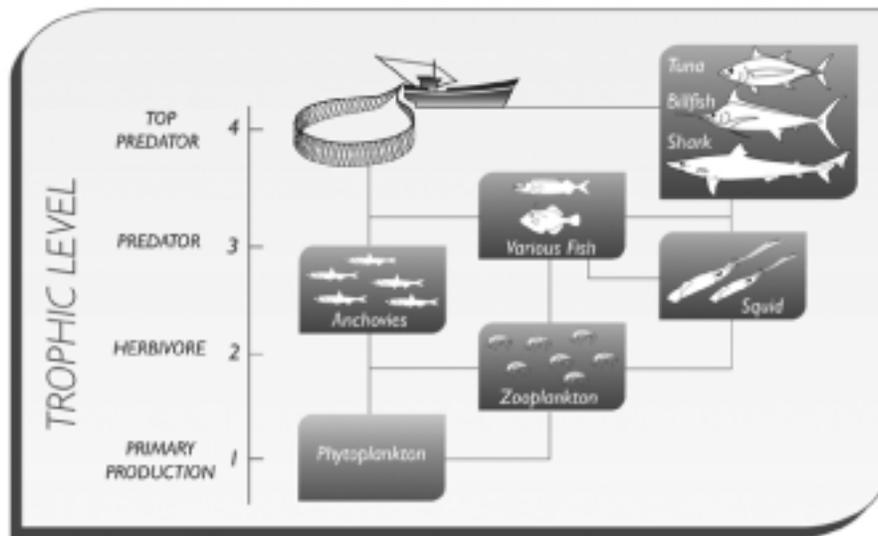


BBRG-5



A preliminary Ecopath model of the warm pool pelagic ecosystem



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Introduction

Up to the 1980s, fisheries have to a large extent focused on obtaining information on the exploited resources in a 'single-species' management style. The concept of ecosystem-based management of fisheries emerged in the 1982 UN convention on the Law of the Sea (UNEP, 2001). In the last two decades, emphasis was put on ecosystem resources interaction, and the fact that these interactions are sometimes more important than the impact of the fisheries (Christensen and Pauly, 1997).

However, adequately assessing the status of an ecosystem would require assessments and monitoring of all major species. Fisheries data are not available for most non-target species, scientific surveys are expensive and time-consuming, and ongoing monitoring may be logistically impossible. The best option seems to be the development of models that represent the principal elements of the ecosystem and description of biomass flows between them, based on the best available information on who eats who (Gibbons-Fly, 2000).

Fisheries research of industrialised countries has lately focused on ecosystem modelling as a result of FAO, UNEP and EU incentives as well as Agenda 21 from Rio de Janeiro 1992 Earth Summit. This has led to the development of different modelling tools such as multispecific models: Multispecies Virtual Population Analysis (MSVPA) (Sparre, 1991) or ecosystem models: Ecopath with Ecosim. They have not as yet proved themselves as management tools, but are paving the way to future implementation of ecosystem-based management of fisheries.

Unfortunately, most existing tools are age-based models, and very data-intensive, which is problematic. Hence, there is wide interest in simple mass-balance models based on food-web analysis, at least in a first descriptive approach (Christensen and Pauly, 1997).

Ecopath with Ecosim has been designed at ICLARM based on the initial work of Polovina (1984) for construction of mass-balance models. An important advantage of the Ecopath approach is that models can be constructed combining local, and previously under-utilised data sets, with regional, published information and estimates from empirical models (Christensen and Pauly, 1997). It is also not very data demanding compared to other modelling software. In the data-scarce Pacific region, Ecopath can therefore be a useful tool to initiate ecosystem research.

The purpose of the present work is to design and parameterise a preliminary Ecopath model of the warm pool pelagic ecosystem, the most productive region in the WCPO. It will ultimately be updated with regional data originating from the food web study, and hopefully result in a better understanding of the warm pool pelagic ecosystem. For this study, it is made with currently available data, comprising other Pacific Ocean based Ecopath models and the first results of the food web study.

This report consists of three main parts. The first part describes quickly the principles of Ecopath with Ecosim and the data necessary to construct the Ecopath model of the warm pool and also their sources. The second part presents the main results of the static picture of the ecosystem obtained from the model and the results of a first simulation to test the reaction of this model to an increase of the fishing catches. In the third part, the limitations

and weaknesses of the model are discussed as well as improvements and interests of the ecosystem modelling.

Methods

Ecopath description

The original Ecopath programme was developed by J.J. Polovina (1984) to describe a coral reef ecosystem in Hawaii. It was a quite simple approach assuming steady state in the system. Since then, it has gone through several changes and developments. Ecopath with Ecosim (EwE) is today well-used in ecosystem modeling. The last version, *EwE 5*, freely available on the Internet (<http://www.ecopath.org>) is used here.

The ecosystem is described using functional groups that can either be made of single species or gather several species with similar characteristics, for example ‘filter feeders’, ‘marine mammals’ or ‘small invertebrates’. Every group must satisfy two equations. The first equation describes the production term, assuming mass-balance:

$$P_i = Y_i + B_i * M2_i + E_i + BA_i + P_i * (1-EE_i)$$

The notations and units are:

P_i : production rate of group i , defined as body mass increase (tWetMass/km²/year)

Y_i : fishery catch rate for this group (year⁻¹)

B_i : biomass of the group averaged on one year (tWM/km²)

$M2_i$: predation mortality (year⁻¹)

E_i : net migration rate (emigration – immigration) (tWM/km²/year)

BA_i : biomass accumulation (or depletion) rate: set to zero by default, used if a group’s biomass is not in equilibrium (tWM/km²/year)

$P * (1-EE_i) = M0$: other mortality rate (year⁻¹)

EE_i : ecotrophic efficiency that can be described as the proportion of the production that is utilized in the system (dimensionless, fraction of 1).

The second ‘master’ equation is based on the principle of conservation of matter within a group:

$$Q_i = P_i + R_i + U_i$$

With:

Q_i : consumption, calculated as $Q/B * B$ (tWM/km²/year)

P_i : production, as calculated in previous equation (tWM/km²/year)

R_i : respiration, accounting for metabolic expenses not usable for any other group (tWM/km²/year)

U_i : unassimilated food, representing feces and urine production (tWM/km²/year).

Ecopath models require the input of three of the following four parameters for each of the groups:

- total biomass, **B** (tWM/km²)
- 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).

The fourth one, if missing, will be estimated by the model assuming mass balance. If the four parameters are provided, the equilibrium will be reached using biomass accumulation or depletion (BA).

Diet composition as well as **fisheries catch** (in tWM/km²/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. The approach is further described with mathematical details in Christensen and Walters (2000).

Ecosim description

Ecosim is a dynamic simulation tool. It 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. The basics of Ecosim consist of a system of coupled differential equations derived from Ecopath first equation, of the form:

$$dB_i/dt = g_i \Sigma C_{ji} - \Sigma C_{ij} + I_i - (M_i + F_i + e_i) * B_i$$

With:

dB_i/dt : growth rate during dt in term of biomass for group i

g_i : net growth efficiency (production/consumption ratio)

C_{ji} : consumption rate of prey j by group i

C_{ij} : consumption rate of prey i by group j

I_i : immigration rate

M_i : natural mortality rate excluding predation

F_i : fishing mortality rate

e_i : emigration rate.

