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Trophic structure of the pelagic ecosystems of the western and central pacific ocean

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1. Introduction

With the long term goal of developing ecosystem approach to fisheries management for the tuna pelagic ecosystem, our first objective is "*to improve understanding of the transboundary oceanic fish resources and related features of the western and central Pacific warm pool large marine ecosystem*" (GEF OFM project). One mean of understanding the functioning of the ecosystem is by building ecosystem models which ultimately will allow assessing fishing and environmental impacts on the whole ecosystem and evaluating management options.

One of the first steps towards building ecosystem models is to quantify and qualify the structure of the ecosystem which is based on prey-predator relationships that are the most important interactions between species. Hence, determining trophic interactions between species by examining stomach contents is the primordial step towards a better understanding and modelling of the ecosystem dynamic.

In this information paper are presented trophic structure information resulting from stomach content examination of 20 top predator species. Results on diversity, prey composition and food webs are provided for 4 pelagic ecosystems as defined by Longhurst in the western and central Pacific.

2. Methods

2.1. Sampling programme

Stomach samples are collected from target fish (tunas) and bycatch species by observers from the different national observer programmes in the area and by scientists during tagging cruises. The majority of the samples were collected onboard longliners (LL), purse-seiners (PS) and pole-and-line vessels (PL). Fishing gears are passive and baited in the case of LL and PL, it is active in the case of PS which can target free schools or aggregated schools around FADs or logs. These fishing methods are targeting different species and catching fish of different sizes, in different areas, at different depth and time. Since the beginning of the study in 2001, a total of 8627 fish from 73 species have been collected.

2.2.Stomach examination procedure

Classical procedure is used to analyze the stomachs. Stomach fullness coefficient is determined from 0-empty to 4 -full. In non-empty stomachs preys are sorted by species or group, identified at the lowest taxonomic level, a digestion state is attributed (from 1-fresh to 4-bone or beak remains), development state is determined (larvae, juvenile, adult); they are counted, weighed and measured.

Since the beginning of the study in 2001, a total of 6438 fish stomachs have been examined (75% of the collection).

2.3.Selection of samples for this study

The goal of this paper being to present the trophic structure of the ecosystem, empty stomachs will not be considered, reducing to 4559 the number of samples included.

2.3.1. Area

Samples being distributed over a very wide area in the Pacific, it is not appropriate to consider all the samples belonging to a unique ecosystem. In this study, we are using the biogeographic partition of the ocean established by Longhurst (Longhurst, 2007) based on various environmental parameters including currents, fronts, depth, water masses, vertical stratification, irradiance, nutrients, phytoplankton production and composition… The spatial distribution of the samples indicates a sufficient number of samples (>200) for only 4 Longhurst provinces (**Error! Reference source not found.**). The analysis will then be limited to ARCH Archipelagic Deep Basins Province (1793 samples), SPSG South Pacific Subtropical Gyre Province (873), SUND Sunda-Arafura Shelves Province in Indonesia (227) and WARM West Pacific Warm Pool Province (1547). Samples outside these 4 provinces will not be considered.

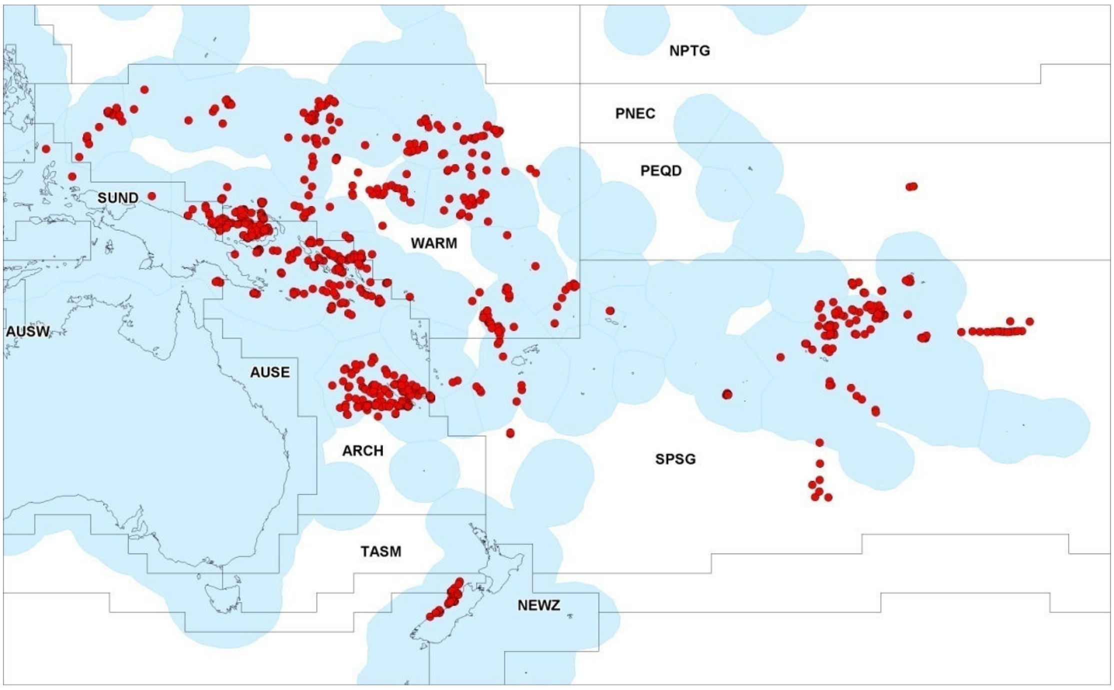


Figure 1. Spatial distribution of the non-empty stomachs examined. Black lines represent the boundaries of the Longhurst areas which are named using a 4-letter code (see text). In blue are represented the EEZ.

