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Review of SEAPODYM, including recent developments and as an ecosystem model for tropical tunas and important bycatch species in the Western Pacific Ocean

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Executive Summary

Scientific research on the spatial distribution and abundance of tunas in the western Pacific Ocean is required by the Pacific Community (SPC) to provide advice to Pacific Island countries and territories and to international tuna management bodies. To reduce uncertainty and enable assessment of climate-driven losses in revenue and related economic benefits from tuna fishing with confidence, research investments are needed to identify the structure of Pacific tuna stocks, understand the response of stocks to climate change scenarios, and develop predictions of the expected redistribution of tuna species under those different scenarios.

The Spatial Ecosystem And POpulation DYnamics Model (SEAPODYM), developed by SPC and Collecte Localisation Satellite (CLS), provides a scientific platform that can be used to model the spatial and temporal distribution and abundance of pelagic species, such as tunas and potentially important bycatch species, at high-resolution spatial scales using environmental scenarios to inform this scientific and management advice.

SEAPODYM is the product of many years' investment and has been used by SPC to assist in its advice. It allows implementation of models that estimate the spatiotemporal distribution of tuna under dynamic processes. SEAPODYM uses maximum likelihood to resolve modelled parameters that 'best-fit' to observational data, and hence allows explicit consideration of plausible models that represent the empirical observations. Currently, SEAPODYM is the best available scientific tool available to SPC for the provision of advice on spatial and temporal changes in tuna distributions, specifically one that that allows consideration of the response of tuna stocks under different greenhouse gas emission scenarios at a high-resolution spatial scale. The review of SEAPODYM in 2016 and this review recognise its importance as a tool for further development in order to meet the outcomes required from scientific research at SPC into tunas and tuna like species.

While alternative high-resolution spatiotemporal population dynamics models are being developed, the only other general framework for implementing these is the Spatial Population Model (SPM). SEAPODYM has been developed further than SPM with regard to modelling tuna and tuna like species, and the use of differentiable computer code has resulted in code efficiencies that significantly reduce model run times.

While species distribution modelling using environmental covariates is becoming relatively common in fisheries research the use of environmental covariates to inform population dynamics and movement is not. Most population dynamics models that include movement use low-resolution spatial-explicit models to inform broad scale species distribution under the effects of fishing.

Understanding high-resolution spatial distributions, how these have changed and may change under future environmental scenarios (e.g., greenhouse gas emission scenarios), requires causal relationships between the species spatiotemporal distribution to the spatial extent of fishing pressure and changes in environmental conditions. The linking of spatial distributions (and hence movement) to habitat and environmental covariates reduces the parameter dimensionality of high-resolution models, and can improve predictions under future environmental conditions — but at the expense of strong assumptions on the nature of the relationship between distribution/movement and the covariates.

While SEAPODYM provides an advanced and reasonably mature product for further development, there are areas where investment could be made to improve its usability and utility to SPC. Different research questions for tropical tunas in the western Pacific Ocean may require alternative research approaches. In part, the research questions required should be clearly identified and the linked with the role of different research tools. While species distributions under GHG emission scenarios could be developed using species

distribution modelling approaches, the relationship to future productivity and spatial distribution requires development of methods to link environmental covariates with productivity. However, species distribution modelling does not currently provide a means to generate operating model suitable for MSE or evaluation of the relative importance of assumptions and data requirements in standard fisheries assessment models used to manage stocks.

Documentation of the underlying SEAPODYM software is available as a draft documents from 2009 and 2013. Full documentation of the current code (and ongoing future modifications) would be most beneficial to allow transparency and collaboration on its development and provide assurance that the outputs represent best available science.

SEAPODYM provides a valuable tool to inform and simulate data to validate the assumptions of management advice from the current assessment (MULTIFAN-CL) models for tunas. However, additional model validation is required in order to verify that the equations and methods can replicate the standard fisheries models — specifically the population dynamics and broad scale movement. Simulation and validation of the SEAPODYM software would also be beneficial (using either MULTIFAN-CL and other spatially explicit models such as SPM or specific case models) to ensure the underlying population dynamics and movement assumptions are robust and consistent, where appropriate, with standard fisheries models used to provide management advice.

Consideration should also be given to the statistical implementation of the underlying estimation equations and assumptions. Specifically, the way in which input data are applied within the model (e.g., the use of kernel smoothed tag recapture data as an input) and the statistical assumptions (e.g., likelihoods) are implemented. Verification of these aspects would not be time consuming and would provide the basis for confirming the best use of input observations and validate that the underlying statistical aspects were consistent with other fisheries assessment practise.

Spatial models, with large numbers of spatial and temporal observations are difficult to validate against statistical assumptions, simply as the dimensionality of observations results in large quantities of model diagnostics and fits that are difficult to distil into easily interpretable but informative summaries. Consideration should be given to further developing the standard model diagnostics, including visual representations of fits, and potentially replicating summaries typically seen with standard fisheries assessment modelling output. Additional development on the SEAPODYM model diagnostics, including reproduction of standard fisheries assessment diagnostics would be beneficial in demonstrating model adequacy, and to highlight those conclusions where spatially explicit models result in alternative predictions of tuna species stock dynamics and status.

As a means of developing the validation and model diagnostics, a key initial test case might be to reproduce a standard fishery model in SEAPODYM where the movement and functional relationships to underlying forage fish and environmental dynamics have been ‘turned off’. Comparison of the model likelihoods, fits, and parameter estimates would then confirm that the underlying processes and statistical equations were correct. Then, iteratively add to this model the specific spatial and environmental functional relationships back, developing an ‘audit trail’ (also known as a bridging analysis’) that demonstrates the effect of additional complexity in movement and population productivity assumptions on the model outputs and management conclusions that could be drawn.

As SEAPODYM provides a well-advanced research tool for the investigation of spatially driven fish dynamics, the requirement for additional research in this area will likely increase in the foreseeable future. Currently, additional research questions that may use SEAPODYM are limited by a small number of individuals who can access or run the program. Considerations should be given to expanding the user base of SEAPODYM, potentially by making the underlying program more available and developing interfaces or tools to allow the investigation of alternative model structures, assumptions, and observational data in an efficient manner; and improving the ability to allow for sensitivity analyses of alternative climate change scenarios and operational fishing scenarios (including total removals, fleet distribution and catch ratios between fleets).

1 Introduction

The Pacific Community (SPC) requires scientific research on the spatial distribution and abundance of tunas in the western Pacific Ocean to provide scientific and management advice to Pacific Island countries and territories (PICTs) and to international tuna management bodies (e.g., the Western and Central Pacific Fisheries Commission, WCPFC). A key input into this advice is on the spatiotemporal distribution, and changes in that spatiotemporal distribution, of commercially important tunas (specifically albacore, bigeye, skipjack, and yellowfin tuna) and associated pelagic bycatch species — specifically resulting from spatiotemporal environmental and oceanographic dynamics, and potential climate change effects on these dynamics.

Recent SPC policy advice in the western Pacific Ocean recognises the importance of industrial tuna fishing licenses for PICT government revenues (Figure 1) and of other socioeconomic benefits derived from tuna (Anon 2019). The predicted eastward redistribution of skipjack and yellowfin tuna due to climate change (Senina et al. 2018) was expected to reduce the total tuna catch within the combined EEZs of the ten PICTs where most purse-seine effort occurs by approximately 10–15% by 2050 (depending on the assumed scenario of greenhouse gas (GHG) emissions used for the climate change projections), potentially reducing annual government revenues by up to US$60 million (Anon 2019). The policy brief noted the contributions that tuna fishing licence fees make to the government revenues, and the potential impact of the predicted decreases in purse-seine catches from climate change induced changes in the spatiotemporal distribution of tunas.

SPC has noted that that to reduce uncertainty and enable PICTs to assess climate-driven losses in government revenues and related economic benefits from tuna fishing with confidence, research investments are needed to (Anon 2019):

- identify the structure of Pacific tuna stocks; i.e., the number of self-replenishing populations ('stocks') within the range of each tuna species;
- model the response of each stock under both high- and low-GHG emissions scenarios; and
- compile integrated maps of the expected redistribution of each tuna species within its range under different GHG emissions scenarios.

The Spatial Ecosystem And POpulation DYnamics Model, SEAPODYM (Bertignac et al. 1998; Lehodey et al. 2008), provides a key tool that can be used to model the spatiotemporal distribution and abundance of pelagic species, such as tunas and potentially important bycatch species, at high-resolution spatial and temporal scales to inform scientific and management advice. SEAPODYM was developed by the Oceanic Fisheries Programme of SPC and Collecte Localisation Satellite (CLS) for investigating spatiotemporal dynamics of tuna populations under the influence of both fishing and environmental assumptions (Lehodey 2004a; Senina et al. 2016), and has been used to consider impacts of changing climate and environmental conditions as well as spatiotemporal effects of fishing. SEAPODYM is the product of many years' work (see, for example, Lehodey 2004b, 2004a; Lehodey et al. 2008, 2015; Lehodey & Senina 2009; Dragon et al. 2015, 2018; Senina et al. 2016, 2018). SEAPODYM spatiotemporal dynamics are modelled using advection-diffusion-reaction equations that describe dynamic processes (e.g., spawning, movement, mortality), which are informed by environmental covariates (e.g., temperature, currents, primary production and dissolved oxygen concentration) (Lehodey 2004b, 2004a), and distributions of mid-trophic level functional groups (e.g., micronektonic tuna forage layers) (Senina et al. 2019a)

Currently, SEAPODYM is the best available scientific tool available to SPC for the provision of advice on spatiotemporal changes in tuna distributions that would allow consideration of the population dynamics of tuna stocks under different GHG scenarios at a high spatial resolution. The continued development and application of SEAPODYM for understanding the population dynamics of tropical tunas in the Pacific region remains a key priority for the Oceanic Fisheries Programme (OFP) at SPC, and for WCPFC under Project 62.