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 25.5 million km², or over 76% of the FAO 71 area of 33.2 million km² (Figure 1).

This study only considers the epipelagic and mesopelagic regions, from the sea surface to 1000 m depth.

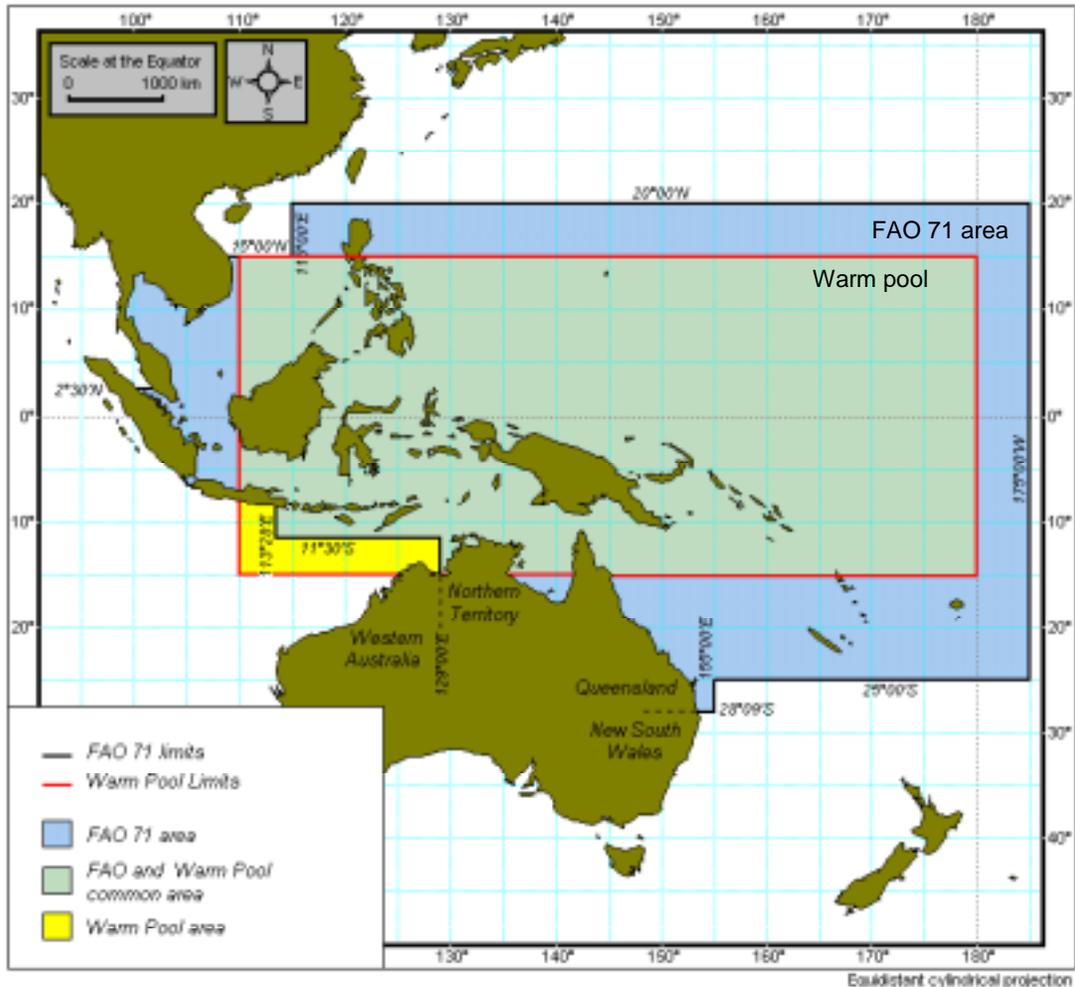


Figure 1: The warm pool limits for this study and the FAO 71 area
(Source: FAO website)

Data acquisition

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

Local data are of various kinds:

- Catch data compiled by OFP and provided by all nations fishing in the WCPO, including distant fishing nations.
- Multifan-CL, a length-based, age-structured statistical model, gives biomass estimates, natural and fishing mortality for the main commercial species of the WCPO.

- The food web study of the WCPO has been launched to collect samples that will be used in the construction of ecosystem models.

However, data holdings essentially concern tuna in the Western Pacific. For the non-target species of the ecosystem, most data were obtained through a literature review, detailed in the appendix.

Sample collection and diet analysis

Stomach samples are collected from target fishes (tunas) and bycatch species following a defined protocol by observers from the different national observer programmes in the area (Cook Islands, Federated States of Micronesia, Fiji, Kiribati, New Caledonia, Papua New Guinea, French Polynesia and Solomon Islands).

Stomach content analysis consists in identifying ingested prey, counting, weighing, measuring and determining their state of digestion. These data are used to estimate the diet composition (%) of four groups in this study: bigeye tuna, skipjack, yellowfin tuna and Piscivorous fish. More details on this study can be found in the paper BBRG-6, V. Allain: Diet of mahi-mahi, wahoo and lancetfish in the western and central Pacific.

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, an extensive fish database (Froese and Pauly, 2000; <http://www.fishbase.org>) as well as Christensen and Pauly's Trophic Models of Aquatic Ecosystems (1993), gathering many detailed Ecopath models from most aquatic ecosystem types.

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 model was built with special interest in tuna. Therefore, the three species of tropical tuna are considered as different groups. All other groups were created depending on available data. They usually are made of several species (Table 1). Biomass, P/B, Q/B, EE, P/Q, U/Q and the diet matrix for each component are detailed in Table 2 and Table 4, sources of information are in appendix.

For the catch estimate five gears/fisheries are considered. Three main fishery types target the tuna in the warm pool: longline, purse seine and pole and line. All other tuna fishing methods are grouped in Tuna Other gears. An average of 1990-2001 yearly catches from SPC data set is used in this study. Other fisheries catch not targeting tuna but species such as billfish, sharks, piscivorous and epipelagic fishes and cephalopods is an average of FAO data on the period 1994-2000 (Table 3). Other fisheries catch is calculated as the difference between tuna fisheries and WP total catch. For tuna and swordfish, tuna fisheries catch is higher than WP total catch. This can be explained by the fact that statistics do not cover the same period and same area. The assumption of homogeneous repartition of tuna might also be

responsible, as we know that most tunas inhabit warm waters. However, the values are close enough to assume that catch estimate for ‘other fisheries’ has the right order of magnitude for the warm pool.

Table 1: Taxonomic composition of the 20 functional groups.