2.3.2. Predator species

In the 4 provinces selected, the number of predator species examined varies, as well as the number of samples per predator. For diversity analyses all predators were selected (**Error! Reference source not found.**).

Table 1. Number of species and stomach samples examined per Longhurst area

	Number of predator species	Number of non-empty stomachs
ARCH	48	1793
SPSG	30	873
SUND	10	227
WARM	40	1547

Of these species, the top-twenty predators in total number of fish examined were selected for analyses on prey composition; for food webs predators with less than 10 samples were not included. Moreover 5 species were split into several groups to account for the various developmental stages (**Error! Reference source not found.**). Split between Small (Sm) and Large (Lg) groups is based on length at maturity. Additional groups of Baby (Bb) were added for SKJ, YFT and BET. For SKJ this limit corresponds to age 3 months as it is used in stock assessment and which is heavily consumed by predators. For YFT, (Graham *et al.*, 2007) showed a diet shift for YFT at around 45cm; it is suspected to be the same for BET.

Predators were identified as deep or surface species according to general knowledge on their behaviour. The number of samples varies per predator and province (**Error! Reference source not found.**).

Table 2. Size (UF-upper jaw to fork length) definition of the developmental stages of 5 predator species.

Species	FAO code	Baby-Bb	Small-Sm	Large-Lg
Skipjack	SKJ	<24cm	24-43cm	≥43cm
Yellowfin	YFT	<45cm	45-120cm	≥120cm
Bigeye	BET	<45cm	45-124cm	≥124cm
Albacore	ALB		<85cm	≥85cm
Lancetfish	ALX		<105cm	≥105cm

Table 3. Number of non-empty stomachs examined per species groups (top-twenty species) and Longhurst area. Orange cells represent predators for which less than 10 samples are available and which are not considered in food web analyses.

Species name	Species scientific name	Species code	Type	ARCH	SPSG	SUND	WARM
Albacore large	Thunnus alalunga	ALBLg	Deep	125	128		16
Albacore small	Thunnus alalunga	AlbSm	Deep	34	1		1
Lancetfish large	Alepisaurus ferox	ALXLg	Deep	56	15		4
Lancetfish small	Alepisaurus ferox	ALXSm	Deep	34	14		
Bigeye baby	Thunnus obesus	BETBb	Surface	12		16	11
Bigeye large	Thunnus obesus	BETLg	Deep	19	28		37
Bigeye small	Thunnus obesus	BETSm	Deep	71	141	10	121
Blue marlin	Makaira nigricans	BUM	Surface	10	20	1	10
Dolphinfish	Coryphaena hippurus	DOL	Surface	74	40	1	27
Silky shark	Carcharhinus falciformis	FAL	Surface	9		1	14
Frigate tuna	Auxis thazard	FRI	Surface	11		1	6
Great barracuda	Sphyraena barracuda	GBA	Surface	24	9		4
Kawakawa	Euthynnus affinis	KAW	Surface	2		8	32
Opah	Lampris guttatus	LAG	Deep	36	34		
Striped marlin	Kajikia audax	MLS	Surface	17	20		4
Pelagic stingray	Dasyatis violacea	PLS	Surface	14	17		
Rainbow runner	Elagatis bipinnulata	RRU	Surface	42		14	81
Sailfish	Istiophorus platypterus	SFA	Surface	13	1		3
Skipjack baby	Katsuwonus pelamis	SKJBb	Surface	6			
Skipjack large	Katsuwonus pelamis	SKJLg	Surface	214	37	38	314
Skipjack small	Katsuwonus pelamis	SKJSm	Surface	159	1	35	176
Shortbill spearfish	Tetrapturus angustirostris	SSP	Surface	22	25		2
Swordfish	Xiphias gladius	SWO	Deep	10	26		10
Triggerfish	Balistidae	TRI	Surface	1			28
Wahoo	Acanthocybium solandri	WAH	Surface	47	92		23
Yellowfin baby	Thunnus albacares	YFTBb	Surface	238		45	195
Yellowfin large	Thunnus albacares	YFTLg	Surface	72	80	3	41
Yellowfin small	Thunnus albacares	YFTSm	Surface	296	90	53	331
			Total	1668	819	226	1491

2.3.3. Prey species

All preys were considered to calculate diversity indices and prey composition by category and vertical class. For more detailed prey composition and food webs, preys were grouped by species, by families or larger groups (named taxa) to obtain a manageable list of preys and create simplified food webs.

Based on literature review each prey is classified according to its vertical distribution and migrating pattern (**Error! Reference source not found.**).

