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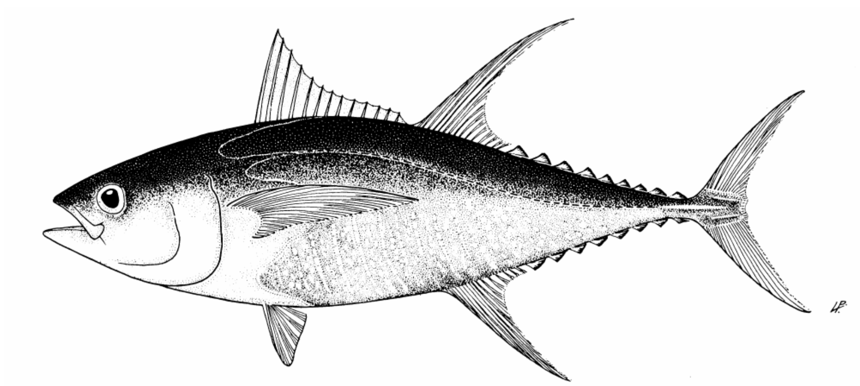
Ecopath model of the pelagic ecosystem of Western and Central Pacific Ocean



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Introduction

With the final objective of managing the fisheries resources through ecosystem-based management, the emphasis has been put lately on the development of ecosystem modelling as a result of FAO, UNEP and EU incentives (UNEP, 2001; Browman and Stergiou, 2004; Pikitch *et al.*, 2004). If the different modelling tools have not yet proved themselves as management tools, they help understanding ecosystem resources interactions that are sometimes more important than the impact of fisheries (Christensen and Pauly, 1997), and are paving the way to future implementation of ecosystem-based management of fisheries.

In the Western and Central Pacific Ocean different types of model have been developed to try and understand the functioning of the pelagic ecosystem: SEAPODYM (Lehodey, 2004, 2005) and ECOPATH/ECOSIM (Godinot and Allain, 2003).

In this paper is presented an updated work on the warm pool ECOPATH model including more local data, particularly diet information, one of the major weakness of the preliminary version being the lack of these local data. A major change is also the use of the 6 forage components defined for the SEAPODYM model that should allow direct comparison between the two models.

Methods

Ecopath description and input parameters

Ecopath is a mass-balance model based on food-web analysis with a simple approach assuming steady state in the system (Christensen and Pauly, 1997). Ecopath with Ecosim (EwE) has been designed at ICLARM based on the initial work of Polovina (1984) for construction of mass-balance models and went through several changes and development; it is now well-used in ecosystem modelling and freely available (http://www.ecopath.org).

The ecosystem is described using functional groups, and every group must satisfy two equations assuming mass-balance and principle of conservation of matter (for details see Godinot and Allain, 2003):

Production = catches + predation mortality + biomass accumulation + net migration + other mortality
and
Consumption = production + respiration + unassimilated food

Ecopath models require the input of three of the following four parameters for each of the groups, the missing parameter will be estimated by the model assuming mass balance:

- total biomass, **B** (tWM/km^2)
- production to biomass ratio, **P/B**, equivalent to total mortality (Allen, 1971) ($year^{-1}$)
- consumption to biomass ratio, **Q/B** ($year^{-1}$)
- ecotrophic efficiency, **EE** (fraction of 1).

Diet composition as well as **fisheries catch** (in tWM/km^2/y) for each group are also needed.

Once all these parameters are entered, the software solves a simultaneous combination of linear equations, one for each group of the system. This results in a mass-balanced trophic model of the ecosystem (Christensen and Walters, 2000).

Based on Ecopath results, Ecosim is a dynamic simulation tool that has been developed to test the effects of given modifications on the ecosystem (new policies, increased fishing effort…). Its goal is to help select the best alternative for the ecosystem as a whole, and not only for a single species (Christensen *et al.*, 2000).

Study area

Longhurst's (1998) biogeochemical classification of the World's oceans and seas defines the Western tropical Pacific Ocean as a 'warm pool' (WP). This region is characterized by a primary production regulated by the input of macronutrients (Le Borgne *et al.*, 2002b) which boundaries in continuous motion can be approximate by the sea surface 29°C isotherm (McPhaden and Picaut, 1990; Lehodey *et al.*, 1997).
The WP moves eastward with El Niño and westward during La Niña events. In the last decade, the 29°C isotherm usually moved between longitude 150°E and 150°W, with a mean around 180°. For reasons of simplicity, we will consider the WP limits to be stable: 110-180°E and 15°N-15°S. This represents an area of 26.9 million km^2, or over 81% of the FAO 71 area of 33.2 million km^2 (Figure 1).
This study only considers the epipelagic and mesopelagic regions, from the sea surface to 1000 m depth.