At the 10th Regular Session of the Scientific Committee in 2014 (Anon 2014), a scientific review of SEAPODYM was requested to help guide the WCPFC in evaluating potential model applications and its future work program under Project 62. The review was presented to the 12th annual meeting of the Scientific Committee of WCPFC (Nicol & Smith 2016). The review summarised the status of the SEAPODYM project at that time, including a review of model assumptions and diagnostics; the immediate and medium-term applications of SEAPODYM; and how SEAPODYM could be modified in order to improve the quality of the science arising from applications of the model. Key recommendations and comments on the recommendations are given below.

Since the 2016 review (Nicol & Smith 2016), SEAPODYM has continued to evolve, which the integration of tagging data to inform movement, production of real-time forecasts of tropical tuna population dynamics, and developments pertaining to climate-change impacts including multi-model ensemble forecasts and predictions of potential ocean acidification effects (Senina et al. 2016, 2018, 2019a, 2019b).

In 2019, SPC commissioned a second review (this report), to provide advice on the current state of SEAPODYM as a tool for understanding the population dynamics of the four tropical tunas of principal commercial interest in the Pacific region (see the full terms of reference in Appendix A below).

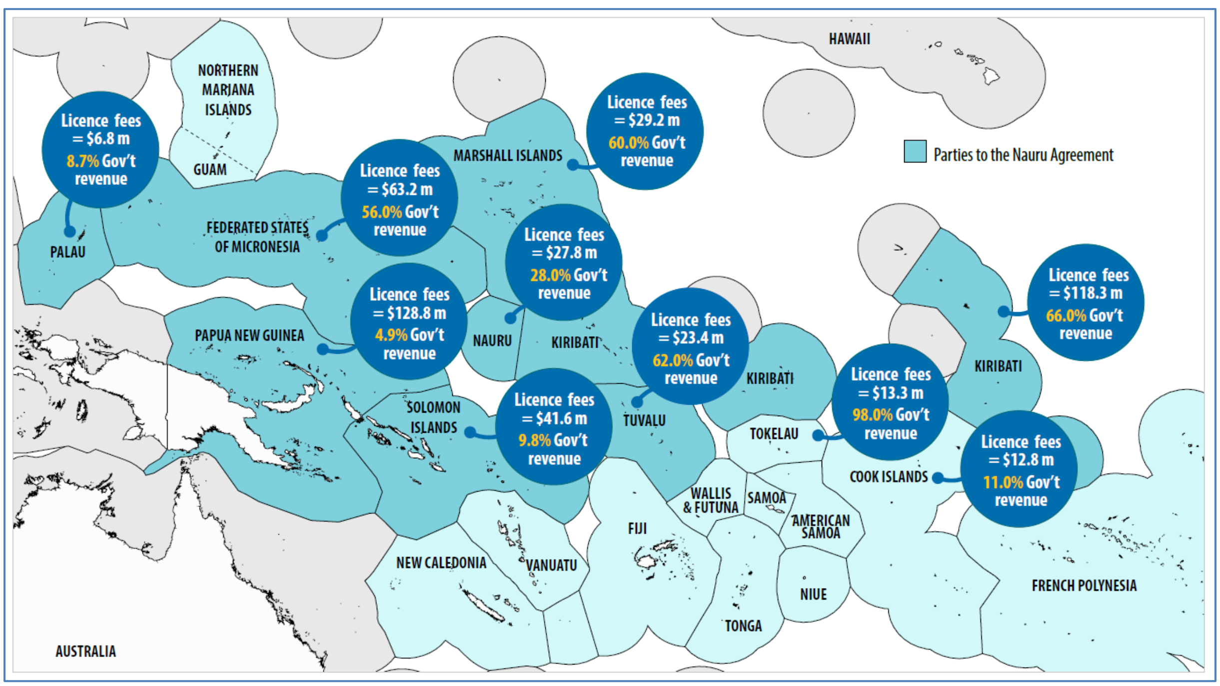

Figure 1: The economic benefits of tuna fishing for Pacific Island countries and territories (2016). (Figure reproduced from Anon 2019)

2 Terms of reference of the 2019 review

The main objective for the second review was to inform SPC of the current state of the SEAPODYM model, its applicability as a scientific tool for research into tuna spatiotemporal distributions (and its use as a tool to predict future change under climate change scenarios); and to inform a future workplan by identifying areas where the model may be improved and the future applications of the model. The specific terms of reference were to provide a review of SEAPODYM for the Pacific Community, and specifically to address the following points:

1. The current state of SEAPODYM as a tool for understanding the population dynamics of the four tropical tunas of principal commercial interest in the Pacific region.
2. Recent SEAPODYM developments since the WCPFC SC 2016 review paper.
3. The current state of the mid-trophic level sub-model influencing the above tuna models, and options for improved sub-model validation.
4. Outstanding gaps and new data requirements for future development of SEAPODYM in the context of i) management strategy evaluation, ii) climate change and iii) ecosystem-based fishery management for tropical tunas in the Western and Central Pacific Ocean (WCPO).
5. Comparison with similar spatially explicit population dynamics model frameworks currently available, not limited to those currently used for tropical tunas.
6. The future of SEAPODYM as an ecosystem-based population dynamics model for tropical tunas and important bycatch species (e.g., mahi mahi, wahoo, sharks) in the WCPO, in both single- and multi-species applications, and not limited to the model's current incarnation.

The complete Terms of Reference (TORs) with annotations and background discussion for the 2019 review are given as Appendix A.

3 The SEAPODYM model

3.1 Background

SEAPODYM is a modelling package that simulates age-structured population dynamics using standard equations for populations in fisheries (although modified to be dependent on habitat suitability functions), and implements movement based on advection-diffusion-reaction equations describing movement, recruitment, natural mortality, and spatially explicit rates of fishing mortality (Lehodey 2004a, 2004b; Lehodey et al. 2008, 2008, 2015; Lehodey & Senina 2009; Titaud et al. 2013; Senina et al. 2015, 2018, 2019a). Biological parameters, with some productivity and the movement parameters are informed by environmental covariates. Observations from catch, length frequencies, and tag data (currently only implemented with full likelihoods for the catch, length, and tagging terms in the skipjack model) provide information to estimate the model parameters, and hence to inform predictions of abundance and distribution over the spatiotemporal domain modelled. The general schema of SEAPODYM is given in Figure 2.

The use of environmental variables to inform distribution and movement has not been widely used in population dynamics models in fisheries, with most models using low-resolution spatially explicit population models to inform species distributions under the effects of fishing (Punt 2019). Understanding the spatiotemporal distributions, how these have changed and may change under future environmental scenarios, requires linking of the species spatiotemporal distribution not only to fishing pressure, but also to environmental covariates (Mackinson et al. 2009). This linking of spatial distributions (and hence movement) to habitat and environmental covariates can improve predictability and greatly reduce the parameter dimensionality (and hence tractability) of the model, but at the expense of assumptions on the functional form and magnitude of the relationship between distribution/movement and the assumed covariates.

The approach of using spatiotemporal models to inform fish species abundance and distribution has support within the literature (see, for example, Punt 2019; Cao et al. 2019) although there are few empirical studies that have validated the best methods for their use. Punt (2019) noted that while additional data in spatially explicit models may lead to less biased and more precise outcomes, the additional complexity and assumptions of spatial assessment models may also lead to model misspecification and poor estimation performance (e.g., see Punt et al. 2015). However, the paper mostly considered only low-resolution spatially explicit models rather than high-resolution models. Punt (2019) recommended that while stock assessment models should be conducted at very fine spatial resolution, the high data requirements, large computational overhead, and difficulties of statistically validating such models make them difficult to use and interpret for management decisions.

SEAPODYM can implement different models, depending on the data and research questions. Typically, the model uses a high-resolution spatial scale and monthly time steps to model the effects of movement, population productivity parameters, and fishing impacts. Both the population and movement parameters are informed by fishery-based observations, estimated using environmental forcing from spatiotemporal layers (primary production (NPZD), temperature (OGCM), currents (OGCM), and oxygen (Levitus database)). The populations are modelled as age-structured, categorised as a series of life-history categories, and uses observations from catch, catch-effort, length frequency, and tag recapture data.

The best description of the SEAPODYM software is detailed in the draft SEAPODYM manual (Lehodey & Senina 2009) a draft unpublished manuscript from 2013 (Titaud et al. 2013), with recent developments in Senina et al. (2019a) and Senina et al. (2019b). Many of the developments since the submission of the draft manual from 2009 are also described in various presentations, reports, and papers (see, for example, Lehodey 2004a, 2004b; Lehodey et al. 2008, 2015; Lehodey & Senina 2009; Senina et al. 2015, 2018), but there is no single comprehensive and up-to-date description of the model software available. The most recent documentation is the draft given by Lehodey & Senina (2009) and a draft unpublished manuscript from 2013 (Titaud et al. 2013). While this review has considered a wide range of reports and papers on SEAPODYM, there may be additional information that would have greatly assisted this review if this were summarised in a single location.

