.4 years of life span. The estimates of length-at-age and maturity-at-age relationships were taken from the 2023 MULTIFAN-CL assessment report (Magnusson *et al.*, 2023) and interpolated to the model age structure. *Von Bertalanffy* parameters from OFP-SPC (2019) were used to compute weight-at-age from length-at-age. As yellowfin tunas are opportunistic spawners, spawning migrations are de-activated in this configuration, so spawning occurs in times and locations of favourable spawning habitat.

The fisheries data used in MLE were structured into eight purse-seine, seven pole-and-line, six longline fisheries and one fishery combining other gears (see Table 4 of Bonnin *et al.* (2026)). Fishing mortality was computed using fishing effort according to Gordon-Schaefer model for the longline and pole-and-line fisheries, and using catch removal method for purse-seine and the fishery combining other gears, as effort data was considered as unreliable.

Larval data was integrated into early-life likelihood by fitting to seasonal averages (1999–2018 time window) of one-month-old larvae densities.

Conventional tagging data was included in the MLE, selecting cohorts of monthly recaptures with a minimum of 50 tags and with recaptures between 2006 and 2012, resulting in 12,962 tags.

Optimisations were run over the 1999–2018 time window, with the predictions of the first five years of simulation excluded from the likelihood to reduce the effect of the initial conditions on the MLE solution.

Fisheries validation datasets were considered, using two time periods out of the MLE: 1983–1998 and 2019–2022. A tagging validation dataset consisted in all cohorts of monthly recaptures with a minimum of 10 tags, and not already included in the MLE dataset, resulting in 2,510 tags.

3.3.3 Bigeye model

Four different life stages are considered: larvae (age 0–1mo), small juveniles (age 1–3mo), juveniles and immature sub-adult (age 4–39mo) and adults, however the transition from immature sub-adult to mature adults is continuous, defined by the smooth maturity function used in the 2020 stock assessment with MULTIFAN-CL (Ducharme-Barth *et al.*, 2020). The age between 0 and 8 years are discretized either into monthly or quarterly

age classes, and 6 more years are modelled as a single A+ class, thus resulting in 97 (33 if quarterly) age classes covering 14 years of life span. For the bigeye tuna growth, which is known to be variable across the Pacific Ocean, the model used in Harley *et al.* (2014) that reflects mainly the growth of bigeye tuna in the EPO was selected previously for its best performance in terms of validation scores and parameter estimates (Senina *et al.*, 2023).

Fisheries data was structured into 17 independent fisheries, comprising nine longline fisheries, six purse-seine fisheries, one pole-and-line and one fishery aggregating other gears. The decision on catch-removal fisheries was taken based on the target species and the quality/availability of the fishing effort. Thus, in fisheries, where bigeye was either a primary target or a secondary target whereas the primary target did not change seasonally, the catch was predicted with the classical Gordon-Schaefer equation based on fishing effort. For all other fisheries, catches were predicted by the catch-removal method. These are four longlines (operating at high latitudes with seasonal shifts in targets), two purse-seines, the pole-and-line (solely because it combines all fleets Pacific-wide) and the other-gears fishery.

For tagging data, 57 most abundant monthly groups with 8923 tag recaptures in total between 2000–2014 were selected for MLE, which differs from the previous work (Senina *et al.*, 2023), where 2000–2007 recaptures, which are located in EPO were left for validation. No larval data were used in the bigeye reference model.

For optimisation, the configuration with degraded age resolution was used. Once parameters were estimated, the model with MLE parameters was simulated and validated with monthly age structure. The MLE time window was 1991–2019, bounded from below to include the development of purse-seine fleets while having enough years to cover at least two lifespans, and from above by the availability of the complete fisheries data. The first four years were skipped to reduce the impact of the initial conditions on MLE.

3.3.4 South Pacific albacore model

Three life stages are considered: larvae and small juveniles (0–3 months old), juveniles and immature sub-adult (age 4 months – 4.5 years corresponding to 50% maturity at a fork length of 84.4 cm), and mature adults. The age between 0 and $a_{max} = 12.5$ years is discretized into quarterly age classes, giving 50 explicit classes (one combined larvae/juvenile class, 17 immature adult classes and 32 mature adult classes), and 7.5 more years are modelled as a single A+ class, thus resulting for albacore in 51 age classes covering 20 years of life span. Estimates of length-at-age, weight-at-age and maturity-at-age relationships were taken from (Harley *et al.*, 2015) and interpolated to the model age structure.

Sixteen fisheries were included in the MLE: 14 longline fleets alongside a drift gillnet and a troll fishery (see Table A1 of (Senina *et al.*, 2020b)). Two approaches were used to compute fishing mortality, depending on data quality and the fishery's targeting behaviour: a Gordon-Schaefer effort-based formulation, or a catch removal method (SEAPODYM Reference Manual, 2022). Eleven of the longline fisheries retained the effort-based approach; the remaining three longline fisheries, together with the drift gillnet and troll fisheries, were modelled through catch removal, either because they target a mix of species, lack reliable effort data, or report effort aggregated over spatial and

temporal scales too coarse to serve as a catchability driver.

