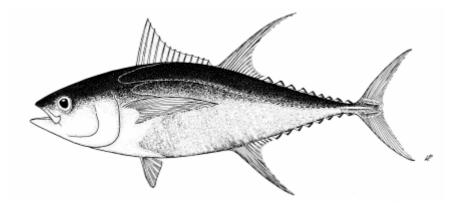
WCPFC-SC1 BI WP-2



Diet of large pelagic predators of the Western and Central Pacific Ocean



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Introduction

To develop ecosystem approaches of fisheries management it is important to take into account species interactions and underlying ecosystem dynamics. Assessing the impact of fisheries and environmental effects on the ecosystem implies a good comprehension of this system. Predation induces an important mortality in the ecosystem that is often higher than fishery mortality, and determining trophic interactions between species is a major step towards a better understanding and modeling of the ecosystem dynamic.

A large sampling programme has been implemented in the western and central Pacific to collect samples and determine the diet of the top predators for a better understanding of the pelagic ecosystem. Based on stomach content data, this paper presents the diet of 4 tuna species, limited to the warm pool area where most of the tropical tuna fisheries occurs. The classification of the preys according to their vertical distribution and migration provides information on the tuna behaviors.

Methods

Sampling programme, sampling protocol

Stomach samples are collected from target fishes (tunas) and bycatch species by observers from the different national observer programmes in the area. Since the beginning of the programme in January 2001, 81 sampling trips have been done, 54 on longline boats, 17 on purse seine vessels and 10 on other boats. Twenty sampling trips were organised by French Polynesia, 13 by New Caledonia, two by Federated States of Micronesia, six by Papua New Guinea, 12 by Solomon Islands, ten by the FSM Arrangement programme, one by Marshall Islands, two by SPC, one by Wallis and Futuna, 12 by ships of opportunity and two by Cook Islands.

For further details on the sampling programme, the sampling protocols and the stomach examination protocol check SCTB16 - BBRG-6

http://www.spc.int/OceanFish/Html/SCTB/SCTB16/bbrg6.pdf and http://www.spc.int/OceanFish/Html/TEB/EcoSystem/index.htm.

Stomach examination

Classical procedure is used to analyze the stomachs:

-Fullness coefficient is determined according to a scale from 0 (empty) to 4 (full) (see caption of Figure 3 for details). If baits are present, they are removed to determine the fullness coefficient. However fullness coefficient is a subjective parameter which determination will vary with the examiner, so another way to evaluate and quantify the stomach fullness is to calculate the stomach content weight – predator weight ratio (= stomach content weight * 100 / predator weight, in %). The weight of the predator is estimated from the measured length and using species-specific length-weight converting factor established by SPC.

-Preys are sorted by species or group, identified at the lowest taxonomic level, a digestion state is attributed (from 1 to 4, see details in caption of Figure 4), development state is determined when possible (larvae, juvenile, adult), they are counted, weighted and measured.

The number of baits, the presence of parasites, the number of cephalopod beaks, gladius and otoliths are recorded.

Data on vertical class and reef association of the prey items in Annexe 1 (p.14) are compiled from literature information and are mainly based, for fish on Fishbase

(http://www.fishbase.org/home.htm), Carpenter & Niem (1999), Granperrin (1975), Smith and Heemstra 1986, for cephalopods on Roper & Young (1975), The Cephalopod page (http://is.doi.org/.com/TCD/index.html). Tree of life/Carbalopods

(http://is.dal.ca/~ceph/TCP/index.html), Tree of life/Cephalopods

(<u>http://is.dal.ca/~ceph/TCP/index.html</u>), for crustacean on Poore (2004), for invertebrates on Wrobel and Mills (1998).

It is important to note that some species are underestimated due to a high digestion rate and/or because of a lack of specific structure that could help for identification. The typical jaws of Tetraodontiformes, *Alepisaurus*, Gempylidae/Trichiuridae, the dorsal spine of Monacanthidae, Balistidae, the photophores of Myctophidae, Ommastrephidae (squids) facilitate identification of these species, even when they are in an advanced state of digestion.

For data analysis, frequency of occurrence (%F), percentage of number (%N) and percentage of weight (%W) were calculated by taxon, cumulating all the data from the same species. Frequency of occurrence of an item is the number of stomachs where this item is present divided by the number of non-empty stomachs. Percentages of number and weight are the respective number and weight of the taxon studied divided by total number or weight of this taxon of all the samples, by species.

Characteristics of the samples

In this study are only presented data from samples collected in the warm pool; 173 yellowfin, 119 bigeye, 300 skipjack, 12 albacore tuna (Figure 1). Due to the small number of ALB samples it will be difficult to conclude anything for this species, but the results are given for information, and further sampling might improve the confidence we can have into the analysis.

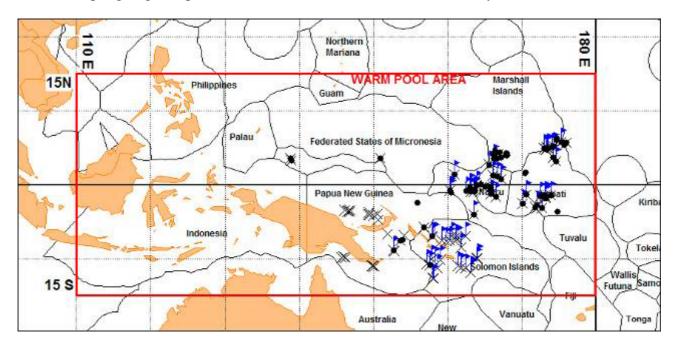


Figure 1. Positions of the tuna sampled for the study in the warm pool. BET (flag), SKJ (circle), YFT (cross).

Most of the fish collected were caught on purse seine but an important portion of the YFT and the BET come from LL fishing as well as the ALB. (Table 1).

The percentage of empty stomachs is just above 50% for YFT and BET while it is nearly 75% for SKJ. The difference in the percentage of empty stomachs observed is partly due to the fishing gear used to catch the fish. Fish caught on the longline are always in an active feeding phase, while schooling fish caught with the purse seine are not necessarily in such a phase and when caught around FADs early in the morning, stomachs are usually empty.