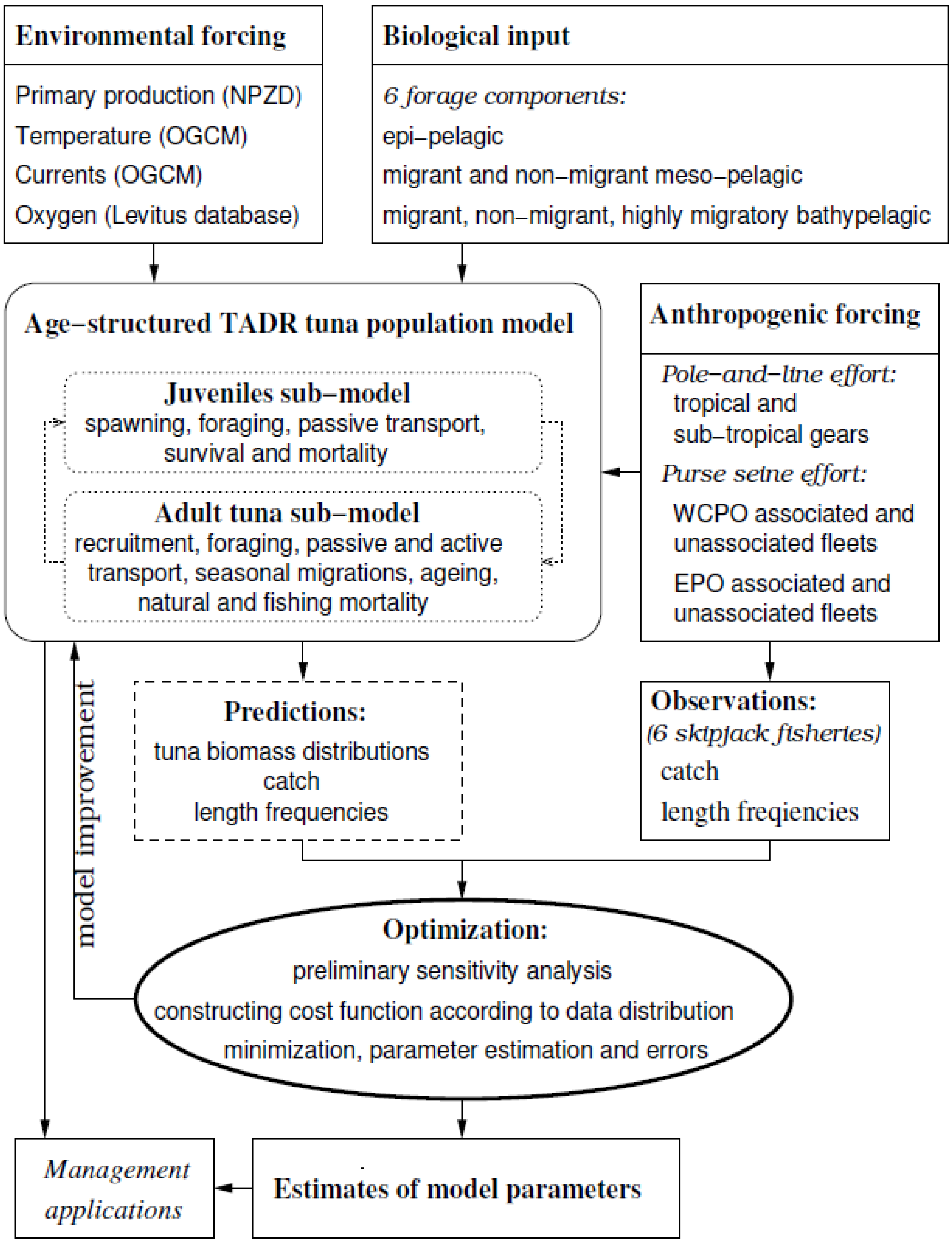

Figure 2: General scheme of the SEAPODYM model with optimization approach. (Reproduced from Figure 3.1 of Lehodey & Senina 2009.)

3.2 Updates and revisions to SEAPODYM following the Nicol & Smith (2016) review

Nicol & Smith (2016) provided a review of SEAPODYM to the 10th annual Scientific Committee meeting of WCPFC. The review recommended that SEAPODYM was ready and available for WCPFC to assist its decision making and made six key recommendations for improvements and additional research. A brief summary of developments since that review is summarised for the six key recommendations.

1. SEAPODYM was ready for application by WCPFC to assist its decision making. By design the model is particularly suited to addressing questions of spatial distribution and the influence of environmental processes on tuna population dynamics. SEAPODYM would be a useful complementary model to MULTIFAN-CL for MSE work that includes spatial management. Similarly, the capacity of SEAPODYM to include alternate oceanographic states (e.g., ENSO phases and climate change projections) would allow climate proofing to be a consideration in the MSE work undertaken by WCPFC.

The recommendation from the 2016 review highlights that SEAPODYM can provide a useful tool to test the current tuna MULTIFAN-CL assessment models for bias and precision from assumptions of spatial structure on management advice and is consistent with the findings of this review.

While there are some alternative high-resolution spatiotemporal models being developed worldwide (e.g., Cao et al. 2019) the only other general fisheries modelling framework for implementing habitat based distributions and movement at this time is SPM (Dunn et al. 2018). SEAPODYM has been developed further than SPM for modelling tuna and tuna like species, and its use of optimised differentiable computer code has resulted in code efficiencies that can significantly reduce model run times.

The approach of using spatiotemporal models to inform fish species abundance and distribution has support within the literature (see, for example, Punt 2019; Cao et al. 2019). Further, as climate variability and change impacts fish distribution and abundance, there is likely to be greater requirements for models that can inform management under such scenarios. However, Punt (2019) noted that while additional data in spatially explicit models may lead to less biased and more precise outcomes, the additional complexity and assumptions of spatial assessment models may also lead to model misspecification and poor estimation performance (e.g., see Punt et al. 2015).

Development of SEAPODYM as a simulator would allow assessment of a range of important research questions, including optimal sampling to reduce uncertainty and bias, inform the choice of potential sensitivities in assessment model management strategy evaluations (MSE), the impacts of spatial heterogeneity on observational data (i.e., length frequency, CPUE, and tag-release and recapture data), as well as inform choices of alternative spatial structure assumptions in the MULTIFAN-CL tuna assessment models.

The use of SEAPODYM as an MSE simulator or to assist as a complimentary model to MULTIFAN-CL (Fournier et al. 1998) that includes evaluation of spatial heterogeneity induced bias has not yet been undertaken. As an example of how this may be implemented, Mormede & Dunn (2013) and Mormede et al. (2014a) used SPM (Dunn et al. 2018) to estimate the high-resolution spatiotemporal structure of Antarctic toothfish in the Ross Sea region, and then used this to simulate the observational data for the single-area population model that had been used for management advice. In this case, they found that the effect of ignoring spatial complexity (specifically, the spatial heterogeneity of the tag release and recapture data) resulted in a significantly biased estimate of the assumed population, underestimating the true population by 19–43% (Mormede et al. 2014a).

Punt (2019) described five stock structure scenarios in spatially explicit fisheries assessment models: (a) a single stock that is found in more than one area, with movement among areas; (b) a single stock that is found in more than one area, but with no movement post- settlement; (c) multiple stocks are located in the region, with movement among areas but no dispersal; (d) multiple stocks/sub-stocks are located in the region, with movement among areas and dispersal among stocks/sub-stocks; and (e) multiple stocks/sub-stocks are located in the region, but there is no movement among areas or dispersal among them. Punt (2019) noted that the assumptions for each scenario would depend on the specific fishery being modelled, but that different assumptions can lead to different levels of bias and precision.

Within MULTIFAN-CL assessments of tunas in the western Pacific Ocean, the populations are typically assumed to follow scenario (a) above. The effect of alternative population scenarios can be simulated using SEAPODYM and hence used to asses bias and precision of choices of assessment models used for management. Further, it can be used to assess the consequence of errors in choice of boundaries and spatial resolution in low-resolution spatially explicit models used to provide management advice.

2. WCPFC should encourage and where feasible support (through Project 62) the continual development of diagnostics to evaluate the fit of the model to data, the validity of underlying assumptions, and allow comparison with alternate population dynamics models.

Since 2016, papers describing SEAPODYM models have provided additional information on model fits and diagnostics (e.g., Senina et al. 2019a). However, while statistical diagnostic summaries have been developed, statistical comparison of alternative model constructs using statistical diagnostics and fits should be more formally undertaken.

Model fits and diagnostics for high-resolution spatiotemporal models is a field of developing research and additional diagnostic and validation methods should be continued to be developed. Such models require the development of graphical and numeric summaries that are both informative and easily digestible. Additional research is required to help inform model developers on where to focus additional consideration of the model and, for users of the outputs, identifying diagnostics that help determine the model reliability and uncertainty.

As noted above, few alternative modelling frameworks exist that allow high-resolution spatiotemporal population dynamics to be fitted to fisheries assessment data. General ecosystem models (see, for example: Allain et al. 2007; Plagányi 2007; Audzijonyte et al. 2019), while modelling a much larger component of the ecosystem, do so at a very low spatial and temporal resolution. The only other generic model that allows the use of a high resolution spatial scale to model the population dynamics is SPM (Dunn et al. 2018). As with SEAPODYM, SPM uses habitat and environmental covariates to inform movement parameters and hence reduce the dimensionality of the high-resolution spatial model to a tractable level. Both models use a discrete space to model populations, unlike methods using gaussian random fields, for example as assumed by Cao et al. (2019).

Bespoke implementations of high resolution spatiotemporal models have been developed for use in fisheries management, for example, a model of snow crab *Chionoecetes opilio* off eastern Canada (Cadigan et al. 2017), but adapting bespoke models for tunas in the Pacific Ocean is likely to be a time-consuming task. More recently, spatiotemporal modelling using high-resolution models that fit both distributions and population dynamics models within a general statistical framework are being developed (Cao et al. 2019). While these methods are still in development, these may provide an alternative approach in the future.

3. An annual review meeting, similar to the pre-assessment workshop held annually to guide the development of the WCPFC stock assessments, would benefit SEAPODYM applications in the

WCPO. This would foster additional collaboration between the modelling team focussed on MULTIFAN-CL applications and development and those focussed on SEAPODYM which would result in more regular sharing of ideas and peer review of models than currently occurs. An option for WCPFC would be resourcing CLS to attend the pre-assessment workshop with potentially an additional day added for the workshop to also discuss any applications of SEAPODYM to WCPFC fisheries that require presentation at the scientific committee of that year.

Greater use and collaboration of the SEAPODYM model in its current and potential future applications would assist in ensuring that the model used the best available science, and that the outcomes of the research can be readily translated into management advice. A formal program for developing collaboration, including making the base models available to other collaboration researchers in a manner that would allow them to quickly test and evaluate alternative observational data, scenarios, and model assumptions would greatly improve the uptake of the model outcomes.