Two early life stage datasets were used to inform the spawning and larval components of the model: a digitised Japanese larval survey (Nishikawa dataset), providing seasonal larval CPUE on a 1° grid across the Pacific, and a South Pacific albacore gonad histology dataset providing spawning status of 1,177 sampled females, used to inform a seasonal spawning index and movements of adults to the spawning sites (Bonnin and Senina, 2024). Both datasets were integrated into the SEAPODYM likelihood following the cost function developments described in (Bonnin and Senina, 2024), and used to re-estimate spawning habitat and spawning season parameters.

Optimisations were run over the 1980–2013 period, long enough to encompass the extended lifespan of albacore, while avoiding the pre-1980s longline fleets' catchability regime associated with pre-monofilament gear. The first five years of the estimation period were used for initialisation and excluded from the likelihood, to reduce the effect of initial conditions on the MLE solution. A validation run, using fisheries data alone, was performed over 1960–1979, to assess model behaviour and stability using the additional available historical catch and effort data. For the early life stage likelihood, larval survey and gonad data were fitted over 1990–2004, a period selected for its climatological similarity to the 1956–1981 Nishikawa survey period, notably with respect to ENSO variability.

Table 1: Configuration of the four SEAPODYM reference models.

	Skipjack	Yellowfin	Bigeye	S. Pacific albacore
Age structure	37 classes, 5 yr[a]	83 classes, 13.4 yr[b]	97 (33) classes, 14 yr[c]	51 classes, 20 yr[d]
Growth (length/weight-at-age)	SA-2016[e]	SA-2023[f]	SA-2014[g]	SA-2015[h]
Maturity-at-age	SA-2016	SA-2023	SA-2020[i]	SA-2015
MLE period	1995–2012	1999–2018	1995–2019	1980–2013
Validation period	2013–2022	1983–2018/ 2019–2022	1960–1994	1960–1979
Fisheries (no.; gears)	13–18 (5–7 PL, 7–9 PS, 1 LL, 1 OT)	22 (8 PS, 7 PL, 6 LL, 1 OT)	17 (9 LL, 6 PS, 1 PL, 1 OT)	16 (14 LL, 1 T, 1 G)
Tagging data	yes	yes	yes	—
Early-life data	yes	yes	—	yes
Spatial resolution MLE	2°	2°	2°	2°
Age resolution MLE	monthly	monthly	quarterly	quarterly
Ocean forcing	ERA5–NEMO–PISCES.v2		JRA55–NEMO–PISCES.v2	

[a] monthly age classes to 3 yr plus a 2-yr A+ class.
[b] monthly age classes to 6.7 yr plus a 6.7-yr A+ class.
[c] monthly (quarterly) age classes to 8 yr plus a 6-yr A+ class.
[d] quarterly age classes to 7.5 yr plus a 12.5-yr A+ class.
[e] SA-2016 = McKechnie *et al.* (2016).
[f] SA-2023 = Magnusson *et al.* (2023).
[g] SA-2014 = Harley *et al.* (2014).
[h] SA-2015 = Harley *et al.* (2015).
[i] SA-2020 = Ducharme-Barth *et al.* (2020).

3.4 Numerical configurations

The model PDE equations (SEAPODYM Reference Manual, 2022) were numerically solved with a monthly time step and two spatial resolutions, on a 1° (simulations) and 2° (MLE) regular grids covering the spatial domain of the Pacific Ocean $\Omega = \{x \in (100°E, 70°W), y \in (59°S, 61°N)\}$ or South Pacific Ocean $\Omega = \{x \in (140°E, 70°W), y \in (59°S, 5°N)\}$. Neumann boundary conditions were used in all runs.

4 Evaluating model performance against previous references

The updated models are compared against the previous reference models of the four species. Those models were built on the earlier SEAPODYM framework and forced by the previous-generation coupled ERA-INTERIM–NEMO–PISCES (hereafter INTERIM) simulations at 2° resolution available over 1979–2010, whereas the updated models are run with ocean forcings of 1° original resolution covering a much longer historical period, 1959–2022. For the updated models, such new forcings provided the flexibility to choose the MLE window and to use the degraded 2° resolution operationally during the development phase, moving to the 1° resolution once the models are fully developed and validated.

All four previous models were fitted to catch and length-frequency data; only the skipjack model used conventional tagging data in the joint likelihood; the yellowfin model was conditioned on habitat and movement parameters estimated from tagging data; and none assimilated early-life-stage data. The models detailed set-up and outcomes can be seen in the following papers and reports: skipjack model in Senina *et al.* (2020a), yellowfin and bigeye models in Senina *et al.* (2023), and albacore model in Senina *et al.* (2020b).

