SCIENTIFIC COMMITTEE
THIRD REGULAR SESSION

13-24 August 2007
Honolulu, United States of America

An Ecopath with Ecosim model of the Western and Central Pacific Ocean warm pool pelagic ecosystem

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WCPFC-SC3-EB SWG/IP-8

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1. Introduction

The warm pool in the western equatorial Pacific is one of the biogeochemical provinces defined by (Longhurst, 1995); it is generally delimited by the 29ºC surface isotherm and a salinity front (Figure 1). It is an oligotrophic system characterized by low salinity, low nitrates, high temperature, deep thermocline, low surface chlorophyll and maximum chlorophyll located at 90m depth. Conversely, the cold tongue in the Eastern equatorial Pacific is an upwelling system with high salinity, high nitrates, low temperature, shallow thermocline, high surface chlorophyll and maximum chlorophyll at the surface. The warm pool-cold tongue system is variable in terms of hydrography, nutrient availability and zonal extension in response to interannual variations such as El Niño Southern Oscillation (ENSO) but also decadal oscillations. These interactions are considerable drivers of ecosystem productivity and high order predator dynamics in the warm pool ecosystem (Lehodey *et al.*, 1997; Lehodey, 2001; Lehodey *et al.*, 2003).

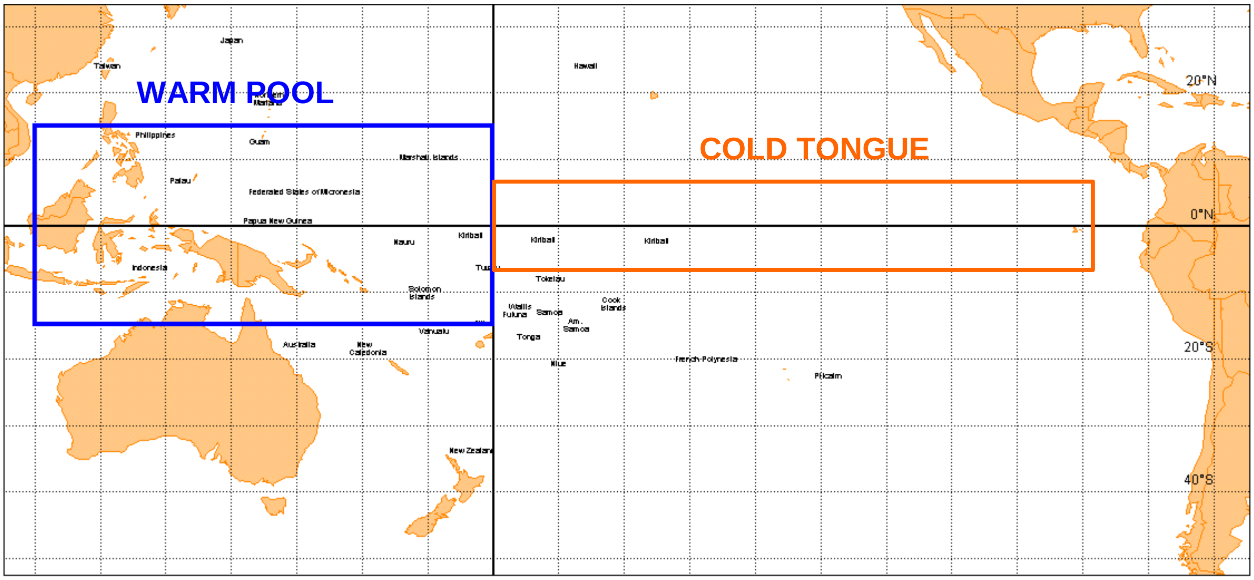

Figure 1. Spatial extent of the warm pool – cold tongue system in the Pacific Ocean.

The western and central Pacific Ocean (WCPO) regions are important for economic, cultural and biodiversity contributions at regional and international scales (Anonymous, 2000). The tuna fishery in the WCPO catches approximately half of the world’s tuna and is of high economic importance to Pacific island countries and territories (Williams & Reid, 2006). Throughout the WCPO, total annual catches of target tuna species (skipjack, yellowfin, bigeye and albacore tuna) are now in excess of 2 million tonnes (Williams & Reid, 2006). Not surprisingly, management concerns arise from potential conflicts in goals that attempt to sustain these economic, cultural and biodiversity values.

Mathematical models that faithfully describe the processes that we understand/observe to influence species and ecosystems are useful for assisting with decision making where such conflicts occur (Burgman *et al.*, 1993; Walters & Martell, 2004). These models allow us to make quantitative predictions about species or ecosystems to different policy alternatives (Hilborn & Mangel, 1997). Our knowledge about all the interactions that sustain the WCPO ecosystem is incomplete, hence any model is a simplification - an abstraction on how we think the ecosystem operates. However, they provide a mechanism for identifying these knowledge gaps and for assessing the influence this uncertainty has on achieving management goals.

Rarely does a single model summarise all the issues faced by managers or provide the opportunity to explore the potential consequences of all management options (Hilborn & Mangel, 1997). Models are constructed with specific questions and consequently have specific purposes and constraints in interpretation and extrapolation. The WCPO stock models provide a description of single species dynamics (tuna) and their interaction with fisheries objectives (Hampton *et al.*, 2006a; Hampton *et al.*, 2006b; Langley & Hampton, 2005; Langley *et al.*, 2005).

Seapodym models are ecosystem models that describe the Pacific Ocean including the warm pool (Lehodey, 2004). They were initially developed for investigating physical-biological interactions between tuna populations and the pelagic ecosystem of the Pacific Ocean. Using predicted environment from ocean-biogeochemical models, Seapodym integrates spatio-temporal and multi-population dynamics and considers interactions among populations of different species and between populations and their physical and biological environment (including intermediate trophic levels). The model also includes a description of multiple fisheries.

While Seapodym models tells us about tuna in a spatially and numerically explicit way, a complimentary model is required that provides the capacity to explicitly examine trade-offs in trophic structure between competing policies. One of the modelling approaches available to explore the ecosystem trophic structure is Ecopath with Ecosim[5], which has been widely used in aquatic and terrestrial system for this purpose. This approach requires that the biomass of the ecosystem is balanced and consequently the effects of altered biomass production or harvest on the entire ecosystem assemblage can be explored. Such a model would complement the existing suite of models available to management. Furthermore models constructed within this context will allow independent exploration of the influence of the assumptions used in both the stock assessment and Seapodym models and vice versa. This paper describes the collaborative approach to develop an Ecopath with Ecosim model for the WCPO warm pool. Specifically it describes:

1- Ecopath model balancing methods and outcomes;
2- Preliminary Ecosim simulations; and
3- Further model development.

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[5] www.ecopath.org

2. Methods

2.1. Model Description

Ecopath models are mass-balance models that describe energy pathways in a food web. Ecosim adds a temporal dynamic to this equilibrium, by adding a time-series of fishery or environmental vectors that allow the influence of these covariates on the distribution of biomass to be explored (Christensen *et al.*, 2000).

The master equation for Ecopath is:

$$B_i(\frac{P}{B})_i EE_i = Y_i + \sum B_j(\frac{Q}{B})_j DC_{ji} + BA_i + NM_i$$

Where B_i and B_j are biomasses of prey (*i*) and predators (*j*), respectively; $(\frac{P}{B})_i$ is the production/biomass ratio, equivalent to total mortality (Z) in most circumstances (Allen, 1971); EE_i is the ecotrophic efficiency, the fraction of the total production of a group that is used in the system; Y_i is the fisheries catch per unit area and time (*i.e.* $Y = F \times B$); $(\frac{Q}{B})_j$ is the food consumption per unit biomass of *j*; and DC_{ji} is the contribution of *i* to the diet of *j*; BA_i is the biomass accumulation of *i* (positive or negative); NM_i is the net migration of i (emigration less immigration).

Consequently for each entity (functional group) modelled in Ecopath, information is required on production/biomass (*P/B*), consumption/biomass (*Q/B*), biomass, proportion of habitat area occupied, biomass in habitat area ($t.km^{-2}$), diet composition and fishing mortality.

In Ecosim the Ecopath equation is re-expressed in a dynamic formulation:

$$\frac{dB_i}{dt} = f(B_i) - MB_i - F_iB_i - \sum_{j=1}^{n} c_{ij}(B_iB_j)$$

Where, $f(B_i)$ is a function of B_i if *i* is a primary producer or $f(B_i) = g_i \sum c_{ij}(B_iB_j)$ if *i* is a consumer, where g_i is the net growth efficiency, and $c_{ij}(B_iB_j)$ is the function used to predict consumption rates from B_i to B_j. A function for c_{ij} is derived from specification of prey vulnerabilities.

2.2. Spatial boundaries of the model and import/export issues

The boundaries of the warm pool vary according to environmental conditions; for the purpose of this study fixed boundaries have been chosen: 110-180ºE[6] and 15ºN-15ºS (Figure 1). It represents a surface area of 26.964 million km^2.

Imports and exports were not considered into this model. All dead organisms end up in the detritus pool, and unused detritus (*i.e.* detritus not consumed by detritivores) is considered to be exported out of the system by sedimentation.

2.3. Functional Groups

The final aggregation of the ecosystem to 31 functional groups was based upon an iterative process of including groups or species of special interest as well as using the pre-existing information available for this ecosystem and aggregating/separating groups in order to account for within group moderated predation (Table 1). A description of the data sources and aggregation issues are described in Appendix 1. Species of special interest such as turtles, marine mammals or birds were not included due to the lack of data, but could be added if information becomes available.

2.4. Ecopath with Ecosim input parameters

To model the warm pool ecosystem data were gathered from different sources (Appendix 1) and classified according to the degree of confidence in their values (high, medium, low confidence and guesstimates) (Table 2). Initial and final parameters for all the components as well as diet matrices and fisheries catches are presented in Table 3, Table 4 and Table 5.

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[6] Mean longitude of the front between the warm pool and the cold tongue for the period 1980-2000 is 178ºW (Le Borgne *et al.*, 2002a).

Prior to balancing the model some simple heuristics to help ensure that the input parameter values were rational were developed. These were:

B *vs.* EE: It was decided to input a B value rather than an EE estimate especially for top predators unless there were good estimates of the lower trophic levels on which the predators are feeding.

Assimilation efficiency U/Q: This parameter is considered of importance only when the detritus component was to be considered in the system. In our model the default value of 0.2 was kept for all the components of the model. This value is recommended for carnivorous fish (Christensen *et al.*, 2000), however the assimilation efficiency is usually lower for omnivores and can reach 0.4 for zooplankton (Christensen *et al.*, 2000; Jarre-Teichmann, 1996).

