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Opportunistic predation in tuna: a size-based approach

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ABSTRACT: To test whether predation is an opportunistic size-based process within a tuna community, analyses were carried out on the size composition of stomach contents of bigeye tuna *Thunnus obesus* (Lowe, 1839) and yellowfin tuna *T. albacares* (Bonnaterre, 1788) caught in 1995 to 1997 during longline scientific surveys in the French Polynesian Exclusive Economic Zone (EEZ). Prey size distributions were compared with the size distribution of organisms collected by pelagic trawls carried out during the same programme. Relationships between prey size and predator size were studied using quantile regressions, and were related to tuna mouth-gape measurements. The results showed that mean and maximum sizes of prey increased with increasing predator size, and that maximum prey sizes (versus tuna size) were below those predicted by tuna mouth-gape size. Minimum prey size varied little with tuna size, and the size distributions of prey in tuna stomachs were very asymmetrical (lognormal type), confirming that during growth, tunas continue to feed on small prey. Comparison with previous studies on other piscivorous species from different ecosystems underlined that tunas feed on very small prey in relation to their own size. However, comparison of size distributions of prey in stomach contents and prey in pelagic trawls revealed that bigeye tuna select larger prey than yellowfin tuna when such prey are available.

KEY WORDS: Tuna · *Thunnus* spp. · Size-based predation · Diet · Quantile regression

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INTRODUCTION

Fish diets are frequently characterised by great diversity of prey species, which can be related to opportunistic predation. Fish predation is often described as an opportunistic (i.e. non-selective) process constrained by local prey availability and predator-prey size ratios (Shin & Cury 2001, 2004). Size is indeed an important factor affecting trophic interactions in marine ecosystems, with most predators being larger than their prey (e.g. Sheldon et al. 1977, Smetacek 1999, Cury et al. 2003). To confirm that prey size and trophic level generally increase with increasing predatory fish size, analyses of stomach contents and nitrogen isotope ratio have been conducted on fish communities in different marine ecosystems (i.e. Scharf et al. 2000, Badalamenti et al. 2002, Jennings et

al. 2002). In open-sea ecosystems, which are less productive than coastal ecosystems (Pauly & Christensen 1995), tuna species represent a high biomass and are considered opportunistic predators in terms of prey species (e.g. Sund et al. 1981). The tunas' prey are micronekton organisms that exhibit different vertical behaviours in the water column, with most undertaking generally large vertical migrations during the twilight phases (Watanabe et al. 1999), but some remaining in the shallow layers both day and night (Marchal & Lebourges 1996). Many studies have reported the size distribution and size range of tuna prey (e.g. Roger 1994), however empirical evidence of opportunistic size-based predation in tuna species has not been well studied. To our knowledge, the only study on size-based predation focused on the size relationships between tunas and cephalopod prey (Rancurel 1976).

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In order to explore whether predation is an opportunistic size-based process for tropical tunas, the present study aimed at specifying the size distribution of the diet of 2 species, *Thunnus obesus* (Lowe, 1839) and *T. albacares* (Bonnaterre, 1788) in the French Polynesia EEZ, using trawling data and stomach content data collected during the ECOTAP programme (Abbes & Bard 1999). Acoustic surveys, pelagic trawling and longline catches of tunas were carried out during the ECOTAP programme, with each data set involving specific bias. Bertrand et al. (1999, 2002a,b) combined these data in order to obtain complementary information about micronekton organisms in their environment, and characterised different types of nocturnal and diurnal scattering structures. They also proposed a typology of the micronekton distribution to predict tuna foraging on a regional scale (Bertrand et al. 1999), and described the pelagic trophic habitat of tunas (Bertrand et al. 2002a,b). The aim of the present study was to identify predation patterns in terms of predator and prey sizes. To this end, we reanalysed the trawling data and the stomach content data of yellowfin and bigeye tunas as a function of size. Firstly, the feeding habits of both tuna species were determined by analysing prey and predator size relationships by quantile regression. Secondly, predator–prey size ratios were determined to obtain an indication of the breadth of the tunas' trophic niche as a function of size. Finally, the size distribution of the prey in the tunas' stomachs was compared to that of micronekton sampled by trawling, and was related to tuna mouth-gape measurements to determine whether this limits the size range of prey ingested.