The percentage of females in the samples is 50% for SKJ and close to 50% for YFT and BET; increasing the number of samples should allow to reach 50% for these species as well as for ALB. Mean length of the fish examined are around 77 cm for YFT and BET, 54 cm for SKJ and 94 cm for ALB. The length distribution has only one mode for SKJ while it is multimodal for YFT and

BET (Figure 2). Fish smaller than 80 cm were caught by PS in general and larger fish were caught on LL.

Nearly all the SKJ examined can be considered as adults while they are all juveniles for BET and more than 2/3 are still juveniles for YFT (Table 1).

	Number of samples	LL	PS	% of empty stomachs (number)	% females (nb of fish sexed)	mean length (UF cm)	length range (UF cm)	Age at maturity (MULTIFAN-CL 2005)	Number of juveniles	Number of adults
YFT	173	54	119	53.76% (93)	45.45% (132)	78.3 5	34-158	Age class with 50% - 2y – 21.28kg – 106.65cm	121	52
BET	119	46	73	56.30% (67)	43.07% (65)	76.0 6	31-175	Age class with 50% - 3.6y – 45.79kg – 129.31cm	115	4
SKJ	300	4	296	73% (219)	50.50% (297)	53.9 6	33-79	Age class with 100% - 0.5y – 1.58kg – 43.03cm	37	263
ALB	12	12	0	0% (0)	20.00% (10)	93.9 2	85-106	Age class with 50% - 5.5y – 10.00kg – 80cm	0	12

Table 1: Characteristics of the samples of the different species sampled in the warm pool.

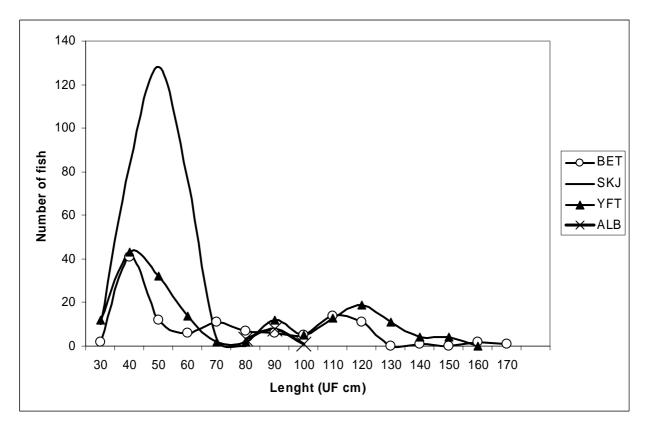


Figure 2: Length distribution of the tuna sampled in the warm pool. UF: upper jaw-fork length, equivalent to SL standard length for tuna.

Results – Discussion

Fullness coefficient

When considering only the non-empty stomachs (stomach fullness >=1), most of them, whatever the species, contain less than half of the stomach volume (Figure 3), and only a very low percentage of samples have full stomachs (2.5% for BET, less than 1% for YFT and SKJ).

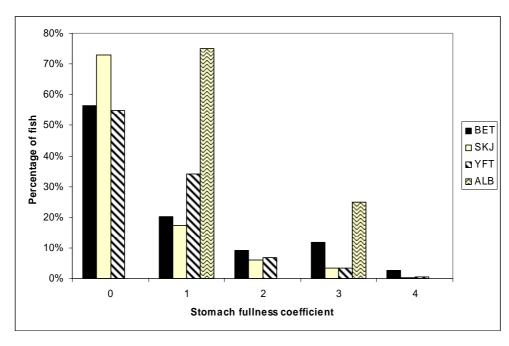


Figure 3: Percentage of stomachs according to their fullness coefficient in the warm pool for the different species. 0: empty stomach, 1: stomach less than half full, 2: stomach half full, 3: stomach more than half full, 4: stomach full.

The mean 'stomach content weight / predator weight ratio' percentage for the non-empty stomachs is low for all species with values less than 1% varying between 0.3 and 1.0% according to the species (Table 2). The maximum values observed for the full stomachs are around 3.5%; the quantity of food in the stomach represents 3.5% of the weight of the fish (except for ALB, but it is probably due to the small sample number).

Species	n	Mean (%)	stdev	Min (%)	Max (%)
BET	51	0.835	0.829	0.002	3.691
YFT	78	0.312	0.497	0.000	3.204
SKJ	81	0.973	0.857	0.005	3.653
ALB	12	0.269	0.408	0.014	1.378

 Table 2: Percentage of 'Stomach content weight / Predator weight ratio' for non-empty stomach of the different species.

The highest mean value is shown by the SKJ (0.97%). If we consider that these values are obtained from the same time period for all the species, this result suggests that SKJ eats more food than the other tuna species; it is in agreement with SKJ high metabolism (Kirby, 2005). However, BET that is supposed to have a much slower metabolism has a mean value of 0.83%, so not very different from SKJ compared to YFT that is only 0.31% with a supposedly intermediate metabolism between BET and SKJ. This subject needs more investigation.

It is important to note that these values does not represent the daily ration of the fish; they only represent a snapshot of the stomach content at the time of the capture. It then can be a long time after a meal (preys are then more or less digested) and the feeding process is probably more or less continuous making difficult the estimation of the daily ration.

State of digestion of the preys

If feeding is supposed more or less continuous, when considering a sample representative of the population, the distribution of the percentage of preys in the different states of digestion can give an indication on the dynamic of the digestion process. State 1 of digestion can be supposed relatively short as once the skin of the fish/mollusc is removed, it is already considered in state 2. States 2 and 3 are two states of disaggregation of soft parts of the preys and once the surface muscles are digested the preys are considered in state 3 that should be a long state. State 4 is probably the longest one as hard parts such as skeletons, cephalopod beaks and gladius are considered in this state, however because of the important loss of biomass in this state, it does not represent an important percentage in weight.

Only a small amount of preys are in digestion state 1 whatever the species (Figure 4): the digestion process starts very quickly once preys are ingested. Two different patterns are then observed according to the species considered: BET, YFT, ALB seem to have a similar digestion process while SKJ is different. For BET, YFT and ALB most of the prey biomass is, as expected, in digestion state 3, a long phase of digestion. For SKJ most of the preys are in digestion state 4 that suggests digestion is very fast for this species compared to the others.