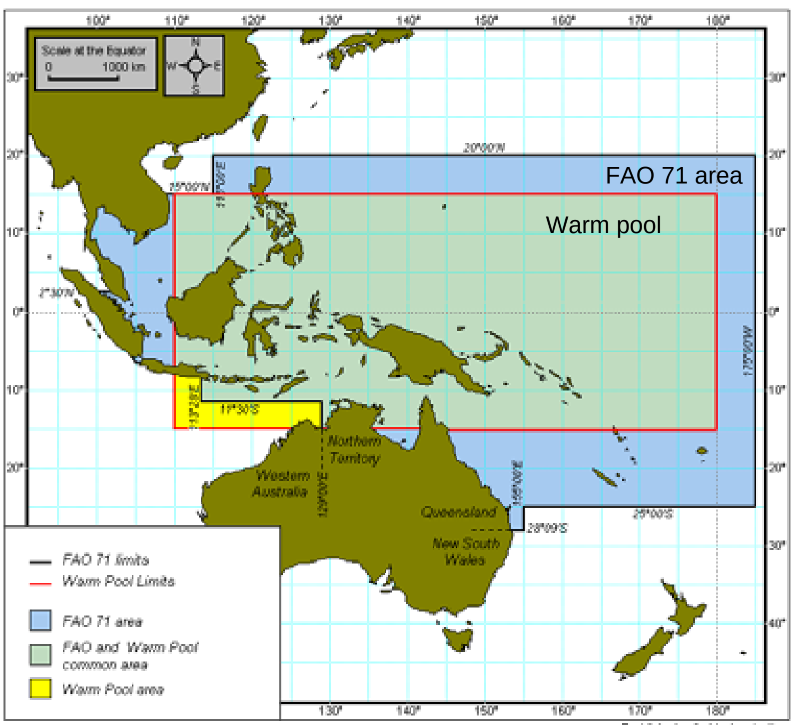

Figure 1: The warm pool limits for this study and the FAO 71 area

Data acquisition

Building an Ecopath model requires several parameters for each defined species or group, (B, P, Q, EE, diet estimate and catch), and 2 types of data were used in this study: local data from the area, and bibliographic data.

Local data:

- Biomass estimates and P/B (equivalent to total mortality) for the tuna species and the forage components
- Catch data for tuna species, swordfish and other billfish
- Q/B estimates from bioenergetic models for SKJ and YFT
- Diet data for tuna species

Bibliographic data:

For most species, field data was not available in the WCPO. Figures from the scientific literature were therefore used. In most cases, we tried to rely on similar studies, *i.e.* tropical Pacific based, to keep the model as realistic as we could. This includes two Ecopath models of the Central Pacific from Kitchell *et al.* (1999, 2002), and a model of the Eastern tropical Pacific from Olson and Watters (2003). Regional FAO catch data were also used. Other important literature includes Fishbase (Froese and Pauly, 2000) as well as Christensen and Pauly's Trophic Models of Aquatic Ecosystems (1993).

Usually, presented data are an average (weighted or not) of various studies. In some cases, it is a 'guesstimate' taken from a range of values found in literature.

Model inputs

This updated model is based on the model developed by Godinot and Allain, 2003. Some of the recommendations for the improvement of the model have been followed and important changes have been done.

About the components, the changes are (Table 1):

- changing the 'Small scombrids' group by 'Small YFT', 'Small BET' and 'Small SKJ'.
- Changing the forage components Epipelagic fish, Mesopelagic fish, Cephalopods and Crustacea by the forage groups used in the SEAPODYM model (mixing of fish, crustacean and molluscs): Epipelagic forage, Migrant mesopelagic forage, Mesopelagic forage, Highly migrant bathypelagic forage, Migrant bathypelagic forage, Bathypelagic forage.

About the data, the changes are (Table 2):

- updated values of B, P/B and catch data for the tuna species from Multifan-CL 2005 runs (average of the decade 1993-2002)
- updated values for catch data for swordfish and other billfish species (average of the decade 1993-2002) (Lawson, 2004; Williams, 2004)
- new data of B and P/B for the forage components extracted from SEAPODYM 2005 runs (average of the decade 1993-2002)
- new data of Q/B values based on a bioenergetic model developed for SKJ and YFT in the WCPO (Kirby, 2005)

- new data on diet of YFT, BET and SKJ from the warm pool area (Allain, 2005)

The list of components and the input data for each group are detailed in Table 1, Table 2 and Table 3; sources of information are in appendix.

Table 1: Taxonomic composition of the 24 functional groups.