Group	Main taxa of group
Swordfish	Large <i>Xiphias gladius</i>
Other billfish	Large <i>Istiophorus platypterus</i> , <i>Makaira indica</i> , <i>Makaira mazara</i> , <i>Tetrapturus audax</i> , <i>Tetrapturus angustirostris</i>
Blue shark	Large <i>Prionace glauca</i>
Other sharks	Large Alopiidae, Carcharhinidae, Lamnidae, Sphyrnidae
Bigeye tuna	Large <i>Thunnus obesus</i>
Yellowfin tuna	Large <i>Thunnus albacares</i>
Skipjack tuna	Large <i>Katsuwonus pelamis</i>
Piscivorous fish	Alepisauridae, Bramidae, Carangidae, Coryphaenidae, Gempylidae, large <i>Acanthocybium solandri</i> . No Scombridae, no billfish, no shark
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
Small scombrids	Small <i>Thunnus obesus</i> , <i>Thunnus albacares</i> , <i>Katsuwonus pelamis</i> , <i>Acanthocybium solandri</i> ; small and large <i>Auxis sp.</i> and other Scombridae
Epipelagic fish	Clupeidae, Engraulidae, Exocoetidae. No Scombridae
Mesopelagic fish	Gonostomatidae, Myctophidae, Phosichthyidae, Sternoptychidae
Cephalopods	Epi- and mesopelagic squids, cuttlefishes and octopi: Cranchiidae, Enoplotheutidae, Loliginidae, Octopoda, Ommastrephidae, Sepiidae
Crustacea	Amphipoda, Euphausiacea, Mysidacea, Penaeidae, Sergestidae, Decapoda larvae
Mesozooplankton	Zooplankton of the class size 200-2000 μm , mostly copepods.
Microzooplankton	Zooplankton of the class size 20-200 μm : copepod nauplii, ciliates, sarcodinids, rotifers, small cladocerans...
Large phytoplankton	All pelagic photosynthetic organisms larger than 2 μm , mainly diatoms
Small phytoplankton	All pelagic photosynthetic organisms smaller than 2 μm
Detritus	All pelagic non-living material, bacterioplankton, pico- and nanozooplankton

Table 2: Input parameters.

Group	Biomass	P/B	Q/B	EE	P/Q
Swordfish	0.002	0.4	5.2		
Other billfish	0.005	0.4	5.3		
Blue shark	0.014	0.3	2.5		
Other sharks	0.010	0.35	4.8		
Bigeye tuna	0.017	0.686	14.5		
Yellowfin tuna	0.045	1.221	15.1		
Skipjack tuna	0.104	2.362	17.0		
Piscivorous fish		1.0	9.0	0.95	
Small billfish	0.011	0.9	9.3		
Small sharks	0.012	0.5	5.2		
Small scombrids	0.214	2.0	17.6		
Epipelagic fish		2.0	13.9	0.95	
Mesopelagic fish	1.722	1.8	13.9		
Cephalopods	0.395	3.1	22.4		
Crustacea	1.000	5.2	20.8		
Mesozooplankton	4.000	33.0			0.3
Microzooplankton	1.724	100.0	300.0		
Large phytoplankton	1.989	134.0			
Small phytoplankton	11.271	94.6			
Detritus	130.000				

Biomass in tWM/km²; P/B and Q/B per year; EE and P/Q dimensionless (fraction of 1).

Table 3: Warm pool fisheries catch.

Group	WP total catch ¹	Tuna LL ²	Tuna PL ²	Tuna PS ²	Tuna OG ²	Other fisheries ³
Swordfish	0.056	0.064				0
Other Billfish	0.482	0.211		0.003		0.268
Blue shark	1.635	0.080				1.555
Other Sharks	1.167	0.057		0.003	0.037	1.070
BET	1.052	0.994		0.584	0.433	0
YFT	8.800	1.437	0.362	7.698	4.163	0
SKJ	27.980	0.031	5.373	24.976	2.900	0
Piscivorous fish	49.334	0.211	0.012	0.013	0.037	49.061
Epipelagic pk fish	46.743			0.013		46.730
Mesopelagic pk fish	0					0
Cephalopods	11.120					11.120

LL: longline. PL: pole and line. PS: purse seine. OG: other gears. ¹ FAO data 1994-2000, ² SPC data 1990-2001, ³ Other fisheries catch = FAO catch – SPC catch. Catch expressed in kg/ km²/ year.

Table 4: Input diet matrix.

#	Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	Swordfish		0.002		0.002													
2	Other billfish		0.002		0.002													
3	Blue shark		0.001		0.003													
4	Other sharks		0.001	0.012	0.001													
5	Bigeye tuna	0.002	0.009		0.005					0.003								
6	Yellowfin tuna	0.003	0.016		0.023		0.002			0.003								
7	Skipjack tuna	0.025	0.146		0.047	0.037	0.018		0.005	0.019	0.064	0.011						
8	Piscivorous fish	0.063	0.143	0.001	0.085	0.115	0.057	0.010	0.043	0.239	0.045	0.025						
9	Small billfish	0.003	0.005		0.002					0.007	0.004							
10	Small sharks		0.003	0.003	0.009				0.001	0.002								
11	Small scombrids	0.067	0.250		0.126	0.017	0.226	0.157	0.065	0.060	0.230	0.063						
12	Epipelagic fish	0.122	0.210	0.301	0.202	0.031	0.388	0.389	0.453	0.330	0.147	0.311	0.052		0.237			
13	Mesopelagic fish	0.156	0.046	0.050	0.096	0.342	0.084	0.105	0.117	0.140	0.125	0.201		0.118	0.326			
14	Cephalopods	0.542	0.164	0.527	0.333	0.379	0.133	0.159	0.120	0.145	0.323	0.152		0.005	0.106			
15	Crustacea	0.017	0.002	0.056	0.018	0.074	0.070	0.118	0.106	0.045	0.031	0.181	0.068	0.307	0.103	0.065		
16	Mesozooplankton			0.050	0.025	0.005	0.022	0.062	0.089	0.007	0.025	0.056	0.633	0.564	0.228	0.507	0.050	
17	Microzooplankton																	0.370
18	Large phytoplankton												0.210			0.247	0.150	
19	Small phytoplankton																	1.000
20	Detritus				0.021				0.001		0.006		0.037	0.006		0.181	0.430	
	SUM	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Predators in columns, preys in lines. Predators are called by their group number. The total diet of each predator is equal to 1.

Results

Balancing the model

Most Ecopath models are built using a set of input parameters consisting of means for the given period. These preliminary inputs are chosen based on the best available information, but the model is likely to be unbalanced at the first run, *i.e.*, not fulfilling realistic thermodynamic constraints. Values of the parameters have to be modified until a balanced model is achieved. The resulting model is one of the many possibilities that fit the defined constraints (Christensen *et al.*, 2000).

In our model, four groups (crustaceans, cephalopods, mesopelagic fish and small scombrids) are “unbalanced”: their ecotrophic efficiency (EE) is greater than one, in the range 2.198-3.086. This means that consumption (predation and fishing) is higher than production. Low EE calculated by the model for the top predators (less than 0.5) seem unrealistic for these heavily fished groups. Moreover, the calculated biomass for piscivorous fish and epipelagic fish is much too high to be realistic, and we can consider them unbalanced as well. Several parameters need to be modified to reach mass-balance.