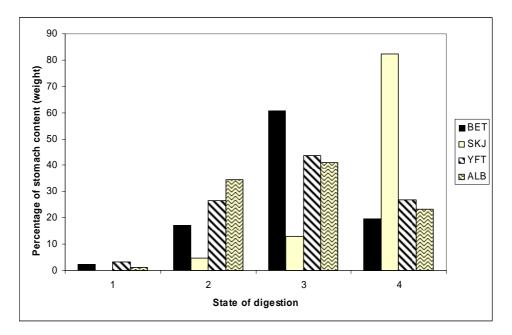


Figure 4: State of digestion of all the preys found in the stomachs, by species. 1: fresh, 2: whole, partially digested, 3: fragmented, advanced digestion, 4: hard part remains and grey mush.

Fast digestion by SKJ is in agreement with the high metabolism of this species (Kirby, 2005). Albeit the large loss of biomass between digestion state 3 and 4, the large amount of preys in state 4 for SKJ also indicates that the digestion of the hard parts of the preys is a long process and that they probably accumulate in the stomach over several meals; it is an important information to know to calculate daily ration.

Description of the diet

Prey groups

The most important prey found in the stomachs are fish, mollusc and crustacea for all tuna species; however, percentages are different according to the species considered (Table 3).

In terms of frequency, Fish preys are found in more than 89% of the non-empty stomachs, it is the most frequent prey for all tuna species. For SKJ the other preys have low frequency (<20%) while for the other tuna species (YFT, BET, ALB), Mollusc and Crustacea are observed in 64 to 90% of the stomachs.

In numbers, Fish is the first group for BET and SKJ (respectively 60 and 77%), followed by Mollusc (27 and 14%) and Crustacea (12 and 8%). For YFT Crustacea is the first group (46%), then Fish (29%) and Mollusc (19%), and for ALB Mollusc is the most important in number (44%) then Crustacea (30%) and Fish (24%). For YFT and ALB, even if Crustacea are important in numbers the small size of Crustacea induce a small percentage in weight.

In weight, the order of prey group by decreasing percentage is identical for the 4 tuna species: Fish (64 to 88%), Mollusc (6 to 25%) and Crustacea (0.2 to 9%). The most piscivorous species is SKJ while ALB presents the lowest percentage of Fish and the highest percentage of Mollusc. Crustacea percentage is the highest for YFT.

	BET				SKJ			YFT			ALB	
Prey Group	%W	%N	%F									
FISH	82.22	60.50	94.23	88.36	77.00	91.36	76.44	28.88	88.75	64.36	23.82	91.67
MOLLUSC	15.27	27.15	90.38	5.98	14.08	18.52	11.26	19.48	63.75	24.90	44.42	83.33
CRUSTACEA	2.50	12.24	78.85	0.21	8.45	4.94	9.24	45.66	72.50	5.65	29.61	75.00
INVERTEBRATE	0.00	0.06	1.92	0.00	0.47	1.23	1.42	4.76	18.75	0.73	2.15	16.67
Unrecognizable	0.00	0.06	3.85	5.45	0.00	14.81	1.18	0.03	18.75	4.33	0.00	58.33
Other	0.00	0.00	0.00	0.00	0.00	0.00	0.47	1.18	11.25	0.02	0.00	8.33

Table 3: Frequency of occurrence (%F) and percentage of the total prey numbers (%N) and weights (%W) of the different prey groups for the different species. Invertebrate: all invertebrates except molluscs and crustacea, *i.e.* mainly worms, salp (see Annexe 1 for details). Unrecognizable: not identifiable prey items. Other: vegetal (floating algae or pieces of wood) + mineral (floating volcanic stones) + rubbish (human products such as plastic pieces) + bird feathers.

SKJ is a true piscivorous while YFT and ALB have a more diversified diet with Crustacea and Molluscs; BET has an intermediate diet with mainly Fish and Molluscs.

Prey items

Prey richness

The number of prey items identified is 93, 77, 42 and 23 respectively for BET, YFT, ALB and SKJ (Table 4). The same order is found when diversity is considered at the family level or at the fish family level (Fish being the most important prey): BET presents the highest diversity and SKJ the lowest one

Predator	Number of prey items	Number of prey families	Number of fish prey families	Percentage of Unidentified and Unrecognizable preys (%W)
BET	93	45	27	22.2
YFT	77	38	23	42.8
ALB	42	25	13	25.5
SKJ	23	12	6	81.9

Table 4: Prey diversity and percentage of unidentified preys in the diet of the different tuna species.

The lowest diversity presented by SKJ diet is probably linked to 2 different factors. A high percentage of its diet could not be identified (81.9%W) underestimating the diversity of the preys, introducing an artefact. However the consumption of preys by SKJ is limited to the epipelagic area (Table 5) while the other tuna species prey also upon deep preys. The availability in prey diversity in different for the 4 species and is reflected in the number of species identified in the diet. Values are lower for ALB but the results are only based on 12 specimens for this species and are probably not representative of the population.

The most important preys in weight and number (Table 5, Figure 5, Annexe 1 p.14)

BET: Not taking into account the undefined items, the most important prey group in terms of weight is the mesopelagic class (36%) with particularly Paralepididae (barracudinas 22.3%), Sternoptychidae (hatchetfish 7%) and the squid *Moroteuthis* (2%). The second prey group is the deep bathypelagic with another Paralepidae: *Magnisudis indica* (10%) but also Diretmidae, Scopelarchidae ans Chiasmodontidae (3, 2 and 1%). Epipelagic preys and surface migrating preys represent 5, 5 and 7% of the diet with SKJ specimens (2%), the squid *Stenoteuthis oualaniensis* (3%) and Myctophidae (4%).