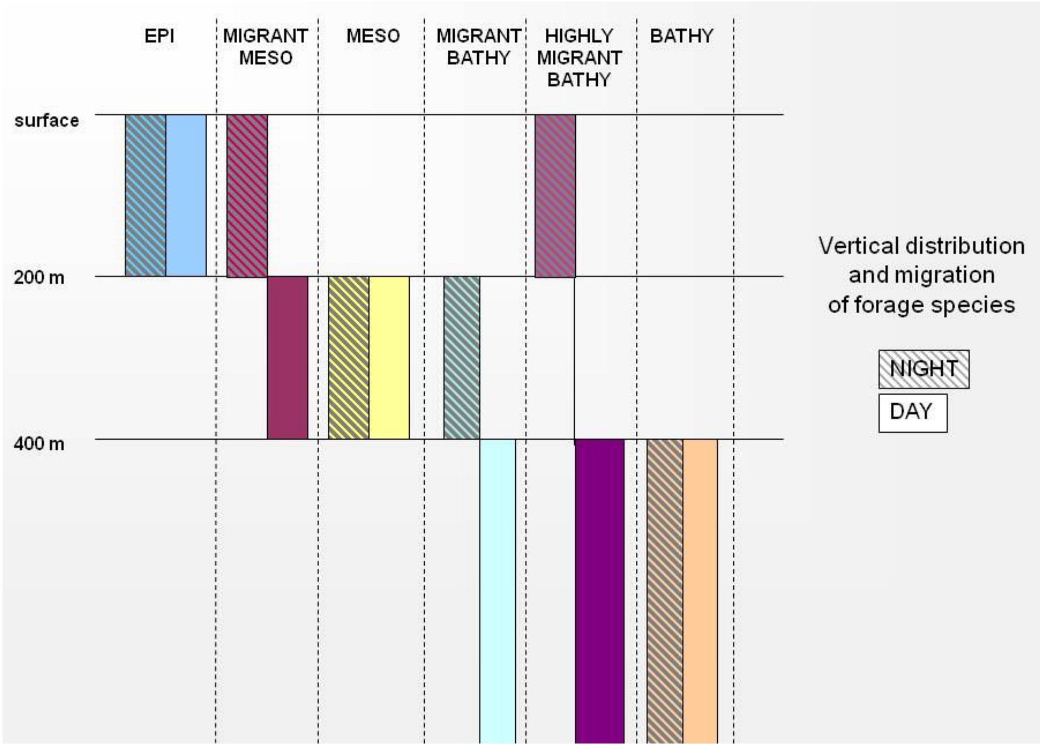


Figure 2. Vertical classification of the prey groups representing their vertical distribution night and day. The epipelagic group is moreover split between oceanic and reef-associated species.

2.3.4. Data analysis

Diversity

Diversity of the 4 Longhurst provinces studied is described by the species richness (total number of prey species observed). However species richness is highly related to the number of samples collected and presents an increasing trend with the number of samples to eventually reach a plateau when the number of samples examined is representative. It is then incorrect to compare areas with different number of samples. This problem can be resolved by calculating the number of species in the different areas if the same number of samples is examined using the rarefaction method (Hurlbert, 1971). The formula computes the expected number of species for a chosen standardized number of samples.

Considering that the number of prey individuals per area ranged from 3874 to 42590 (considered as the sample size), using the rarefaction method we calculated the expected number of species for samples of 3800 and 15000 individual preys. The same method was used to establish cumulative expected prey species richness.

Total species richness is calculated using all the preys species, but the rarefaction method was applied to non-rare preys only which are defined as prey for which the total number of individuals is strictly superior to 5.

The Shannon's diversity index H (Legendre & Legendre, 1998) was also calculated using non-rare prey species. H takes into account the number of species and the number of individuals per species; it increases with the number of species and for a given number of species it is maximum when the individuals are equally distributed among the species.

Prey composition

For prey composition, data was analyzed using weight of prey (W) cumulated for all the samples in a province. Results are presented for various degree of aggregation of the preys: by broad category (Fish, Mollusc, Crustacea, Other), by vertical class (**Error! Reference source not found.**) or by detailed composition of the prey items by taxa (species, family or group).

Food webs

From detailed diet data per predator, food webs can be built. They are usually compiled into diet matrices that can be directly included into models such as Ecopath. Food webs can also be presented in a more graphic manner allowing apprehending the complexity of the ecosystem. Simplified food webs were constructed by transforming the predator diet data into prey-predator matrices (matrices are not provided in this paper) for each province based on the top-twenty predators with more than 10 non-empty stomachs and prey taxa.

Three descriptors are used to characterise the food webs: S, the number of taxa, L, the number of interspecific links and D, the link density (D=L/S) (Dambacher *et al.*, 2010). Simplified food webs were further reduced to create food web graphs, including only the top-five preys of each predator (in %W, not including unidentified and miscellaneous preys).

3. Results

3.1. Diversity of preys

A grand total of 466 different species were identified from the 106,480 prey individuals extracted from the 4,440 stomachs examined (**Error! Reference source not found.**). Per Longhurst area, the total species richness varied from 77 in SUND to 378 in ARCH, SPSG and WARM presenting intermediate values of 270 and 249 species respectively. When only non-rare species are considered the number of species is inferior, but the ranking between provinces stays the same (**Error! Reference source not found.**).

However the number of samples examined (in stomach and prey individual numbers) being different, comparison between provinces is more suitable using the rarefaction method. Cumulative prey species richness indicates clearly that the number of samples examined in ARCH, SPSG and WARM are sufficient to describe the diversity of these provinces while it is not the case for SUND for which the curve does not clearly reach a plateau (**Error! Reference source not found.**). Species richness rarefied for a sample of 3800 prey individuals demonstrate that species richness is the highest in the ARCH province (173 species), it is the smallest for the SUND province (72) and it is intermediate and similar in SPSG and WARM (140 and 130 respectively). The Shannon's diversity index indicates the same trend.