Group	Main taxa of group
Swordfish	Large *Xiphias gladius*
Other billfish	Large *Istiophorus platypterus, Makaira indica, Makaira mazara, Tetrapturus audax, Tetrapturus angustirostris*
Blue shark	Large *Prionace glauca*
Other sharks	Large Alopiidae, Carcharhinidae, Lamnidae, Sphyrnidae
Bigeye tuna	*Thunnus obesus* larger than class size/age at 50% of maturity 129cm/3.6y
Yellowfin tuna	*Thunnus albacares* larger than class size/age at 50% of maturity 107cm/2y
Skipjack tuna	*Katsuwonus pelamis* larger than class size/age at 100% of maturity 43cm/0.5y
Piscivorous fish	Alepisauridae, Bramidae, Carangidae, dolphinfish *Coryphaena hippurus*, Gempylidae, wahoo *Acanthocybium solandri*, opah *Lampris guttatus*, small Scombridae
Small bigeye tuna	*Thunnus obesus* smaller than class size/age at 50% of maturity 129cm/3.6y
Small yellowfin tuna	*Thunnus albacares* smaller than class size/age at 50% of maturity 107cm/2y
Small skipjack tuna	*Katsuwonus pelamis* smaller than class size/age at 100% of maturity 43cm/0.5y
Small billfish	Small billfish, same species as large groups swordfish and other billfish
Small sharks	Small sharks, same species as large groups blue shark and other sharks
Epipelagic forage	Euphausids, shrimps, Stomatopoda, Decapoda, Amphipoda, Hyperiidae, Phronima, Megalopa, Palinuridae, Scyllaridae, Engraulidae, Clupeidae, Exocoetidae, small Carangidae Bramidae Scombridae, juveniles of reef fish Acanthuridae Holocentridae Chaetodontidae Malacanthidae Serranidae Tetraodontiformes, juveniles of Octopoda Onychoteuthidae Cranchidae, Carinaria, Argonauta, Loliginidae, Cavolinia
Migrant mesopelagic forage	Nemichthyidae, Myctophidae, Gempylidae, Phosichthyidae, Enoploteuthidae, Stenoteuthis, Pterygioteuthis
Mesopelagic forage	Juvenile Alepisauridae, Omosudidae, Paralepididae, Ophiididae, Trichiuridae, Caristiidae, Ostracoberycidae, Percophidae, Scombrolabracidae, Scorpaenidae, Argyropelecus, Triacanthidae, Macrurocyttidae, Octopoteuthidae, Ommastrephidae, Moroteuthis, Ancistrocheiridae, Oplophoridae
Highly migrant bathypelagic forage	Myctophidae, Maurolicus, Sternoptyx, Liocranchia, Caridae, Oplophorus, Sergestidae, Euphausiidae
Migrant bathypelagic forage	Histioteuthidae, Penaeoidea, Acanthephyra
Bathypelagic forage	Paralepididae, Scopelarchidae, Diretmidae, Chiasmodontidae, Bolitaenidae
Mesozooplankton	Zooplankton of the class size 200-2000 mm, mostly copepods.
Microzooplankton	Zooplankton of the class size 20-200 mm: copepod nauplii, ciliates, sarcodinids, rotifers, small cladocerans…
Large phytoplankton	All pelagic photosynthetic organisms larger than 2 mm, mainly diatoms
Small phytoplankton	All pelagic photosynthetic organisms smaller than 2 mm
Detritus	All pelagic non-living material, bacterioplankton, pico- and nanozooplankton

Table 2: Initial input parameters.

Group name	Biomass t/km²	P/B /year	Q/B /year	EE P/Q	Catch t/km²/year
SWO	0.002	0.4	5.2		0.000101
Other billfish	0.005	0.4	5.3		0.000289
BSH	0.014	0.3	2.5		0.00163*
Other Shark	0.01	0.35	4.8		0.00117*
Adult BET	0.00148	1.026	14.5		0.000724
Adult YFT	0.0112	1.446	16.14		0.00561
Adult SKJ	0.103	2.046	26		0.0204
Small billfish	0.011	0.9	9.3		
Small Shark	0.012	0.5	5.2		
Small SKJ	0.0282	2.539	50		0.000761
Small BET	0.00393	0.755	18		0.0011
Small YFT	0.00953	1.936	18		0.00276
Piscivorous Fish		1	9	EE = 0.95	0.0493*
Forage epipelagic	0.35	3.691	13.9		0.0467*
Forage migrant mesopelagic	0.42	2.132	13.9		
Forage mesopelagic	0.17	2.435	13.9		
Forage H migrant bathypelagic	0.64	1.189	13.9		
Forage migrant bathypelagic	0.35	1.338	13.9		
Forage bathypelagic	0.77	0.845	13.9		
Mesozooplankton	4	33		P/Q = 0.3	
Microzooplankton	1.724	100	300		
Large Phytoplankton	1.989	134			
Small Phytoplankton	11.271	94.6			
Detritus	130				

* Catch data obtained from FAO 1994-2000 average for area 71.

Table 3: Initial input diet matrix.

Prey	Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	SWO		0.002		0.002																	
2	Other billfish		0.002		0.002																	
3	BSH		0.001		0.003																	
4	Other Shark		0.001	0.012	0.001																	
5	Adult BET	0.002	0.009		0.005																	
6	Adult YFT	0.003	0.016		0.023																	
7	Adult SKJ	0.025	0.146		0.047				0.019													
8	Small billfish	0.003	0.005		0.002				0.007	0.004												
9	Small Shark		0.003	0.003	0.009				0.002													
10	Small SKJ	0.060	0.105		0.066		0.025	0.915	0.060	0.264	0.010	0.031	0.134	0.608	0.050							
11	Small BET	0.002	0.010		0.040				0.003	0.001												
12	Small YFT	0.005	0.020		0.020		0.116		0.003	0.002												
13	Piscivorous Fish	0.063	0.193	0.010	0.085				0.239	0.045												
14	Forage epipelagic	0.182	0.272	0.357	0.220	0.005	0.610	0.075	0.435	0.180	0.900	0.046	0.660	0.374	0.050	0.300		0.250				
15	Forage migrant mesopelagic	0.100	0.064	0.098	0.019	0.033	0.032	0.004	0.040	0.073	0.040	0.079	0.120	0.011	0.050	0.050	0.300	0.100	0.050			
16	Forage mesopelagic	0.305	0.146	0.450	0.410	0.681	0.129	0.006	0.185	0.400		0.495	0.037			0.100	0.100	0.050	0.200			
17	Forage H migrant bathypelagic	0.100	0.005			0.131	0.012					0.090	0.043	0.000	0.050				0.050	0.200		
18	Forage migrant bathypelagic	0.100				0.106	0.001					0.004	0.002	0.002		0.050	0.100	0.050	0.050	0.200		
19	Forage bathypelagic	0.050				0.044	0.075					0.255	0.004	0.005				0.050	0.150	0.100		
20	Mesozooplankton			0.050	0.025				0.007	0.025	0.050				0.600	0.500	0.500	0.500	0.500	0.500	0.050	
21	Microzooplankton																				0.370	
22	Large Phytoplankton														0.200						0.150	
23	Small Phytoplankton																					1.000
24	Detritus			0.020	0.021					0.006											0.430	

Results

The initial input data are chosen based on the best available information, and the resulting model is one of the many possibilities that fit the defined constraints (Christensen *et al.*, 2000). However the model is likely to be unbalanced at the first run, *i.e.*, not fulfilling realistic thermodynamic constraints.