This diet composition is in agreement with the vertical behaviour of BET known from electronic tagging: at night time they stay between the surface and 250m while during daytime they dive between 200 and 500m and on rare occasion up to 900m depth (Allain et al., 2005; Musyl et al. 2003). It suggests then that this species eats during day and night at all depths and it is in agreement with its eye characteristics that makes of BET an efficient visual hunter even in dim light (Fritsches and Warrant, 2001).

YFT: A large portion of the YFT diet is composed of epipelagic preys (40%) and particularly of *Elagatis bipinnulatus* (rainbow runner 7%), Exocoetidae (flying fish 4%), SKJ (4%), YFT (3%), juveniles of reef fish: Acanthuridae (surgeon fish 2%), Balistidae (trigger fish 3%), Tetraodontidae (puffer fish 2%) and small crustacea (megalopa, Amphipoda, Stomatopoda, *Phronima*). The reef-associated preys represent 10% in weight of the diet of the YFT (Table 6). YFT also consumes deeper preys: Mesopelagics (5%) with Paralepididae (3%), Bathypelagic Chiasmodontidae (2%) and migrant deep preys with the squid *Stenoteuthis oualaniensis* (2%) and Myctophidae (1%).

It is interesting to note the presence in the diet of juveniles of tuna species demonstrating predation pressure on SKJ (4%) and cannibalism (3%). It also appears that YFT can have an important impact on the mortality of the juveniles of reef-associated fish; this predation is opportunistic and depends on the area considered and on the presence of islands (Allain, 2004). The predominantly epipelagic diet is in agreement with what is know of the vertical distribution of the YFT that stays day and night between the surface and 200m and dives on rare occasions up to 500m (Dagorn et al. 2001).

SKJ: Because of the large portion of preys in digestion state 4, unrecognizable, and which vertical class could not be defined, less than 13% of the preys in weight could be classified but 12% were epipelagic preys. The most important prey is SKJ with 11%, the other preys represent altogether less than 1% (Bramidae, Acanthuridae, Pomacanthidae, Stomatopoda). Deeper preys are less than 0.1%.

According to prey items identified, SKJ is exclusively an epipelagic predator and shows an important cannibalism. It will be important to try and improve the percentage of identified preys to validate this high rate of cannibalism. Genetic techniques coupled with examination of hard part is a promising technique to identify highly digested preys (Smith et al. 2005) and could be applied to the case of SKJ to obtain a more accurate estimate of cannibalism. SKJ is an epipelagic predator that stays between the surface and 100m day and night and dives on rare occasions up to 250m (Ogura, 2003) and the fact that no deep preys migrating at the surface at night are found in their stomach suggests that they only feed during the day. It is in agreement with the fact that all the SKJ caught early in the morning around FADs have empty stomachs, however the hypothesis of daily feeding only needs to be confirmed by increasing the percentage of identified preys, and the effect on FADs on feeding strategy needs to be clarifies (Musyl et al. 2003).

ALB: The most important prey group in ALB diet is the Mesopelagics (47%) with particularly Paralepidae (25%), the squid *Ancistrocheirus lesueuri* (9%), the squid *Moroteuthis* (7%) and the fish *Scombrolabrax heterolepis* (black mackerel 3%). Epipelagics and surface migrating bathypelagics represent both 8% with the cephalopoda Sepiida (1%), small crustacea (megalopa 1% and Stomatopoda 1%), Acanthuridae (1%) and Myctophidae (8%). Reef-associated preys represent 5% of the diet of ALB (Table 6). ALB also consumes deep bathypelagic preys (4%) such as Chiasmodontidae (3%) and *Sternoptyx sp.* (hatchet fish 1%).

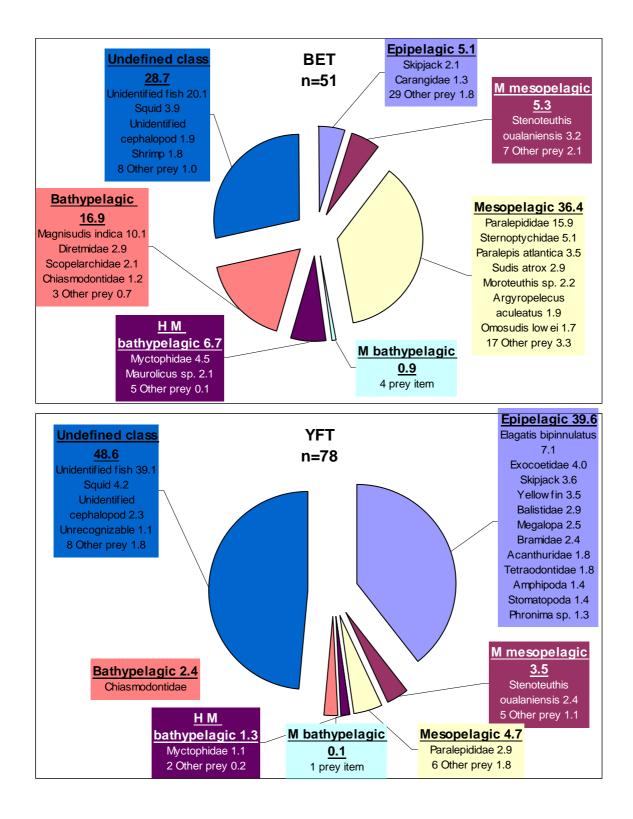
ALB has a diet similar to BET's but does not seem to dive as deep as BET;, it relies more on mesopelagics and epipelagics (including reef-associated preys) or surface migrating preys. The portion of deep preys (bathypelagics) is less important then in BET (respectively 4 and 17%).

	В	ET	S	KJ	Y	FT	ALB		
Prey items	%W	%N	%W	%N	%W	%N	%W	%N	
Epipelagic	5.1	5.2	12.1	25.8	39.6	55.9	8.5	33.0	
M mesopelagic	5.3	5.2	0.0	0.5	3.5	0.9	0.4	0.6	
Mesopelagic	36.4	18.6	0.1	0.9	4.7	1.4	47.2	7.9	
M bathypelagic	0.9	0.4			0.1	0.1			
H M bathypelagic	6.7	13.5			1.3	2.0	8.1	5.8	
Bathypelagic	16.9	12.4			2.4	1.6	4.0	0.6	
Undefined class	28.7	44.6	87.8	72.8	48.6	38.2	31.7	51.9	

Table 5: Percentages in weight (%W) and number (%N) of preys classified by vertical class for the four predators. See Annexe 1 caption for definitions of prey types. Shaded cells: >5%.