MATERIALS AND METHODS

Data. Data was collected within the framework of the ECOTAP programme (Abbes & Bard 1999); the sampling design has been described by Bertrand et al. (2002a). Yellowfin *Thunnus albacares* and bigeye *T. obesus* tunas were caught from October 1995 to August 1997 in the French Polynesian EEZ, between 4 and 20° S and 134 and 154° W, by instrumental longline fishing (Bach et al. 2003). Longlines were set to sample deep strata, i.e. from 100 to 400 m, thus targeting mostly large tunas. Several small juveniles of both species were also caught by trolling. Tuna size was recorded as fork length, FL (cm) (see Table 1). The tunas were divided into 4 length classes in order to study potential changes during ontogeny. Stomachs were immediately removed from freshly caught fish, and the contents sifted and rinsed on ship deck. The stomach contents were fixed in 10% formalin onboard ship. In the laboratory, prey items were sorted into

main prey classes (crustaceans, fishes, squids, gelatinous), which were then weighed (wet mass) to calculate their proportions in the tunas' diet. Prey sizes were measured according to prey morphology: standard length, SL (cm) for fishes, mantle length for squids, distance from eye to end of abdomen for crustaceans, and total length for gelatinous organisms. Highly digested prey were not measured. Assuming that prey height is more a constraint than length for a potential predator, we examined whether prey body height (and tuna mouth gape) limit the size of ingested prey. Only body lengths were available for our data set (no measure of prey body height), but Scharf et al. (1998b) estimated the relationship between fish height (defined as the maximum linear dorsoventral distance) and SL for several fish species, and from among those relationships, we selected their estimate for the butterflyfish *Peprius triacanthus*, because this species has the largest height compared to its length. The SL of our fish prey were converted to height according to

$$H = \frac{(SL - 5.638)}{2.384}$$

with H representing fish height (all measurements in mm; Scharf et al. 1998b). This ensured that a conservative hypothesis was tested, since it overestimated the height of the fish prey.

A total of 105 pelagic trawls were carried out during the ECOTAP programme with a fry pelagic trawl (5 mm mesh, mouth 18 m high) coupled with echosounding. The trawls were deployed according to nocturnal and diurnal scattering layers revealed by the echosounder: 69 trawls were conducted in diffuse and thick scattering layers during the night, and 36 trawls during the day for various forms of micronektonic aggregations; some organisms may have been collected during deployment and retrieval of the trawls. Most trawling was between the surface and intermediate layers (~250 m), with 1 trawl extending below 400 m in depth. The biomass (weight) of the scattering layers was dominated by myctophids (see Bertrand et al. 2002a for more details). Samples were immediately frozen onboard ship. In the laboratory, micronekton organisms were sorted into the 4 main prey classes used for the stomach content analyses and counted and measured as for the tuna prey. All trawling data was combined in order to obtain a large-scale estimate of the size spectrum of the organisms sampled.

Data analysis. Scatter diagrams of raw data linking prey and predator body sizes typically comprise a variety of polygonal structures, suggesting that upper and lower size boundaries change at different rates (Blackburn et al. 1992, Scharf et al. 1998a). Therefore, analysing changes in the highest and lowest sizes may be more informative than analysing changes in the mean