4.1 Comparison between models

The models are compared over 1986–2010, the common period available for all four previous reference models; its start is set by the yellowfin previous-generation INTERIM outputs, which begin in 1986, the other three species extending back to 1979. This window favours the previous models, which over 1986–2010 were evaluated entirely within their estimation period. The updated skipjack, bigeye and yellowfin models, by contrast, have estimation periods beginning in 1991, of which the first four to five years serve as model spin-up and are excluded from the likelihood, so that their fitted period starts in 1995–1996 (Table 1). Hence, for these three species, roughly the first decade of the comparison window, 1986 to the mid-1990s, is independent, out-of-sample data. The updated albacore model is an exception: its estimation period of 1980–2012 uses the same fisheries data as the previous albacore model, so for albacore the two models are compared over a shared estimation period. The improvements reported below for skipjack, bigeye and yellowfin are therefore obtained under a comparison that, if anything, favours the previous models.

Figure 1 compares the total-biomass distributions predicted by the previous and updated models. The estimated parameters of the updated models are collected in Table 2.

Table 3 reports the global validation scores of the previous and updated reference models by data type.

Table 2: Estimated parameters of the four updated SEAPODYM reference models; notations follow SEAPODYM Reference Manual (2022). Skipjack parameters are from the MLE with SEAPODYM under ERA5–NEMO–PISCES.v2 reference solution; Yellowfin values are for the `jra55` best solution; † marks parameters held fixed (not estimated).

θ	Description	Skipjack	Yellowfin	Bigeye	Albacore
Reproduction and spawning habitat					
T_s^*	optimal spawning SST, °C	30.0†	19.3–32	28.5	24.71
σ_s	SST-Gaussian std. dev. or logistic slopes (H_s), °C	10.0†/1.0†	0.6/0.01	4.0/2.5	1.517
α	prey (NPP) function shape (Holling-III)	11.98	0.0454	≈ 0	10^{-5}†
α_F	predation function amplitude	2.50†	4.74	1.0†	1†
β_F	predation function shape	2.63	3.28	2.66	2.5†
r	reproduction rate, in mo^{-1}	3.5†	0.065	0.04†	0.007
b	reproduction slope parameter	0.09	10.1	5.15	1.5†
Adult thermal and oxygen habitat					
σ_0	SST-Gaussian std. dev. age 0, °C	1.06	0.031	1.89	2.754
σ_K	SST-Gaussian std. dev. oldest cohort, °C	2.0	4.48†	1.5	2.5†
T_0	optimal SST, age 0, °C	31.5†	29.2	22.5	28†
T_K	optimal SST, oldest cohort, °C	27.15	26.6†	9.36†	12.86
b_T	thermal-preference age slope	0.50	3.0	0.20†	0.6918†
$\hat{O}$	dissolved-oxygen threshold, $\mathrm{ml\,l^{-1}}$	3.97	1.8†	0.53	3.5†
Forage (feeding-habitat) accessibility					
E_{11}	epipelagic forage	1.5	1.72	0†	3†
E_{22}	upper-mesopelagic forage	1†	10	≈ 0	4.5
E_{21}	migrant upper-mesopelagic forage	3†	0.087	0†	0†
E_{31}	highly migrant lower mesopelagic forage	1.3	0.87	≈ 0	1†
E_{32}	migrant lower mesopelagic forage	0†	0†	0.23	0†
Movement					
V_m	max. sustainable speed (taxis), $\mathrm{BL\,s^{-1}}$	0.256	0.211†	2.82	1.98
σ	diffusion-rate multiplier	0.366	0.5†	1.24	4.39
c	diffusion–habitat coefficient	0.500	$1.85 \cdot 10^{-10}$	0.75†	$1.2 \cdot 10^{-9}$†
Natural mortality					
$\bar{m}_p$	predation mortality rate, $\mathrm{mo^{-1}}$	0.25†	0.13	0.15†	0.05†
β_p	predation mortality slope, $\mathrm{mo^{-1}}$	0.12	0.382	0.047	0.059
$\bar{m}_s$	senescence mortality rate, $\mathrm{mo^{-1}}$	0.0138†	$4.58 \cdot 10^{-5}$	$2.05 \cdot 10^{-5}$ †	0.0004†
β_s	senescence mortality slope, $\mathrm{mo^{-1}}$	0.77	1.42	1.73	1.10
ε	habitat-dependent mortality amplitude	0	4.97†	$2.4 \cdot 10^{-4}$	1.09
ε_{larvae}	habitat-dependent larval mortality amplitude	20†	4.7†	2.7†	0†