	BI	ET	SI	۲J	YI	-T	ALB		
Reef Associated preys	W	Ν	W	Ν	W	Ν	W	Ν	
No	99.58%	97.88%	99.64%	90.61%	90.03%	67.79%	95.22%	77.25%	
Yes	0.42%	2.12%	0.36%	9.39%	9.97%	32.21%	4.78%	22.75%	

Table 6: Percentages in weight (%W) and number (%N) of preys classified by reef association for the four predators. See Annexe 1 for classification of the preys. Shaded cells: reef-associated preys>5%.



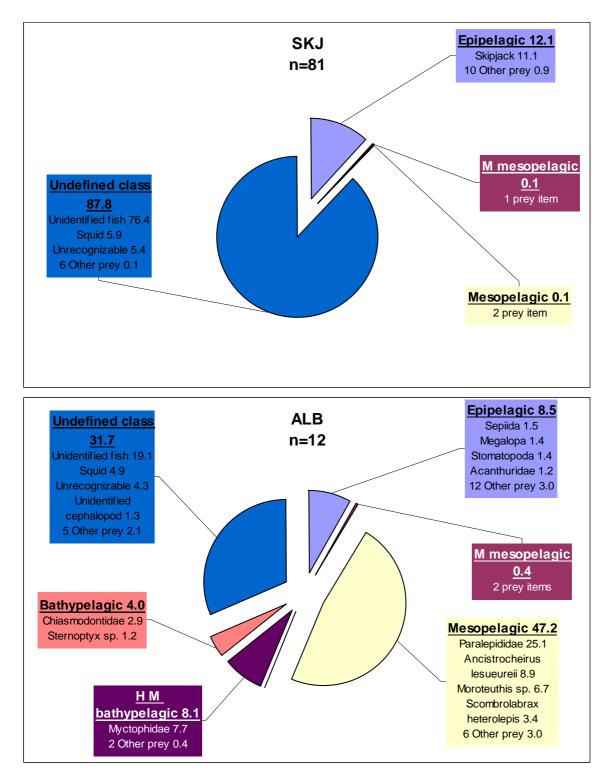


Figure 5: Percentages in weight of the preys by vertical class in the diet of the four tuna species. Vertical class: Epi=Epipelagic= pelagic species between the sea-surface and 200 m depth, Meso=Mesopelagic= pelagic species between 200 and 500 m depth, M Meso=Migrant Mesopelagic= mesopelagic species migrating in the epipelagic area at night, Bathy=Bathypelagic= pelagic species between 400 and 1000 m depth, HM Bathy=Highly Migrant Bathypelagic= bathypelagic species migrating in the epipelagic area at night, M Bathy=Migrant Bathypelagic= bathypelagic species migrating in the mesopelagic area at night.

Size-distribution of the preys

BET ingests preys between 0 and 690 mm with a mean value of 73.8 mm and most of the preys in the 50-60 mm length class, 42% of the preys are less than 5cm (Figure 6). The other tuna species eat smaller preys. Length ranges of the preys are respectively for SKJ, YFT and ALB of 0-109mm, 0-387mm and 2-203mm while the mean is 37.9mm, 47.8mm and 39.7mm and the mode is length class 10-20, 20-30 and 10-20mm. Preys less than 5cm represent 74%, 65% and 78% of the preys consumed by SKJ, YFT and ALB.

According to the list of prey items consumed and their vertical classification, BET and ALB on one hand and YFT and SKJ on the other hand have similar diets. However the size distribution of the preys shows that ALB and SKJ eat smaller preys than BET and YFT respectively. It then seems there is little overlap in the diet of the 4 tuna species.

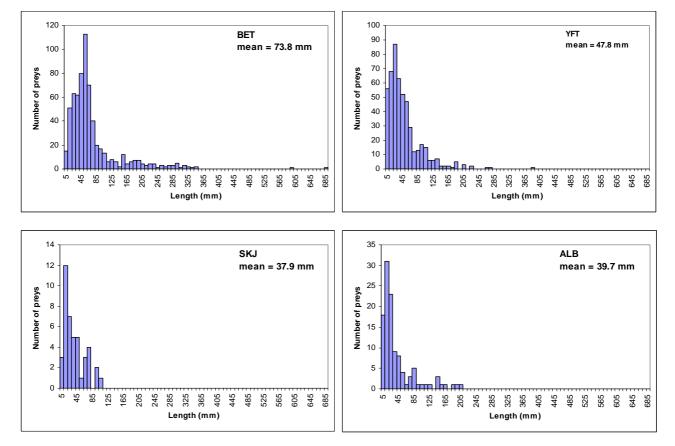


Figure 6: Length-frequency distribution of the preys consumed by the different predators.

Conclusion.

Examination of the stomach content provides important information on feeding strategies. It seems that to balance its high metabolism SKJ eats more and digest faster than the other tuna species. Due to their vertical distribution and behaviour the 4 tuna species have access to different depth strata and it is noticeable in the composition of their diet. SKJ that stays closer to the surface eats only epipelagic preys, mainly fish, with a very high cannibalism rate, and shows a low diversity in prey. YFT eats also mainly surface preys but also deep organisms. BET and ALB have a high percentage of deep preys in their diet. If SKJ and YFT on one hand and ALB and BET diet on the other hand are similar there are differences in the size of the preys consumed. The diet of the 4 tuna species shows relatively low overlap.

This diet study is not limited to the tuna species and the main large predators are also examined to obtain detailed data on the different components of the ecosystem. The diet studies are also complemented by isotope studies that give more information on the trophic structure of the ecosystem. For example, it appears that the observed isotope values of SKJ are higher than the expected values that correspond to a strict epipelagic diet; the higher value could be induced by the consumption of deep preys; it is then important to reduce the high percentage of unidentified preys for this species.