The most recent SEAPODYM (draft) user manual was Lehodey & Senina (2009) and a draft unpublished manuscript from 2013 (Titaud et al. 2013). Since then there have been substantial model enhancements and modifications as the software has been applied to growing areas of research. An updated and complete documentation of SEAPODYM would greatly assist collaborators and end-users of the outcomes of the models better understand the model assumptions and outcomes when applying these to management decision making. In addition, access to the underlying documented source code would help encourage collaboration and transparency in its use.

4. WCPFC and other sub-regional organisations should consider options for industry support for research and data that would enhance SEAPODYM's forage component. Acoustic data provided opportunistically by fishing vessels would allow for optimisation routines to be applied to the estimation of the forage biomass.

High-resolution spatially explicit population models rely on large amounts of data and assumptions in order to provide robust outcomes. Additional observational data (e.g., length frequencies, catch estimates, and tag-release and recapture data) would benefit the model by validating current predictions and improving functional relationships estimated in the model. Additional data from, for example, wide-spread acoustic programs to inform the forage fish component would also lead to greater confidence that model outputs were consistent with the real world.

Since 2016, the potential for the additional opportunistic data from industry vessels has been considered but not implemented. Simulation testing of data requirements would also assist in the focusing of efforts to collect data that would most likely provide the determination of alternative hypotheses of relationships or reduce model uncertainty.

Development of the best information required to inform the model would need to be the topic of a specific research project — underpinned by simulation and empirical studies that allow for the generation of structural and environmental hypothesis that targeted observational data would be likely to inform.

5. SEAPODYM could be used as a tag simulator to test assumptions and/or provide priors or fixed values for the inclusion of the PTTP data in MULTIFAN-CL applications.

Tag-release and -recapture data can provide assessment models with estimates of relative or absolute abundance, fish movement rates, and growth estimates. However, tag data are often spatially biased —both releases and recaptures are often concentrated in specific locations over time due to the expense of release programmes and the spatiotemporal concentration of fishing vessels that record recaptures. Bias resulting from spatial and temporal heterogeneity is well documented in fisheries tagging programmes (Gwinn et al.

2010, 2011; Mormede & Dunn 2013; Sippel et al. 2015; Punt 2019), and much of this results from spatial heterogeneity.

The use of SEAPODYM as a simulator for targeting tag-releases and tag-recapture data collection would be of great benefit to improved understanding of fish abundance, movement, mortality, and fishing pressure. As tag programmes are often expensive and time consuming to undertake, simulation testing to evaluate the best locations and time periods to undertake such programs would improve the efficiency of these programmes and the value of the resulting data collected.

In addition, simulating from SEAPODYM would provide observational data to test within the current tuna assessment models in MULTIFAN-CL for bias and uncertainty (e.g., see Mormede & Dunn 2013; Mormede et al. 2014a).

6. A detailed technical document which describes reviews to date, developments implemented, and developments planned should be developed to support future SEAPODYM work (including for example criteria for reference models).

Since 2016, papers that use the SEAPODYM model have improved the descriptions of the underlying methods and approaches (e.g., Senina et al. 2019a), however documentation of the underlying model software is available as a draft document from 2009 (Lehodey & Senina 2009) and a draft unpublished manuscript from 2013 (Titaud et al. 2013). Many of the model equations and assumptions are only available for specific details across a variety of reports, presentations and published papers(see, for example, Lehodey 2004a, 2004b; Lehodey et al. 2008, 2015; Lehodey & Senina 2009; Senina et al. 2015, 2018). Full documentation of the model, model equations, and implementation would be beneficial as the code is currently proprietary and unavailable in a manner that would allow transparency and collaboration to ensure it's the best available science.

4 Consideration of the terms of reference for the 2019 review

4.1 The current state of SEAPODYM as a tool for understanding the population dynamics of the four tropical tunas of principal commercial interest in the Pacific region.

4.1.1 Introduction

SPC has been developing SEAPODYM for a number of years, and it has been used to provide scientific advice on key tuna population distribution and dynamics and to forecast tuna availability and abundance under climate change scenarios combined with fishing effects (Lehodey 2004a, 2004b; Lehodey et al. 2008, 2015; Lehodey & Senina 2009; Senina et al. 2015, 2018).

A key question for SEAPODYM as a tool for understanding the population dynamics of the four commercially important tropical tunas (albacore, bigeye, skipjack, and yellowfin) of principal commercial interest in the Pacific region are the management requirements and issues that research is required to address. SPC (Anon 2019) notes that research to identify the structure of Pacific tuna stocks i.e., the number of self-replenishing populations ('stocks') within the range of each tuna species; the response of each stock under both high- and low-GHG emissions scenarios; and production of integrated maps of the expected redistribution of each tuna species within its range under different GHG emissions scenarios are high priorities for research into tunas in the western Pacific Ocean..

Different approaches and research development would depend on the priority of research to inform management. The EcoSEA workshop (EcoSEA, Noumea, New Caledonia, 28 October–1 November 2019) identified a number of potential research questions, including:

- Modelling and validation of eastward movement of tunas under GHG emission scenarios
- Efficient evaluation of the effects of alternative IPCC scenarios when predicting future tuna distributions
- Development of tools to inform distant water nation fishery effects
- Consequences of the spatial distribution and population productivity on allocation decision making, including the distribution of tuna populations inside and outside of PICT EEZs,
- Developing of tools to inform fishery operational decision making
- Potential effects of spatial management, including potential effects of choices of areas for fishery exclusions, and static MPA and spatiotemporal MPA designation,
- Development of fishery scenario modelling, including economic consequences of ports of departure and landing in relation to the spatial distribution of tunas,
- Development and evaluation of information to assist in fishery compliance monitoring
- Development of upscaled and downscales models that could inform local (i.e., costal) changes in tuna distribution.

Consideration of the specific objectives for that research, and a prioritised program to develop work in this area would assist the SEAPODYM developers and funders of how SEAPODYM should be developed.

The SEAPODYM model represents a long-term investment into a high resolution spatially explicit mode suitable for tunas and tuna like species in the Western Pacific Ocean. Spatially explicit models are complex and require an understanding of the population and spatial dynamics of researched species, as well as the ecological and biological relationships with environmental covariates. They are, by the nature of the higher spatial resolution, more complex than standard single area or low-resolution spatially explicit fisheries assessment models, and a wider range of structural and parameter assumptions are typically required. Data requirements to evaluate functional relationships are higher, model run times are much slower, and evaluating fits and model adequacy is more difficult due to the large amount of input and output data. Currently, SEAPODYM is reasonably mature software and has the benefit of optimised and differentiable computer code to enable tractable model estimation and minimisation in reasonable run times.

4.1.2 Spatial processes

SEAPODYM provides a valuable tool to inform and simulate data to validate the assumptions of management advice from the current assessment (MULTIFAN-CL) models for tunas. However, additional model validation is required in order to verify that the equations and methods can replicate the standard fisheries models — specifically the population dynamics and broad scale movement. Simulation and validation of the SEAPODYM software would also be beneficial (using either MULTIFAN-CL and other spatially explicit models such as SPM or specific case models) to ensure the underlying population dynamics and movement assumptions are robust and consistent, where appropriate, with standard fisheries models used to provide management advice.

The use of environmental variables to inform distribution and movement is not widely used in population dynamics models in fisheries, with most models using low-resolution spatially explicit population models to inform species distributions under the effects of fishing. However, understanding the spatiotemporal distributions, how these have changed and may change under future environmental scenarios, requires linking of the species spatiotemporal distribution not only to fishing pressure but also to environmental covariates. This linking of spatial distributions (and hence movement) to habitat and environmental covariates greatly reduces the parameter dimensionality (and hence tractability) of these models, but at the expense of strong assumptions on the functional form and strength of the relationship between distribution/movement and the assumed covariates. The use of environmental forcing to inform movement is a key attribute of the SEAPODYM software, and hence is the most applicable to developing models that forecast future states under climate and environmental change.

However, spatially explicit models require large amounts of input data and observations, are time consuming to run, and model validation and model fitting require caution when determining 'best-fit' outputs. Punt (2019) noted that while additional data in spatially explicit models may lead to less biased and more precise outcomes, the additional complexity and assumptions of spatial assessment models may lead to model misspecification and poor estimation performance (e.g., see Punt et al. 2015). However, the paper mostly considered only low-resolution spatially explicit models rather than high-resolution models.

4.1.3 Model description and documentation

Documentation of the underlying SEAPODYM software is available as a draft document from 2009 (Lehodey & Senina 2009) and a draft unpublished manuscript from 2013 (Titaud et al. 2013), and many of the model equations and assumptions are available only for specific aspects contained within a variety of reports, presentations, and published papers. Full documentation of the current code (and ongoing future modifications) would be most beneficial to allow transparency and collaboration on its development and provide assurance that the outputs represent best available science.

One of the most likely future uses of SEAPODYM is as a tool to investigate the potential effects of greenhouse gas emissions (climate change) on population abundance and distribution (e.g., as in Senina et al. 2018, 2019a, 2019b). SEAPODYM provides a unique framework for the investigation of spatially and temporally resolved scientific investigation into the plausible future abundance and distribution scenarios of tuna (specifically skipjack, yellowfin, and albacore tunas), and includes key population dynamics processes (i.e., spawning, movement, mortality). Environmental covariates that define distribution and movement within the model (i.e., temperature, ocean currents, primary production and dissolved oxygen concentration) derived from ocean forecasting models provide the inputs that SEAPODYM uses to forecast distributions of key species.

By parameterising movement and distribution of species using habitat and environmental covariates, the model can be used to predict potential future distributions from oceanographic model forecasts of environmental conditions. Assumptions of habitat linked preferences for some marine species are well documented in the scientific literature (e.g., see Mackinson et al. 2009; Ottersen et al. 2010; Overland et al. 2010).

Parameterising spatial complexity using environmental covariates has the advantage of reducing the dimensionality of the model with a much smaller number of parameters but requires strong assumptions on the nature of the relationships between (i) environmental covariates and distribution, and (ii) biological productivity parameters and environmental covariates. Distributional assumptions are more easily identified, and studies linking the distribution of species, particularly pelagic species such as tunas, has been well described in the scientific literature. Model fits and evaluations of species distribution are less problematic to assess and evaluate.