Biomass, P/B and Q/B ratios are less subject to variation in space and time than diets. Therefore, we decided to modify diets in order to achieve mass balance (Table 6 p.12):

- Christensen *et al.* (2002) recommend minimizing cannibalism, as this has a strong artificial effect on the group’s biomass in the model. It was reduced to zero for crustaceans, cephalopods, mesopelagic, epipelagic and piscivorous fish and small scombrids;
- The main predator of each unbalanced species had its diet modified so that the prey was no more unbalanced;
- The overall predation on piscivorous and epipelagic fish was decreased to result in realistic biomass for those groups.
- Diets were also adapted so that EE approached 0.95 for microzooplankton, mesozooplankton, crustacea, cephalopods, mesopelagic fish and small scombrids. However it would not have been possible to reach this EE for other species without major diet changes.

Top predator EE were modified to reach higher values by exporting a fraction of the biomass out of the system.

Balanced model

The resulting model (Table 5) is one of the many possibilities that fit the defined constraints (Christensen *et al.*, 2000). Modified diets are presented in Table 7.

Table 5: Outputs of the modified model.

	Group name	Trophic level	Habitat area	Biomass in habitat area (t/km ²)	Biomass (t/km ²)	Prod./ biom. (/year)	Cons./ biom. (/year)	Ecotrophic efficiency	Production / consumption
1	Swordfish	4,70	1,000	0,002	0,002	0,400	5,200	0,900	0,077
2	Other billfish	4,20	1,000	0,005	0,005	0,400	5,300	0,900	0,075
3	Blue shark	4,50	1,000	0,014	0,014	0,300	2,500	0,900	0,120
4	Other sharks	4,70	1,000	0,010	0,010	0,350	4,800	0,900	0,093
5	Bigeye tuna	4,70	1,000	0,017	0,017	0,686	14,500	0,900	0,087
6	Yellowfin tuna	4,00	1,000	0,045	0,045	1,221	15,100	0,900	0,100
7	Skipjack tuna	4,20	1,000	0,104	0,104	2,362	17,000	0,900	0,100
8	Piscivorous fish	4,20	1,000	0,100	0,100	1,000	9,000	0,950	0,111
9	Small billfish	4,40	1,000	0,011	0,011	0,900	9,300	0,900	0,097
10	Small sharks	4,40	1,000	0,012	0,012	0,500	5,200	0,900	0,090
11	Small scombrids	4,10	1,000	0,214	0,214	2,000	17,600	0,940	0,114
12	Epipelagic fish	3,70	1,000	2,000	2,000	2,000	13,900	0,950	0,100
13	Mesopelagic fish	3,00	1,000	1,722	1,722	1,800	13,900	0,900	0,100
14	Cephalopods	3,00	1,000	0,395	0,395	3,100	22,400	0,907	0,100
15	Crustacea	2,80	1,000	1,000	1,000	5,200	20,800	0,900	0,200
16	Mesozooplankton	2,80	1,000	4,000	4,000	33,000	100,000	0,900	0,300
17	Microzooplankton	2,00	1,000	1,724	1,724	100,000	300,000	0,900	0,300
18	Large phytoplankton	1,00	1,000	1,989	1,989	134,000	-	0,900	-
19	Small phytoplankton	1,00	1,000	11,271	11,271	94,600	-	0,900	-
20	Detritus	1,00	1,000	130,000	130,000	-	-	0,200	-

The missing parameters are calculated by Ecopath software, and represented in shaded cells. Biomass in tWM/km²; P/B and Q/B per year; EE and P/Q dimensionless (fraction of 1).

Table 6: Balanced diet matrix.

#	Prey \ Predator	1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17
1	Swordfish		0.002		0.002													
2	Other billfish		0.002		0.002													
3	Blue shark		0.001		0.003													
4	Other sharks		0.001	0.012	0.001													
5	Bigeye tuna	0.002	0.009		0.005					0.003								
6	Yellowfin tuna	0.003	0.016		0.023		0.002			0.003								
7	Skipjack tuna	0.025	0.146		0.047	0.037	0.018		0.005	0.019	0.010	0.011						
8	Piscivorous fish	0.063	0.143	0.001	0.085	0.115	0.057	0.010	0.000	0.100	0.045	0.007						
9	Small billfish	0.003	0.005		0.002					0.007	0.004							
10	Small sharks		0.003	0.003	0.009				0.001	0.002								
11	Small scombrids	0.067	0.250		0.126	0.017	0.180	0.080	0.065	0.060	0.100	0.000						
12	Epipelagic fish	0.122	0.210	0.301	0.202	0.031	0.388	0.389	0.453	0.330	0.147	0.250	0.000		0.120			
13	Mesopelagic fish	0.156	0.046	0.050	0.096	0.342	0.130	0.105	0.117	0.140	0.125	0.201		0.000	0.180			
14	Cephalopods	0.542	0.164	0.527	0.333	0.379	0.133	0.159	0.132	0.145	0.323	0.100		0.000	0.000			
15	Crustacea	0.017	0.002	0.056	0.018	0.074	0.070	0.169	0.137	0.091	0.120	0.181	0.050	0.054	0.100	0.000		
16	Mesozooplankton			0.050	0.025	0.005	0.022	0.088	0.089	0.100	0.120	0.250	0.633	0.940	0.600	0.507	0.150	
17	Microzooplankton																	0.370
18	Large phytoplankton												0.280				0.312	0.150
19	Small phytoplankton																	1.000
20	Detritus				0.021				0.001		0.006		0.037	0.006		0.181	0.330	
	SUM	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1

Predators in columns, preys in lines. Predators are called by their group number. The total diet of each predator is equal to 1. Changes compared to unbalanced diet (Table 4 p.9) are highlighted in bold.

Consistency check

Model balancing was done manually. To ensure that our adjustments are realistic, it is important to check that the model parameters comply with physiological and thermodynamic constraints. Three important diagnostic indices were considered.

Gross food conversion efficiency (P/Q)

P/Q typically ranges from 0.05 to 0.15 for fish and from 0.1 to 0.3 for other organisms, but can be higher for very fast growing organisms such as bacteria (Jones, 1982 in Christensen, 1995; Paloheimo and Dickie, 1966 in Christensen, 1995).

Our model produced P/Q values ranging from 0.047 (bigeye tuna) to 0.144 (epipelagic fish) for fish, and from 0.138 (cephalopods) to 0.333 (microzooplankton) for non-fish groups (Table 5 p.11). These values are in the expected range.

However, the high value for large blue shark seems quite high for a top predator. It might indicate that blue shark, which P/Q value is higher than small sharks or small scombrids, is not very well parameterised.

Trophic levels

Trophic levels range from 1 (detritus and both phytoplankton groups) to 4.91 (other billfish). This is somewhat higher than the average value of Pauly and Christensen (1997). However, this is only due to a difference in zooplankton diet (Godinot, 2002). Apart from this minor difference, trophic levels are in the right order of magnitude. Top predators are the higher organisms of the food web, followed by small top predators, and piscivorous fish. Micronekton species (cephalopods, fish and crustaceans) are the link between plankton and fish, and zooplankton between phytoplankton and micronekton.

Turnover time

The turnover time is calculated as B/P , and expressed in years. It represents the necessary time for one group to renew its biomass. Figure 2 represents the turnover time, in $\log(\text{years})$, as a function of trophic level. Turnovers almost follow an exponential trajectory. Top predators and their young are a very homogeneous population, but blue shark is standing out with the slowest turnover (3.3 years). We can conclude that its P/B is probably too low. Micronekton have a slower turnover than expected by their trophic level according to the regression curve. On the contrary, micro and mesozooplankton have a faster turnover than expected.