			All prey species	Non-rare prey species			
Longhurst Province	Number of non-empty stomachs	Number of prey individuals observed	Total Species Richness	Species Richness for non-rare preys	Rarefied Species Richness at 3800	Rarefied Species Richness at 15000	Shannon's diversity index (H)
ARCH	1793	42590	378	247	173	229	3.708
SPSG	873	25050	270	206	140	193	3.061
SUND	227	3874	77	72	72		2.568
WARM	1547	34966	249	199	130	176	3.163
Grand Total	4440	106480	466	262	173	238	3.566

Table 4. Prey species richness and diversity indices of the 4 Longhurst provinces

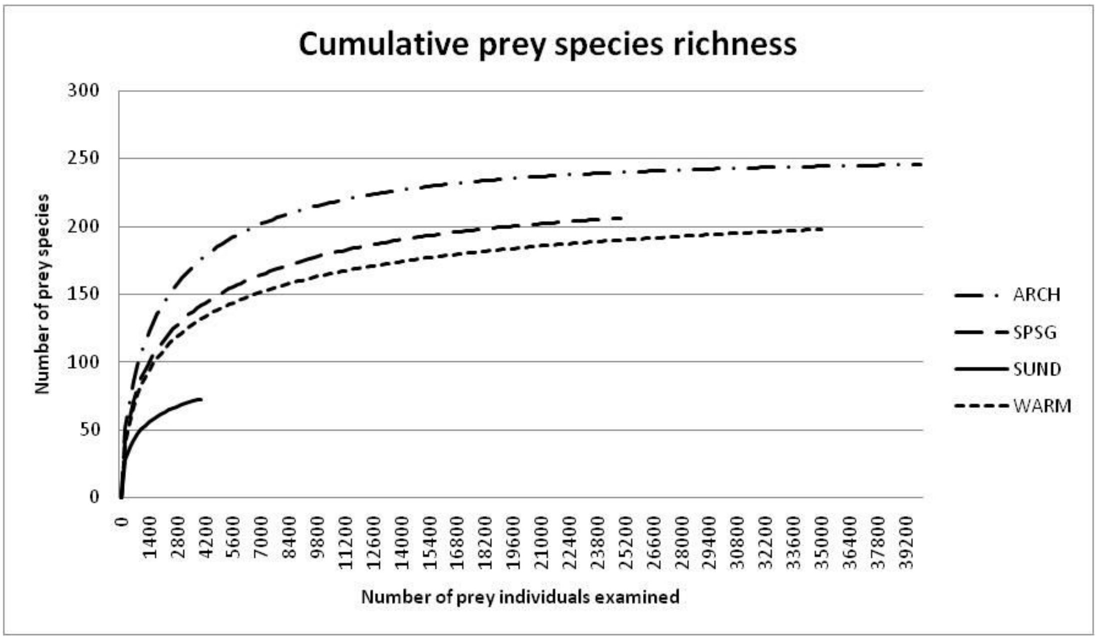


Figure 3. Cumulative prey richness calculated by the rarefaction method for non-rare prey species, per Longhurst province

3.2. Prey composition

3.2.1. By prey category

In the 4 provinces Fish is the dominant prey category with a maximum in SUND (86%), a minimum in SPSG (76%) and intermediate identical values in ARCH and WARM (81%) (**Error! Reference source not found.**). Molluscs are the second prey for SPSG (20%), ARCH and WARM (16%-13%); it is the third prey for SUND (4%). Crustaceans are the second prey for SUND (8%) and third prey in the other provinces (less than 5%).

	ARCH	SPSG	SUND	WARM	All
CRUSTACEA	2.59%	3.08%	7.53%	4.17%	3.14%
FISH	80.68%	76.08%	86.35%	81.08%	79.63%
MOLLUSC	15.71%	19.59%	4.01%	13.46%	16.07%
OTHER	1.02%	1.25%	2.11%	1.28%	1.15%

Table 5. Diet prey composition by category in %W in the 4 Longhurst provinces. Colour-code: red >50%, orange=20-50%, green=10-20%, blue=5-10%, purple=2-5%.

3.2.2. By prey vertical distribution

When preys are classified according to their vertical distribution, it appears that the primary prey in all provinces is epipelagic (>32%) (**Error! Reference source not found.**). In the SUND province the other main prey are epipelagic-reef related species (25%). In the other provinces the mesopelagic preys represent 10 to 15%. ARCH and WARM present similar profiles with identical values of epipelagic and mesopelagic, low bathypelagic preys and medium-low values of mesopelagic migrant and epipelagic reef preys. SPSG demonstrates a different pattern with lower epipelagic preys, and medium bathypelagic highly migrant preys which are not present in other provinces.

Prey class		ARCH	SPSG	SUND	WARM
Epipelagic	1	47.56%	32.60%	42.24%	49.20%
Epipelagic-Reef	1r	4.60%	4.85%	24.75%	5.91%
Mesopelagic migrant	2	3.53%	8.15%	2.26%	8.03%
Mesopelagic	3	13.64%	14.61%	2.56%	10.34%
Bathypelagic migrant	4b	0.22%	0.05%	0.00%	0.06%
Bathypelagic highly migrant	4c	1.68%	5.77%	0.16%	1.01%
Bathypelagic	5	3.92%	3.23%	0.00%	2.40%
Not classified	NC	24.85%	30.75%	28.04%	23.05%

Table 6. Diet prey composition by prey vertical class in %W in the 4 Longhurst provinces. Colour-code, see caption of Error! Reference source not found.**.**

3.2.3. By prey taxa

In the 4 provinces fish of the Scombridae family (tuna, mackerels…) are the primary preys of the top predators (**Error! Reference source not found.**). "Epipelagic Scombridae" are prey 1 in SPSG and SUND, "large skipjack" is prey 1 in WARM, "small skipjack" are prey 1 or 2 in the 4 provinces. Besides "small skipjack" and "epipelagic Scombridae", the "Baby skipjack" is the only other species ranked in the top-ten preys that is present in the 4 provinces; it is ranked 5 for ARCH and WARM, 8 for SUND and 9 for SPSG. Overall skipjack represent 26.7% of the diet of WARM predators, 17.5% in SUND, 9.5% in ARCH and 10.7% in SPSG. This species is then the number 1 prey in the 4 provinces.