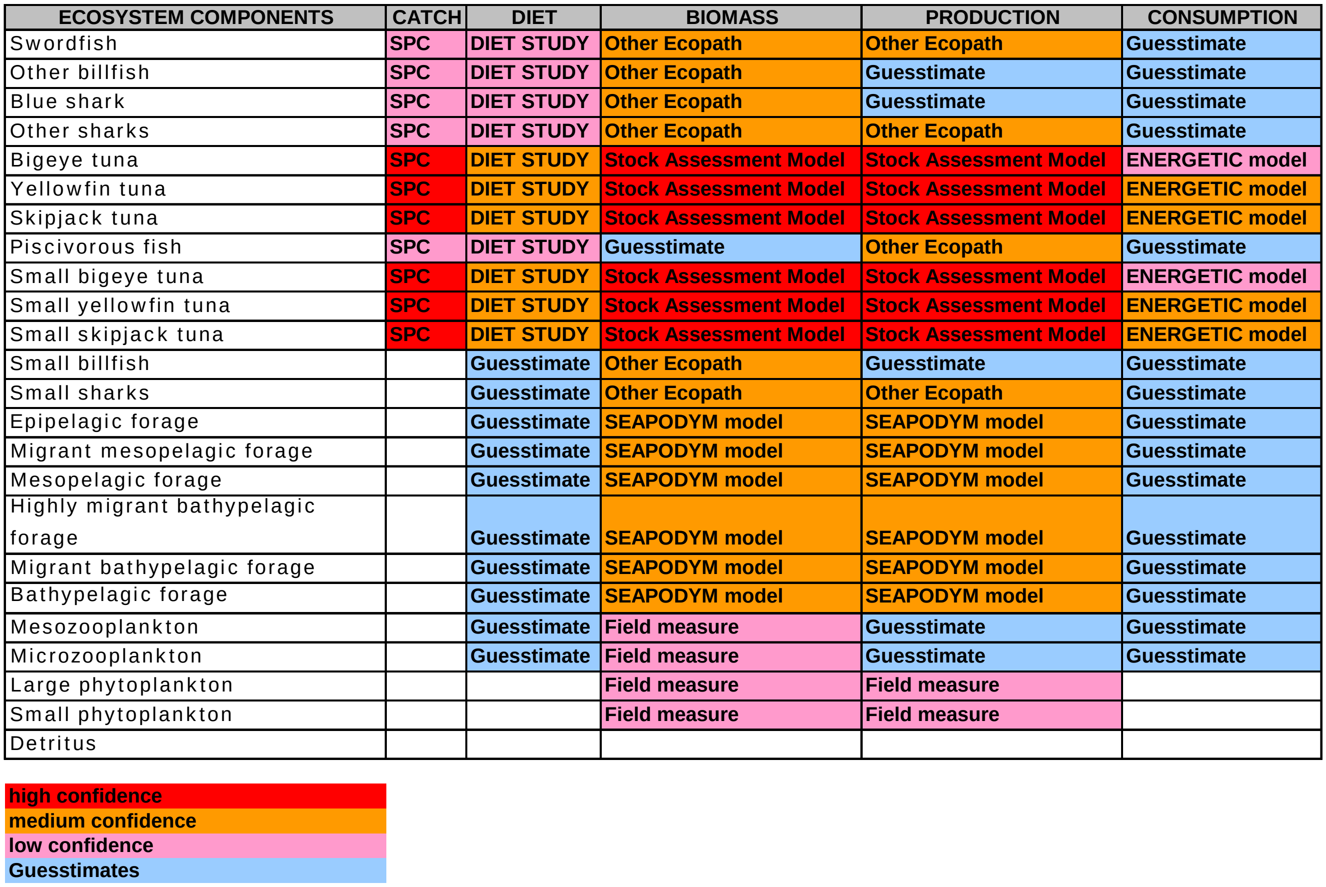
Gross efficiency P/Q (P/B / Q/B): This ratio was expected to be less than 0.3; this high value was reached by species with very efficient and rapid growth.

2.5. Modelling approach

A collaborative approach was used to build this Ecopath model. Seven participants with diverse expertises on Ecopath modelling, other modelling and pelagic research contributed to the development of the model during a workshop organised at the Secretariat of the Pacific Community, Noumea, New Caledonia, March 5-9, 2007.

Functional group name	Functional group description	Justification
Swordfish	Large *Xiphias gladius*	Bycatch species of interest for fisheries and ecosystem management
Other billfish	Large *Istiophorus platypterus, Makaira indica, Makaira mazara, Tetrapturus audax, Tetrapturus angustirostris*	
Blue shark	Large *Prionace glauca*	Bycatch species of interest for ecosystem management
Other sharks	Large Alopiidae, Carcharhinidae, Lamnidae, Sphyrnidae	
Bigeye tuna	*Thunnus obesus* larger than class size/age/weight at 50% of maturity 124cm/3.85y-46.2months/43kg*	Target species of interest for fisheries and management
Yellowfin tuna	*Thunnus albacares* larger than class size/age/weight at 50% of maturity 120cm/2.25y-27months/33kg*	
Skipjack tuna	*Katsuwonus pelamis* larger than class size/age/weight at 100% of maturity 43cm/0.75y-9months/1.6kg*	
Piscivorous fish	Alepisauridae, Bramidae, Carangidae, Coryphaenidae, Gempylidae, wahoo *Acanthocybium solandri*, opah *Lampris guttatus*, small Scombridae	Bycatch species of interest for ecosystem management but species by species information not available.
Small billfish	Small billfish, same species as large groups swordfish and other billfish	Bycatch species of interest for fisheries and ecosystem management
Small sharks	Small sharks, same species as large groups blue shark and other sharks	
Small bigeye tuna	*Thunnus obesus* smaller than class size/age/weight at 50% of maturity 124cm/3.85y-46.2months/43kg and larger than 20cm/3 months/0.18kg*	Target species of interest for fisheries and management
Small yellowfin tuna	*Thunnus albacares* smaller than class size/age/weight at 50% of maturity 120cm/2.25y-27months/33kg and larger than 24cm/3 months/0.33kg*	
Small skipjack tuna	*Katsuwonus pelamis* smaller than class size/age/weight at 100% of maturity 43cm/0.75y-9months/1.6kg and larger than 24cm/3 months/0.25kg*	
Baby SKJ	*Katsuwonus pelamis* from hatching to recruitement = 0 to 3 months, smaller than 24cm/0.25kg*	Additional group required to decrease the importance of cannibalism and balance the model
Epipelagic forage	Euphausids, shrimps, Stomatopoda, Decapoda, Amphipoda, Hyperiidae, Phronima, Megalopa, Palinuridae, Scyllaridae...; Engraulidae, Clupeidae, Exocoetidae, small Carangidae Bramidae Scombridae, juveniles of reef fish Acanthuridae, Balistidae, Chaetodontidae, Diodontidae, Holocentridae, Kyphosidae, Lethrinidae, Malacanthidae, Monacanthidae, Nomeidae, Ostraciidae, Pomacanthidae, Priacanthidae, Scaridae...; Argonautidae, Carinariidae, Cavoliniidae, Loliginidae, Eucleoteuthis luminosa, Hyaloteuthis pelagica, Moroteuthis lonnbergi, Onychoteuthidae, Sepiolidae, Thysanoteuthidae...	Species by species information was not available. Pre-existing aggregated information available.
Epipelagic crustaceans	Stomatopoda, Megalopa stage, Hyperiidea, Amphipoda, Palinura, Enoplometopidae, Phronima sp., Thalassocaris sp., Scyllaridae, Harpiosquillidae…	Additional groups required to decrease the importance of cannibalism and balance the model
Epipelagic fish	Acanthuridae, Balistidae, Bramidae, Carangidae, Chaetodontidae, Diodontidae, Echeneidae, Engraulidae, Exocoetidae, Holocentridae, Kyphosidae, Lethrinidae, Malacanthidae, Molidae, Monacanthidae, Nomeidae, Ostraciidae, Pomacanthidae, Priacanthidae, Scaridae, Scombridae, Serranidae, Tetraodontidae, Zanclidae...	
Epipelagic small fish	Larval and juvenile stages of the "Epipelagic fish" species	
Epipelagic molluscs	Argonautidae, Carinariidae, Cavoliniidae, Loliginidae, Eucleoteuthis luminosa, Hyaloteuthis pelagica, Moroteuthis lonnbergi, Onychoteuthidae, Sepiolidae, Thysanoteuthidae…	
Epipelagic small molluscs	Larval and juvenile stages of the "Epipelagic molluscs" species	
Migrant mesopelagic forage	Nemichthyidae, Myctophidae, Gempylidae, Phosichthyidae…; Enoploteuthidae, Stenoteuthis, Pterygioteuthis, Heteroteuthinae…	Species by species information was not available. Pre-existing aggregated information available.
Migrant mesopelagic fish	Nemichthyidae, Myctophidae, Gempylidae, Phosichthyidae…	Additional groups required to decrease the importance of cannibalism and balance the model
Migrant mesopelagic molluscs	Enoploteuthidae, Stenoteuthis, Pterygioteuthis, Heteroteuthinae…	
Mesopelagic forage	Juvenile Alepisauridae, Omosudidae, Paralepididae, Ophiididae, Trichiuridae, Caristiidae, Ostracoberycidae, Percophidae, Scombrolabracidae, Scorpaenidae, Argyropelecus, Triacanthidae, Macrurocyttidae...; Octopoteuthidae, Ommastrephidae, Moroteuthis, Ancistrocheirus, Amphitretidae...	Species by species information was not available. Pre-existing aggregated information available.
Mesopelagic fish	Juvenile Alepisauridae, Omosudidae, Paralepididae, Ophiididae, Trichiuridae, Caristiidae, Ostracoberycidae, Percophidae, Scombrolabracidae, Scorpaenidae, Argyropelecus, Triacanthidae, Macrurocyttidae…	Additional groups required to decrease the importance of cannibalism and balance the model
Mesopelagic molluscs	Octopoteuthidae, Ommastrephidae, Moroteuthis, Ancistrocheirus, Amphitretidae…	
Highly migrant bathypelagic forage	Myctophidae, Maurolicus, Sternoptyx, Liocranchia, Caridae, Oplophorus, Sergestidae, Euphausiidae…	Species by species information was not available. Pre-existing aggregated information available.
Migrant bathypelagic forage	Histioteuthidae, Penaeoidea, Acanthephyra…	
Bathypelagic forage	Paralepididae, Scopelarchidae, Diretmidae, Chiasmodontidae, Bolitaenidae…	
Mesozooplankton	Zooplankton of the class size 200-2000µm, mostly copepods.	Secondary production. Species by species information was not available. Size-class information available.
Microzooplankton	Zooplankton of the class size 20-200µm: copepod nauplii, ciliates, sarcodinids, rotifers, small cladocerans…	
Large phytoplankton	All pelagic photosynthetic organisms larger than 2-8µm, mainly diatoms, autotrophic dinoflagellates, pelagophytes, prymnesiophytes	Primary production driving the bottom-up mechanisms
Small phytoplankton	All pelagic photosynthetic organisms smaller than 2-8µm, mainly Prochhlorococcus, Synechococcus and autotrophic eukaryotes	
Detritus	All pelagic non-living material, bacterioplankton, heterotrophic pico- and nanozooplankton (<20µm)	Group required in Ecopath model