A set of parameters can be checked to evaluate if the model is balanced and realistic (P/Q, trophic level, turn-over, Christensen *et al.* 2000), and the first parameter is the EE ecotrophic efficiency that is usually calculated by the model. EE represents the fraction of the production used in the system (by predation, fishing, biomass accumulation, migration, export…) and its dimensionless values vary between 0 and 1. Values close to 0 means the group considered is not preyed upon or fished and the animals die of old age, while a value close to 1 indicates a high predation and/or fishing pressure. In general, except for top predators and primary producers, EE should be close to 1 (Christensen *et al.* 2000). So values larger than 1 are not possible as they mean that there is more of the group eaten than produced.

It is the case for 9 groups in our model after the first run (Table 4): the 3 small tuna and particularly small SKJ which presents a EE larger than 50, and the 6 forage components.

Table 4: Basic estimates after the first run with initial input parameters. Shaded cells are the values estimated by the model.

Group name	Trophic level	Biomass (t/km²)	Prod./ biom. (/year)	Cons./ biom. (/year)	EE	Prod. / cons.
SWO	5.23	0.002	0.4	5.2	0.313	0.077
Other billfish	5.44	0.005	0.4	5.3	0.219	0.075
BSH	4.86	0.014	0.3	2.5	0.041	0.12
Other Shark	5.22	0.01	0.35	4.8	0.141	0.073
Adult BET	5.3	0.00148	1.026	14.5	0.807	0.071
Adult YFT	4.85	0.0112	1.446	16.14	0.444	0.09
Adult SKJ	5.38	0.103	2.046	33.475	0.136	0.061
Small billfish	5.16	0.011	0.9	9.3	0.124	0.097
Small Shark	5.17	0.012	0.5	5.2	0.137	0.096
Small SKJ	4.46	0.0282	2.539	69.288	51.605	0.037
Small BET	5.27	0.00393	0.755	18	1.238	0.042
Small YFT	4.75	0.00953	1.936	18.009	1.392	0.107
Piscivorous Fish	5.09	0.0394	1	9	0.95	0.111
Forage epipelagic	3.48	0.339	3.691	13.9	5.292	0.266
Forage migrant mesopelagic	4.12	0.417	2.132	13.9	2.772	0.153
Forage mesopelagic	4.33	0.164	2.435	13.9	5.976	0.175
Forage H migrant bathypelagic	4.16	0.629	1.189	13.9	3.482	0.086
Forage migrant bathypelagic	4.37	0.343	1.338	13.9	7.207	0.096
Forage bathypelagic	4.36	0.759	0.845	13.9	3.499	0.061
Mesozooplankton	2.44	4	33	110	0.311	0.3
Microzooplankton	2	1.724	100	300	0.944	0.333
Large Phytoplankton	1	1.989	134	-	0.251	-
Small Phytoplankton	1	11.271	94.6	-	0.485	-
Detritus	1	130	-	-	0.184	-

To try and balance the model, values of the parameters have to be modified, and because biomass, P/B and Q/B ratios are less subject to variation in space and time than diets, we decided to modify diets in priority:

- diet modifications were done to reduce the predation (and the EE) on the unbalanced groups and particularly on small SKJ. For example, in the first diet matrix, adult SKJ were feeding at 90% on small SKJ based on diet studies (Allain, 2005). However in this study 70% of the diet of SKJ is unrecognizable, the value has then been considerably reduced. Predation of forage components on mesozooplankton has been increased to try and increase predation on this components that has relatively low EE (0.311) and then to decrease predation and EE on the other forage components. A large number of changes has been done in the diet of most of the components.
- as SKJ represents a high biomass with very high consumption they have an important impact on their preys. Their Q/B values were reduced to try to decrease the predation and the EE on their preys, particularly the small SKJ and the epipelagic forage.
- while modifying the diet matrix and recalculating the parameters after each modification, it appears that the estimated biomass of the piscivorous group presented important fluctuations, it was then decided to input the biomass instead of the EE in the second set of input data.

After numerous changes a second set of input data have been entered (Table 5 and Table 6) and run for the estimation of the basic estimates.

Table 5: Second set of input parameters.