However, forecasting future *abundance* is more difficult as it requires using predicted environmental variables to inform future fish productivity (e.g., growth, recruitment, and natural mortality). The experimental observations that link environmental covariates to tuna and tuna-like species abundance and productivity are less clear than those for tuna distributions. Functional or even correlations between fishery observations and spatially explicit abundance are often extremely difficult to determine.

Typically, the confounding between catchability, availability, and species abundance means that determining spatially explicit abundance is difficult to resolve for oceanic marine species. The functional link between key population productivity parameters (e.g., natural mortality, growth, and mean recruitment) can be even more difficult to determine, and hence parameterise and evaluate within a model. Forecasting and predicting potential future abundance based on environmental variables for such species requires strong assumptions but may not be tractable with current levels of understanding.

The SEAPODYM model has movement dynamics that appear to represent the spatiotemporal distribution of tunas reasonably well — the diagnostic plots presented for example species have showed that the SEAPODYM models can reproduce observed spatial distributions (e.g., Senina et al. 2019a). Diagnostic plots and evaluations of the population dynamics at a spatiotemporal level are less well developed, specifically the link to changes in underlying productivity parameters (e.g., natural mortality, recruitment or growth). In part this is because observations of these parameters are not easy to obtain (e.g., estimates of natural mortality are difficult to determine ignoring spatial complexity in non-spatially resolved fish species, and potentially not plausible at all with current techniques at a highly resolved spatiotemporal resolution).

The associated uncertainty of the model predictions under climate and environmental change would likely depend on the choice of the functional relationships between environmental covariates and spatiotemporal changes in productivity. While SEAPODYM can use an underlying forage fish model to inform the relationship between natural mortality and recruitment (see Senina et al. 2019b), growth is assumed to be non-adaptive and is therefore constant both spatially and temporally. However, the lack of empirical observations means that the adequacy of these relationships may be difficult to validate.

Underpinning the future use and utility of SEAPODYM is the requirement for a model that can be used by other researchers to compare and evaluate its outputs, test alternative assumption, and understand the model assumptions, equations, and underlying code. In undertaking this review, understanding the specific processes used in the models, the implementation of the equations used, and how these assumptions may impact the conclusions is difficult without access to an up-to-date description of the model, model assumptions and equations, and possibly even the underlying model computer code.

4.1.4 Data inputs and dynamic processes

The dynamic processes are constrained/informed by environmental data (and potentially distributions of prey species) by fitting to observations of catch, catch-effort, length frequency and tag data. Natural mortality is estimated as a function of age and is assumed to be the sum of predation and senescence mortality. Recruitment follows a Beverton-Holt relationship, with local recruitment informed by a local habitat index (Senina et al. 2019a). SEAPODYM uses ages within categorical groups (larvae, immature, and mature) to model the age structure of the populations, with specific life-history traits associated with each phase. Larvae stages use oceanic currents to inform movement and later life stages are modelled assuming active movement driven by the underlying forage food availability and environmental covariate layers. Fishing effort and catch is accounted for within the model, and outputs include predictions of recruitment, length frequencies, and the resulting spatiotemporal distributions of tuna. Different life stages (larvae, juveniles, immature and mature adults) are modelled with different environmental relationships. The use of categorical relationships simplifies the underlying dynamics and is likely to be the best approach to modelling the fish characteristics in response to environmental covariates.

Catch and catch-effort data are an important input into the SEAPODYM model. In Senina et al. (2019a), catch is estimated within the model, presumably to resolve the Baranov catch equation with multiple fisheries as well as allowing for spatial heterogeneity in the recording of catch locations with respect to the model. Senina et al. (2019a) reports that "*ideally the level of biomass should always be higher than observed catch, however up to 20% local errors are allowed because of biases in the physical forcing, the errors in the fishing data and the coarse spatial resolution of the numerical model*". Two approaches were considered by Senina et al. (2019a) — (i) the first estimated catch based on effort via an assumption of constant catchability and selectivity within the model, using an *F* mortality rate, and then compared with the recorded catch. And (ii) a similar approach but with disaggregation using the observed age composition, and then aggregated across multiple fisheries to subtract the total catch at age and spatial location from species biomass. Spatiotemporal recording of catch in tuna fisheries can contain inaccuracies – both in the specific location and in the amount of catch taken (Senina et al. 2019a). Model fitting to these data therefore can be problematic, especially when the level of fishing mortality can influence overall abundance. The unavailability of local biomass to support local catches is not an unusual problem in spatially explicit models (due to the inaccuracies in modelled movement, and in the choice of spatial scale of both catch and environmental covariates) — but requires careful consideration where and when the catch:biomass ratios exceed plausible exploitation rates and model inconsistencies are present. The choice of the catch equation is unlikely to be influential in the model outcomes, but may be material when comparing to alternative models such as MULTIFAN-CL. The choice in catch equation used can also influence the stability of the model and potentially model inference (i.e., the Baranov catch equation adds many model parameters). Hence, some comparisons of the alternative approaches may be required when validating SEAPODYM against MULTIFAN-CL in the future.

The use of the tag data in the SEAPODYM model may require additional consideration — specifically the choices of likelihood; use of the recaptured releases only in the model; and 'smoothing' using kernel density estimates of the tag data and aggregation over larger spatiotemporal scales should be considered.

In the current implementation, SEAPODYM uses tag-releases from the subset of released tags that were recaptured only. It is not known if this introduces a bias into the resulting estimates or if the estimates of movement and population processes resulting from this choice are robust to this assumption. Information from tags not recaptured can provide additional information to the model, specifically by assisting in estimates of fishing mortality (if recapture detection rates are known) and on movement parameters from comparing the rate of recapture between areas. Simulation testing should be undertaken to evaluate if any bias from this assumption affected the conclusions of the model.

In the Senina et al. (2019a) application of SEAPODYM, a bivariate Gaussian kernel for two independent variables (longitudinal and latitudinal coordinates) was applied to the observed tag recapture records. This was to account for the uncertainty in location of capture, and to obtain smooth densities of the recaptures that could be compared to the continuous fields of modelled densities in the likelihood framework (Senina et al. 2019a). This essentially applied a spatial smoother to the recapture data before it enters the model. This approach of smoothing input observations is not unusual in fisheries modelling but can introduce bias, as well as biasing the estimated uncertainty. Modelling the observations directly in this instance would be the preferred approach.

As noted in Senina et al. (2019a), additional tagged cohorts increases the underlying model complexity, and hence computational times significantly, and only a subset of the available tag data were used. This represents a pragmatic trade-off between choices of suitable data and the overall time taken to run the models. The current choices of categories and tag cohorts likely represent a reasonable trade-off. However, this choice should be validated using simulation studies where appropriate.

The length frequency data for many of the SEAPODYM implementations is the same as that used for the standard integrated MULTIFAN models (Brouwer et al. 2019). However, consideration should be given to the choice of selectivity associated with length frequency data, specifically how these data are fitted within the model. Comparison of a simple 'test' model in SEAPODYM with MULTIFAN-CL would allow detailed comparison to be made, and, at the same time, assist with the validation of the SEAPODYM model.

4.1.5 Model fitting and estimation

SEAPODYM uses maximum likelihood estimation to fit and estimate parameters. The three observation types used in the model are catch data (determined from effort data), length frequency data, and tag recapture data. The likelihoods defined are an important component of the estimation process. The likelihoods used in SEAPODYM and detailed in Senina et al. (2019a) should be reviewed and updated. Other likelihoods are available within SEAPODYM (including Poisson, truncated Poisson, exponential, Weibull, negative binomial, zero-inflated negative binomial, lognormal, concentrated, normal and robust normal likelihoods), but these are currently undocumented (I. Senina, pers. Comm, March 2020).

The likelihood for the catch data, where the method is by removals, assume a normal distribution "as the errors are proportional to the modelled biomass" (Senina et al. 2019a) for fishery *f*, timesteps *t*, and region *i*,

$$-LL = \frac{1}{2\sigma^2}\sum_{fti}\left(E_{fti} - O_{fti}\right)^2$$

The choice of a normal likelihood is unusual as this does not adequately deal with proportional errors (typically assumed in fisheries catch data), nor observed or expected values close to or equalling zero. Otherwise for catch predicted by fishing effort, a Poisson likelihood was assumed (Senina et al. 2019a).

Hampton & Fournier (2001) use a robustified lognormal distribution, i.e., for fishery *f*, timesteps *t*, and region *i*,

$$-LL = \frac{1}{2\sigma^2}\sum_{fti}\left(\log\left(1 + E_{fti}\right) - \log\left(1 + O_{fti}\right)\right)^2$$

Other likelihoods for catch data (e.g., Methot 2009; Bull et al. 2012; Williams & Shertzer 2015) are available and may be better suited to these data, for example (Bull et al. 2012), i.e., for observation *i*,

$$-LL = \sum_{i}^{n}\left(log(c_i E_i) + 0.5\left(\frac{O_i - E_i}{c_i E_i}\right)^2\right)$$

Note that the constant term in the likelihoods may or may not be required, depending on how these are used for between-model comparisons. Often these are ignored to reduce the number of computations required in a specific implementation (although may be important when, for example, comparing models using Bayes factors or when comparing calculations between packages that treat these differently).