"Engraulidae (anchovies)"is prey 2 and 3 respectively in ARCH and WARM. The "mesopelagic Paralepididae (barracudina)" and the "mesopelagic migrant purple squid *Sthenoteuthis oualaniensis*" are important preys in ARCH, SPSG and WARM. "Bathypelagic highly migrant Myctophidae (lanternfish)" are highly ranked in SPSG along with other deep preys while "epipelagic-reef associated Synodontidae larvae (lizardfish)" are important in SUND with other reef-associated preys. There is only one crustacean in the top-ten preys, it is "epipelagic-reef associated Stomatopoda larvae" in the SUND province (ranked 6). Top-ten preys vary according to provinces.

Prey	Category	Prey class		ARCH		SPSG		SUND		WARM	
SKJLg	FISH	Epipelagic	1		0.01%		1.24%			1	10.90%
SKJSm	FISH	Epipelagic	1	1	6.11%	2	7.10%	2	15.21%	2	9.41%
Engraulidae	FISH	Epipelagic	1	2	3.90%		0.15%			3	7.19%
Myctophidae	FISH	Bathypelagic highly migrant	4c		1.44%	3	4.12%		0.13%		0.70%
Synodontidae	FISH	Epipelagic-Reef	1r					3	12.83%		
Tetraodontidae	FISH	Epipelagic	1	4	3.74%		0.86%		0.07%		0.09%
Scombridae	FISH	Epipelagic-Reef	1r				0.02%	4	6.36%		
Scombridae	FISH	Epipelagic	1	9	2.63%	1	7.76%	1	15.76%	6	3.75%
Alepisauridae	FISH	Mesopelagic	3		2.38%	5	3.80%				0.55%
Hemiramphidae	FISH	Epipelagic	1		0.32%		0.01%	5	2.93%		0.64%
Paralepididae	FISH	Mesopelagic	3	3	3.90%	6	3.42%		0.29%	7	3.57%
Sthenoteuthis oualaniensis	MOLLUSC	Mesopelagic migrant	2	10	2.50%	4	3.85%		0.28%	4	6.90%
ALXSm	FISH	Mesopelagic	3	6	3.16%		0.38%				
Stomatopoda	CRUSTACEA	Epipelagic-Reef	1r		0.49%		0.12%	6	2.92%		0.96%
SKJBb	FISH	Epipelagic	1	5	3.37%	9	2.38%	8	2.26%	5	6.38%
Lagocephalus spp.	FISH	Epipelagic	1	7	2.95%		0.29%				0.04%
Gempylidae/Trichiuridae	FISH	Mesopelagic	3		0.74%	7	3.00%		0.35%	8	3.16%
Bramidae	FISH	Epipelagic	1	8	2.79%		1.06%	7	2.41%		0.65%
Exocoetidae	FISH	Epipelagic	1		2.44%	8	2.60%				0.81%
Decapterus ssp.	FISH	Epipelagic	1		1.81%		0.11%		0.64%	9	2.14%
Gempylidae/Trichiuridae	FISH	Mesopelagic migrant	2		1.14%	10	2.43%	9	1.95%		0.30%
Ommastrephidae	MOLLUSC	Mesopelagic	3		2.50%		1.04%	10	1.76%		0.22%
Scombrolabrax heterolepis	FISH	Mesopelagic	3		0.13%		0.24%			10	1.61%

Table 7. Diet prey composition by prey taxa in %W in the 4 Longhurst provinces; rank of the top-ten preys is indicated. Colour-code for ranked preys: red >10%, orange 5-10%, green 2-5%, blue <2%).

3.3.Food webs

In the simplified food webs, as previously observed, the number of species is maximum for ARCH, minimum for SUND and intermediate for SPSG and WARM (**Error! Reference source not found.**). The number of links in the food web follows the same ranking as well as the density of links. SPSG and WARM are remarkably similar.

	S	L	D=L/S
ARCH	129	928	7.19
SPSG	111	603	5.43
SUND	52	164	3.15
WARM	101	547	5.42

Table 8. Descriptors of the pelagic food webs of the 4 Longhurst provinces, including number of species (S), interspecific predation links (L) and link density (D=L/S).

Despite being simplified and limited to the top-five preys of each predator, the food web graphs visually highlight the complexity of the pelagic ecosystems of the western and central Pacific and the differences between provinces (**Error! Reference source not found.Error! Reference source not found.**). The ARCH systems appears to be the more complex one with a large number of species and connections. The SUND system is very limited in comparison and highly dependent on epipelagic layer. SPSG and WARM present similar complexity but the higher importance of the deep layer appears clearly in SPSG.