Group name	Biomass t/km²	P/B /year	Q/B /year	P/Q	Catch t/km²/year
SWO	0.002	0.4	5.2		0.000101
Other billfish	0.005	0.4	5.3		0.000289
BSH	0.014	0.3	2.5		0.00163
Other Shark	0.01	0.35	4.8		0.00117
Adult BET	0.00148	1.026	14.5		0.000724
Adult YFT	0.0112	1.446	16.14		0.00561
Adult SKJ	0.103	2.046	26		0.0204
Small billfish	0.011	0.9	9.3		
Small Shark	0.012	0.5	5.2		
Small SKJ	0.0282	2.539	50		0.000761
Small BET	0.00393	0.755	18		0.0011
Small YFT	0.00953	1.936	18		0.00276
Piscivorous Fish	0.15	1	9		0.0493
Forage epipelagic	0.35	3.691	13.9		0.0467
Forage migrant mesopelagic	0.42	2.132	13.9		
Forage mesopelagic	0.17	2.435	13.9		
Forage H migrant bathypelagic	0.64	1.189	13.9		
Forage migrant bathypelagic	0.35	1.338	13.9		
Forage bathypelagic	0.77	0.845	13.9		
Mesozooplankton	4	33		0.3	
Microzooplankton	1.724	100	300		
Large Phytoplankton	1.989	134			
Small Phytoplankton	11.271	94.6			
Detritus	130				

Table 6: Second set of input diet matrix.

Prey	Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	21
1	SWO		0.002		0.002																	
2	Other billfish		0.002		0.002																	
3	BSH		0.001		0.003																	
4	Other Shark		0.001	0.012	0.001																	
5	Adult BET	0.002	0.009		0.02																	
6	Adult YFT	0.003	0.016		0.04																	
7	Adult SKJ	0.025	0.146		0.1	0.05	0.05		0.019	0.05												
8	Small billfish	0.003	0.005		0.002				0.007	0.004												
9	Small Shark		0.003	0.003	0.009				0.002													
10	Small SKJ	0.06	0.105		0.05	0.05	0.025	0.215	0.06	0.114	0.01	0.031	0.104	0.25	0.001							
11	Small BET	0.002	0.01		0.01			0.005	0.003	0.001			0.005	0.001								
12	Small YFT	0.005	0.02		0.02		0.116	0.005	0.003	0.002		0.005		0.001								
13	Piscivorous Fish	0.063	0.193	0.16	0.156	0.05	0.05	0.3	0.239	0.125	0.1	0.1	0.1	0.005	0.001							
14	Forage epipelagic	0.182	0.272	0.257	0.22	0.005	0.51	0.305	0.435	0.2	0.7	0.046	0.46	0.374	0.05	0.1		0.14				
15	Forage migrant mesopelagic	0.1	0.064	0.098	0.019	0.033	0.032	0.124	0.04	0.073	0.04	0.069	0.1	0.011	0.002	0.05	0.15	0.025	0.025			
16	Forage mesopelagic	0.305	0.146	0.3	0.2	0.531	0.129	0.006	0.185	0.3		0.305	0.032	0.2		0.05	0.05	0.025	0.075			
17	Forage H migrant bathypelagic	0.1	0.005	0.05	0.05	0.131	0.012			0.05		0.09	0.043	4E-04	0.002				0.025	0.1		
18	Forage migrant bathypelagic	0.1		0.05	0.05	0.106	0.001			0.05		0.004	0.002	0.003		0.05	0.05	0.03	0.025	0.1		
19	Forage bathypelagic	0.05				0.044	0.075					0.2	0.004	0.005				0.03	0.1	0.05		
20	Mesozooplankton			0.05	0.025			0.04	0.007	0.025	0.15	0.15	0.15	0.15	0.7	0.7	0.7	0.7	0.7	0.7	0.05	
21	Microzooplankton														0.094	0.05	0.05	0.05	0.05	0.05	0.37	
22	Large Phytoplankton														0.15						0.15	
23	Small Phytoplankton																					1
24	Detritus			0.02	0.021					0.006											0.43	

After a large number of successive changes in the diet matrix and runs, the model is still unbalanced with EE values higher than 1 for 10 groups (Table 7): the 3 small tuna, piscivorous fish and the 6 forage components. However, the small SKJ EE has been considerably reduced, from 51.6 to 9.8.

Table 7: Basic estimates after the last run with the second set of input parameters. Shaded cells are the values estimated by the model.

Group name	Trophic level	Biomass (t/km²)	Prod./ biom. (/year)	Cons./ biom. (/year)	EE	Prod. / cons.
SWO	4.74	0.002	0.4	5.2	0.313	0.077
Other billfish	4.98	0.005	0.4	5.3	0.219	0.075
BSH	4.61	0.014	0.3	2.5	0.43	0.12
Other Shark	4.86	0.01	0.35	4.8	0.475	0.073
Adult BET	4.83	0.00148	1.026	14.5	0.9	0.071
Adult YFT	4.65	0.0112	1.446	16.14	0.525	0.09
Adult SKJ	4.67	0.103	2.046	26	0.932	0.079
Small billfish	4.79	0.011	0.9	9.3	0.124	0.097
Small Shark	4.78	0.012	0.5	5.2	0.137	0.096
Small SKJ	4.16	0.0282	2.539	50	9.796	0.051
Small BET	4.6	0.00393	0.755	18	2.399	0.042
Small YFT	4.42	0.00953	1.936	18	1.776	0.108
Piscivorous Fish	4.47	0.15	1	9	5.837	0.111
Forage epipelagic	3.23	0.35	3.691	13.9	3.629	0.266
Forage migrant mesopelagic	3.69	0.42	2.132	13.9	1.617	0.153
Forage mesopelagic	3.74	0.17	2.435	13.9	3.406	0.175
Forage H migrant bathypelagic	3.67	0.64	1.189	13.9	1.616	0.086
Forage migrant bathypelagic	3.74	0.35	1.338	13.9	4.024	0.096
Forage bathypelagic	3.74	0.77	0.845	13.9	2.037	0.061
Mesozooplankton	2.44	4	33	110	0.373	0.3
Microzooplankton	2	1.724	100	300	0.956	0.333
Large Phytoplankton	1	1.989	134	-	0.25	-
Small Phytoplankton	1	11.271	94.6	-	0.485	-
Detritus	1	130	-	-	0.184	-