Table 1. Initial and final functional groups included in the warm pool ecosystem Ecopath model. ***White cells: in initial and final iterations, red cells: added in the final iteration, blue cells: removed from the final iteration. * age at maturity, length at age, weight at age according to Multifan-CL 2006 parameterisation; biomass and mortality information from Multifan-CL are provided for fish older than 3 months only.***



ECOSYSTEM COMPONENTS	CATCH	DIET	BIOMASS	PRODUCTION	CONSUMPTION
Swordfish	SPC	DIET STUDY	Other Ecopath	Other Ecopath	Guesstimate
Other billfish	SPC	DIET STUDY	Other Ecopath	Guesstimate	Guesstimate
Blue shark	SPC	DIET STUDY	Other Ecopath	Guesstimate	Guesstimate
Other sharks	SPC	DIET STUDY	Other Ecopath	Other Ecopath	Guesstimate
Bigeye tuna	SPC	DIET STUDY	Stock Assessment Model	Stock Assessment Model	ENERGETIC model
Yellowfin tuna	SPC	DIET STUDY	Stock Assessment Model	Stock Assessment Model	ENERGETIC model
Skipjack tuna	SPC	DIET STUDY	Stock Assessment Model	Stock Assessment Model	ENERGETIC model
Piscivorous fish	SPC	DIET STUDY	Guesstimate	Other Ecopath	Guesstimate
Small bigeye tuna	SPC	DIET STUDY	Stock Assessment Model	Stock Assessment Model	ENERGETIC model
Small yellowfin tuna	SPC	DIET STUDY	Stock Assessment Model	Stock Assessment Model	ENERGETIC model
Small skipjack tuna	SPC	DIET STUDY	Stock Assessment Model	Stock Assessment Model	ENERGETIC model
Small billfish		Guesstimate	Other Ecopath	Guesstimate	Guesstimate
Small sharks		Guesstimate	Other Ecopath	Other Ecopath	Guesstimate
Epipelagic forage		Guesstimate	SEAPODYM model	SEAPODYM model	Guesstimate
Migrant mesopelagic forage		Guesstimate	SEAPODYM model	SEAPODYM model	Guesstimate
Mesopelagic forage		Guesstimate	SEAPODYM model	SEAPODYM model	Guesstimate
Highly migrant bathypelagic forage		Guesstimate	SEAPODYM model	SEAPODYM model	Guesstimate
Migrant bathypelagic forage		Guesstimate	SEAPODYM model	SEAPODYM model	Guesstimate
Bathypelagic forage		Guesstimate	SEAPODYM model	SEAPODYM model	Guesstimate
Mesozooplankton		Guesstimate	Field measure	Guesstimate	Guesstimate
Microzooplankton		Guesstimate	Field measure	Guesstimate	Guesstimate
Large phytoplankton			Field measure	Field measure	
Small phytoplankton			Field measure	Field measure	
Detritus					

🟥 high confidence
🟧 medium confidence
🟪 low confidence
🟦 Guesstimates

Table 2. Origin of the data of the input parameters for the initial iteration of the model with the degree of confidence in the data quality.

	Biomass		Production / biomass		Consumption / biomass		Ecotrophic efficiency		Unassim./Cons.	
	Initial	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final
Swordfish	0.0036	0.0036	0.4	0.4	5	5			0.2	0.2
Other Billfish	0.0052	0.0052	0.6	0.6	5	5			0.2	0.2
Blue Shark	0.016	0.016	0.3	0.3	5	3			0.2	0.2
Other Sharks	0.0012	0.0012	0.3	0.3	5	3			0.2	0.2
BET	0.00162	0.00162	0.95	0.95	24.728	15			0.2	0.2
YFT	0.00799	0.00799	1.537	1.537	16.14	16.14			0.2	0.2
SKJ	0.0842	0.0842	2.046	2.046	33.475	25			0.2	0.2
Piscivorous fish	0.05	0.025	1.5	1.5	10	10			0.2	0.2
Small Billfish	0.0106	0.0106	1	1	10	10			0.2	0.2
Small Sharks	0.0118	0.0118	0.5	0.5	10	5			0.2	0.2
Small BET	0.00356	0.00241	0.834	0.834	22.387	26.159			0.2	0.2
Small YFT	0.0157	0.0128	1.983	1.983	18.009	33.964			0.2	0.2
Small SKJ	0.0275	0.0194	2.539	2.539	69.288	50.698			0.2	0.2
Baby SKJ		0.00659		25		191.81				0.2
Epi forage	0.339		3.691		15				0.2	
Epi crust				8		30		0.98		0.2
Epi fish				3		15		0.95		0.2
Epi small fish				10		60		0.98		0.2
Epi mollusc				7		20		0.95		0.2
Epi small mollusc				15		100		0.98		0.2
M Meso forage	0.417		2.132		15				0.2	
M Meso fish				2.2		10		0.95		0.2
M meso mollusc				3		10		0.95		0.2
Meso forage	0.164		2.435		15				0.2	
Meso fish				2.5		10		0.95		0.2
Meso mollusc				3		10		0.95		0.2
HM Bathy forage	0.629		1.189	1.189	15	8		0.95	0.2	0.2
M Bathy forage	0.343		1.338	1.338	15	8		0.95	0.2	0.2
Bathy forage	0.759		0.845	0.845	15	8		0.95	0.2	0.2
Mesozpk	4.358	4.4	38	50	230	230			0.2	0.35
Microzpk	1.461	2	120	120	382	382			0.2	0.4
Large phyto	1.849	1.849	120.3	120.3						
Small phyto	10.477	8	109.44	109.44						
Detritus		100								

Table 3. Initial and final input parameters for the Ecopath model. Biomass in tons/km^2, Production/Biomass and Consumption/Biomass in /year, Unassim./Cons.= Unassimilated/Consumption with no unit. ***White cells: no changes, red cells: modified or added in the final iteration, blue cells: removed in the final iteration.***

Prey \ Predator	Swordfish		Other Billfish		Blue Shark		Other Sharks		BET		YFT		SKJ		Piscivorous fish		Small Billfish		Small Sharks		Small BET		Small YFT		Small SKJ		baby SKJ
	Initial	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final	Final
Swordfish																											
Other Billfish																											
Blue Shark					0.01		0.001	0.001																			
Other Sharks							0.01	0.01																			
BET	0.001	0.001	0.001	0.001	0.001		0.001	0.001									0.003	0.003									
YFT	0.001	0.001	0.001	0.001	0.011		0.001	0.001									0.003	0.003									
SKJ	0.006	0.006	0.55	0.55	0.1		0.2	0.15	0.01	0.01		0.02					0.019	0.019	0.07	0.072							
Piscivorous fish	0.075	0.075	0.05	0.05	0.353		0.272	0.262	0.06	0.061	0.05	0.05			0.008	0.009	0.1	0.082	0.145	0.15	0.06	0.0607					
Small Billfish	0.001	0.001	0.001	0.001	0.001		0.001	0.001	0.001	0.001		0.001					0.007	0.007	0.004	0.004							
Small Sharks					0.02		0.01	0.01									0.002	0.002									
Small BET	0.001	0.001	0.01	0.01	0.01		0.01	0.01	0.02	0.001	0.01	0.001					0.01	0.005	0.01	0.005							
Small YFT	0.01	0.01	0.01	0.01	0.09	0.014	0.104	0.104	0.03	0.031	0.05	0.03	0.03		0.05	0.026	0.05	0.051	0.05	0.052	0.008	0.0081					
Small SKJ	0.055	0.035	0.2	0.1	0.3		0.2	0.1	0.08	0.041	0.23	0.03	0.65		0.34	0.054	0.2	0.051	0.15	0.052	0.017	0.00506	0.14	0.0304			
baby SKJ		0.02		0.1				0.1		0.041		0.101		0.02		0.053		0.154		0.077		0.0101		0.0323		0.02	
Epi forage			0.05		0.054		0.15		0.04		0.35		0.255		0.504		0.306		0.2		0.06		0.59				
Epi crust										0.01		0.101		0.074		0.059		0.006				0.0506		0.0754		0.309	0.2
Epi fish				0.02				0.05		0.01		0.151		0.186		0.173		0.103		0.103		0.0709		0.205		0.155	0.02
Epi small fish																						0.506					0.08
Epi mollusc		0.05		0.03		0.07		0.1		0.02		0.151		0.31		0.163		0.205		0.103		0.0709		0.323		0.155	0.02
Epi small mollusc																						0.00202					0.08
M Meso forage	0.1		0.01						0.08		0.055		0.05		0.02		0.14		0.1		0.07		0.09		0.58		
M Meso fish+other		0.025		0.005		0.07		0.02		0.031		0.02		0.099		0.065		0.041		0.052		0.215		0.0215		0.083	0.075
M meso mollusc		0.075		0.005				0.03		0.051		0.039		0.186		0.108		0.103		0.052		0.00101		0.108		0.103	0.075
Meso forage	0.3		0.02		0.05		0.05		0.6		0.13		0.005		0.02		0.14		0.171		0.5		0.06		0.34		
Meso fish + other		0.05		0.005		0.141		0.02		0.204		0.076		0.037		0.087		0.041		0.073				0.0323		0.021	0.05
Meso mollusc		0.25		0.015		0.282		0.03		0.408		0.101		0.062		0.087		0.103		0.103				0.0538			
HM Bathy forage	0.2	0.15	0.027	0.027		0.141			0.034	0.035	0.01	0.01			0.03	0.033			0.1	0.103	0.07		0.025	0.0269		0.052	
M Bathy forage	0.1	0.1	0.02	0.02		0.282			0.022	0.022	0.005	0.005			0.001	0.001					0.002		0.0004	0.000431	0.005		
Bathy forage	0.15	0.15	0.05	0.05					0.02	0.02	0.04	0.04			0.007	0.062					0.212		0.066	0.0711			
Mesozpk									0.003	0.003	0.07	0.071	0.01	0.025	0.02	0.022	0.02	0.021			0.001		0.029	0.0205	0.075	0.103	0.4
Microzpk																											
Large phyto																											
Small phyto																											
Detritus																											