However, with a R^2 over 0.9, this lets us conclude that production and biomass are coherent with trophic level for most of the groups.

Subsequently to those tests, we can conclude that no data is completely out of range, even after the modifications necessary to reach mass- balance.

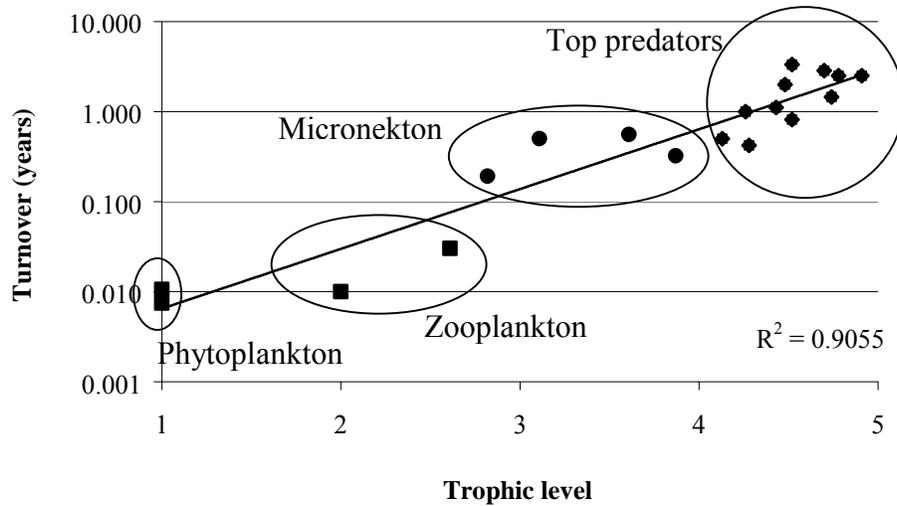


Figure 2: Turnover time as a function of trophic level

Y-axis is logarithmic. Squares: plankton; circles: micronekton; diamonds: top predators.

Sensitivity analysis

The software includes a sensitivity routine. For each group, each of the three input parameters (B, Q/B and P/B for most groups) varies from -50% to $+50\%$. The output parameters of all other groups (EE for most groups) are more or less modified in order to preserve mass-balance.

Here we counted how many output parameters were modified by more than 5% for a $\pm 50\%$ input parameter change (Figure 3).

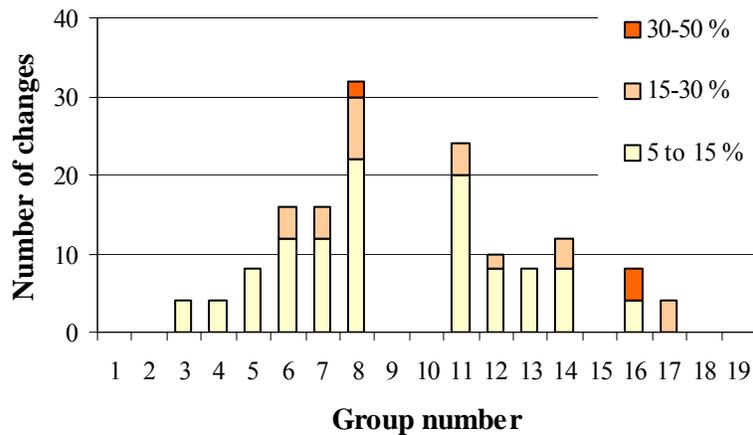


Figure 3: Sensitivity of the model to input parameter variations ($\pm 50\%$).

Groups for which biomass is estimated (group 8 Piscivorous fish and group 12 Epipelagic fish) can undermine the stability of the model by affecting numerous groups at the same time: increased biomass for a top-predator leads to increased prey consumption. If the preys' calculated parameter is biomass, high predation mortality will result in high biomass estimation (and hence high consumption), leading in turn to increased biomass

and consumption for the preys' own preys... This is known as a 'cascading effect' (Christensen, 1995). Groups for which Ecopath estimates EE induce less change in the ecosystem, as they do not produce cascading effects.

In our case, 17 out of 19 groups' estimated parameters are EE. The network absorbs strong input parameters variations in most cases. We can conclude that our model is not sensitive to relatively important variations of input parameters. It is nonetheless important to highlight that piscivorous fish and small scombrids are the most sensitive groups of the model.

Response of the model to an increase of fishing catches

The Ecopath model developed in this study is still preliminary, mostly due to the lack of local data. Albeit the lack of reliability of the model, Ecosim was used to test the response of the model to perturbation. The catches of all five fleets was doubled after 5 years and maintained at this high level during 25 more years to allow biomasses to stabilize.

For a more realistic result, juvenile and adult groups were linked in the model. The links were not parameterized and the default values of the model were used. It was necessary to create new juvenile groups as Ecosim does not allow to link one group to several others. Then small sharks, small billfish and small scombrids were split into small BSH, small other sharks, small SWO, small other billfish and small SKJ, small YFT and small BET respectively. A group of small scombrids was also kept to represent *Auxis sp.*, juvenile wahoo, mackerels... Input parameters of these groups were roughly parameterised according to importance of the corresponding large groups.

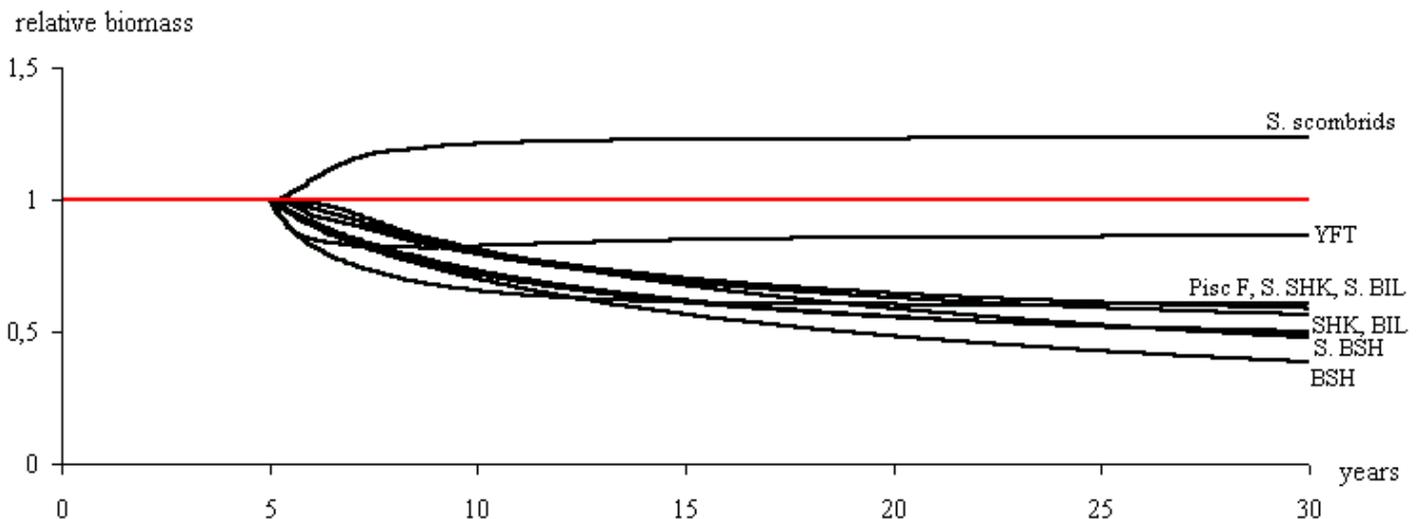


Figure 4: Evolution of relative biomass for linked groups after a fishing mortality increase

Fishing mortality is doubled at year 5 and maintained. Adult tuna, shark and billfish groups linked with juveniles. Only biomasses changing more than ± 0.1 are represented on the graph. BIL: billfish; BSH: blue shark; Pisc F: piscivorous fish; SHK: other sharks; YFT: yellowfin tuna. S.scombrids not including small tunas.