Discussion

The Ecopath model of the pelagic ecosystem of the warm pool could not be balanced, preventing the use of Ecosim for the simulation of management scenarios.
Balancing the model will necessitate more work and these first runs allowed to identify the parts of the model that need closer examination:

Introducing variability in the diet matrix
The very high EE have been reduced by many modifications of the diet. We did not want to make major changes to the diets of the tuna which are based on local data, however these diets are not fixed and introducing some variability in them by the use of the

Ecoranger module of the software might help balancing the model. As a general comment, introducing a range of data rather than a mean value for all the parameters might allow more flexibility in the model.

Obtaining more accurate data on critical components of the ecosystem
However, it seems that slight modifications of the diet are not enough to induce important changes in the EE. To reach the balance of the model, dramatic changes in the diet might be necessary and/or changes in the other input parameters that might have more effects such as biomass, consumption or production. If major plausible changes in the diet are not enough to balance the model it will be necessary to consider these other factors and try and obtain more accurate data. In our model the most problematic components are the small tunas, the piscivorous group and the forage components.
The piscivorous group is of main concern as it regroups all the large predators other than tunas, sharks and billfish, that is dolphinfish, wahoo, opah, pomfrets, trevally… These predators can have very different life characteristics but they are grouped under the same component as their common characteristic is the lack of any data. Some of these species are fished as bycatch in the tuna fisheries but unfortunately we don’t even have good estimates of the total catch even if more and more data are collected on these species and if catch data are now estimated. Information on biomass is inexistent and there are few information on their biology and physiology, including consumption and diet. Obtaining more information on these predators, that are important bycatch, seems primordial to hope to improve the accuracy of the ecosystem model, but it will probably necessitate a long time before obtaining good statistics on these species.
All the forage components in our model were unbalanced. Again for these groups the lack of information is very high and obtaining data on these non-exploited species is very challenging. Moreover these groups are composed of very different species including fish, cephalopods and crustacea making more difficult the assessment of the necessary parameters for these species. These intermediate groups have a very important role in the ecosystem as already noticed (Olson and Watters, 2003) and improving our knowledge on the forage components might be considered as a priority for the better comprehension of the functioning of the ecosystem as it was pointed during the PFRP PI Meeting in Hawaii in 2004 on Ecosystem Approaches to Fishery Management (processes occuring at mid-trophic levels).

Conclusion

The new runs of the Ecopath model of the warm pool pelagic ecosystem did not allow to obtain an improved model, and simulations could not be conducted to test management policies and to assess the impact of fisheries and environmental factors. However this work helped understanding a little bit more the functioning of the ecosystem and highlighted some factors or groups that need better parameterisation (variability in diet matrix and input parameter, more accurate information on bycatch piscivorous species and on forage components).

Ecopath with Ecosim is still potentially an interesting model to try and understand how the ecosystem works, and even if we are not sure to have an accurate model, by building it we gain in the comprehension of some of the mechanisms occurring in the ecosystem. Concerning the use of this type of models for management issue, at this stage, they cannot probably be considered as management tools and the uncertainties and approximations prevent to rely on them to make management decisions. However they are a good complement of single-species models as they provide information on the non-target species of the ecosystem. Even if the results emerging from simulations can be highly speculative because of important uncertainties in the model, Ecopath and Ecosim still provide a documented information that is valuable in the absence of any other source of data.

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NOAA website, monthly atmospheric and SST indices: http://www.cpc.ncep.noaa.gov/data/indices/index.html
SeaWiFS project website: http://seawifs.gsfc.nasa.gov/SEAWIFS.html

Appendix: sources of parameter and diet estimates for the model of the warm pool pelagic ecosystem