Prey \ Predator	Epi forage	Epi crust	Epi fish	Epi small fish	Epi mollusc	Epi small mollusc	M Meso forage	M Meso fish+other	M meso mollusc	Meso forage	Meso fish + other	Meso mollusc	HM Bathy forage		M Bathy forage		Bathy forage		Mesozpk		Microzpk	
	Initial	Final	Final	Final	Final	Final	Initial	Final	Final	Initial	Final	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final	Initial	Final
Swordfish																						
Other Billfish																						
Blue Shark																						
Other Sharks																						
BET																						
YFT																						
SKJ																						
Piscivorous fish																						
Small Billfish																						
Small Sharks																						
Small BET																						
Small YFT																						
Small SKJ																						
baby SKJ																						
Epi forage	0.05						0.2						0.1									
Epi crust			0.097	0.1	0.176	0.1		0.211	0.2					0.4								
Epi fish								0.113	0.1													
Epi small fish			0.101		0.176				0.2													
Epi mollusc									0.1													
Epi small mollusc			0.193					0.141	0.2													
M Meso forage	0.05						0.1			0.2			0.1		0.05							
M Meso fish+other					0.235				0.15		0.3	0.2				0.15						
M meso mollusc					0.118						0.3	0.2				0.15						
Meso forage							0.1			0.1			0.1		0.2							
Meso fish + other												0.3				0.3						
Meso mollusc																0.15						
HM Bathy forage	0.05				0.235								0.05		0.2		0.3	0.25				
M Bathy forage												0.1	0.1		0.1		0.3	0.25				
Bathy forage													0.05		0.2		0.1					
Mesozpk	0.7	0.45	0.609	0.9	0.059	0.7	0.5	0.465	0.05	0.6	0.3	0.2	0.5	0.6	0.25	0.25	0.1	0.1	0.1			
Microzpk	0.1	0.1				0.2	0.1	0.07		0.1	0.1								0.5	0.2	0.05	
Large phyto	0.05	0.05																	0.1	0.1	0.05	0.1
Small phyto																			0.05	0.05	0.8	0.8
Detritus		0.4															0.2	0.4	0.25	0.65	0.1	0.1

Table 4. Initial and final diet matrices for the Ecopath model. Preys in rows, predators in column. Diet is expressed in fraction and total of each column is 1. ***White cells: no changes, red cells: modified or added in the final iteration, purple cells: slightly modified in the final iteration, blue cells: removed in the final iteration.***

	Longline	PS Unass	PS FAD	Domestic ID PHL	Total
Swordfish	0.0000714				0
Other Billfish	0.000219		0.0000141		0
Blue Shark	0.000144				0
Other Sharks	0.0000479		0.0000444		0
BET	0.00041	0.0000012	0.0000218	0.000386	0.001
YFT	0.000803	0.00136	0.000197	0.00414	0.007
SKJ	0.00184	0.00995	0.0126	0.0113	0.036
Piscivorous fish	0.000157		0.000223		0
Small Billfish					0
Small Sharks					0
Small BET	0.000504	0.0000525	0.000555	0.000286	0.001
Small YFT	0.000763	0.00174	0.00217	0.0023	0.007
Small SKJ	0.000011	0.000072	0.000197	0.00144	0.002
Epi forage					0
M Meso forage					0
Meso forage					0
HM Bathy forage					0
M Bathy forage					0
Bathy forage					0
Mesozpk					0
Microzpk					0
Large phyto					0
Small phyto					0
Detritus					0
Sum	0.005	0.013	0.016	0.02	0.054

Table 5. Fisheries landings in tons/km^2/year for the Ecopath model.

3. Results

3.1. First run and balancing strategy

The first run, which was based on literature estimates, stock assessment estimates for tuna biomass, Seapodym model estimates of forage biomass and empirical data from stomach analysis for the diet matrix indicated that the model was not balanced. Ecotrophic efficiency was higher than 1[7] for most of the lower trophic level components: microzooplankton; forage groups; small tuna groups and the aggregated group of piscivorous fish. The most unbalanced groups were skipjack tuna (SKJ).

The strategy chosen to improve the model was to adjust first the most unbalanced components (highest EE), one after the other, by changing the input data. Diet composition modifications were preferred to other parameter changes such as biomass or production rate, particularly for the species for which stock assessment existed. We

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[7] EE>1 indicates that consumption of this group is higher than the quantity available in the system, the group is unbalanced.

considered that confidence was higher in stock assessments[8] than in diet composition which is known to be highly uncertain. However, disequilibrium in some groups was so high that only drastic changes of biomass, consumption or production could balance them. During the balancing process we realised that it was necessary to disaggregate some components in the model and to take into account the linkages between the different age groups of the same species by implementing the "multi-stanza' routine in Ecopath. The changes made are reported below.

3.2. Multi-stanza and new groups

With the objective of using the Ecopath model to conduct Ecosim simulations, it was necessary to link together the different stages of yellowfin (YFT), bigeye (BET) and skipjack (SKJ) using the multi-stanza tool. Starting age of each group was specified as well as their total mortality (Z), B, Q/B for the adult group, and the curvature parameter K of the Von Bertalanffy growth curve (VBGF) (respectively 0.3, 0.32 and 0.8 for BET, YFT and SKJ). For the other parameters the default values were used (recruitment power=1, BA/B=0, Wmaturity/Winf=0, no fixed fecundity). This option allows Ecosim to link different stages of the same species with recruitment factor.

SKJ was the most unbalanced species, largely due to predation by other tuna and cannibalism. Because much of the predation on SKJ was exerted on the very small individuals (less than 10cm), a third group of SKJ, "baby SKJ", which described individuals from 0 to 3 months, was added to the model.

Balancing problems were encountered in some of the aggregated forage groups, despite many changes in the diet composition. This was due to over-aggregation of different species within the same group creating overly simplified trophic connections (*i.e.* equilibrium could not be achieved because of cannibalism - a high proportion of the group's diet was itself - and small trophic loops - one order cycle: when group 1 feeds on group 2 that in return feeds on group 1). To solve this problem the forage groups were

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[8] It is important to notice that SKJ stock assessment is probably the less reliable of the 3 tuna species assessments (Simon Hoyle, SPC, *pers. comm.*).

disaggregated into: crustaceans, fish and molluscs for the epipelagic component; and into fish + others and molluscs for migrant mesopelagic and for mesopelagic (Table 1). Bathypelagic components were not disaggregated. Furthermore for the epipelagic component small molluscs and small fish groups were created to avoid cannibalism.

3.3. Parameter changes (Table 3)

Piscivorous fish biomass was decreased by half to reduce the predation pressure on its preys. Small tuna group biomasses were recalculated using the muti-stanza tools. These estimates were lower in comparison to initial parameters. Meso and micro-zooplankton biomasses were slightly increased to sustain the forage feeding on them. Small zooplankton biomass was decreased, to increase the EE. In this oligotrophic area it was assumed that most of the phytoplankton is used in the system. Detritus biomass was added (see Appendix 1).

The baby SKJ group was assumed to be productive with a high mortality rate, an initial value of P/B ratio value of 5 was chosen, slightly higher than that estimated for forage species. Under this construct the SKJ group did not balance (EE>400). The group could not be balanced through modifications of the diet compositions as baby SKJ were prey for many different predators and small changes in the diet composition resulted in these groups and lower trophic groups no longer balancing. A change in P/B ratio from 5 to 25 reduced the EE from 400 to 10. New forage groups P/B values were estimated following the principles that crustaceans are more productive than molluscs which, in turn, are more productive than fish; that small components are more productive than large components and that productivity is higher in shallow waters than in deep waters. Mesozooplankton P/B was also increased to sustain predation on this group.

Q/B was decreased for most of the top predator groups to reduce the predation pressure on their preys. Adult SKJ consumption (Q/B=33) was initially estimated to represent a daily ration of *ca.* 9% (Q/B / 3.65 = % bodyW/day=daily ration); a ration of 5-6% was considered more realistic and Q/B was revised to 25. After multi-stanza calculations Q/B values for young groups of SKJ were adjusted. Similarly, other small tuna Q/B's were recalculated using the multi-stanza tool.

Biomasses of the initial forage groups were re-distributed among the disaggregated new forage groups based upon available information. The predation impacts from upper trophic levels, however was too high to allow balancing of these forage groups. The possibility of an advection of forage at the edge of the warm pool close to the cold tongue was explored; however calculations indicated that plausible quantities that could be advected would be insufficient to balance the model. This crude estimate was based on advection (flow) rate, biologically plausible forage concentration, the size of the ecosystem boundary and the total area of the ecosystem modelled here. It was found that advection could only account for a trivial fraction (ca. 10^{-4}) of the production needed to balance the model. This process of balancing the model through Q/B and the diet matrix indicated that existing information on biomass estimates for the forage components were highly uncertain. To obtain an estimate of the required biomass of forage to sustain the system, EE values for the forage groups were fixed and biomass estimated. It was assumed that nearly all the forage was used in the system so an EE of 0.95 was used for all forage components and 0.98 was used for the epipelagic small fish and small molluscs.

Unassimilated to consumption ratio or assimilation efficiency of meso- and micro-zooplankton were increased from 0.2 initially to respectively 0.35 and 0.4 in agreement with literature information.

3.4. Diet composition changes

Ecopath-calculated predation mortalities allowed the identification of groups that induced a high predation pressure on "unbalanced groups", and consequently modification of their diet composition to decrease predation resolved many of the balancing issues. Changes made are detailed in Table 4.

Disaggregating groups induced major modifications in the diet matrix. Introducing new forage species required changes in the diet of all the components of the ecosystem. For top predators in general the proportions of a particular forage category was transferred and split in the different sub-groups of this category; *e.g.* swordfish foraging on 0.3 of mesopelagic in the initial model was changed into 0.05 of mesopelagic fish and 0.25 of mesopelagic mollusc in the final iteration. However this rule could not always be followed and extensive modifications were required:

- the proportions of epipelagic and mesopelagic forage were increased for YFT, SKJ and Small YFT;
- the epipelagic proportion was reduced but mesopelagics were increased for piscivorous fish;
- the epipelagic and migrant mesopelagic groups were increased and mesopelagic group reduced for small BET;
- epipelagics were increased but mesopelagics reduced for small SKJ;
- the initial predation on Small SKJ was reassigned to baby SKJ;
- the dietary proportion of baby SKJ for YFT, SKJ, piscivorous fish and small YFT was decreased;
- the diet of baby SKJ was assumed to be dominated by mesozooplankton and epipelagic preys;
- predation on small YFT and small BET was also reduced in the diet of blue shark and YFT;
- small BET proportions were decreased in the diet of BET, small billfish and small sharks; and
- small YFT was also reduced in the diets of SKJ and piscivorous fish.

The consequence of the high biomass and high consumption rate for SKJ in the model was a very high predation pressure on SKJ prey. Cannibalism had been observed in the diet studies (initial diet proportion of 0.65 of Small SKJ), however this value had to be reduced drastically to achieve balance. All the SKJ predation on small SKJ was transferred to baby SKJ (0.65 to 0.02). Similarly because of the high biomass and consumption of the SKJ, small YFT in their diet was removed. The diet was reassigned to epipelagic and migrant mesopelagic forage. Small SKJ diet was reviewed to include some predation on baby SKJ, but with epipelagic forage dominating their diet.

Blue shark diet was entirely revised: predation on top predators was removed and consumption of mesopelagic and bathypelagic forage increased. Cannibalism was removed from mesozooplankton and microzooplankton. Trophic loops were identified as a major problem for balancing the model, so for example all the loops were removed in the diet composition of the different forage components. Mesozooplankton predation on microzooplankton was decreased, as it was hypothesised that mesozooplankton feeds predominantly on the microbial loop that in this model was captured in the detritus group.

3.5. Basic estimates of the balanced model

The parameter values for the balanced model are presented in Table 6.