It is quite complex to study the evolution of biomasses that are based on numerous predator-prey relationships inducing direct and indirect effects, but several factors can be invoked to explain tendencies observed (Figure 4).

The more impacted groups are the shark and billfish top predators, juveniles and adults. When the fishing mortality is doubled, it also concerns non-tuna fisheries (Table 3) and fisheries targeting sharks and billfish are large enough to have a strong impact on these species considering their low P/B.

Piscivorous fish are also highly fished and although most of their predators are negatively impacted, it does not allow them to maintain their biomass. Epipelagic fish does not present any noticeable variation albeit an important fishery and a decrease of their predators, a P/B of 2.0 could explain the difference of reaction compared to piscivorous fish that have a P/B of 1.0.

Surprisingly BET are not impacted when YFT show a decrease of its biomass. The decrease of their predators that are very similar could balance the effect of the fishery in the case of the BET. A noticeable difference in the diet matrix is a cannibalism component in the case of YFT that becomes probably an important part of the predation as the other predators decrease. SKJ does not show any variation; high P/B, more available food as S scombrids increase and less predation as top predators decrease seem to balance the increased fishing pressure.

Small scombrids not submitted to fishing in this model benefit of important decrease of predation by top predators and less competition for food by the same top predators that allows an increase of its biomass. They are in fact submitted to other fisheries and a better parameterization should allow correcting this somewhat artificially enhanced effect.

To conclude, doubling the fishing effort during 25 years reduces the biomass of sharks, billfish, YFT and piscivorous fish. The only top-down effect is shown by small scombrids which biomass increase. This quasi-absence of top-down cascade is also documented by Cox *et al.* (2002), who had difficulty detecting any substantial ecosystem-scale impacts of fishing in the pelagic Pacific. However it is important to remind that this very preliminary simulation is based on an Ecopath model with many uncertainties concerning input data, as most of the information is based on literature and not local data. Hence, at this stage, no confidence can be given to the variations observed, nonetheless, it is useful to show what kind of results can be expected from such model and simulations.

Discussion – Conclusion

This model has been developed as a preliminary model of the WCPO. It is important to recall that it is one of several alternative equilibria fitting our input requirements, and that much of the information synthesized in this model is uncertain.

Ecopath limitations

It is also crucial to remember the pitfalls of Ecopath when using it.

The general assumption in this software is that, considering a long period of time, a mass-balanced model should correctly represent the basic trophic interactions between groups

in the ecosystem. This working hypothesis is questionable especially in exploited ecosystems.

One of the major sources of errors comes from the estimation of rare prey types in a given predator's diet. It is easy to overlook a minor diet item in specifying diet composition for some predator. Unfortunately, while that prey type may not be important for the predator, it may represent a very large component of total mortality for the prey type and enhanced the sensitivity of the model (Christensen and Walters, 2000). Additionally, Ecopath cannot explain all relationships in the ecosystem. The only considered interaction mechanism is direct consumption. The model ignores factors like habitat alteration, diet shifts, and other trophic interactions ... For example, the rarefaction of a predator will be predicted to result in an increase of its prey. However, the prey's biomass could as well stay stable –or even decrease– due to increased predation mortality from another, less competitive predator (Christensen and Walters, 2000).

Finally several parameters that are tackled in most single-species models are not considered in EwE software. There is no explicit consideration of seasonal changes or directed migration (Walters *et al.*, 1999), and size-selectivity of predation is ignored. Abiotic phenomenon such as nutrient uptake by phytoplankton or temperature preferences cannot be considered.

Weaknesses of the warm pool ecosystem model

The major weakness of our Ecopath model is the uncertainty of most parameters and diets. Most species are poorly known, and input parameters used are usually not based on local data. An effect of the lack of local data is the use of data originating from other regions. This leads to great uncertainty in the estimation of B, P/B and Q/B values, as biological factors and abundance can vary strongly with the area.

Our model counts 19 living groups, a relatively small number compared to other existing models. This is not due to a reduced biodiversity but to an over-aggregation of some groups due to a lack of detailed information. Many groups were not even included in the model due to the lack of information, for instance whales, dolphins, marine birds, rays, skates and turtles. These species inhabit the warm pool either temporarily or permanently, and they certainly have an effect upon the ecosystem. Other species such as bluefin tuna or albacore tuna were not included as they are mostly temperate species. Nonetheless, they can be caught in relatively important numbers in the warm pool and should be included as temporary visitors of the area.

Improvements to the model

The first improvement should be to replace current data with local data both on target and bycatch species as well as on non-exploited species. It is important to enrich the model as soon as information is gained on these species. The sampling programme implemented to collect stomachs of top predators should allow improving the diet matrix. Biomass, production and consumption estimates also need to be improved. Fisheries catch could also be more precise by including discard data.

Linking large and small groups has important effects on the quality of the predictions. Thus, creating one small group for each group of interest could be a useful improvement as well as precisely defining the link parameters between juveniles and adults.

It would be an important improvement of the model to realise comparisons of obtained results with historical data. Comparisons using Ecosim are the only way to judge the quality of the predictions of the model. A model that can reproduce historical data and dynamics at least provides a good starting point, even if it is very roughly parameterised (Cox *et al.*, 2002). Thus, trying to reproduce historical SPC data, by introducing data series in the simulation, could be very rewarding and help improve the design of the model.

Further work is needed on Ecosim scenario to obtain better results when simulating fishing scenarios, but also variations of phytoplankton due to phenomenon such as ENSO variations to test the bottom-up effect. Preliminary tests were conducted with this model and it seems that the bottom-up effect is much more accentuated than the top-down effect observed with fishery impact.

Interest of the ecosystem modeling

First of all, such exercises helps spot the most important data gaps and define priorities in data refinement needs. Priority is related with uncertainty of the group's input parameters, overall influence on the system and other user-defined factors such as preservation of rare or valuable species. As Okey (2001) and Christensen and Walters (2000) underlined, the construction of a preliminary Ecopath model is useful, as it pinpoints what is *not* known about the ecosystem, be it biomass, production, or even trophic links between groups (predator-prey relationships).