Diet studies provide information on basic biology and behaviour of the fish but they are also an important part of the parameterization of ecosystem models such as Ecopath/Ecosim (Allain, 2005); and information such as prey diversity, size of the preys, composition of the diet can be used as ecosystem indicators in conjunction with other indicators to detect changes in the ecosystem (Kirby *et al.*, 2005).

Bibliography.

- Allain, V. 2005. Ecopath model of the pelagic ecosystem of the WCPO. WCPFC-SC1, EB-WP10. Noumea, New Caledonia, 9-18 Aug. 2005.
- Allain V. 2004. Diet of yellowfin tuna in different areas of the western and central Pacific Ocean. SCTB17 – BIO1. Majuro, Marshall Islands. 9-18 Aug 2004.
- Allain, G., Lehodey, P. and Kirby, D. 2005. The influence of the environment on horizontal and vertical bigeye tuna movements investigated by analysis of archival tag records and ecosystem model outputs. WCPFC-SC1, BI-WP3. Noumea, New Caledonia, 9-18 Aug. 2005.
- Carpenter, K. and Niem, V. (Eds.). 1999. FAO species identification guide for fishery purposes. FAO. Rome. 6 volumes.
- Dagorn, L., Josse, E. and Bach, P. 2001. Association of yellowfin tuna with tracking vessels during ultrasonic telemetry experiments. *Fishery Bulletin.* **99**: 40-48.
- Fritsches, K. and Warrant, E. 2001. New discoveries in visual performance of pelagic fishes. *PFRP Newsletter*. **6**(3): 1-3.
- Grandperrin, R. 1975. Structures trophiques aboutissant aux thons de longue ligne dans le Pacifique Sud-Ouest tropical. Thèse d'état. Université d'Aix-Marseille II. 296p.
- Kirby, D. 2005. Prey consumption estimates for tunas in the WCPO. WCPFC-SC1, EB-WP4. Noumea, New Caledonia, 9-18 Aug. 2005.
- Kirby, D., Allain, V. and Molony, B. 2005. Potential ecosystem indicators for the WCPO. WCPFC-SC1, EB-WP5. Noumea, New Caledonia, 9-18 Aug. 2005.
- Musyl, M., Brill, R., Boggs, C., Curran, D., Kazama, T. and Seki, M. 2003. Vertical movements of bigeye tuna associated with islands, buoys, and seamounts near the main Hawaiian islands from archival tagging data. *Fisheries Oceanography*. **12**(3): 152-169.
- Ogura, M. 2003. Swimming behavior of skipjack, observed by the DST at the NW Pacific. SCTB16 SKJ7. Mooloolaba, Australia. 9-16 Jul 2003.
- Poore, G. 2004. Marine decapod crustacean of Southern Australia. A guide to identification. CSIRO publishing. Collingwood. 574p.
- Roper, C. and Young, R. 1975. Vertical distribution of pelagic cephalopods. Smithsonian contributions to zoology. 209: 1-51.
- Smith P.J., McVeagh S.M., Allain V.& Sanchez C. 2005. DNA identification of gut contents of large pelagic fishes. *Journal of Fish Biology. In press.*
- Smith, M. and Heemstra, P. 1986. Smiths' sea fishes. Springer-Verlag. Berlin. 1047p.
- Wrobel, D. and Mills, C. 1998. Pacific coast pelagic invertebrates. A guide to the common gelatinous animals. Sea Challengers, Monterey Bay Aquarium. Monterey. 108p.

Annexe 1: Percentages of weight (%W) and number (%N) of the different prey items for the different predators. Vertical class: Epi=Epipelagic= pelagic species between the sea-surface and 200 m depth, Meso=Mesopelagic= pelagic species between 200 and 500 m depth, M Meso=Migrant Mesopelagic= mesopelagic species migrating in the epipelagic area at night, Bathy=Bathypelagic= pelagic species between 400 and 1000 m depth, HM Bathy=Highly Migrant Bathypelagic= bathypelagic species migrating in the epipelagic area at night, M Bathy=Migrant Bathypelagic= bathypelagic species migrating in the mesopelagic area at night. Shaded cells: green >5%, yellow between 1% and 5%.

					BET		SKJ		YFT		ALB	
			Vertical	Reef								
Order	Family	Prey item	class	associated	%W	%N	%W	%N	%W	%N	%W	%N
FISH												
		long orange fish			0.00	0.06						
		Mesopelagic fish	Meso		0.72	1.12						
		Unidentified fish			20.10	15.03	76.40	58.22	39.10	16.02	19.07	5.79
Anguilliformes	Nemichthyidae	Nemichthyidae	M meso		0.14	0.34						
Aulopiformes	Alepisauridae	Alepisaurus sp.	Meso						0.24	0.06	0.67	0.64
Aulopiformes	Omosudidae	Omosudis lowei	Meso		1.73	0.28						
Aulopiformes	Paralepididae	Lestidium sp.	Meso		0.10	0.06						
Aulopiformes	Paralepididae	Magnisudis indica	Bathy		10.09	0.95						
Aulopiformes	Paralepididae	Paralepididae	Meso		15.93	5.31			2.89	0.78	25.11	2.58
Aulopiformes	Paralepididae	Paralepis atlantica	Meso		3.45	0.28						
Aulopiformes	Paralepididae	Sudis atrox	Meso		2.86	1.28			0.29	0.06	0.41	
Aulopiformes	Scopelarchidae	Scopelarchidae	Bathy		2.08	4.13						
Beloniformes	Exocoetidae	Exocoetidae	Epi						3.96	0.06		
Beryciformes		Beryciformes									0.06	0.21
Beryciformes	Diretmidae	Diretmidae	Bathy		2.86	2.91						
Beryciformes	Holocentridae	Holocentridae	Epi	yes					0.07	0.15		
Clupeiformes		Clupeiformes	Epi						0.40	0.03		
Clupeiformes	Engraulidae	Engraulidae	Epi						0.15	0.45		
			HM									
Myctophiformes	Myctophidae	Bolinichthys sp.	bathy		0.02	0.06						
			HM			0.70			1.00	4.00	7.00	1.00
Myctophiformes	Myctophidae	Myctophidae	bathy		4.47	8.72			1.09	1.02	7.68	4.29
Myctophiformes	Myctophidae	Myctophum selenops	M meso HM		0.14	0.17						
Myctophiformes	Myctophidae	Myctophum sp.	bathy		0.02	0.06						
Ophidiiformes	Ophiididae	Ophiididae	Meso		0.02	0.06						
Perciformes		Trichiuridae/Gempylidae	Meso		0.53	0.06	0.06	0.47				
Perciformes	Acanthuridae	Acanthuridae	Epi	yes	0.00	0.00	0.13	1.88	1.80	1.80	1.18	1.72
Perciformes	Bramidae	Brama sp.	Epi	ycc	0.07	0.11	0.10	1.00	1.00	1.00	1.10	1.72