Group name	Trophic level	Biomass (t/km^2)	Prod./ biom. (/year)	Cons./ biom. (/year)	Ecotrophic efficiency	Production / consumption
Swordfish	5.24	0.0036	0.4	5	0.05	0.08
Other Billfish	5.58	0.0052	0.6	5	0.075	0.12
Blue Shark	5.35	0.016	0.3	3	0.031	0.1
Other Sharks	5.57	0.0012	0.3	3	0.356	0.1
BET	5.41	0.00162	0.95	15	0.777	0.063
YFT	4.88	0.00799	1.537	16.14	0.56	0.095
SKJ	4.92	0.0842	2.046	25	0.347	0.082
Piscivorous fish	4.93	0.025	1.5	10	0.946	0.15
Small Billfish	5.22	0.0106	1	10	0.114	0.1
Small Sharks	5.27	0.0118	0.5	5	0.043	0.1
Small BET	4.51	0.00241	0.834	26.159	0.644	0.032
Small YFT	4.89	0.0128	1.983	33.964	0.849	0.058
Small SKJ	4.33	0.0194	2.539	50.698	0.927	0.05
baby SKJ	3.88	0.00659	25	191.81	0.776	0.13
Epi crust	2.64	4.515	8	30	0.98	0.267
Epi fish	3.54	2.127	3	15	0.95	0.2
Epi small fish	3.24	0.785	10	60	0.98	0.167
Epi mollusc	4.3	0.384	7	20	0.95	0.35
Epi small mollusc	3.2	0.955	15	100	0.98	0.15
M Meso fish+other	3.57	3.404	2.2	10	0.95	0.22
M meso mollusc	4.25	1.484	3	10	0.95	0.3
Meso fish + other	4.21	0.634	2.5	10	0.95	0.25
Meso mollusc	4.74	0.201	3	10	0.95	0.3
HM Bathy forage	3.38	1.803	1.189	8	0.95	0.149
M Bathy forage	4.7	0.282	1.338	8	0.95	0.167
Bathy forage	3.64	0.0698	0.845	8	0.95	0.106
Mesozpk	2.2	4.4	50	230	0.995	0.217
Microzpk	2	2	120	382	0.992	0.314
Large phyto	1	1.849	120.3	-	0.829	-
Small phyto	1	8	109.44	-	0.756	-
Detritus	1	100	-	-	0.791	-

Table 6. Basic estimates of the balanced model. ***Blue cells represent the parameters calculated by the model.***

3.6. Model Structure and Sensitivity

The balanced model presented is one of the many possibilities that could fit the defined constraints of the warm pool ecosystem. Alternative structures are yet to be explored. The mixed-trophic impact routine in Ecopath provides a summary of the diet structure of all groups on each other group; the impact can be positive (a prey will have a positive impact on its predator) or negative (a predator will have a negative impact on its prey). The mixed-trophic impact matrix for the balanced model (Figure 2) indicates that higher order predators in the balanced model exert negative effects upon each other. The lower-order groups typically exert negative effects upon each other and positive effects on higher order predators.

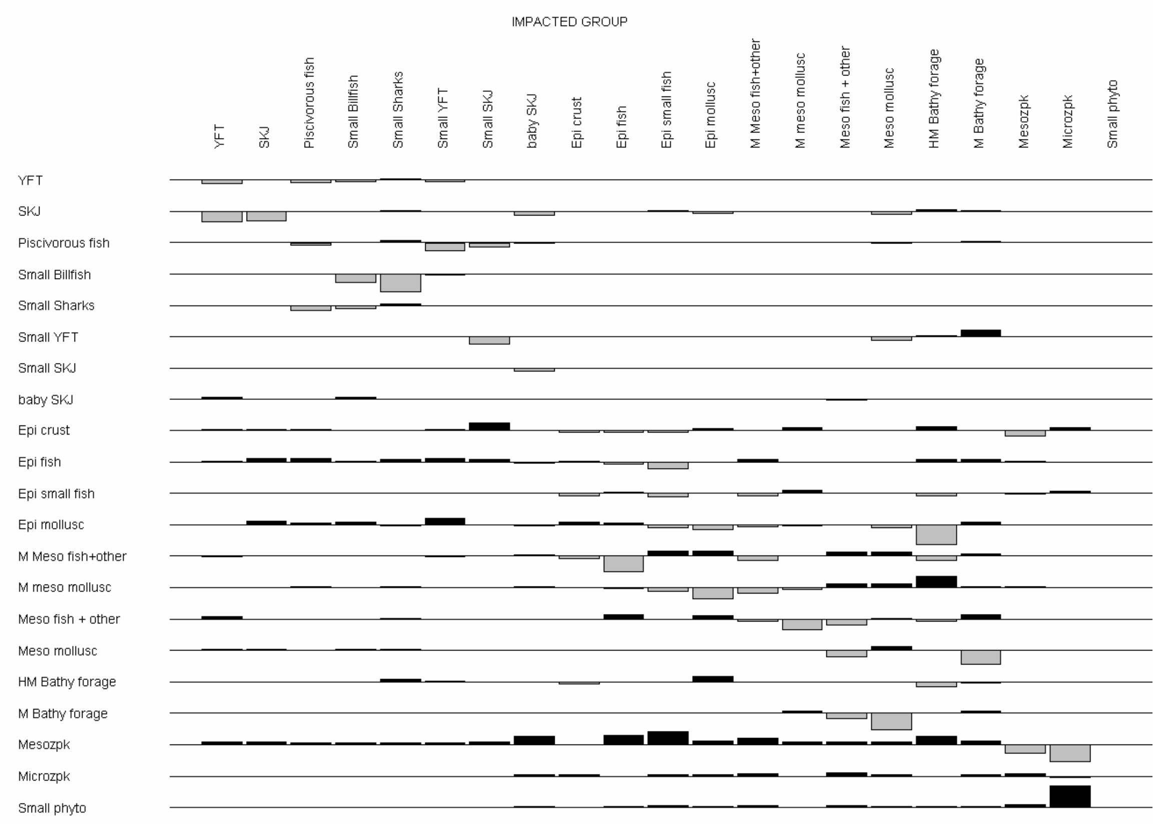

Figure 2. Mixed trophic impact matrix of selected components of the ecosystem. ***Impacting groups on the left, impacted groups on top; grey box below the line represents a negative impact, black box above the line represents a positive impact.***

The sensitivity routine included in Ecopath modified each of the 3 input parameters per species group from -50% to +50% in 10% steps and calculated the fourth parameter to maintain mass-balance. A table of the magnitude of changes of the fourth parameters for each species according to the % of variation of the input parameters can be extracted from Ecopath. This large table can be summarised by calculating a simple index of sensitivity per component following the methodology outlined in Olson & Watters (2003) (see caption Figure 3). Components where changes will induce large variations in the overall system can then be identified. In the balanced model migrant bathypelagic forage and molluscs (mesopelagic, migrant mesopelagic and epipelagic) were the components inducing large changes (Figure 3). In general, the model was more sensitive to changes in the lower trophic levels rather than variations in the top predators.

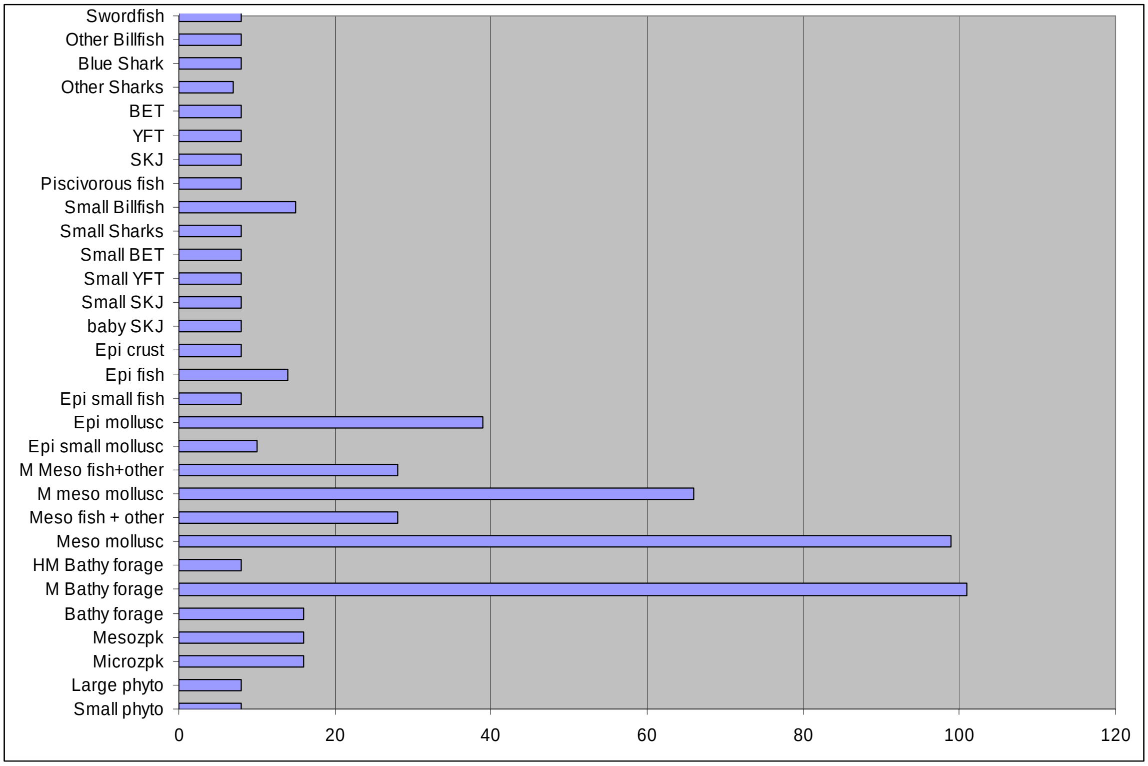

Figure 3. Sensitivity analysis of the Ecopath model. ***Results are presented with an index of sensitivity which is the count of estimated parameters of the model that are affected by at least 30% given +-10-50% changes in the input parameters of the y-axis components following the method presented in (Olson & Watters, 2003).***

3.7. ECOSIM simulation

The Ecosim application was briefly explored to check the stability of the model and further potential sensitivities. Three simple top-down scenarios were tested: (1) complete removal of all the fisheries after 5 years; (2) removal of FAD purse seine fisheries after 5 years, other fisheries maintained at current level; and (3) all fisheries doubled after 5 years and maintained at that level. These scenarios provided trajectories that allowed identifying the most reactive species, the species with very stable behaviour whatever the conditions, and the groups of species evolving in conjunction or in opposition. The default value of 2 was used for the Vulnerability coefficients[9]; this value represents a mix between bottom-up and top-down controls.