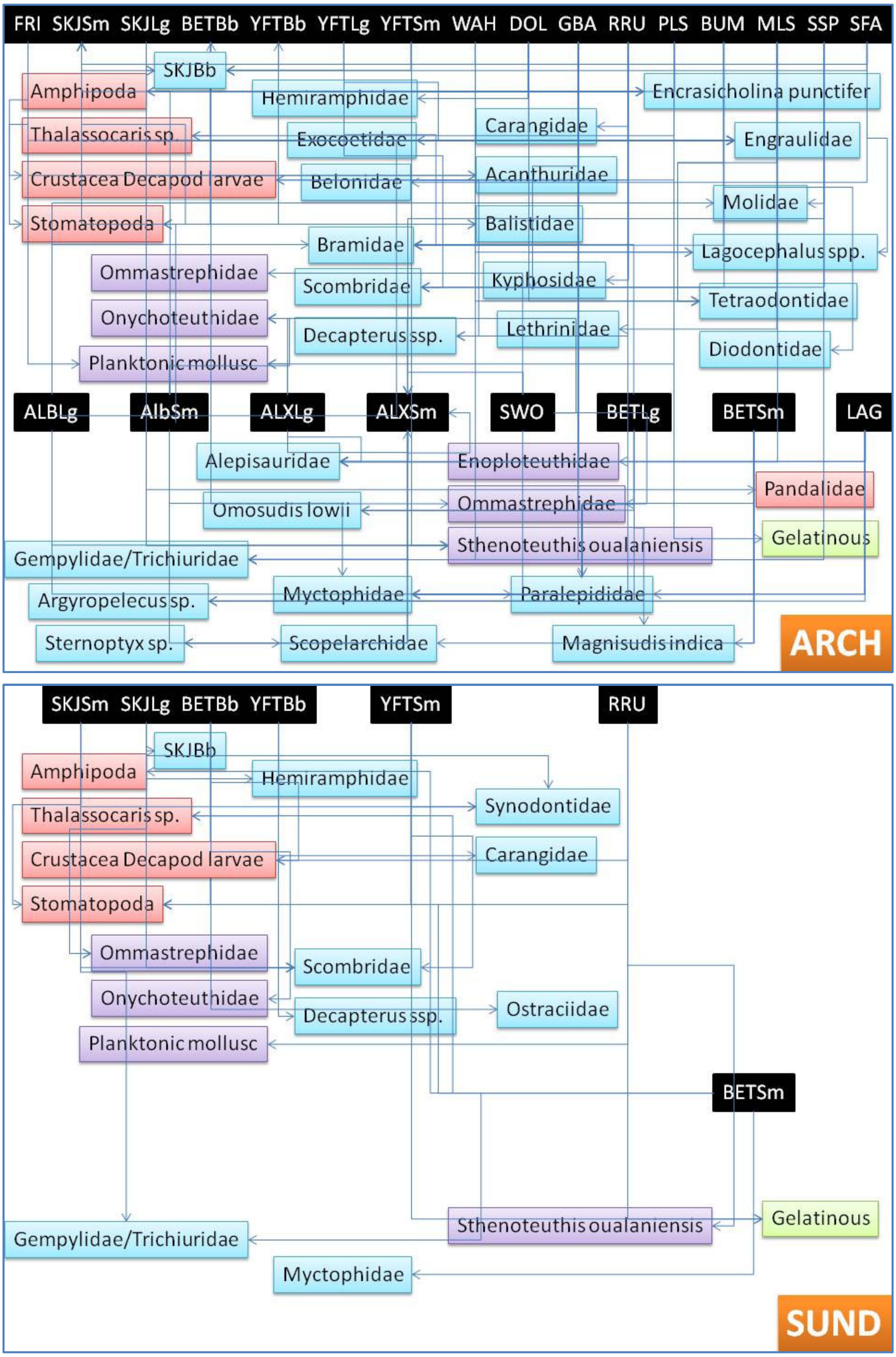
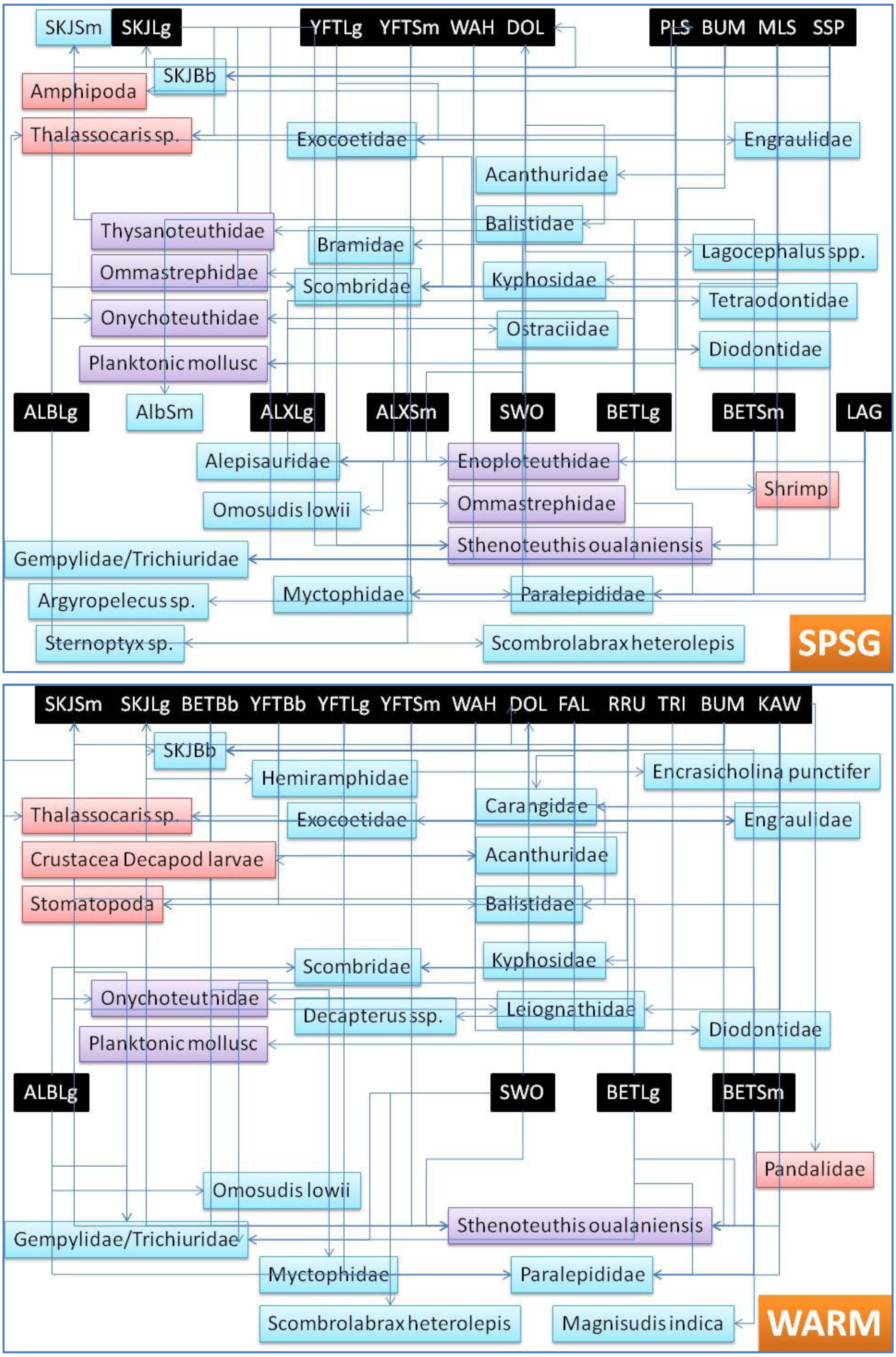