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Perciformes	Bramidae	Bramidae	Epi		0.26	0.34	0.49	2.35	2.42	0.90	0.10	0.21
Perciformes	Carangidae	Carangidae	Epi		1.26	0.06			0.18	0.06		
Perciformes	Carangidae	Decapterus tabl	Epi	yes					0.29	0.03		
Perciformes	Carangidae	Elagatis bipinnulatus	Epi						7.11	0.03		
Perciformes	Carangidae	Selar crumenophthulmus	Epi	yes					0.15	0.03		
Perciformes	Caristiidae	Caristiidae	Meso		0.01	0.06						
Perciformes	Chaetodontidae	Chaetodontidae	Epi	yes	0.01	0.06			0.17	0.45	0.37	1.72
Perciformes	Chiasmodontidae	Chiasmodontidae	Bathy		1.20	3.35			2.39	1.56	2.86	0.43
Perciformes	Gempylidae	Gempylidae	M meso		0.57	0.22	0.04	0.47	0.53	0.12	0.27	0.21
Perciformes	Gempylidae	Lepidocybium flavobrunneum	M meso						0.26	0.03		
Perciformes	Malacanthidae	Malacanthidae	Epi		0.00	0.06						
Perciformes	Ostracoberycidae	Ostracoberyx dorygenys	Meso		0.31	1.01			0.16	0.30		
Perciformes	Percophidae	Percophidae	Meso		0.01	0.06						
Perciformes	Pomacanthidae	Pomacanthidae	Epi	yes	0.01	0.28	0.08	3.76	0.26	2.31	0.49	3.65
Perciformes	Priacanthidae	Priacanthidae	Epi	yes					0.06	0.03		
Perciformes	Scombridae	Katsuwonus pelamis	Epi	-	2.08	0.06	11.14	9.39	3.56	0.45		
Perciformes	Scombridae	Scombridae	Epi						0.58	0.12		
Perciformes	Scombridae	Thunnus alalunga	Epi						0.05	0.03		
Perciformes	Scombridae	Thunnus albacares	Epi						3.53	0.03		
Perciformes	Scombrolabracidae	Scombrolabrax heterolepis	Meso		0.48	0.39			0.33	0.09	3.39	0.43
Perciformes	Serranidae	Anthiinae	Epi		0.01	0.17						
Perciformes	Serranidae	Serranidae	Epi	yes	0.02	0.06			0.04	0.09		
Perciformes	Zanclidae	Zanclidae	Epi	yes					0.04	0.03		
Scorpaeniformes	Scorpaenidae	Scorpaenidae	Meso		0.03	0.22						
Stomiiformes	Phosichthyidae	Phosichthyidae	M meso		0.12	0.17						
Stomiiformes	Sternoptychidae	Argyropelecus aculeatus	Meso		1.88	1.06						
Stomiiformes	Sternoptychidae	Argyropelecus sladeni	Meso		0.03	0.06						
Stomiiformes	Sternoptychidae	Argyropelecus sp.	Meso		0.23	0.28						
			HM									
Stomiiformes	Sternoptychidae	Maurolicus sp.	bathy		2.08	4.13						
Stomiiformes	Sternoptychidae	Sternoptychidae	Meso		5.10	4.02					0.49	0.21
Stomiiformes	Sternoptychidae	Sternoptyx pseudobscura	Bathy		0.06	0.06						
Stomiiformes	Sternoptychidae	Sternoptyx sp.	Bathy		0.42	0.67					1.18	0.21
Tetraodontiformes		Tetraodontiformes	Epi						0.00	0.03		
Tetraodontiformes	Balistidae	Balistidae	Epi	yes	0.07	0.06			2.93	2.07		
Tetraodontiformes	Monacanthidae	Monacanthidae	Epi	yes					0.08	0.09		
Tetraodontiformes	Ostraciidae	Ostraciidae	Epi						0.05	0.12		
Tetraodontiformes	Tetraodontidae	Tetraodontidae	Epi						1.77	0.15	0.18	0.43