4.1.1 Skipjack

Both reported MLEs converged and were found to be at a minimum. The updated skipjack model improves on the previous reference across every data type, although each metric improves only marginally. The basin-aggregate catch fit strengthens on all three Taylor components (r^2 0.93 → 0.95, VR 0.88 → 0.92, *err* 0.27 → 0.23); the length-frequency shape is essentially unchanged ($\mathrm{NRMSE}_{\bar{x}}$ 0.40 → 0.39) while its mean bias is removed (SMD 0.11 → 0.00); and every tagging metric improves (NRMSE_{σ} 0.57 → 0.52, KGE 0.73 → 0.77, PC 0.86 → 0.89). The updated model additionally assimilates early-life-stage data, absent from the previous model, reproducing the larval distribution with $\mathrm{NRMSE}_{\sigma} = 0.45$. For a controlled comparison, the previous skipjack INTERIM reference was re-run and re-validated using the same fishery structure as the updated models

Table 3: Global validation scores by data type over the common 1986–2010 period, for the previous (Prev.) and updated (Upd.) reference models: C catch, L length-frequency, T tagging, E early-life. Catch scores are the basin-aggregate Taylor triple, PC is the pattern correlation, and KGE is Kling-Gupta efficiency metric (see Senina *et al.* (2026), Section 8.2). **Bold** marks the better score in each Prev./Upd. pair. — = *data type not used for that species.*

		Skipjack		Yellowfin		Bigeye		Albacore	
Data	Metric	Prev.	Upd.	Prev.	Upd.	Prev.	Upd.	Prev.	Upd.
Catch (C)	r^2	0.93	**0.95**	0.45*	**0.51***	0.71	**0.81**	0.71	**0.72**
	VR	0.88	**0.92**	0.50*	**0.94***	0.67	**0.85**	0.6	**0.73**
	err	0.27	**0.23**	0.75*	0.75*	0.54	**0.43**	0.54	**0.53**
Length (L)	$\text{NRMSE}_{\bar{x}}$	0.40	**0.39**	**0.47**	0.53	0.68	**0.41**	**0.44**	0.52
	SMD	0.11	**0.00**	0.08	**-0.07**	0.15	**0.02**	-0.061	**0.058**
Tagging (T)	NRMSE_{σ}	0.57	**0.52**	**0.36**	0.5	0.74	**0.70**	—	
	KGE	0.73	**0.77**	**0.85**	0.73	0.35	**0.55**	—	
	PC	0.86	**0.89**	**0.93**	0.87	0.64	**0.76**	—	
Early-life (E)	NRMSE_{σ}	—	0.45	0.68	**0.67**	—		0.98	**0.72**

* Yellowfin catch scores compare longline (LL) data only: they are the catch-weighted aggregate over the LL fisheries, because the updated yellowfin model imposes its purse-seine catch by removal, which would artificially inflate the basin-aggregate fit.

(Senina *et al.*, 2025, Table 2), so that the score differences reflect the model and forcing update rather than a change in the definition of the fisheries. As about the first decade of the window is out-of-sample, these gains are obtained partly on independent data.

4.1.2 Yellowfin

The development of the yellowfin model is still a work in progress, and the current best model solution presented here shows some deficiencies in fitting tagging data and in predicting stock level. Indeed, this solution is a hybrid configuration combining the biological and fisheries parameters from one MLE solution with the movement parameters from a separate solution (Bonnin *et al.*, 2026). Future work will focus on including the estimation of movement and fisheries selectivity parameters into an MLE.

The updated yellowfin model comparisons are not straightforward. Because the previous model was informed by purse-seine fisheries effort and catch and in the updated model the purse-seine fleets inform model parameters only in grid cells where there is not enough biomass to sustain observed catches, the catch comparison for purse-seine fisheries is meaningless and hence is restricted to longline fisheries (Table 3, note). There the pronounced under-dispersion of the previous model is corrected (VR 0.50 → 0.94), while spatial correlation and error are either slightly improved or unchanged (r^2 0.45 → 0.51, *err* 0.75). Note, however, that the 1986–1995 period is out-of-sample for the updated model, while entirely within the fitting period of the previous model. The length-frequency shape fit degrades slightly ($\text{NRMSE}_{\bar{x}}$ 0.47 → 0.53), though the mean-length bias stays small (SMD 0.08 → −0.07). The early-life-stage global error is similar to the previous model's (0.68 → 0.67), but with notable difference for the SST (0.63 → 1.45) and MNK profiles

(1.18 → 0.41).

The previous model attains the better tagging scores, but its tagging fit derives from a stand-alone tag-movement model by keeping the movement and habitat parameters conditioned on that tag-likelihood maximisation rather than the fully re-estimating them with the joint likelihood, so the two are not directly comparable and we draw no conclusion from them here. The updated yellowfin model therefore corrects the catch dispersion and largely preserves its fit elsewhere, but does not uniformly surpass the previous reference.