The likelihood for the length frequency data use a version of a robustified multivariate normal from (Hampton & Fournier 2001), defined in Senina et al. (2019a) for fishery *f*, timesteps *t*, and region *i* as,

$$-LL = 0.5\sum_{fti} log\left(2\pi\left(\xi_{fti} + \frac{1}{I}\right)\right) + I\sum_{ft} log\left(\tau_{ft}\right) + \sum_{fti}\frac{(O - E)^2}{2\tau_{ft}^2\left(\xi_{fti} + \frac{1}{I}\right)}$$

Note that this likelihood, almost the same as that described in Senina et al. (2019a), is incorrect as written in the paper (ignoring the robustification term). The last component should be subtracted, not added, i.e., (given here with the robustification term),

$$-LL = 0.5\sum_{fti} log\left(2\pi\left(\xi_{fti} + \frac{1}{I}\right)\right) + I\sum_{ft} log(\tau_{ft}) - \sum_{fti} log\left[exp\left(\frac{(O-E)^2}{2\tau_{ft}^2\left(\xi_{fti} + \frac{1}{I}\right)}\right) + 0.001\right]$$

Note that alternative likelihoods for length frequency data can be used and recent fisheries assessments have tended to use the multinomial, multinomial-Dirichlet, or Dirichlet likelihoods (Methot 2009; Bull et al. 2012; Williams & Shertzer 2015; Dunn et al. 2018). More recently, the logistic-normal (Martell & Lima 2014) has been proposed as this, along with the multinomial-Dirichlet and Dirichlet, allows estimation of the variance terms to adjust the likelihood instead of using iterative data weighing. See Francis (2017) for a more comprehensive discussion of likelihoods and data weighting in fisheries modelling applications.

The likelihood for the tag data uses a least squares 'likelihood' which was determined from "assuming a normal distribution" (Senina et al. 2019a) for fishery *f*, timesteps *t*, region *i* and tag recapture *j*, with,

$$-LL = w\sum_{ftij}(E-O)^2$$

The choice of tag 'likelihood' is also unusual and, while analogous to a least squares implementation of the normal likelihood, it is not in a form typically used in maximum likelihood theory. Alternative likelihoods include the binomial distribution (e.g., Bull et al. 2012) or potentially the lognormal or Poisson distribution. A more appropriate likelihood should be considered as a part of revising and updating SEAPODYM.

Choice of variance estimates (i.e., multinomial N's or lognormal c.v.s) in the likelihoods is an important part of any model assumptions, as these influence model fits and allow reconciliation of conflicting data within the model (Francis 2017). From Senina et al. (2019a), it appears that only the weighting factor (*w*) for the likelihood associated with the tag data is estimated or evaluated within the model (in order to upweight the tag data) — suggesting that the length frequency data are given priority on the model fitting procedure. As data weightings can have considerable impact on model fits, future work should consider how data weightings are applied, and develop diagnostics to investigate the effect of downweighting on variance assumptions and model fits.

Note that future developments in computing power (specifically in multi-threaded CPUs) may assist in reducing the run time of complex spatial models by implementing parallel processing into the model code (e.g., see Dunn et al. 2018 for multi-threaded movement preference function dynamics in SPM). Recent CPUS are now available with much larger numbers of cores and hence threads, than available even recently. However, such applications require software architecture planning and reasonably sophisticated programming skills and is not easily retrofitted into generic modelling software.

4.2 Recent SEAPODYM developments since the WCPFC SC 2016 review paper

Developments since the 2016 review are described in Senina et al. (2018, 2019a, 2019b). SEAPODYM has been used to develop predictions of climate change induced distribution changes and has been extended to include tag data, alternative catch estimation assumptions, and revisions to the modelling assumptions.

The 2016 review noted that SEAPODYM could provide a useful tool to test the current tuna MULTIFAN-

CL assessment models for bias and precision from assumptions of spatial structure on management advice, however use of SEAPODYM as a simulator for the current MULTIFAN-CL assessments has not yet been developed. Development of SEAPODYM as a simulator would allow assessment of a range of important research questions, including optimal sampling to reduce uncertainty and bias, inform the choice of potential sensitivities in assessment model management strategy evaluations (MSE), the impacts of spatial heterogeneity on observational data (i.e., length frequency, CPUE, and tag-release and recapture data), as well as inform potential for future research.

Model diagnostics and evaluation of model fits have been developed since 2016 (see, for example, Senina et al. 2019a). However further development would be beneficial. In particular, replicating standard model diagnostics and fits used in the current MULTIFAN-CL tuna assessments would allow direct comparison of the model outcomes between SEAPODYM and those used to directly inform stock status and catch limit management.

Senina et al. (2019a) evaluated the performance of SEAPODYM with tagging data by undertaking sensitivity analysis, optimisation and validation comparisons to verify that the model with tagging data performed better than the model with fisheries only data. While these considerations are important, stimulation testing of the underlying framework should be undertaken to assess the potential bias and levels of uncertainty that may result from different modelling assumptions and data choice.

4.3 The current state of the mid-trophic level sub-model influencing the above tuna models, and options for improved sub-model validation

The underlying mid-trophic level sub-model (SEAPODYM-LMTL) has previously been considered an important input into the SEAPODYM models of tuna and tuna-like species, being an important driver for tuna movement and distribution. This arises as it is assumed that tunas will likely move to and reside in areas where there is greater abundance of available food (micronekton). The sub-model provides this prediction based on environmental covariates and assumptions about the link between these covariates and the micronekton.

Development of the mid-trophic level sub-model has not been progressed by SPC in recent years as far as the main SEAPODYM program for modelling of tunas and tuna-like species, although the underlying LMTL model has continued to be developed. Estimates from the LMTL model have been made publically available (see http://www.seapodym.eu/zooplankton-and-micronekton-model-for-cmems-now-available, accessed 31 January 2020) by week for 1998–2016 at 1/4° resolution.

Consideration could be given to implementations of SEAPODYM for tunas that forgo the LMTL sub-model and use the environmental covariates directly. It may be that this investigation has been undertaken, although there are no published comparisons between the choice of inclusion of the underlying mid-trophic level sub-model or direct environmental covariates on model outcomes. This would provide information on if the mid-trophic level sub-model therefore is required for tuna and tuna-like modelling. While additional research to further develop the mid-trophic level sub-model could be undertaken — specifically in the collection of spatiotemporal data (i.e., acoustic data from vessels of opportunity) to inform model assumptions —whether it is required as an input into the SEAPODYM models for tunas should first be addressed.

We note, however, that the 2D micronekton and zooplankton fields derived from this model are being used within a new Ecopath with Ecosim (EwE) ecosystem model currently under development for the tropical western Pacific (EcoSEA workshop, 2019), and as such may be required for other research being developed by SPC.

4.4 Outstanding gaps and new data requirements for future development of SEAPODYM in the context of i) management strategy evaluation, ii) climate change and iii) ecosystem-based fishery management for tropical tunas in the Western and Central Pacific Ocean (WCPO)

SEAPODYM provides a key scientific platform that can be used to model the spatiotemporal distribution and abundance of pelagic species, such as tunas and potentially important bycatch species, at high-resolution spatial scales using environmental scenarios to inform this scientific and management advice.

Development of how to characterise uncertainty, both in statistical interpretation of observations and in the structural uncertainty in model parameterisation should be considered. Both statistical and structural uncertainty is influenced by biased and/or misleading assumptions, data, and spatiotemporal heterogeneity of observational data. Development of SEAPODYM as a simulator would enable this assessment of uncertainty and other important research questions, including optimal sampling to reduce uncertainty and bias, inform the choice of potential sensitivities in assessment model management strategy evaluations (MSE), the impacts of spatial heterogeneity of current observational data (i.e., length frequency, CPUE, and tag-release and recapture data), as well as inform research questions on choices of alternative spatial structure assumptions in the MULTIFAN-CL tuna assessment models.

While the structure of the underlying SEAPODYM code is not readily available, in general, adding simulations should be relatively easy to add, and should be considered for SEAPODYM. Both SPM (Dunn et al. 2018) and CASAL (Bull et al. 2012) both implement observation simulations by using either assumed or estimated model parameters to generate 'expected' values for each observation, and then add random error according to the likelihood and variance term specified by the user (analogous to the Bayesian posterior-predictive distributions). This allows models to be run that generate alternative sets of observations, with different levels of precision, to undertake simulation experiments using the same or even alternative underlying operating models. See Mormede & Dunn (2013) and Mormede et al. (2014a) for an example of simulations from a spatial model used to evaluate bias and precision resulting when tag data were used within a non-spatial model. Alternatively, an R package or other similar tool could be developed that uses SEAPODYM and the model parameters to generate simulated observations, similar to that for Stock Synthesis (Anderson et al. 2014).

Yates et al. (2018) identified a summary of challenges in ecological modelling from a large number of ecological modelling experts using the Delphi method (Mukherjee et al. 2015). They noted that an understanding of the factors that affect ecological model predictability were still insufficiently understood, and proposed that the most immediate obstacle to improving understanding was with the absence of a widely applicable set of metrics for assessing model suitability when applied to new and novel questions (Yates et al. 2018).

Spatial models, with large numbers of spatial and temporal observations are difficult to validate against statistical assumptions, simply as the dimensionality of observations results in large quantities of model diagnostics and fits that are difficult to distil into easily interpretable but informative summaries. While consideration should be given to further developing the standard model diagnostics (i.e., patterns in normalised and Pearson residuals for biomass series and by cohort, time, and space for length frequency or tagging data), additional data is likely to improve model predictability.

The investigation of the type and amount of new observational and research data that would have the most impact requires additional research. Simulations from the SEAPODYM model would assist in developing this understanding. However, it is likely that the most important requirements would be for data that directly informs the model of dispersal and movement, for example tag data. Given the difficulties and costs in implementing large scale tagging programs, simulations that evaluate the most efficient deployment of tags should be undertaken and SEAPODYM would provide a suitable package for simulations.

As environmental conditions alter due to climate change, validation of model forecasts against observed changes would provide validation of the predictions in the short term and improve understanding of where the likely effects of change are most apparent. Development of ongoing monitoring, data collection, and observational data in these areas should be considered. The response of species and how they may adapt to a changing environment is a key gap in current knowledge for ecological models: how do animals respond to a changing environment?; do they evolve to adapt to change, and if so, how and over what time scale?; what happens to the underlying food web from plankton through to higher trophic levels under ocean warming, variability, and chemical changes due to climate change? Fisher behaviour will most likely also need to adapt to changing environmental conditions and changes in target species' distribution and abundance. Consideration should be given to hypotheses on how adaption may occur when forecasting, combined with monitoring to validate that predicted changes in both the underlying environmental drivers and fish species responses are consistent with those forecasted. Such comparison using monitoring programmes and SEAPODYM forecasts could be easily incorporated within broader ecosystem reporting requirements at national and regional levels.