Prior to simulation exercises, this model tells us little about the system that was not already known. However, it offers an easily accessible view of the system. Moreover, it is a powerful tool to aggregate ecosystem data from different sources. In the end, it represents a necessary framework for the refinement of input parameters so that a cohesive view of the whole marine ecosystem can emerge, and so that questions about the system mechanisms and dynamics can be explored (Okey, 2001; Okey and Pugliese, 2001). It is probably in this exploratory approach that the model is the most useful. The software developers identified various potential uses for the model, including testing hypotheses about ecosystem functions, policy screening of proposed ecosystem management strategies and better understanding of the possible impacts of long-term regime shifts (Gibbons-Fly, 2000). In our case, the splitting of fisheries into four tuna fleets and another miscellaneous fleet could for example allow the investigation of various policy measures at the fleet level. However, depending on the level of uncertainty of the model, results emerging from these scenarios would likely be highly speculative. Polovina (1996) also stressed that Ecopath can be used to explore ecosystem responses to environmental variations, by explicitly describing biological parameters (such as phytoplankton biomass) as functions of physical variables (such as light and nutrient concentration) and then drive Ecosim with physical time series. Another, more intuitive method is to translate physical variations into biological effects. For example, increasing larval advection can be expressed as decreasing recruitment or increasing mortality.

Ecosystem modeling, or multispecies modeling is a tool for learning about a system. It has the potential to indicate which of several management options available may be the most effective. Alternatively, and just as valuable, it can indicate which will be least

effective (Gibbons-Fly, 2000). Ecosystem modeling provides the facility to answer questions that cannot be solved with single-species models, such as the effects of fishing on non-target species and efficiency of policy interventions aimed to limit side-effects of fishing.

However, the point of this report is not to compare or oppose ecosystem-based and single-species modeling. Both present advantages and drawbacks, but more importantly they are not incompatible: EwE can integrate time series data from single-species models, and use split pools for each age class of a given species. Single-species models can therefore improve Ecopath inputs (Christensen and Walters, 2000).

Embedding single species models for a small number of species of interest into an ecosystem model could be very useful, as they would combine the reduced uncertainty of single-species models together with the capacity of examination of various measures at the ecosystem scale (Mace, 2001). Ecopath is a model, and as any other model it has limitations that produce uncertainty on the results. It can complement other management tools to help in the development of ecosystem-based management, but sensitivity and uncertainty need to be clearly identified and quantified, and results validated.

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CSIRO website, Australian JGOFS programme:

http://www.marine.csiro.au/datacentre/JGOFSweb/cmr_jgofs.htm

FAO website, Fisheries Databases and Statistics:

ftp://ftp.fao.org/fi/maps/fig_h4_71_0.gif

GLOBEC website, working group reports:

<http://www.usglobec.org/reports/ebcccs/ebcccs.wg5.html>

Fishbase website:

<http://www.fishbase.org>

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 <i>et al.</i> , 1999, 2002; Kleiber and Yokawa, 2002; Olson and Watters, 2003	Guénette and Morato, 1997; Kitchell <i>et al.</i> , 1999, 2002; Olson and Watters, 2003		Cox <i>et al.</i> , 2002; Guénette and Morato, 1997; Kitchell <i>et al.</i> , 2002; Olson and Watters, 2003
Other billfish	Kitchell <i>et al.</i> , 1999, 2002; Okey and Pugliese, 2001	Kitchell <i>et al.</i> , 1999, 2002; Kleiber <i>et al.</i> , 2001b, 2002; Okey and Pugliese, 2001; Olson and Watters, 2003	Browder, 1993; Kitchell <i>et al.</i> , 1999, 2002; Okey and Pugliese, 2001; Olson and Watters, 2003		Abitia-Cardenas <i>et al.</i> , 1999; Cox <i>et al.</i> , 2002; Kitchell <i>et al.</i> , 2002; Olson and Watters, 2003; Fishbase
Blue shark	Kitchell <i>et al.</i> , 1999, 2002	Kitchell <i>et al.</i> , 1999, 2002; Kleiber <i>et al.</i> , 2001a	Kitchell <i>et al.</i> , 1999, 2002		Cortés, 1999; Kitchell <i>et al.</i> , 2002; Fishbase
Other sharks	Kitchell <i>et al.</i> , 2002	Arreguín-Sánchez <i>et al.</i> , 1993a, b; Browder, 1993; De Paula E Silva <i>et al.</i> , 1993; Guénette and Morato, 1997; Kitchell <i>et al.</i> , 1999, 2002; Okey and Pugliese, 2001; Olson and Watters, 2003; Opitz, 1993; Polovina and Ow, 1983; Sheridan <i>et al.</i> , 1984; Wolff <i>et al.</i> , 1996	Arreguín-Sánchez <i>et al.</i> , 1993a, b; Browder, 1993; De Paula E Silva <i>et al.</i> , 1993; Guénette and Morato, 1997; Kitchell <i>et al.</i> , 1999, 2002; Okey and Pugliese, 2001; Olson and Watters, 2003; Opitz, 1993; Polovina and Ow, 1983; Wolff <i>et al.</i> , 1996		Cox <i>et al.</i> , 2002; Guénette and Morato, 1997; Kitchell <i>et al.</i> , 2002; Olson and Watters, 2003; Fishbase
Bigeye tuna	SPC data	SPC data	Kitchell <i>et al.</i> , 1999, 2002; Olson and Watters, 2003		Cox <i>et al.</i> , 2002; Kitchell <i>et al.</i> , 2002; Olson and Watters, 2003; Fishbase; SPC data
Yellowfin tuna	SPC data	SPC data	Kitchell <i>et al.</i> , 1999, 2002; Olson and Watters, 2003; Fishbase		Cox <i>et al.</i> , 2002; Kitchell <i>et al.</i> , 2002; Olson and Watters, 2003; Roger, 1973b; Fishbase; SPC data
Skipjack tuna	SPC data	SPC data	Kitchell <i>et al.</i> , 1999, 2002; Olson and Watters, 2003; Fishbase		Cox <i>et al.</i> , 2002; Kitchell <i>et al.</i> , 2002; Olson and Watters, 2003; SPC data
Piscivorous fish		Abarca-Arenas and Valero-Pachero, 1993; Aliño <i>et al.</i> 1993; Arreguín-Sánchez <i>et al.</i> , 1993a, b; De La Cruz-Aguero, 1993; De Paula E Silva <i>et al.</i> , 1993; Kitchell <i>et al.</i> , 1999; Mendoza, 1993; Okey and Pugliese, 2001; Olson and Watters, 2003; Opitz, 1993; Silvestre <i>et al.</i> , 1993; Fishbase	Abarca-Arenas and Valero-Pachero, 1993; Aliño <i>et al.</i> 1993; Arreguín-Sánchez <i>et al.</i> , 1993a, b; De La Cruz-Aguero, 1993; De Paula E Silva <i>et al.</i> , 1993; Kitchell <i>et al.</i> , 1999; Mendoza, 1993; Okey and Pugliese, 2001; Olson and Watters, 2003; Opitz, 1993; Silvestre <i>et al.</i> , 1993; Fishbase	EE: High value based on assumption that most of the production is consumed by predators	Cox <i>et al.</i> , 2002; Kitchell <i>et al.</i> , 2002; Olson and Watters, 2003; Fishbase; SPC data
Small billfish	Kitchell <i>et al.</i> , 1999	Olson and Watters, 2003	Olson and Watters, 2003		Olson and Watters, 2003
Small sharks	Kitchell <i>et al.</i> , 1999	Cox <i>et al.</i> , 2002; Kitchell <i>et al.</i> , 1999; Olson and Watters, 2003	Cox <i>et al.</i> , 2002; Kitchell <i>et al.</i> , 1999; Olson and Watters, 2003		Cox <i>et al.</i> , 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
Small scombrids	Cox <i>et al.</i> , 2002; Kitchell <i>et al.</i> , 1999, 2002; Olson and Watters, 2003	Cox <i>et al.</i> , 2002; De Paula E Silva <i>et al.</i> , 1993; Kitchell <i>et al.</i> , 1999, 2002; Olson and Watters, 2003; Suda and Kume, 1967; Fishbase	Cox <i>et al.</i> , 2002; De Paula E Silva <i>et al.</i> , 1993; Kitchell <i>et al.</i> , 1999, 2002; Olson and Watters, 2003; Pauly <i>et al.</i> , 1993a		Cox <i>et al.</i> , 2002; Olson and Watters, 2003
Epipelagic fish		Abarca-Arenas and Valero-Pachero, 1993; Arreguín-Sánchez <i>et al.</i> , 1993a; Cox <i>et al.</i> , 2002; De La Cruz-Aguero, 1993; De Paula E Silva <i>et al.</i> , 1993; Kitchell <i>et al.</i> , 1999, 2002; Mendoza, 1993; Olivieri <i>et al.</i> , 1993; Olson and Watters, 2003; Silvestre <i>et al.</i> , 1993; Fishbase	Abarca-Arenas and Valero-Pachero, 1993; Arreguín-Sánchez <i>et al.</i> , 1993a; Cox <i>et al.</i> , 2002; De La Cruz-Aguero, 1993; De Paula E Silva <i>et al.</i> , 1993; Kitchell <i>et al.</i> , 1999, 2002; Mendoza, 1993; Olivieri <i>et al.</i> , 1993; Olson and Watters, 2003; Silvestre <i>et al.</i> , 1993; Fishbase	EE : High value based on assumption that most of the production is consumed by predators	De Paula E Silva <i>et al.</i> , 1993; Guénette and Morato, 1997; Mendoza, 1993; Olivieri <i>et al.</i> , 1993; Olson and Watters, 2003; Silvestre <i>et al.</i> , 1993; Fishbase
Mesopelagic fish	Grandperrin, 1975; Legand <i>et al.</i> , 1972	Cox <i>et al.</i> , 2002; Kitchell <i>et al.</i> , 2002; Olson and Watters, 2003; Fishbase	Considered same as epipelagic fish, like in Kitchell <i>et al.</i> (2002) and Olson and Watters (2003)		Legand <i>et al.</i> , 1972; Williams <i>et al.</i> , 2001; Fishbase
Cephalopods	Kitchell <i>et al.</i> , 1999, 2002	Aliño <i>et al.</i> , 1993; Arreguín-Sánchez <i>et al.</i> , 1993b; Cox <i>et al.</i> , 2002; Kitchell <i>et al.</i> , 1999, 2002; Mendoza, 1993; Okey and Pugliese, 2001; Olson and Watters, 2003; Opitz, 1993;	Aliño <i>et al.</i> , 1993; Arreguín-Sánchez <i>et al.</i> , 1993b; Cox <i>et al.</i> , 2002; Kitchell <i>et al.</i> , 1999, 2002; Mendoza, 1993; Okey and Pugliese, 2001; Olson and Watters, 2003; Opitz, 1993;		Coelho <i>et al.</i> , 1997; Cox <i>et al.</i> , 2002; Guénette and Morato, 1997; Kitchell <i>et al.</i> , 2002; Martins, 1985; Mendoza, 1993; Olson and Watters, 2003;
Crustacea	Grandperrin, 1975; Legand <i>et al.</i> , 1972	Abarca-Arenas and Valero-Pachero, 1993; Aliño <i>et al.</i> , 1993; Arreguín-Sánchez <i>et al.</i> , 1993a, b; Beamish <i>et al.</i> , 2000; Browder, 1993; De La Cruz-Aguero, 1993; Guénette and Morato, 1997; Lapko <i>et al.</i> , 2000; Mc Farlane <i>et al.</i> , 2001; Olivieri <i>et al.</i> , 1993; Olson and Watters, 2003; Vega-Cendejas <i>et al.</i> , 1993	Abarca-Arenas and Valero-Pachero, 1993; Aliño <i>et al.</i> , 1993; Arreguín-Sánchez <i>et al.</i> , 1993a, b; Beamish <i>et al.</i> , 2000; Browder, 1993; De La Cruz-Aguero, 1993; Guénette and Morato, 1997; Lapko <i>et al.</i> , 2000; Mc Farlane <i>et al.</i> , 2001; Olivieri <i>et al.</i> , 1993; Olson and Watters, 2003; Vega-Cendejas <i>et al.</i> , 1993		Arreguín-Sánchez <i>et al.</i> , 1993a, b; Guénette and Morato, 1997; Morissette, 2001; Olivieri <i>et al.</i> , 1993; Roger, 1973a
Mesozooplankton	Le Borgne and Rodier, 1997	Aliño <i>et al.</i> , 1993; Arreguín-Sánchez <i>et al.</i> , 1993a, b; Browder, 1993; Chai <i>et al.</i> , 2002; Chávez <i>et al.</i> , 1993; De La Cruz-Aguero, 1993; De Paula E Silva <i>et al.</i> , 1993; Mendoza, 1993; Olivieri <i>et al.</i> , 1993; Opitz, 1993; Roman <i>et al.</i> , 2002a, b; Silvestre <i>et al.</i> , 1993; Vega-Cendejas <i>et al.</i> , 1993		P/Q : Dalsgaard and Pauly, 1997; Omori and Ikeda, 1984 in Roman <i>et al.</i> , 2002a; Straile, 1997 in Roman <i>et al.</i> , 2002a U/Q : Conover, 1978 in Roman <i>et al.</i> , 2002a	Parts calculated from various sources, see (3); Olivieri <i>et al.</i> , 1993
Microzooplankton	Le Borgne and Rodier, 1997	Olivieri <i>et al.</i> , 1993	Olivieri <i>et al.</i> , 1993		Assumed to feed exclusively on small phytoplankton, like in Chai <i>et al.</i> , 2002.
Large phyto	Various sources, see (1)	Various sources, see (2)			
Small phyto	Various sources, see (1)	Various sources, see (2)			
Detritus	Pauly <i>et al.</i> , 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/km².

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/km²**, and thus the biomass of small plankton around **11.3 tWM/km²**.

(2) phytoplankton P/B ratios

Le Borgne *et al.* (2002b) estimated primary production at 0.32 gC/m²/d, or 1333 tWM/km²/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.

$$0.05 * 1333 = 66.65 \text{ tWM/km}^2/\text{y}$$

$$Q_{\text{mesozooplankton}} = Q/B * B = 110 * 4 = 440 \text{ tWM/km}^2/\text{y}$$

$$66.65 / 440 = 0.15$$

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.