The trajectories from the 3 scenarios identify that BET and YFT (juveniles and adults), other sharks, other billfish, piscivorous fish (Figure 4) were the more reactive species to top-down forcing (fishing harvest changes). The tunas mentioned above, sharks and billfish increased when the fishing pressure was removed. BET was the species that showed the highest increase particularly when the FAD fisheries are removed. YFT was the species increasing the most when the Domestic Indonesian and Phillipino fisheries were removed. YFT decreased dramatically when fishing pressure increased and BET became extinct 15 years after the fishing harvest rate was doubled (Figure 4C). Sharks and other billfish biomass also decreased with a doubling of fishing harvest rate. Piscivorous fish behaviour differed, responding positively to the decrease in predation pressure caused by the major decline in biomasses of BET and YFT to a doubling of fishing harvest rate. SKJ did not show much variation when fishing harvest was changed. No cascading effect to the forage level was observed for the scenarios explored; the forage component is probably more sensitive to bottom-up control that needs to be tested.

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[9] Vulnerability coefficients are based on the foraging arena theory developed by Walters and Juanes (1993). The theory assumes that prey exchange between vulnerable and safe habitats, and that only when in vulnerable habitats are they susceptible to predation. When exchange rates are slow, the model acts like a “donor controlled” predator prey system. When exchange rates are rapid, the model acts like a joint “donor-recipient” control, analogous to the basic predator prey models (e.g. Lotka Volterra).

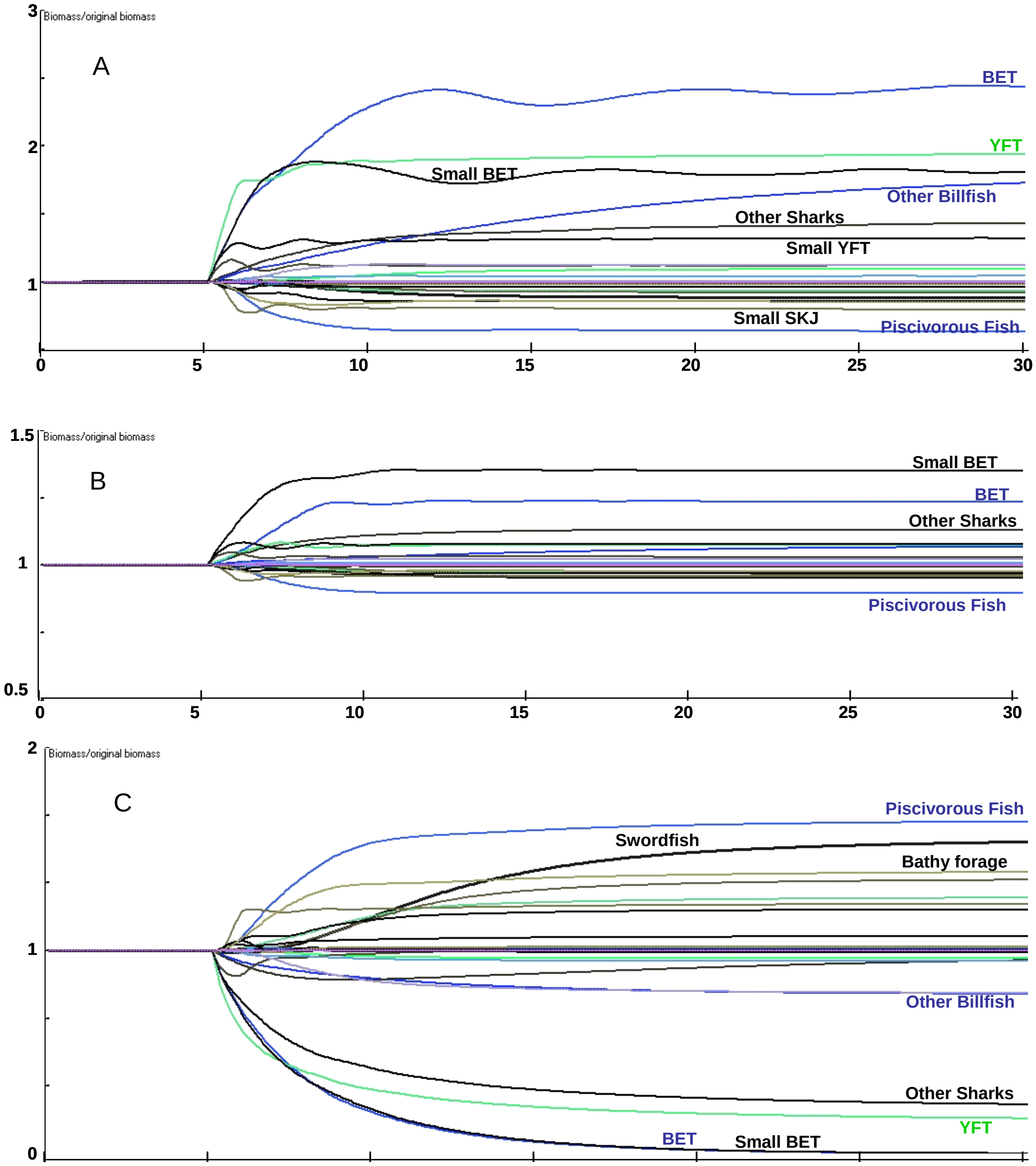

Figure 4. Biomass/Original Biomass ratio trajectories of the ecosystem components over 30 years with 3 different Ecosim scenarios: A) complete removal of all the fisheries after 5 years, B) removal of FAD purse seine fisheries after 5 years, other fisheries maintained at current level, C) all fisheries doubled after 5 years and maintained at that level.

4. Discussion

The balanced model represents an alternative to Godinot & Allain (2003) model which was constructed without much of the dietary information currently available. Both constructs demonstrate sensitivity to groups in the lower trophic groups. The Ecosim simulations identified that the higher order trophic levels are sensitive to changes in fishing harvest rate, except for skipjack which remained stable to the perturbations of fishing harvest rate.

The balancing process revealed a disagreement in the input data: the forage biomass estimates extracted from the Seapodym model and the field measurements of zooplankton biomass could not sustain the biomass of tuna estimated from the stock assessment model MULTIFAN-CL. Initial biomass values for forage groups summed to 2.6 tons/km^2, however that needed to be increased to 16.7 tons/km^2 (x6.4) to balance the model. Four hypotheses could be considered to explain this discrepancy:

-the system is not well captured because of too much overaggregation;

-there is an underestimation of forage, particularly epipelagic and mesopelagic component and possibly a bad repartition of the diet proportions among the different forage components;

-there is an overestimation of tuna biomass;

-a potential importation of forage/zooplankton from the East that would interact with the West is not captured in the model.

Because little information was available on forage we chose to consider tuna biomass estimates as more reliable than forage estimates when balancing the model. This assumption identified, along with the sensitivity analysis, the high dependence of the model to forage changes. Testing hypotheses about the reliability of forage component information and the validity of the tuna biomasses estimates within the Ecopath with Ecosim framework would provide a better understanding of where the important uncertainty occurs.

The construction of the Ecopath model provided important lessons on the technical aspect and limits of mass-balance modelling, but also on the functioning of the pelagic warm pool ecosystem itself. We encountered two major problems that created balancing difficulties: cannibalism and diet loops. We managed to overcome these problems by disaggregating some groups (*i.e.* SKJ or forage) and by modifying the diet matrix. Overaggregation of groups and species allowed a simple model with few components, however as observed in this example it induces structural problems in the model that can prove difficult to overcome. Obtaining a balanced model required a compromise between simplification and complexity.

The balancing process also identified potential consequences of data uncertainty and knowledge gaps about the functioning of the pelagic ecosystem of the western and central Pacific Ocean. SKJ appear to have a key role in the system because of its high biomass, high production, high consumption and important cannibalism. This species was the most difficult to balance and the changes carried out on this group had important impacts on the other components of the system. It was necessary to divide this species into 3 age classes to balance the model. The SKJ consumption rate was high in order to maintain their high productivity and because cannibalism is high, the species exerts important pressure on its juveniles. Juvenile SKJ was also a major source of food for all the top predators. Consequently, in the balanced model SKJ occupied a central position in the system that might be comparable in a way to the position of *Auxis sp.* in the Eastern Pacific (Olson & Watters, 2003). Given this construct, SKJ was driving our Ecopath model and draft Ecosim simulations showed a very high resilience of this species to perturbations, it was nearly impossible to eliminate this species from the system with a top-down control. SKJ resiliency is probably related to the high production rate and the internal density-dependence induced by cannibalism.

5. Future developments

The Ecopath model developed here has proven to be a very useful learning tool. The ultimate goal of this exercise is to provide ecosystem models with the capacity of testing different fishing policies and environmental change scenarios to assist managers with identifying the most robust and reliable management options that will achieve their objectives. Before reaching this end point, model development will require:

- model parameter and structural uncertainty analysis;
- model validation through the fitting of historical fishing data; and
- the testing of management options and environmental impact.

Model parameter and structural uncertainty analysis will provide a better understanding of the model's behaviour and dependencies. A synthesis of data from other ecosystems (*i.e.* establishing a list of input values with all the context information for reference) would help with bounding parameter inputs where specific knowledge uncertainty is high. Consultation with experts is the best way to insure that the values extracted from the literature are well adapted to the study case (Okey & Pauly, 1999). An important step will be the construction of alternate Ecopath models of the warm pool with different structures particularly in the components (more or less size-classes for the species of interest, aggregation or disaggregation of the forage groups, different organisation of the forage groups, etc). The results from such structural analysis will provide important insights into the reliability of stock assessment, the Seapodym model, dietary and literature information. A further level of exploration that will help with understanding the functioning of the model will be the testing of simulation scenarios. As applied by Olson & Watters (2003), fitting fishing effort time-series was a good method for validating and exploring the properties of the model associated with top-down processes. The fitting of an index of environmental variability in primary production (to mimic the SOI index variation for example) would provide an alternate bottom-up exploration of model properties.

Potential outcomes of a realistic and validated Ecopath model and Ecosim simulations are multiple and are of particular interest for managers. Ecosim allows testing of scenarios that will provide information on the impact on non-target species and on the overall ecosystem that can be evaluated in conjunction with stock assessment models. The impact of changes in environmental parameters such as global warming, increase of the frequency and/or strength of El Niño events could be assessed as well as the consequence of the implementation of fishing policies such as regulation of the FAD fisheries.

Another potential of the model that has not been explored is the Ecospace module. Specifying habitats in the modelled area and allowing spatially-explicit expression of the functional groups and fisheries in the model area will allow exploration of the potential effects of marine protected areas on the high seas, as well as evaluations of the robustness of temporal simulations in a spatially-explicit context. This would also provide further opportunity for comparison and cross-validation with stock assessment models and Seapodym models.

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Appendix 1. Data sources and description for the functional groups

Detritus

Detritus biomass was estimated in a previous study (Godinot, 2002) to be approximately 130gWM/m^2 after the empirical method given by Pauly *et al.* (1993).

Phytoplankton groups

Data on primary producers came from an intensive bibliographic search that gathered a large amount of information from the western oligotrophic Pacific area and the oligotrophic parts of the central Pacific that are north and south of the equatorial mesotrophic region. The most reliable information was selected as input parameters in consultation with Robert Le Borgne[10].