4.1.3 Bigeye

The best-configuration MLE converged with Gmax=96 and the full convergence diagnostics were not yet run for this model pending a few additional tests to explore the overestimation of bigeye biomass in the high latitudes, in particular in the southern ocean. The updated bigeye model improves on the previous reference across every data type, and by the widest margins of the four species. The catch fit improves on all three Taylor components (r^2 0.71 → 0.81, VR 0.67 → 0.85, *err* 0.54 → 0.43), and the length-frequency fit improves markedly in both shape and bias ($\text{NRMSE}_{\bar{x}}$ 0.68 → 0.41, SMD 0.15 → 0.02). All three tagging metrics improve as well (NRMSE_{σ} 0.74 → 0.70, KGE 0.35 → 0.55, PC 0.64 → 0.76). Note, as the previous bigeye reference was fitted to catch and length-frequency data only, this is an out-of-sample tag validation, and the improvement reflects the assimilation of tagging data in the updated model.

4.1.4 Albacore

The updated albacore model is also a work in progress. It improves the catch variance ratio (VR 0.60 → 0.73) with little change in correlation or error (r^2 0.71 → 0.72, *err* 0.54 → 0.53), and significantly improves the early-life-stage error (0.98 → 0.72); the mean-length bias is marginally smaller (SMD −0.061 → 0.058). The length-frequency shape fit is the only metric that does not improve ($\text{NRMSE}_{\bar{x}}$ 0.44 → 0.52). Albacore integrates no tagging data. As the two models share their estimation period, these differences are entirely in-sample.

Figure 1 compares the mean total-biomass distributions, averaged over a decade 2001–2010, predicted by the previous and updated models. Across the four species the updated models retain the main large-scale features of their predecessors – the equatorial aggregation of the three tropical tunas and the south-western subtropical band of albacore – while resolving sharper spatial contrasts and additional basin- and boundary-scale structure, consistent with the higher-resolution ocean forcing. Each panel is drawn on its own colour scale, spanning the intrinsic range of the distribution it depicts, so the maps are compared here in spatial pattern only, not in absolute level.

For skipjack, both models place the highest densities in a zonal equatorial band along the western and central Pacific warm pool, coincident with the bulk of the catch. The updated model sharpens this pattern: the equatorial band is more strongly contrasted against the surrounding waters, and distinct concentrations emerge at higher latitudes and along eastern-boundary systems – notably higher densities in the Kuroshio region off Japan (although being seasonal they are poorly depicted on the average map) and near the Central American coast – that are smoothed out in the more diffuse previous field. The EPO sub-stock is hence substantially higher than in the previous model.