Group	Biomass	P/B	Q/B	Other parameter	Diet
Swordfish	Kleiber and Yokawa, 2002	Guénette and Morato, 1997; Kitchell *et al.*, 1999, 2002; Kleiber and Yokawa, 2002; Olson and Watters, 2003	Guénette and Morato, 1997; Kitchell *et al.*, 1999, 2002; Olson and Watters, 2003		Cox *et al.*, 2002; Guénette and Morato, 1997; Kitchell *et al.*, 2002; Olson and Watters, 2003
Other billfish	Kitchell *et al.*, 1999, 2002; Okey and Pugliese, 2001	Kitchell *et al.*, 1999, 2002; Kleiber *et al.*, 2001b, 2002; Okey and Pugliese, 2001; Olson and Watters, 2003	Browder, 1993; Kitchell *et al.*, 1999, 2002; Okey and Pugliese, 2001; Olson and Watters, 2003		Abitia-Cardenas *et al.*, 1999; Cox *et al.*, 2002; Kitchell *et al.*, 2002; Olson and Watters, 2003; Fishbase
Blue shark	Kitchell *et al.*, 1999, 2002	Kitchell *et al.*, 1999, 2002; Kleiber *et al.*, 2001a	Kitchell *et al.*, 1999, 2002		Cortés, 1999; Kitchell *et al.*, 2002; Fishbase
Other sharks	Kitchell *et al.*, 2002	Arreguín-Sánchez *et al.*, 1993a, b; Browder, 1993; De Paula E Silva *et al.*, 1993; Guénette and Morato, 1997; Kitchell *et al.*, 1999, 2002; Okey and Pugliese, 2001; Olson and Watters, 2003; Opitz, 1993; Polovina and Ow, 1983; Sheridan *et al.*, 1984; Wolff *et al.*, 1996	Arreguín-Sánchez *et al.*, 1993a, b; Browder, 1993; De Paula E Silva *et al.*, 1993; Guénette and Morato, 1997; Kitchell *et al.*, 1999, 2002; Okey and Pugliese, 2001; Olson and Watters, 2003; Opitz, 1993; Polovina and Ow, 1983; Wolff *et al.*, 1996		Cox *et al.*, 2002; Guénette and Morato, 1997; Kitchell *et al.*, 2002; Olson and Watters, 2003; Fishbase
Large Bigeye tuna	MULTIFAN-CL 2005 estimates SPC data from areas 3 and 4	MULTIFAN-CL 2005 estimates SPC data from areas 3 and 4	Kitchell *et al.*, 1999, 2002; Olson and Watters, 2003		Allain 2005
Large Yellowfin tuna	MULTIFAN-CL 2005 estimates SPC data from areas 3 and 4	MULTIFAN-CL 2005 estimates SPC data from areas 3 and 4	Kirby 2005: bioenergetics model SPC data		*Allain 2005*
Large Skipjack tuna	MULTIFAN-CL 2005 estimates SPC data from areas 5 and 6	MULTIFAN-CL 2005 estimates SPC data from areas 5 and 6	Kirby 2005: bioenergetics model SPC data		*Allain 2005*
Small Bigeye tuna	MULTIFAN-CL 2005 estimates SPC data from areas 3 and 4	MULTIFAN-CL 2005 estimates SPC data from areas 3 and 4	Assumed identical to small YFT		Allain 2005
Small Yellowfin tuna	MULTIFAN-CL 2005 estimates SPC data from areas 3 and 4	MULTIFAN-CL 2005 estimates SPC data from areas 3 and 4	Kirby 2005: bioenergetics model SPC data		*Allain 2005*
Small Skipjack tuna	MULTIFAN-CL 2005 estimates SPC data from areas 5 and 6	MULTIFAN-CL 2005 estimates SPC data from areas 5 and 6	Kirby 2005: bioenergetics model SPC data		*Allain 2005*
Piscivorous fish	*Olson and Watters, 2003*	Abarca-Arenas and Valero-Pachero, 1993; Aliño *et al.* 1993; Arreguín-Sánchez *et al.*, 1993a, b; De La Cruz-Aguero, 1993; De Paula E Silva *et al.*, 1993; Kitchell *et al.*, 1999; Mendoza, 1993; Okey and Pugliese, 2001; Olson and Watters, 2003; Opitz, 1993; Silvestre *et al.*, 1993; Fishbase	Abarca-Arenas and Valero-Pachero, 1993; Aliño *et al.* 1993; Arreguín-Sánchez *et al.*, 1993a, b; De La Cruz-Aguero, 1993; De Paula E Silva *et al.*, 1993; Kitchell *et al.*, 1999; Mendoza, 1993; Okey and Pugliese, 2001; Olson and Watters, 2003; Opitz, 1993; Silvestre *et al.*, 1993; Fishbase	**EE**: High value based on assumption that most of the production is consumed by predators	Cox *et al.*, 2002; Kitchell *et al.*, 2002; Olson and Watters, 2003; Fishbase; SPC data
Small billfish	Kitchell *et al.*, 1999	Olson and Watters, 2003	Olson and Watters, 2003		Olson and Watters, 2003
Small sharks	Kitchell *et al.*, 1999	Cox *et al.*, 2002; Kitchell *et al.*, 1999; Olson and Watters, 2003	Cox *et al.*, 2002; Kitchell *et al.*, 1999; Olson and Watters, 2003		Cox *et al.*, 2002; Olson and Watters, 2003

Sources of parameter and diet estimates for the improved model of the warm pool pelagic ecosystem (Continued)