COMPOSITION: Two groups of primary producers are considered: small and large phytoplankton with a theoretical size limit of approximately 2 to 8µm. In general biomass and production estimates of primary producers were estimated by size-class rather than by taxons. Unfortunately, there has been no consistent size limit differentiation used in the literature (*e.g.* 8µm (Brown *et al.*, 2003; Le Borgne & Landry, 2003), 1 and 3 µm (Rodier & Le Borgne, 1997), 3 and 10µm (Ishizaka *et al.*, 1997), 3µm (Le Bouteiller *et al.*, 2003; Champalbert *et al.*, 2003), 5µm (Chai *et al.*, 2002), 2µm (Dam *et al.*, 1995)) which added uncertainty to the parameterisation. In the oligotrophic waters of the western Pacific the small producers are considered dominant (Chai *et al.*, 2002; Champalbert *et al.*, 2003; Dam *et al.*, 1995; Ishizaka *et al.*, 1997; Le Borgne *et al.*, 2002b; Le Bouteiller *et al.*, 2003; Rodier & Le Borgne, 1997; Verity *et al.*, 1996) and we assumed that large phytoplankton is about 15% of the primary producers biomass as stated by Le Borgne *et al.* (2002b). Information on the taxonomic composition for each group is provided in Table 1.

BIOMASS: Phytoplankton biomass is mainly estimated by 2 techniques: measurements of *Chlorophyll a* concentration or counting of phytoplankton cells. Both techniques imply the use of conversion factors (C/Chla and C/cell) to obtain values in grams of C. C/Chla

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ratio varies with light, nutrient and temperature (Wang *et al.*, 2007): due to photoacclimation the ratio decreases from high to low light; there is then a decrease of the ratio with depth (Chavez *et al.*, 1996; Le Borgne *et al.*, 2002b; Le Bouteiller *et al.*, 2003). C/Chla ratio can vary from 200 at the surface to 40 in deeper waters; in the warm pool maximum of chlorophyll is at *ca.* 90m depth, a C/Chla ratio of 40 was considered in this study (Brown *et al.*, 2003). C/cell ratio depends on the taxons considered (Brown *et al.*, 2003; Le Bouteiller *et al.*, 2003). Carbon biomass is converted into wet mass (WM) with the conversion factor: 11.539gWM/gC (ICES, 1989 and Jones, 1984 in Christensen, 1995).

Counting is considered the most reliable technique (Le Borgne, *pers.comm.*) and the minimum and maximum values provided by Brown *et al.* (2003) and Ishizaka *et al.* (1997) were averaged to obtain a total depth-integrated phytoplankton biomass of 1068mgC/m^2 or 12.3265gWM/m^2. This value is divided into 1.84898gWM/m^2 for large phytoplankton (15%) and 10.4775 gWM/m^2 for small phytoplankton.

PRODUCTION: Total primary production between 96.4 and 624mgC/m^2/day have been determined by several studies providing a rough average of 325mgC/m^2/day (Barber *et al.*, 1996; Ishizaka *et al.*, 1997; Le Borgne *et al.*, 2002a; Le Bouteiller *et al.*, 2003; Mackey *et al.*, 1995; McClain *et al.*, 2002; Rodier & Le Borgne, 1997; Vinogradov *et al.*, 1997). Production can be considered roughly constant in the 0-100m depth layer in the warm pool (Le Borgne, *pers.comm.*) allowing to calculate conversion factors: $P_{\text{large ppk}} = P_{\text{tot ppk}}/6.1558$ and $P_{\text{small ppk}} = P_{\text{tot ppk}}/1.193956$ (Le Borgne & Landry, 2003). Hence production of large phytoplankton is 52.8mgC/m^2/day and production of small phytoplankton is estimated at 272.2mgC/m^2/day. According to the biomass estimations, productions to biomass ratios are: $P/B_{\text{small ppk}}$=109.44/y and $P/B_{\text{large ppk}}$=120.3/y.

Zooplankton groups

Numerous references were reviewed to gather information on zooplankton in the Pacific. Similarly to phytoplankton the more relevant and accurate information has been selected in collaboration with Robert Le Borgne to parameterise the model.

COMPOSITION: In our model we defined 2 zooplankton functional groups: microzooplankton (20-200µm) and mesozooplankton (200-2000µm). Smaller zooplankton: nano- and picozooplankton (<20µm) are assumed to be involved only in the microbial loop along with the heterotrophic bacteria and are considered in the model in the detritus group, they are thought to have a minor role in the classical food chain. Larger zooplankton: macrozooplankton (>2000µm) is assimilated to micronekton/forage in our model.

Microzooplankton is comprised primarily of copepod nauplii but also ciliates, foraminiferans, acantharians, and heterotrophic dinoflagellates (Roman *et al.*, 2002; Ishizaka *et al.*, 1997; Verity *et al.*, 1996; Calbet & Landry, 1999). Mesozooplankon group is dominated by copepods but also contains ostracods, larval euphausiids, chaetognaths, amphipods, pteropods, siphonophores, foraminiferans and radiolarians among others (Le Borgne & Rodier, 1997; Ishizaka *et al.*, 1997; Le Borgne *et al.*, 2003). The proportions between the different groups can be considered *ca.* 20% microzooplankton and 80% mesozooplankton of the cumulated micro- and mesozooplankton; if nanoplankton is also considered then nano- and microzooplankton represent 40% and mesozooplankton 60% (Ishizaka *et al.*, 1997; Rodier & Le Borgne, 1997; Roman *et al.*, 2002).

BIOMASS: Biomass estimates of zooplankton in oligotrophic conditions are provided by numerous authors and range between 439 and 2111mgWetWeight/m^2 for microzooplankton and between 1216 and 8158mgWW/m^2 for macrozooplankton (Calbet & Landry, 1999; Ishizaka *et al.*, 1997; Le Borgne & Rodier, 1997; Le Borgne *et al.*, 2003; Rodier & Le Borgne, 1997; Roman *et al.*, 2002; Vinogradov *et al.*, 1997; White *et al.*, 1995). In our model we considered depth-integrated average values of 1461mgWW/m^2 for microzooplankton and 4358mgWW/m^2 for mesozooplankton.

Biomasses are provided with different units and conversion factors were used to transform them in wet weight (WW). The following conversion factors are valid for zooplankton: C/N=5.9 and N/P=20 (atomic in mol.), gC/gDW=0.36, gAFDW/gDW=0.74 (Le Borgne *et al.*, 2003), gN/gDW=0.038, gP/gDW=0.0075, gDW/gWW=0.16 (Champalbert *et al.*, 2003).

PRODUCTION: There is little information available on production. P/B ratio is equivalent to growth rate in a steady state situation and estimates using this hypothesis (P/B = 38-150/y (Roman *et al.*, 2002)) are much lower than the estimates calculated from ingestion rates (P/B=153-1164/y (Ishizaka *et al.*, 1997)). Growth rates and then P/B ratios for the microzooplankton community are roughly comparable to those of their phytoplankton preys (Landry & Calbet, 2004) for which the production estimations are more reliable; moreover mesozooplankton should have a lower P/B. We assumed the values estimated from growth rates: $P/B_{microzooplankton}$=120/y and $P/B_{mesozooplankton}$=38/y.

CONSUMPTION: Consumption, grazing and predation studies have been conducted by several authors and indicate Q/B values ranging from 77 to 1204/y for microzooplankton and from 80 to 985/y for mesozooplankton (Chai *et al.*, 2002; Landry *et al.*, 1995; Le Borgne & Landry, 2003; Verity *et al.*, 1996; Wang *et al.*, 2007; Gaudy *et al.*, 2003). Average values of $Q/B_{mesozooplankton}$=230/y and $Q/B_{microzooplankton}$=382/y were included into the model.

DIET COMPOSITION: The compilation of the information found in different publications allowed establishing the following approximate diet composition (Calbet & Landry, 1999; Chai *et al.*, 2002; Dam *et al.*, 1995; Gaudy *et al.*, 2003; Landry & Calbet, 2004; Le Borgne & Landry, 2003; Zhang *et al.*, 1995). Microzooplankton would eat 80% of small phytoplankton, 5% of large phytoplankton, 10% of heterotrophic bacteria associated to detritus and 5% of cannibalism while mesozooplankton would consume 5% of small phytoplankton, 10% of large phytoplankton, 40% of microzooplankton, 10% of cannibalism and 35% of detritus.

Micronekton/forage groups

Micronekton or forage describes the organisms in the 2-20cm size class. Under this denomination are included numerous species of crustaceans, fish, cephalopods and other invertebrates for which information is very scarce. The availability of information on ecological groups of forage rather than on taxonomic groups leaded us to consider these ecological groups (Lehodey, 2004).

COMPOSITION: Based on the work of Blackburn (1968), Grandperrin (1975), Legand *et al.* (1972) and Roger (1974)) among others, Lehodey (2004; 2005) defined 6 classes of pelagic micronekton according to their vertical distribution and vertical migratory behaviour: epipelagic (0- ~200m), mesopelagic (~200- ~400m) and bathypelagic

(>~400m) components including migrant and non-migrant groups (Figure 5). These classes were used in our model.

To identify the species included in the different forage classes, information has been compiled from literature, the main references being Fishbase[11], Carpenter & Niem (1999), Grandperrin (1975), Smith & Heemstra (1986) for fish, Roper & Young (1975), The Cephalopod page[12], and Tree of life/Cephalopods[13] for cephalopods, Poore (2004) for crustacean, and Wrobel & Mills (1998) for invertebrates. Taxonomic composition of these groups is detailed in Table 1.

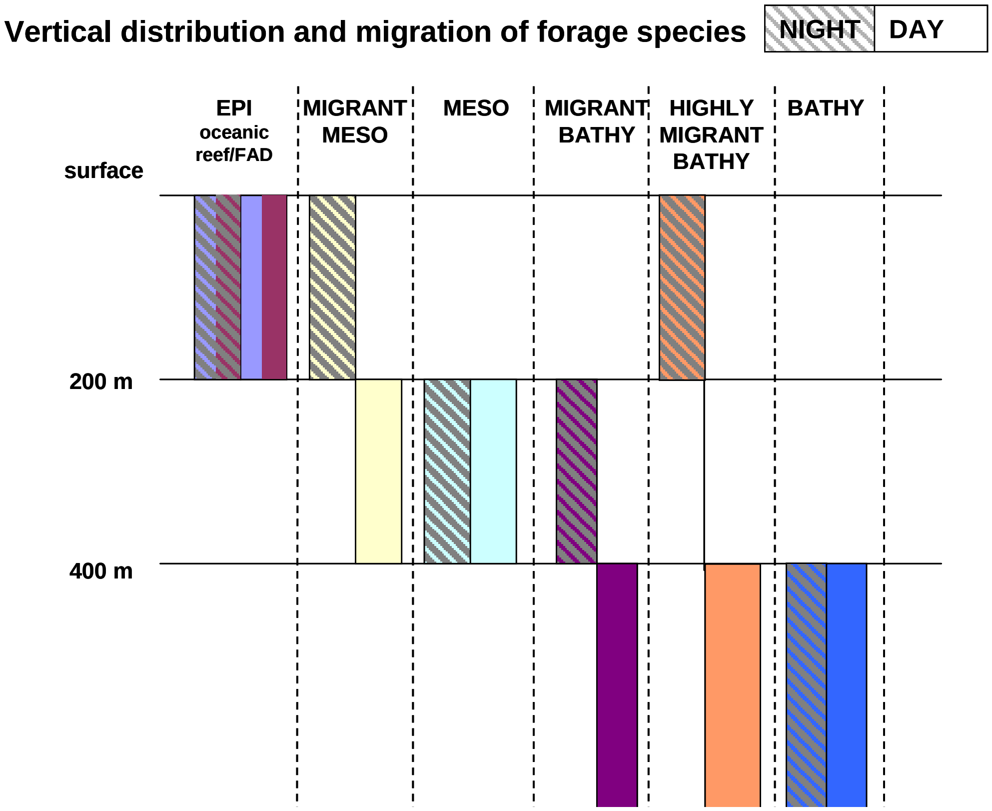

Figure 5. Schematic view of the different forage components according to their vertical distribution and their vertical day/night migratory behaviour.