Figure 4. Reduced simplified food webs of the pelagic ecosystem in the 4 Longhurst provinces. Top predators (in black) for which more than 10 samples have been analysed are including along with their top-five preys (fish in blue, crustaceans in red and molluscs in purple). The top part of each graph represents roughly the epipelagic layer of the ecosystem; the lower part of the graph represents the deep layer.



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4. Discussion-Conclusion

It is important to remind that the pelagic ecosystems presented in this paper represent only a partial vision of the system. As they are based on sampling of top predators, if the trophic links created by these top predators are well described, no analyses were conducted on the species of intermediate trophic level. In this paper is only described the "upper" part of the trophic structure.

The analysis of the trophic structure indicates that the pelagic ecosystems of the 4 provinces have different structures and functioning even if all of them heavily rely on the skipjack as a major prey.

SUND is a province with little similarities with the other provinces except that skipjack is a major prey as for the other areas. SUND shows little diversity and link density, giving the impression it is a simpler system. It is an area where crustaceans are particularly important in the diet while molluscs are minor, and the system really focuses on the epipelagic prey, and particularly reef-associated preys.

At the other extreme ARCH demonstrates a very high diversity of prey and density links between preys and predators. It is a very complex ecosystem. The prey composition is very similar to WARM in prey category (Fish, Mollusc and then Crustaceans), prey vertical distribution (Epipelagic, mesopelagic and little bathypelagic) and taxa. Skipjack and Engraulidae are primary preys in both provinces but their percentage is lower in ARCH than in WARM and predation is widespread on many more preys in ARCH. It is a very complex ecosystem which is balanced between surface and deep layers.

SPSG and WARM present very similar diversity and density links (which is intermediate between SUND and ARCH). However they differ in prey composition. There are more molluscs consumed in SPSG, less epipelagic preys and more bathypelagic highly migrant preys. Skipjack is less important in the SPSG system and Engraulidae which are dominant in WARM are absent from SPSG. These 2 systems have an intermediate degree of complexity implying both the surface and the deep layers, the deep layer being more important in the case of SPSG.

As observed in a previous analysis and modelling of the warm pool (Allain *et al.*, 2007), skipjack appears to be a major prey in the pelagic systems of the western and central Pacific; not only in the warm pool, but also in the other provinces described in this study. All developmental stages of SKJ are consumed: small, large and then baby in terms of weight but baby, small and large in terms of numbers. The highest percentages of SKJ preys in WARM and SUND are in agreement with the SKJ distribution as predicted by Seapodum models (Figure 5). Because of its high biomass, high production, high consumption and important cannibalism, skipjack occupies a central position in the system being both an important predator and prey. Modelling work also proved that it was a species very resilient to perturbation (Allain *et al.*, 2007) and consequently it probably brings some degree of stability into the ecosystem. Skipjack does not have the same role in the eastern tropical Pacific where diet studies and ecosystem modelling indicated that another fish of the same Scombridae family is central to the system: *Auxis sp.*(Olson & Watters, 2003).