Use of an eco-system modelling approach would allow supplementary advice on interactions with dependent and associated species (e.g., pelagic sharks). Integration of research from SEAPODYM, full ecosystem models such as EwE, and integrated assessment model (MULTIFAN-CL) should be considered. The EcoSEA workshop, recently held by SPC (EcoSEA, Noumea, New Caledonia, 28 October–1 November 2019) provided an opportunity to understand the strengths and weaknesses of each approach, and to begin to construct a common framework behind these programs that would allow future integration of the scientific understanding and management outcomes.

The current tuna assessment models implemented in MULTIFAN-CL allow for modelling of single species and determine consequences of alternative management approaches. This modelling framework provides the scientific advice for management advice on catch limits for tunas, management policy (fleets, areas, data requirements, etc), and is used to undertake tactical decision making in response to management objectives. While SEAPODYM may also be able to reproduce similar outcomes, confounding between spatial and abundance information and the longer run times to undertake modelling may not make it suitable for tactical management advice in the same manner as the current MULTIFAN-CL models.

However, SEAPODYM does provide an important alternative model to develop model validations, evaluate alternative assumptions of spatiotemporal confounding that may bias the current management models, and to generate alternative scenarios for MSE. In addition, the predictions of future climate change induced changes in fishery abundance and distribution can provide alternative future scenarios for MULTIFAN-CL MSE modelling and predictions. For example, changes in the underlying productivity parameters (natural mortality, growth, recruitment, etc.) and broad scale distributional changes, from SEAPODYM can be used as scenario modelling in the MSE for the current assessment models to evaluate how different strategies responds to these changes.

In this context, SEAPODYM provides both a strategic and a tactical modelling approach as an estimation model for comparing with single species assessment models, an operating model for Management Procedure Evaluations (MPEs), developing scenarios of fleet responses to changing environmental conditions, and a hypothesis generating model for climate change scenarios.

SPC is currently investigating updating and further developing the 'warm pool' EcoPath model from 2007 (Allain et al. 2007). This model has much lower spatial resolution and is 'tuned' rather than fitted to data.

This provides a strategic modelling approach to investigating the consequential effects of fishing and exploitation on the ecosystem through Ecosim. As this model includes a greater component of the ecosystem, it allows modelling of the changes in species relationships under different scenarios. Here, SEAPODYM can also be used to inform potential changes in distribution and productivity of tunas under climate change scenarios that would enhance its utility for developing advice.

Comparisons with the suite of models available — from single species assessments in MULTIFAN-CL, high-resolution spatiotemporal models in SEAPODYM, and full ecosystem broad scale models in EcoPath — provides an opportunity to investigate how different aspects of important target species will respond to exploitation, the consequences on fishing fleets and PICTs of changes in management and spatial distribution resulting from climate change, and the consequential ecosystem changes that may arise.

Depending on the research requirements of SPC, alternative approaches also include species distribution modelling to determine spatial distribution changes under GHG emission scenarios and environmental change. Development of species distribution models (i.e., including boosted regression trees, random forests, maximum entropy, gaussian random fields, and GLM/GAMs) will not be adequate for investigating population composition research questions, but will provide alternative and comparable overall species distributions predictions with SEAPODYM. Robinson et al. (2017) provides a 'best practise' framework for constructing marine species distribution models, which provides a method for defining research goals, data selection, GIS, and model implementation, calibration, and validation (see Figure 7 in Robinson et al. 2017). Such modelling approaches would allow validation of SEAPODYM predictions, and an evaluation of the additional insights obtained from modelling the population composition and its relationship to environmental covariates.

Peck et al. (2018) reviewed spatially-explicit modelling approaches used to model changes in the distribution and productivity of living marine resources, including: species distribution models; physiology-based, biophysical models of single life stages or the whole life cycle of species; food web models; and end-to-end ecosystem models.. The review by Peck et al. (2018) recommended development of models that "encompass more realism in ecophysiology and behaviour of individuals, life history strategies of species, as well as trophodynamic interactions occurring at different spatial scales". But they also noted that species distribution models can help identify those factors that have the most influence on spatiotemporal distributions and provide an important step in developing understanding of potential changes in species under environmental change. The review concluded that confidence in projections of changes in the distribution and productivity would be increased by evaluating and comparing a range of alternative approaches (e.g., ensemble modelling).

4.5 Comparison with similar spatially explicit population dynamics model frameworks currently available, not limited to those currently used for tropical tunas

SEAPODYM is a complex forage and environmentally driven population dynamics model for tunas. While there are some alternative high-resolution spatiotemporal models being developed worldwide (e.g., Cao et al. 2019) the only other generic model that allows the use of a high resolution spatial scale to model movement and population dynamics is SPM (Dunn et al. 2018, see also https://github.com/alistairdunn1/SPM). As with SEAPODYM, this uses habitat and environmental covariates to inform movement parameters, and hence reduce the dimensionality of the high-resolution spatial model to a tractable level. However, SEAPODYM has been developed further than SPM for modelling tuna and tuna like species, and its use of differentiable computer code has resulted in code efficiencies that can significantly reduce model run times.

Specific implementations of high resolution spatiotemporal models that include population dynamics have been developed for use in fisheries management, including a model of snow crab *Chionoecetes opilio* off eastern Canada by Cadigan et al. (2017). This used a high-resolution spatiotemporal population model to fit to spatially explicit Snow crab CPUE, and hence estimated depletion and fishery saturation. An alternative approach to modelling spatiotemporal change was recently developed by Cao et al. (2019). The spatiotemporal model builds on the VAST model (Thorson & Barnett 2017) and links species distribution and population dynamic models within a single statistical framework. While this method is still in development, it may provide an alternative approach in the future. Furthermore, the VAST model is open-source software available on GitHub and was written in Template Model Builder (TMB), a software package that makes model development easier for other researchers.

However, high-resolution spatiotemporal population dynamics models have generally only been applied in simulations and as research models, rather than being used to provide specific stock status and management advice (e.g., Mormede et al. 2014a, 2017; Kristensen et al. 2014).

Spatial distribution models that include population dynamics also include agent based models (e.g., Ikamoana, Scutt Phillips et al. 2018), full end-to-end ecosystem models (e.g., EwE, Allain et al. 2007; and ATLANTIS, Audzijonyte et al. 2019) and MICE models (Plaganyi et al. 2012).

End-to-end ecosystem models are often large and complex and require a long lead time to develop. These also tend to operate at a low-resolution spatial scale due to the model complexity and lack of highly resolved ecosystem data. Agent based models rely on habitat relationships and may have similar complexity to high-resolution spatiotemporal population dynamics models. Generalised agent based models are being developed (see, for example, Marsh (2019) at https://github.com/Craig44/IBM), that may provide an alternative platforms for developing agent based models in the future.

Depending on the nature of the available data, these may provide a better understanding of tag-release and recapture data as they can identify individual tagged fish and environmental response, rather than evaluating these as homogenously behaving tagged cohorts as in cohort models like SEAPODYM. MICE models provide an intermediate approach, and "are context- and question-driven and limit complexity by restricting the focus to those components of the ecosystem needed to address the main effects of the management question under consideration" (Plaganyi et al. 2012). Under this definition, SEAPODYM mostly meets the criteria of a MICE model.

4.6 The future of SEAPODYM as an ecosystem-based population dynamics model for tropical tunas and important bycatch species (e.g., mahi mahi, wahoo, sharks) in the WCPO, in both single- and multi-species applications, and not limited to the model's current incarnation

SEAPODYM has had a long development history and condenses a wide variety of scientific understanding into a single framework. This has the advantage that it is a powerful tool that can be used to further to investigate a wide range of assessment and ecosystem influences on current and future fisheries utilisation for Western Central Pacific Region tunas.

SEAPODYM clearly has a key role in providing scientific advice for understanding spatiotemporal impacts of fishing and of environmental variability and change of tuna populations in the western Pacific Ocean. Modelled distributions and changes can provide a useful contrast and potentially input assumptions into EwE, in particular for the mid-level trophic sub model.

The development of the EwE model provides an opportunity to use both EwE and SEAPODYM as a closely integrated research program — scenarios in EwE can be used as input assumptions in SEAPODYM, and specific SEAPODYM models can be used to validate the EwE conclusions. For example, as EwE scenarios develop and are able to provide future scenarios of abundance and productivity parameters, these could be used by SEAPODYM to model the resulting distributional changes, effects of CPUE for fishing, and the hence consequences for PICTs and fishing nations in the Pacific Ocean for specific species.

The high level of spatial resolution in SEAPODYM also allows for the development of spatial allocation management scenarios. For example, investigating the impacts of spatial closures, MPAs, or distributional changes in fleet activity as a result of potential management changes (e.g., Sibert et al. 2012). For example, Mormede et al. (2017) used SPM to investigate the potential consequences of the Ross Sea region MPA on spatial distribution of Antarctic toothfish fishing activity, local density change in toothfish abundance as a result of those changes in fishing distributions and the resulting fishing CPUE and catch composition. Such research may assist in informing management as to the consequences of different choices of spatial and fleet management, including assisting PICTs and fishing nations in the western Pacific develop management options and evaluate trade-offs between alternative choices. For example, research possibilities include fishery scenario modelling, including economic models of distance to fishing and ports of departure and unloading, and other similar economic consequences due to potential changes in fish distribution and abundance.

Multispecies models, particularly where there are strong relationships between species being modelled, would also assist in understanding inter-species relationships and consequences of the spatiotemporal effects of fishing on associated and dependent species. For example, Mormede et al. (2014b) used a multi-species spatial model of target fisheries and bycatch species with predator-prey relationships to investigate the effect of target and bycatch fishing on resulting catch and abundance of the bycatch species.