BIOMASS: In the SEAPODYM[14] model developed by Lehodey the forage components are modelled as single populations composed of different species (Lehodey *et al.*, 1998;

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[11] http://www.fishbase.org/home.htm

[12] http://www.thecephalopodpage.org/

[13] http://www.tolweb.org/Cephalopoda/19386

[14] SEAPODYM model and associated programs and documentation are made available to the scientific community free of charge. For more information consult http://www.seapodym.org/.

Lehodey, 2001; Lehodey *et al.*, 2003; Lehodey, 2004; Lehodey, 2005). Forage biomass originates from the trophic conversion of primary production to secondary production applying energy transfer coefficients variable according to the forage classes. A growth model is not used to estimate forage biomass, it is a simple conversion (Lehodey, 2004). In the SEAPODYM model primary production is predicted from a coupled general circulation model and bio-geochemical model. Average forage biomasses for the 6 components were extracted from the model for the warm pool region for the period January 1993 to December 2002. Values vary between 0.759 and 0.164 g/m^2 (or tons/km^2) according to the component considered (Table 3). Cumulated mesopelagic and bathypelagic biomass indicates a depth integrated biomass of 2.31 tons/km^2 very similar to 2 tons/km^2, the value provided by Gjøsaeter & Kawaguchi (1980) in the western Pacific for the 200-1000m depth mesopelagic biomass and of the same order to the values calculated by Lam & Pauly (2005).

PRODUCTION: Production values were also extracted from SEAPODYM model for the same area and time period and allowed to calculate a P/B between 3.69 and 0.84 according to the forage component considered. Production values decrease from the surface to deep areas with faster turnover in the epipelagic strata due to higher temperature than in the deeper layers.

CONSUMPTION: A Q/B value of 15 was chosen for all the forage components. This value is a guesstimate and is coherent with the values found in the literature for forage species (4.6 to 36) and compiled in a previous Ecopath model (Godinot, 2002; Godinot, 2003; Godinot & Allain, 2003).

DIET COMPOSITION: Very little information is available on diet of micronekton species and considering the aggregation of very different species in unknown proportions in our model it was not realistic to try and base the diet composition on studies found in the literature. Diet composition was arbitrarily determined according to the vertical/temporal distribution of the different forage components in the water column. Two forage components occurring in the same depth strata at the same time can forage on each other. Zooplankton groups were also considered as potential preys as well as large phytoplankton in the epipelagic strata.

Piscivorous fish

There is a large number of piscivorous species. For some of them individual information is available but it is not a general rule. Also, to avoid a too large number of components in the model, it has been decided to aggregate all these species in the same group.

COMPOSITION: This group is very heterogeneous including all the predators except tuna, billfish and sharks. It is composed of non-target species with commercial value as well as discarded species (Table 1). These species can have very different behaviours, for example opah and Alepisauridae are known to spend most of their time in deep waters while Coryphaenidae are surface dwellers.

BIOMASS: No information could be obtained on the biomass of the piscivorous fish. The value included in our model is a guesstimate of the same order of the value calculated in a preliminary model of the warm pool based on ecotrophic efficiency (Godinot & Allain, 2003).

PRODUCTION: Based on a compilation of data, mainly from Ecopath models described in Anon. (1993) but also from other models (Kitchell *et al.*, 1999; Kitchell *et al.*, 2002; Olson & Watters, 2003; Anon., 2000), a range of P/B values from 0.3 to 3 has been determined and an average value of 1.5 has been chosen.

CONSUMPTION: As for P/B, Q/B values were compiled from the same publications and a range from 2.9 to 20 was determined, an averaged value of 10 was included into the model.

DIET COMPOSITION: Diet composition is based on the analysis of 181 non-empty stomachs of predators collected in the warm pool area between 2001 and 2007 as part of an extensive trophic study in the Pacific (Allain, 2003; 2004; 2005). Predators considered to determine the diet of the piscivorous group are 1 *Lepidocybium flavobrunneum*, 1 *Lobotes surinamensis*, 1 *Platax spp.*, 1 *Platax teira*, 3 *Ruvettus pretiosus*, 8 *Sphyraena barracuda*, 4 *Sphyraena spp.*, 4 *Taractichthys longipinnis*, 23 *Acanthocybium solandri*, 1 *Allothunnus fallai*, 1 *Assurger anzac*, 5 Bramidae, 1 *Caranx sexfasciatus*, 24 *Coryphaena hippurus*, 2 *Euthynnus affinis*, 88 *Elagatis bipinnulata*, 2 *Gempylus serpens*, 4 *Gnathanodon speciosus* and 7 *Lampris guttatus*.

Tuna

Tuna are the target species of oceanic pelagic fisheries in the Pacific, they are of high interest for management, they have been monitored for a long time and therefore they have been detailed in the model.

COMPOSITION: In the warm pool area the tuna species constituting most of the catches are skipjack *Katsuwonus pelamis*, yellowfin *Thunnus albacares* and bigeye *Thunnus obesus*; albacore *Thunnus alalunga* is only present on the north and south boundaries of the warm pool and has not been considered in the model. Each species has been split into 2 groups: adults and juveniles according to 50% of maturity for the populations of YFT and BET and 100% of maturity for the population of SKJ. In this model, age, size and weight at maturity (Table 1) correspond to the values used in MULTIFAN-CL[15], the stock assessment model used by SPC to provide annual estimates to the WCPFC[16] scientific committee.

BIOMASS: Biomasses are extracted from 2006 MULTIFAN-CL regions 3 assessments for YFT and BET and 2005 region 5 assessment for SKJ (no assessment was provided in 2006 for SKJ). MULTIFAN-CL is an age-structured model allowing to differentiate biomasses for adults and juveniles.

PRODUCTION: Ecopath is a mass-balanced model and under this condition, total mortality equals to production over biomass (Allen, 1971 in Christensen *et al.*, 2000). Total mortality was calculated for adults and juveniles using MULTIFAN-CL data.

CONSUMPTION: Tuna consumption has been modelled with a bioenergetic model per age class (Kirby, 2005). Models have been developed for YFT and SKJ, however the absence of data did not allow to parameterise a bioenergetic model for BET; YFT consumption rates were simply applied to BET making the estimates for this species less reliable.

DIET COMPOSITION: As for piscivorous fish, diet composition is based on the stomach content analysis of tuna collected in the warm pool area between 2001 and 2007. 143 non-empty stomachs of SKJ were examined (48 juveniles, 95 adults), 283 YFT (192 juv.,

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[15] http://www.multifan-cl.org/

[16] WCPFC: Western and Central Pacific Fisheries Commission; http://www.wcpfc.int

89 ad.) and 137 BET (15 juv., 120 ad.). However values were modified to account for species not observed in stomach but that are probably part of the diet.

Sharks and billfish

Little information is available for billfish and sharks and it is variable according to the species considered.

COMPOSITION: Swordfish *Xiphias gladius* and blue shark *Prionace glauca* constitute 2 individual groups. Swordfish is particularly targeted by some fisheries and blue shark is the most common shark bycatch. Blue, black and striped marlin (*Makaira mazara, M. indica, Tetrapturus audax),* sailfish *Istiophorus platypterus* and spearfish *T. angustirostris* are aggregated in the "other billfish" component and Alopiidae, Carcharhinidae, Lamnidae and Sphyrnidae shark families are aggregated in the "other shark" component. Juvenile components are also taken into consideration, "small billfish" include juvenile swordfish and other billfish, "small sharks" include juvenile blue and other sharks. Age/size/weight defining juvenile and adult groups have not been specified.

BIOMASS: Biomass values included in this model are the ones used in the Central Pacific Ecopath model developed by Kitchell *et al*. (1999).

PRODUCTION: P/B ratios are guesstimates based on other Ecopath models or studies. Compilation of publications detailed in Godinot (2002) provided P/B ranges of 0.14-0.41 for blue shark, 0.1-0.6 for other sharks, 0.35-0.5 for swordfish and 0.3-1 for other billfish.

CONSUMPTION: In the same report Q/B ranges can be found: 2.1-2.8 for blue sharks, 1.5-9.7 for other sharks, 2.8-7.8 for swordfish and 4-7.8 for other sharks.

DIET COMPOSITION: As for piscivorous fish and tuna, diet composition is based on the stomach content analysis of tuna collected between 2001 and 2007. However number of samples being small in the warm pool area, all the samples from the western and central Pacific have been considered: 27 non-empty stomachs of swordfish, 13 blue sharks, 36 other sharks and 17 other billfish. The small number of samples does not allow a good level of confidence in the data and values were modified to account for species not observed in the stomachs but that are probably part of the diet.

Fisheries information

Fisheries information has been extracted from SPC fisheries database system CES Tuna fishery Catch and Effort query System[17] and from Lawson (2006). Four fisheries have been considered: longline, purse seine unassociated schools, purse seine FAD schools and domestic fisheries of Indonesia and Philippines (Table 5). For sharks, billfish and piscivorous fish groups, longline data are extracted from the database for the warm pool area and the average values for years 1995 to 2004 were considered. In CES shark information is not provided on a species by species basis, blue sharks were then assumed to constitute 75% of shark catches as calculated from the data provided in Lawson (2006) for the WCPFC area. Billfish information is provided by species. CES does not provide detailed information on bycatch species caught by purse seine; they were then extracted from Lawson (2006) for the whole WCPFC area. Catch per km^2 was assumed identical for WCPFC and WCPO as purse seine fisheries operate mainly around the equator. All the bycatch caught with purse seine were assumed to be FAD associated.

Catch data for tuna were extracted from the stock assessment 2006 for yellowfin and bigeye and stock assessment 2005 for skipjack. For YFT and BET data are annual averages of the years 1995 to 2004 for region 3 (in the model 1 of MUFDAGER). For SKJ catch data is an annual average of the years 1993 to 2002 and longline data are in fact pole-and-line data for region 5 (in the model 4 of MUFDAGER).

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[17] http://www.spc.int/oceanfish/html/statistics/Ces/index.htm