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Tetraodontiformes	Triacanthidae	Triacanthidae	Meso		0.01	0.06						
Zeiformes	Macrurocyttidae	Macrurocyttidae	Meso		0.35	1.90	0.01	0.47			0.86	1.07
Zeiformes	Macrurocyttidae	Zenion sp.	Meso	_	0.11	0.34						
MOLLUSC												
		cephalopod beak			0.34	11.17	0.01	0.94	0.43	11.52	0.90	35.19
		Gastropoda							0.01	0.54	0.02	0.21
		Unidentified cephalopoda			1.88	4.41	0.03	0.94	2.29	2.10	1.29	2.36
Architaenioglossa	Carinariidae	Carinaria sp.	Epi		0.03	0.45	0.00	0.47	0.18	1.80	0.02	0.21
Neotaenioglossa	Atlantidae	Atlanta sp.	Epi						0.01	0.12		
Octopoda		Octopoda			0.21	0.17						
Octopoda	Argonautidae	Argonauta sp.	Epi						0.03	0.12		
Octopoda	Bolitaenidae	Bolitaenidae	Bathy		0.22	0.34						
Octopoda	Octopodidae	Octopodidae			0.14	0.34						
Octopoda	Octopodidae	Octopus sp.	Epi	yes	0.07	0.11			0.01	0.03		
Teuthida		Teuthida			3.93	4.41	5.93	11.27	4.21	1.89	4.90	4.08
Teuthida	Enoploteuthidae	Abralia sp.	M meso						0.09	0.06		
Teuthida	Enoploteuthidae	Enoploteuthidae	M meso						0.04	0.03		
Teuthida	Enoploteuthidae	Enoploteuthis sp.	M meso		0.43	0.28			0.12	0.12		
Teuthida	Enoploteuthidae	Pyroteuthis sp.	M meso		0.40	0.84						
Teuthida	Histioteuthidae	Histioteuthidae	M bathy		0.11	0.11						
Teuthida	Histioteuthidae	Histioteuthis sp.	M bathy		0.73	0.22						
Teuthida	Loliginidae	Loliginidae	Epi		0.03	0.17						
Teuthida	Octopoteuthidae	Octopoteuthidae	Meso		0.32	0.06						
Teuthida	Ommastrephidae	Ommastrephidae	Meso						0.53	0.03		
Teuthida	Ommastrephidae	Stenoteuthis oualaniensis	M meso		3.24	2.35			2.43	0.51		
Teuthida	Onychoteuthidae	Moroteuthis lonnbergi	Epi						0.31	0.03		
Teuthida	Onychoteuthidae	Moroteuthis sp.	Meso		2.16	0.56			0.27	0.06	6.72	0.21
Teuthida	Onychoteuthidae	Onychoteuthidae	Epi		0.26	0.06						
Teuthida	Onychoteuthidae	Walvisteuthis sp.	Epi		0.32	0.06						
Teuthida	Pyroteuthidae	Pterygioteuthis sp.	M meso		0.30	0.89					0.18	0.43
Teuthida	Thysanoteuthidae	Thysanoteuthidae	Epi		0.28	0.06		1				
Teuthida	Ancistrocheiridae	Ancistrocheirus lesueurii	Meso					1			8.94	0.21
			HM									
Teuthida	Cranchiidae	Liocranchia reinhardti	bathy								0.41	0.21
Thecosomata	Cavoliniidae	Cavolinia sp.	Epi				0.00	0.47	0.04	0.33	0.02	0.21
Thecosomata	Cavoliniidae	Clio pyramidata	Epi		0.00	0.28						
Sepiida		Sepiida	Epi								1.51	1.07
CRUSTACEA												

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		Unidentified crustacea			0.23	0.06	0.00		0.20	0.21	0.80	0.21
Amphipoda		Amphipoda	Epi		0.01	0.28			1.43	6.03		
Amphipoda		Hyperiidea	Epi		0.03	0.56	0.04	2.35	0.44	2.22	0.45	3.22
Amphipoda	Phronimidae	Phronima sp.	Epi		0.04	0.11	0.01	0.94	1.29	3.24	0.22	0.64
Amphipoda	Oxycephalidae	Streetsia sp.	Epi								0.02	0.21
			HM									
Decapoda		Caridea	bathy		0.01	0.34			0.04	0.72		
Decapoda		Dendrobranchiata			0.02	0.17						
Decapoda		Megalopa stage	Epi	yes	0.00	0.06			2.47	19.71	1.37	11.80
Decapoda		Palinura	Epi	yes	0.03	0.06			0.14	0.18		
Decapoda		Penaeoidea	M bathy		0.01	0.06						
Decapoda		Shrimp			1.82	8.60	0.00	0.47	0.60	4.47	0.37	3.86
Decapoda	Enoplometopidae	Enoplometopus sp.	Epi		0.03	0.28	0.00	0.47	0.75	2.64	0.41	1.93
Decapoda	Galatheidae	Galatheidae	Epi						0.01	0.09		
Decapoda	Oplophoridae	Acanthephyra sp.	M bathy		0.02	0.06			0.06	0.12		
Decapoda	Oplophoridae	Oplophoridae	Meso		0.01	0.06					0.06	0.21
Decapoda	Oplophoridae	Oplophorus sp.	Meso		0.01	0.11					0.55	2.36
			HM									
Decapoda	Oplophoridae	Oplophorus spinosus	bathy		0.02	0.06			0.13	0.30		
Decapoda	Palinuridae	Palinuridae	Epi	yes	0.05	0.34			0.01	0.03		
Decapoda	Palinuridae	Panulirus sp.	Epi	yes	0.01	0.11						
Decapoda	Palinuridae	Puerulus angulatus	Epi	yes	0.05	0.28						
Decapoda	Palinuridae	Puerulus sp.	Epi	yes	0.01	0.06			0.01	0.03		
Decapoda	Scyllaridae	Parribacus sp.	Epi	yes	0.06	0.11						
Decapoda	Scyllaridae	Scyllaridae	Epi	yes					0.01	0.06		
Decapoda	Scyllaridae	Scyllarus sp.	Epi	yes	0.02	0.11			0.02	0.06		
			HM									
Decapoda	Sergestidae	Sergestidae	bathy		0.05	0.17						
Isopoda		Isopoda					0.00	0.47				
Stomatopoda		Stomatopoda	Epi	yes	0.02	0.34	0.12	3.29	1.41	5.04	1.37	3.86
Stomatopoda	Harpiosquillidae	Harpiosquilla stephensoni	Epi	yes			0.03	0.47				
Euphausiacea	Euphausiidae	Euphausiidae	HM bathy								0.04	1.29
INVERTEBRATE												
		Cnidaria (phylum)							0.01	0.03		
		Gelatinous plankton							0.47	1.20		
		Polychaeta (Annelida)							0.05	0.03		
		Unidentified invertebrate			0.00	0.06			0.03	0.12		
Hemiptera	Geriidae	Halobates sp,			1	T	0.00	0.47				

										18
Salpida	Salpidae	Salp	Epi				0.86	3.42	0.73	2.15
MISCELLANEOUS										
		Bird feathers	Epi				0.00	0.03		
		Vegetal	Epi				0.08	0.15	0.02	
		Stone	Epi				0.34	0.96		
		Rubbish (human product)	Epi				0.03	0.03		
UNRECOGNIZABLE										
		Unrecognizable		0.01	0.06	5.45	1.15	0.03	4.33	