Plaganyi et al. (2012) noted that quantitative models to support fisheries decision-making may be either strategic (conceptual and broad scale) or tactical (inform short term management decisions such as target species catch limit setting), with outcomes from strategic models informing the choices in tactical models. The authors proposed Models of Intermediate Complexity for Ecosystems (MICE) as tactical tool to inform management. These models provide a useful tool as ecosystem assessment tools, with the advantage that "they limit complexity by restricting the focus to those components of the ecosystem needed to address the main effects of the management question under consideration" (Plaganyi et al. 2012). They noted that an important application includes the prediction of future productivity (and hence sustainable catches/potential rebuilding rates) given environmental factors and the implications for yield and population structure arising from consideration of different management controls on different areas. In this context, SEAPODYM contains the necessary functions to be a MICE tactical tool, through the inclusion of spatiotemporal variability driven by environmental covariates,

The development of model and related observational indicators would provide validation of SEAPODYM modelled outcomes, and likely be an important input into management decision making. Consideration should be given to the development of potential indicators that are useful for management including, for example, spatiotemporal predictions over short time scales, "early warning" indicators that provide short term predictions of adverse or significant events, and indicators that measure previous predictions against observed outcomes to assist with quantifying prediction accuracy.

5 Conclusions

Scientific research on the spatial distribution and abundance of tunas in the western Pacific Ocean is required by the Pacific Community (SPC) to provide advice to Pacific Island countries and territories and to international tuna management bodies. The Spatial Ecosystem And POpulation DYnamics Model (SEAPODYM), developed by The Pacific Community (SPC) and Collecte Localisation Satellite (CLS), provides a key scientific platform that can be used to model the spatiotemporal distribution and abundance of pelagic species, such as tunas and potentially important bycatch species, at high-resolution spatial scales using environmental scenarios to inform this scientific and management advice.

SPC has noted that to reduce the uncertainty and enable assessment of climate-driven changes in the tuna fisheries and related economic benefits from tuna fishing, research investments are needed to identify the structure of Pacific tuna stocks, understand the response of stocks to climate change scenarios, and develop predictions of the expected redistribution of tuna species under those different scenarios (Anon 2019).

Currently, SEAPODYM provides the best available scientific tool available to SPC for the provision of advice on spatiotemporal changes in tuna distributions that include population dynamics — specifically one that that allows consideration of the response of tuna stocks under different greenhouse gas emission scenarios at a high-resolution spatiotemporal scale. SEAPODYM provides a strong platform for developing this advice.

SEAPODYM has the potential provide a link between the targeted single species assessment models (e.g., MULTIFAN-CL) used to provide tactical management advice on key tuna stocks, and full simulation based ecosystem models (e.g., EwE) that allow understanding of the ecosystem relationships from climate change and fishing at a broad spatial and temporal scale. Consideration of how the advice from these different work streams can be more fully integrated would be beneficial and assist when developing the medium-long term research program for SEAPODYM. Clear identification of the research questions required by SPC and the role of the different tools available would be beneficial to informing future development.

While SEAPODYM provides an advanced and reasonably mature product suitable for generating advice, there are a number of key areas where research investment could be considered that would improve its usability and utility to SPC. Documentation of the underlying SEAPODYM software is available as a draft document from 2009 (updqated as a draft unpublished manuscript in 2013). Full documentation of the current code (and ongoing future modifications) would be most beneficial to allow transparency and collaboration on its development and provide assurance that the outputs represent best available science.

SEAPODYM provides a valuable tool to inform and simulate data to validate the assumptions of management advice from the current assessment (MULTIFAN-CL) models for tunas. Additional model validation is required in order to verify that the equations and methods can replicate the standard fisheries models — specifically the population dynamics and broad scale movement. Simulation and validation of the SEAPODYM software would also be beneficial (using either MULTIFAN-CL and other spatially explicit models such as SPM or specific case models) to ensure the underlying population dynamics and movement assumptions are robust and consistent, where appropriate, with standard fisheries models used to provide management advice.

Consideration should also be given to the statistical implementation of the underlying estimation equations and assumptions. Specifically, the way in which input data are applied within the model (e.g., the use of kernel smoothed tag recapture data as an input) and the statistical assumptions (e.g., likelihoods) are implemented. Verification of these aspects would not be time consuming and would provide the basis for confirming the best use of input observations and validate that the underlying statistical aspects were consistent with other fisheries assessment practise.

Spatial models, with large numbers of spatial and temporal observations are difficult to validate against statistical assumptions, simply as the dimensionality of observations results in large quantities of model diagnostics and fits that are difficult to distil into easily interpretable but informative summaries.

Consideration should be given to further developing the standard model diagnostics, including visual representations of fits, and potentially replicating summaries typically seen with standard fisheries assessment modelling output. Additional development on the SEAPODYM model diagnostics, including reproduction of standard fisheries assessment diagnostics would be beneficial in demonstrating model adequacy, and to highlight those conclusions where spatially explicit models result in alternative predictions of tuna species stock dynamics and status.

As a means of developing the validation and model diagnostics, a key initial test case might be to reproduce a standard fishery model in SEAPODYM where the movement and functional relationships to underlying forage fish and environmental dynamics have been 'turned off'. Comparison of the model likelihoods, fits, and parameter estimates would then confirm that the underlying processes and statistical equations were correct. Then, iteratively add to this model the specific spatial and environmental functional relationships back, developing an 'audit trail' (also known as a bridging analysis') that demonstrates the effect of additional complexity in movement and population productivity assumptions on the model outputs and management conclusions that could be drawn.

As SEAPODYM provides a well-advanced research tool for the investigation of spatially driven fish dynamics, the requirement for additional research in this area will likely increase in the future. Currently, additional research questions that may use SEAPODYM are limited by a small number of individuals who can access or run the program. Considerations should be given to expanding the user base of SEAPODYM, potentially by making the underlying program more available and developing interfaces or tools to allow the investigation of alternative model structures, assumptions, and observational data in an efficient manner; and improving the ability to allow for sensitivity analyses of alternative climate change scenarios and operational fishing scenarios (including total removals, fleet distribution and fleet catch ratios between fleets).

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8 Appendix A: Terms of reference for the review of SEAPODYM as a population dynamics model for tunas and tuna-like species

Project title: A review of SEAPODYM as a population dynamics model for tunas and tuna-like species

8.1 Background

The continued development and application of the Spatial Ecosystem And POpulation DYnamics Model (SEAPODYM) for understanding the population dynamics of tropical tunas in the Pacific region remains a key priority for the Oceanic Fisheries Programme (OFP) at the Pacific Community (SPC), and for the Western & Central Pacific Fisheries Commission (WCPFC) under Project 62.

SEAPODYM is a model for investigating the spatiotemporal dynamics of fish populations under the influence of both fishing and environment (www.seapodym.org), and its current implementation is the product of many years' work (see Lehodey 2004a, b; Lehodey et al. 2008; Senina et al. 2008; Lehodey and Senina 2009; Senina et al. 2015, 2018). The model is based on advection-diffusion-reaction equations that describe the distribution of tuna under dynamic processes (i.e. spawning, movement, mortality), which are constrained by environmental data (i.e. temperature, ocean currents, primary production and dissolved oxygen concentration) and distributions of mid-trophic level functional groups (e.g. micronektonic tuna forage).

The model simulates age-structured population processes with length and weight relationships obtained from independent studies. Various life stages are considered: larvae, young, immature and mature adults. In the larval and young phases, tuna drift with currents; later on, they become autonomous — their movement influenced by an additional component linked to fish size and habitat quality in conjunction with current velocity fields. From the age at first maturity, tuna begin spawning, and if appropriate, their displacements are governed by a seasonal switch between feeding and spawning habitats (e.g. in the case of South Pacific albacore tuna). The last age stage in the model is a 'plus class' where the oldest individuals are considered. The model takes into account fishing activity and predicts total catch and size frequencies of catch by the fishery when spatially explicit fishing data are available. A Maximum Likelihood Estimation approach is used to estimate model parameters, including fishery parameters, and conventional release-recapture tagging data were recently integrated within MLE framework to allow better estimation of movement and habitat parameters.

At the 10th Regular Session of the Scientific Committee (SC10) in 2014, a scientific review of SEAPODYM was requested to help guide the WCPFC in evaluating potential model applications and its future work program under Project 62. The review was presented at SC12 in 2016 (see Nicol and Smith 2016, Appendix 1). It documented 1) the status of the SEAPODYM project at that time, including a review of model assumptions and diagnostics; 2) the immediate and medium-term applications of SEAPODYM; and 3) how SEAPODYM could be modified in order to improve the quality of the science arising from applications of the model.

Since this 2016 review, SEAPODYM has continued to evolve, with the inclusion of new micronekton fields, production of real-time forecasts of tropical tuna population dynamics, and developments pertaining to climate-change impacts including multi-model ensemble forecasts and predictions of potential ocean acidification effects.

8.2 Terms of reference

Given these developments, the substantial uncertainties remaining around tropical tuna stock structure and life histories in the Pacific region (Moore et al. 2018), and questions regarding the direction of the SEAPODYM project into the future, the following aspects should be reviewed:

1. The current state of SEAPODYM as a tool for understanding the population dynamics of the four tropical tunas of principal commercial interest in the Pacific region.
2. Recent SEAPODYM developments since the WCPFC SC 2016 review paper.
3. The current state of the mid-trophic level sub-model influencing the above tuna models, and options for improved sub-model validation.
4. Outstanding gaps and new data requirements for future development of SEAPODYM in the context of i) management strategy evaluation, ii) climate change and iii) ecosystem-based fishery management for tropical tunas in the Western and Central Pacific Ocean (WCPO).
5. Comparison with similar spatially explicit population dynamics model frameworks currently available, not limited to those currently used for tropical tunas.
6. The future of SEAPODYM as an ecosystem-based population dynamics model for tropical tunas and important bycatch species (e.g. mahi mahi, wahoo, sharks) in the WCPO, in both single- and multi-species applications, and not limited to the model's current incarnation.