Group	Biomass	P/B	Q/B	Other parameter	Diet
Epipelagic forage	SEAPODYM 2005 estimates SPC data: Warm pool, 1993-2002	SEAPODYM 2005 estimates SPC data: Warm pool, 1993-2002	Abarca-Arenas and Valero-Pachero, 1993; Arreguín-Sánchez *et al.*, 1993a; Cox *et al.*, 2002; De La Cruz-Aguero, 1993; De Paula E Silva *et al.*, 1993; Kitchell *et al.*, 1999, 2002; Mendoza, 1993; Olivieri *et al.*, 1993; Olson and Watters, 2003; Silvestre *et al.*, 1993; Fishbase		De Paula E Silva *et al.*, 1993; Guénette and Morato, 1997; Mendoza, 1993; Olivieri *et al.*, 1993; Olson and Watters, 2003; Silvestre *et al.*, 1993; Fishbase
Migrant mesopelagic forage	SEAPODYM 2005 estimates SPC data: Warm pool, 1993-2002	SEAPODYM 2005 estimates SPC data: Warm pool, 1993-2002	Considered same as epipelagic fish, like in Kitchell *et al.* (2002) and Olson and Watters (2003)		Based on mesopelagic and vertical behavior
Mesopelagic forage	SEAPODYM 2005 estimates SPC data: Warm pool, 1993-2002	SEAPODYM 2005 estimates SPC data: Warm pool, 1993-2002	Considered same as epipelagic fish, like in Kitchell *et al.* (2002) and Olson and Watters (2003)		Legand *et al.*, 1972; Williams *et al.*, 2001; Fishbase
Highly migrant bathypelagic forage	SEAPODYM 2005 estimates SPC data: Warm pool, 1993-2002	SEAPODYM 2005 estimates SPC data: Warm pool, 1993-2002	Considered same as epipelagic fish, like in Kitchell *et al.* (2002) and Olson and Watters (2003)		Based on mesopelagic and vertical behavior
Migrant bathypelagic forage	SEAPODYM 2005 estimates SPC data: Warm pool, 1993-2002	SEAPODYM 2005 estimates SPC data: Warm pool, 1993-2002	Considered same as epipelagic fish, like in Kitchell *et al.* (2002) and Olson and Watters (2003)		Based on mesopelagic and vertical behavior
Bathypelagic forage	SEAPODYM 2005 estimates SPC data: Warm pool, 1993-2002	SEAPODYM 2005 estimates SPC data: Warm pool, 1993-2002	Considered same as epipelagic fish, like in Kitchell *et al.* (2002) and Olson and Watters (2003)		Based on mesopelagic and vertical behavior
Mesozooplankton	Le Borgne and Rodier, 1997	Aliño *et al.* 1993; Arreguín-Sánchez *et al.*, 1993a, b; Browder, 1993; Chai *et al.*, 2002; Chávez *et al.*, 1993; De La Cruz-Aguero, 1993; De Paula E Silva *et al.*, 1993; Mendoza, 1993; Olivieri *et al.*, 1993; Opitz, 1993; Roman *et al.*, 2002a, b; Silvestre *et al.*, 1993; Vega-Cendejas *et al.*, 1993		**P/Q**: Dalsgaard and Pauly, 1997; Omori and Ikeda, 1984 in Roman *et al.*, 2002a; Straile, 1997 in Roman *et al.*, 2002a **U/Q**: Conover, 1978 in Roman *et al.*, 2002a	Parts calculated from various sources, see (3); Olivieri *et al.*, 1993
Microzooplankton	Le Borgne and Rodier, 1997	Olivieri *et al.*, 1993	Olivieri *et al.*, 1993		Assumed to feed exclusively on small phytoplankton, like in Chai *et al.*, 2002.
Large phyto	Various sources, see (1)	Various sources, see (2)			
Small phyto	Various sources, see (1)	Various sources, see (2)			
Detritus	Pauly *et al.*, 1993b				

(1) Phytoplankton biomass

Total phytoplankton biomass was calculated using data from French JGOFS cruises Flupac and Zonalflux (courtesy of Dr. R. Le Borgne, IRD Nouméa), as well as Australian JGOFS cruises FR 9008, FR 9205 and FR 9308 (CSIRO website) and publications from Kirchman *et al.* (1995), Mackey *et al.* (1995) and Chavez *et al.* (1996).

To convert these data into wet mass estimates, we used a **C:Chla ratio of 40** (Chavez *et al.*, 1996; Brown *et al.*, submitted) and a conversion factor of **11.539 gWM/gC** (Jones, 1984 and ICES, 1989 in Christensen, 1995). This led to a total phytoplankton biomass of 13.3 tWM/km^2.

In the western Pacific, diatoms only represent 15% of phytoplankton biomass (Le Borgne *et al.*, 2002a). We can estimate their biomass around **2.0 tWM/km^2**, and thus the biomass of small plankton around **11.3 tWM/km^2**.

(2) phytoplankton P/B ratios

Le Borgne *et al.* (2002b) estimated primary production at 0.32 gC/m^2/d, or 1333 tWM/km^2/y in the warm pool. Diatom contribution to total primary production can reach 20% in the warm pool (Blain *et al.*, 1997).

0.2 * 1333 / 2.0 = 134
0.8 * 1333 / 11.3 = 95
Diatoms have a P/B of **134 year^{-1}**, and small phytoplankton a P/B ratio of **95 year^{-1}**.

(3) Mesozooplankton diet

Daily consumption of phytoplankton biomass by mesozooplankton (>200 µm) is generally **<**5% of the phytoplankton standing crop per day in the equatorial Pacific (Dam *et al.*, 1995, Roman and Gauzens, 1997). Small phytoplankton is not edible for mesozooplankton, due to its small size (Dam *et al.*, 1995). Therefore, the phytoplankton consumed is only composed of large phytoplankton, mainly diatoms.
0.05 * 1333 = 66.65 tWM/km^2/y
$Q_{mesozooplankton}$ = Q/B * B = 110 * 4 = 440 tWM/km^2/y
66.65 / 440 = 0.15
15% of mesozooplankton diet is composed of large phytoplankton.

Food requirements suggest that most of the diet of equatorial Pacific Ocean mesozooplankton is microzooplankton (Roman *et al.*, 2002b). We considered that microzooplankton is edible only to mesozooplankton due to its very small size. We calculated mesozooplankton feeding rate so that it led to a final EE of 0.95 for microzooplankton. It results that **37%** of mesozooplankton diet is microzooplankton.

We used a value of **5%** for intraguild predation (Olivieri *et al.*, 1993). The remaining **43%** of the diet is detritus.