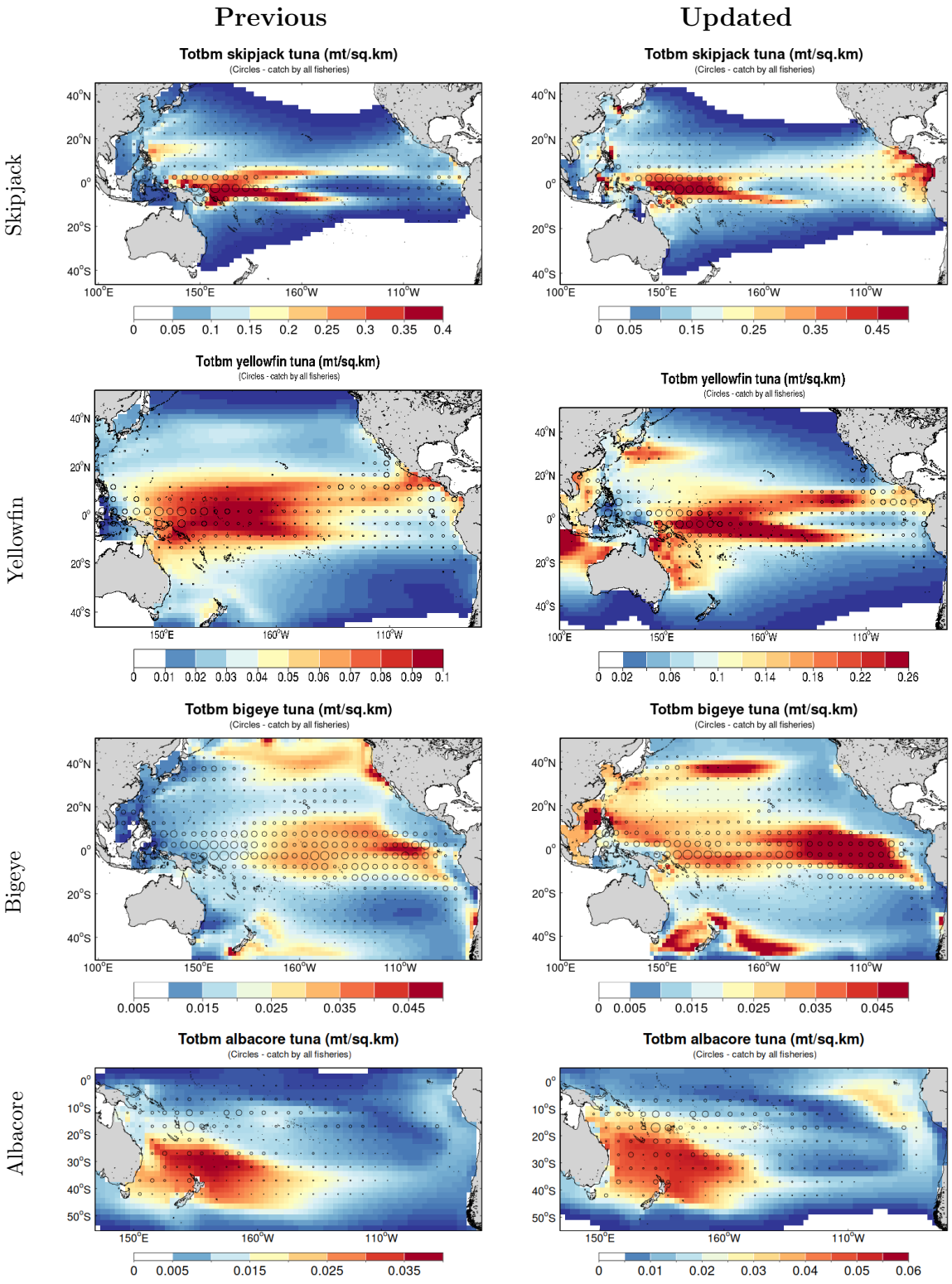

Figure 1: Spatial distribution of total biomass from the previous (left) and updated (right) reference models, for the four species (rows). Mean distributions were computed over the last decade of the common time period between previous and updated reference models, 2001–2010. Each panel uses its own colour scale, spanning the intrinsic range of the distribution shown, so the maps are comparable in spatial pattern but not in absolute magnitude.

While both yellowfin models show similarities in highest biomass concentrations within the tropical band, extending from the western Pacific warm pool across the central Pacific and north-eastward toward the coast of the Americas, the updated model exhibits stronger spatial contrasts and a more heterogeneous biomass pattern. In the updated model, the equatorial biomass band is narrower and the hotspot extends eastward on either side of the equator, forming northern and southern branches. In addition to the main equatorial aggregation, the updated model predicts pronounced biomass concentrations at higher latitudes, particularly in the Kuroshio region and along the East Australian Current in the Coral Sea.

The bigeye comparison shows the most pronounced structural change. The previous model spreads biomass diffusely across the central and eastern tropical Pacific with weak spatial contrast, and into the high latitudes with hotspots not supported by fisheries data. The updated model organises it into a well-defined equatorial core extending eastward, flanked by subtropical bands and by distinct concentrations along the Kuroshio Current in the north and, in the south, the Tasman Sea and the East Australian Current. The updated distribution is thus markedly more heterogeneous, with the two equatorial interconnected sub-stocks and the higher-latitude features more clearly separated.

For albacore, both models concentrate biomass in the south-western subtropical Pacific, around the Tasman Sea and north of New Zealand, in line with the fishery. The updated model renders this core more sharply and adds a north-eastward branch extending across the South Pacific toward lower latitudes in the east, following the subtropical front, giving a more structured distribution than the smoother previous field.

5 Discussion

All updated reference models mostly improve on their predecessors across the data types to which they were fitted (Table 3). The magnitude of the improvement is not uniform, and it tracks how developed each previous reference model was. The skipjack model shows the smallest gain – its catch fit was already very good (basin-aggregate r^2 rising only from 0.93 to 0.95), and its length and tagging scores improve modestly – because the previous skipjack reference assimilated conventional tagging data in the joint likelihood (Senina *et al.*, 2020a) and was thus the most advanced of the four. The bigeye model, whose previous reference left more room, improves substantially, with the catch r^2 rising from 0.71 to 0.81 and the catch-weighted length NRMSE falling from 0.68 to 0.41. The remaining two species, yellowfin and albacore, *a priori* have even more room for improvement as their previous references made the weakest use of the movement information and no use at all of early-life information.

Two changes underlie the improvement common to all four models. First, the new coupled NEMO–PISCES simulations are run at higher spatial resolution, which sharpens the representation of the equatorial circulation and, in particular, of the equatorial upwelling and the associated primary production that drive the forage and spawning habitats. Second, the estimation framework is more flexible and computationally performant (see Section 3 and Senina *et al.* (2026)), allowing a larger set of observable parameters and a wider range of data to be assimilated. Beyond these common factors, the gains are shaped by species-specific differences in the MLE and in the representation of the

fisheries.