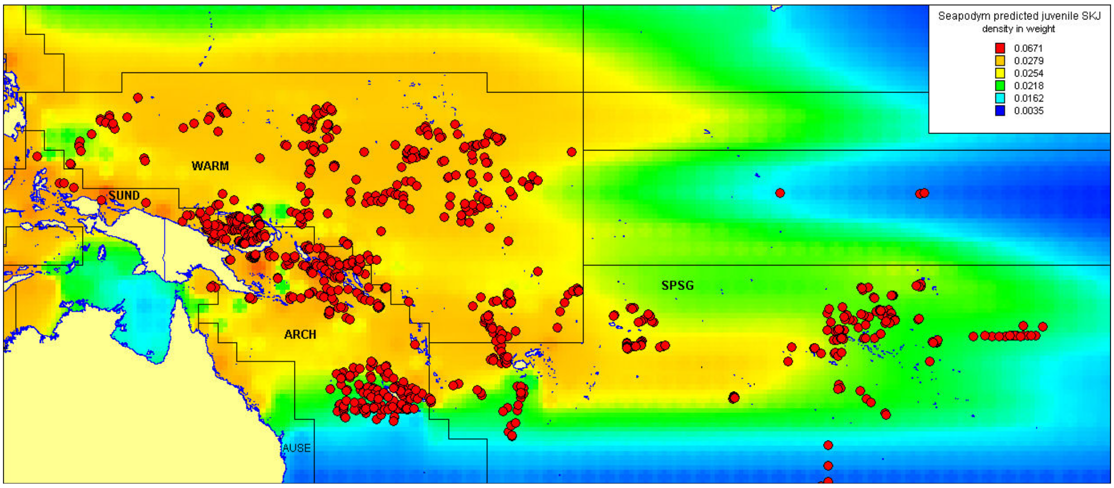

Figure 5. Baby skipjack average spatial distribution (2001-2005) as predicted by Seapodym model in the western and central Pacific ocean. Longhurst province are superimposed to the map as well as sample distribution (red dots).

The very high species diversity observed in ARCH can probably be attributed to the complexity of this province. It is very complex in terms of topography and hydrography. It covers deep basins open to the ocean and is scattered by numerous small and large islands, atolls and seamounts (Allain *et al.*, 2008) that induce disturbance to the circulation of the main current systems and creates specific hydrographic features such as eddies. This complex habitat favours a high species diversity which is utilised by tuna feeding on all the preys available from the surface to the deep. This high diversity induces a strong potential resilience of the ARCH system to perturbations.

On the other hand SUND is a less diverse system. If the lower number of samples does not allow obtaining the total diversity of this province, the rarefied diversity calculation allows comparing it to other provinces, and it appears lower. In this province the samples collected are mainly representative of surface species; there are only 10 small bigeyes in the sample which can be considered as deep predators. Hence there is a bias in the sample as the deep ocean layer is not evaluated in our sample. However, if our samples are mainly located at the eastern margin of the province in waters with intermediate depth, on the broad scale SUND is considered as the shallow-water counterpart of the ARCH province (Longhurst, 2007) and it mainly covers continental shelves spread with many islands, large and small, with coastal fringes of shallow waters. The sampling bias but also the nature of the SUND province explains why it is an epipelagic-centred ecosystem. And the coastal nature of this province can also explain the high percentage of reef-associated species in the stomach contents.

The WARM and the SPSG show many similarities in terms of biodiversity and prey composition that could be explained by a shared oceanic nature scattered by small islands. However the vertical structure is different with a very deep thermocline and a low thermal gradient in SPSG and a shallower thermocline (80m in normal condition, 40m during El Niño) with a very strong thermal gradient in WARM. The weaker (low gradient) and deeper thermocline in SPSG could allow an easier access to the deep preys including the molluscs.

The nature of the habitat (topography, hydrography and degree of complexity) can help explaining the variability in the ecosystem structures.

5. References

1. Allain, V., Kerandel, J.-A., Andréfouët, S., Magron, F., Clark, M. R., Kirby, D. S., & Muller-Karger, F. E. 2008. Enhanced seamount location database for the western and central Pacific Ocean: screening and cross-checking of 20 existing datasets. *Deep-Sea Research I*. **55**(8), 1035-1047.

2. Allain, V., Nicol, S., Essington, T. E., Okey, T. A., Olson, R. J., & Kirby, D. S. 2007. An Ecopath with Ecosim model of the Western and Central Pacific Ocean warm pool pelagic ecosystem. *3rd Meeting of the Scientific Committee of the Western and Central Pacific Fisheries Commission, WCPFC-SC3, Honolulu, Hawaii, USA, 13-24 August 2007*. **EB SWG/IP-8**, 1-42.

3. Dambacher, J. M., Young, J. W., Olson, R. J., Allain, V., Galván-Magaña, F., Lansdell, M. J., Bocanegra-Castillo, N., Alatorre-Ramírez, V., Cooper, S. P., & Duffy, L. M. 2010. Analyzing pelagic food webs leading to top predators in the Pacific Ocean: A graph-theoretic approach. *Progress in Oceanography*. **86**, 152-165.

4. Graham, B. S., Grubbs, D., Holland, K. N., & Popp, B. N. 2007. A rapid ontogenetic shift in the diet of juvenile yellowfin tuna from Hawaii. *Marine Biology*. **150**(4), 647-658.

5. Hurlbert, S. H. 1971. The nonconcept of species diversity: a critique and alternative parameters. *Ecology*. **52**, 577-586.

6. Legendre, P. & Legendre, L. 1998. Numerical ecology. Elsevier, Amsterdam, pp. 1-853.

7. Longhurst, A. 2007. Ecological geography of the sea. Academic Press, pp. 1-542.

8. Olson, R. J. & Watters, G. M. 2003. A model of the pelagic ecosystem in the eastern tropical Pacific Ocean. *IATTC Bulletin*. **22**(3).