For skipjack, the decisive addition is the assimilation of early-life-stage data through a dedicated early-larvae observation model, which constrains the modelled distribution of mature, spawning fish and thereby the spatial structure of recruitment. Bigeye benefits chiefly from the integration of tagging data, absent from its previous reference, which accounts for both its out-of-sample tagging improvement and the widest overall gains of the four species. For albacore, in the absence of usable tagging data, larval and gonad data inform the adult movements, as well as the spawning location and seasonality, which all together improve the estimation of recruitment.

Yellowfin appears the least improved in this validation, and is the most instructive case. Its representation gains from the advanced longline fishery structure (Forestier *et al.*, 2025) and from the validation of habitat parameters against archival-tagging records of vertical behaviour (Scutt Phillips *et al.*, 2022). At the same time, the revised protocol for integrating the purse-seine fisheries – whose catch is imposed by removal rather than fitted – may have withdrawn information that previously constrained the juvenile biomass, so that the updated model tends to over-predict density of young yellowfin in the equatorial zone while the adult stock remains only weakly constrained by the longline fisheries, whose low catch rates carry little weight in the likelihood. A further possible reason that the larval data did not sharpen the yellowfin fit as expected is one of sampling and scale: the larvae are predicted at the end of the month, by which time only a small fraction of a cohort survives, and the observed individuals, at 4–6 mm in length, are only a few days old. Since the density distribution of a monthly aged cohort, which survived predation, starvation and several temperature-dependent developmental stages, may be very different from the density distributions of observed larvae, so fitting them likely leads to additional bias of the model solution.

Note that all gains are reported under a comparison that favours the previous models: over the common 1986–2010 window the previous models are evaluated entirely within their estimation period, whereas the updated skipjack, bigeye and yellowfin models are held partly to independent, out-of-sample data. That the models still improve under this stricter evaluation indicates that the gains reflect a genuine improvement in fit rather than an artefact of the updated estimation.

The updated models remain a work in progress; albacore and yellowfin require further development before they can serve as references; the present results should nonetheless be read as demonstrating that the update generally improves the fit to the fisheries and biological data relative to the previous references.

6 Declaration of generative AI and AI-assisted technologies in the SC paper preparation process

The generative AI tool Claude was used to assist with drafting and editing text in this document, with tabulating and summarising the validation results, and with a minor utility script for exporting those results for tabulation. All analytical choices, model specifications, diagnostic interpretations, and conclusions are those of the authors, who reviewed and verified all AI-assisted output. The methodology, model implementation, and scientific conclusions were developed by, and are the sole responsibility of, the authors. The SEAPODYM model and its codebase were developed independently, without generative-AI assistance.

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A Sensitivity of the skipjack model to ocean forcing

The skipjack reference model was fitted to data under three updated ocean forcings, ERA5 and JRA55 (both coupled to NEMO–PISCES), the latter using the PISCES.v1 and PISCES.v2 parameterisations (Aumont *et al.*, 2015), called JRA55.v1 and JRA55.v2 respectively. This is to assess the sensitivity of the fit and of the estimated parameters to the choice of atmospheric reanalysis. The ERA5 solution is used as the reference in the main text, as it is the most recent forcing and the one adopted in the companion methodology paper (Senina *et al.*, 2026). The two PISCES.v2 solutions (ERA5 and JRA55.v2) are statistically almost indistinguishable and both improve markedly on the previous (INTERIM) reference across every data type (Table A1); their spatial biomass distributions are nearly identical (Figure A1); and their estimated parameters differ only modestly (the ERA5 and JRA55.v2 columns of Table A2). The skipjack model is thus robust to the choice of reanalysis, provided the PISCES parameterisation is unchanged. This does not hold for the JRA55.v1 solution, which by contrast shows strong sensitivity to the forcing, entirely due to a change in the tropical distribution of primary production, with a marked decline of productivity in the warm pool and the WCPO more generally.

Table A1: Skipjack global validation scores over the 1986–2010 period under the previous (INTERIM) forcing and the three updated forcings (ERA5, JRA55.v1, JRA55.v2); metrics as in Table 3. **Bold** marks the best score in each row across the four forcings.

Data	Metric	INTERIM	ERA5	JRA55.v1	JRA55.v2
Catch (C)	r^2	0.930	**0.950**	0.930	**0.950**
	VR	0.880	**0.920**	0.860	0.900
	err	0.270	**0.230**	0.270	**0.230**
Length (L)	$\mathrm{NRMSE}_{\bar{x}}$	0.403	0.395	**0.177**	0.374
	SMD	0.110	0.005	−0.027	**−0.001**
Tagging (T)	NRMSE_{σ}	0.568	**0.517**	0.527	0.522
	KGE	0.732	0.774	**0.794**	0.773
	PC	0.862	0.898	**0.918**	0.899
Early-life (E)	NRMSE_{σ}	—	0.447	**0.391**	0.450

Table A2: Estimated skipjack parameters under the previous (INTERIM) and the three updated forcings (ERA5, JRA55.v1, JRA55.v2; symbols as in Table 2).

θ	Description	INTERIM	ERA5	JRA55.v1	JRA55.v2
α	prey (NPP) function shape (Holling-III)	$5.7 \cdot 10^{-4}$	11.98	4.75	12.0
β_F	predation function shape	1.53	2.63	2.45	2.91
T_K	optimal SST, oldest cohort, °C	26.05	27.15	27.0	27.5
b_T	thermal-preference age slope	2.83	0.50	0.31	0.29
$\hat{O}$	dissolved-oxygen threshold, $\mathrm{ml\,l^{-1}}$	3.76	3.97	4.02	4.13
V_m	max. sustainable speed (taxis), $\mathrm{BL\,s^{-1}}$	0.489	0.256	0.096	0.324
σ	diffusion-rate multiplier	0.160	0.366	0.235	0.500
$\bar{m}_p$	predation mortality rate, $\mathrm{mo^{-1}}$	0.25	0.25	0.35	0.25
β_p	predation mortality slope, $\mathrm{mo^{-1}}$	0.066	0.115	0.750	0.155
β_s	senescence mortality slope, $\mathrm{mo^{-1}}$	1.137	0.774	0.736	0.824

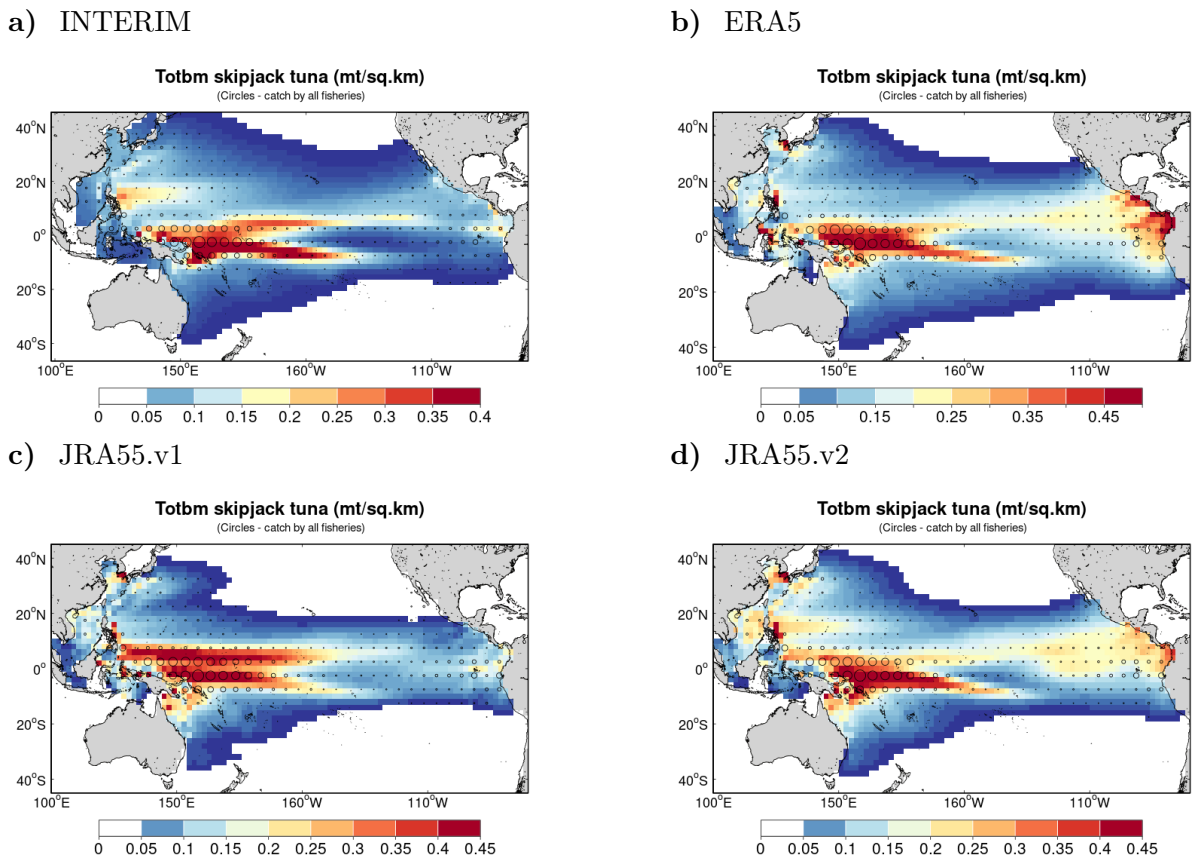

Figure A1: Skipjack total biomass distribution (mean over 2001–2010) under (a) the previous INTERIM–NEMO(ORCA2)–PISCES forcing and the updated (b) ERA5–NEMO(ORCA1)–PISCES, (c) JRA55–NEMO(ORCA1)–PISCES.v1 and (d) JRA55–NEMO(ORCA1)–PISCES.v2 forcings.

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