sizes (Cade et al. 1999). Cohen et al. (1993) showed that positive correlation between the body size of a predator and that of its prey is rarely high (and even negative in some cases), whereas upper boundaries of prey size tend to increase with predator size. Quantile regressions, as defined by Koenker & Bassett (1978), are well adapted for estimating changes near the upper boundaries of data distributions (Scharf et al. 2000, Eastwood et al. 2001, Cade 2003, Juanes 2003). Quantile regression is an extension to quantiles of the least-absolute deviation regression, whereby 50% of the observations are less than and 50% are greater than the fitted line (Scharf et al. 1998a, Cade et al. 1999). The package ‘quantreg’ of R available from the Comprehensive R Archive Network (<http://lib.stat.cmu.edu/R/CRAN>) was used in this study; it incorporates an estimation of the standard errors of the regression parameters. The choice of the quantiles used to represent upper and lower boundaries is subjective (Scharf et al. 1998a). Therefore, we first documented the variations in the slopes of the quantile regression according to quantiles ranging from 0.05 to 0.95. Slope estimates were compared using an *F*-like test (a variant of the Wald test) proposed in the R package, whereby the linear predictors of the fits are all the same, but the specified quantiles are different. The null hypothesis is that the slope coefficients of the models are identical. Ordinary least-squares regressions were also performed to estimate the relationship between mean prey size and predator size. Furthermore, quantile regression of prey body height versus predator body size was compared to the ordinary least-squares regression of predator mouth-gape size versus predator body size. For this latter analysis, data of mouth-gape size for bigeye and yellowfin tuna were pooled, since the mouth morphology of both species is similar. Trophic-niche breadth for each species was examined on a ratio scale, following the approach of Scharf et al. (2000). Quantile regressions (5th and 95th) were fitted to prey:predator size ratios versus predator sizes. Slopes between upper and lower limits were

compared using an *F*-like test: a significant difference corresponding to a divergence (convergence) of the slopes indicates an increase (decrease) of the ratio-based trophic-niche breadth.

RESULTS

A total of 136 bigeye and 97 yellow fin tunas with non-empty stomachs were analysed (Table 1). Fishes and squid were the most important food source by wet weight, gelatinous organisms were less commonly preyed on by both tuna species, and crustaceans were significant in the yellowfin tuna diet only (Fig. 1). Diet composition as a function of size class did not reveal

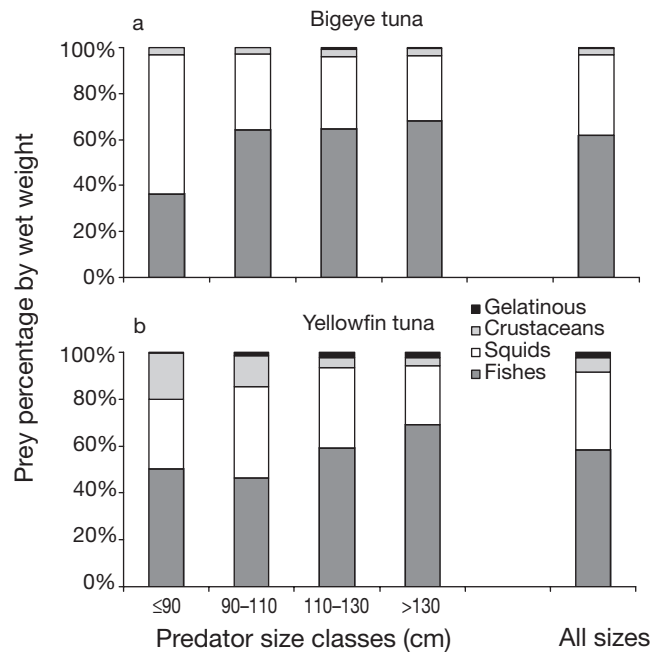


Fig. 1. (a) *Thunnus obesus*, (b) *T. albacares*. Contribution of main functional prey groups (fishes, squids, crustaceans, gelatinous organisms) to diet. Tunas are divided into 4 size classes (fork length)

Table 1. *Thunnus albacares* and *T. obesus*. Number and size descriptors (mean, minimum, maximum) of sampled tuna and number (n) and mean size of their prey. Tunas are divided into 4 size classes (fork length)

Parameter	<i>T. obesus</i>					<i>T. albacares</i>				
	≤90 cm	90–110	110–130	>130 cm	Total	≤90 cm	90–110	110–130	>130cm	Total
Predator n	18	65	46	7	136	14	14	57	12	97
Prey n	184	974	650	90	1898	453	307	1152	201	2113
Mean prey size (cm)	5.66	6.67	6.92	7.86	6.71	2.60	3.23	4.26	4.95	3.82
Predator size (cm)										
mean			106.6					113.8		
min.			47					51		
max.			159					147		

strong differences with tuna ontogeny. However, we did find that squid dominated the diet of small bigeye tuna (FL < 90 cm; mean size = 75.2 cm), whereas fishes dominated (>60%) the diet of bigeye tuna larger than 90 cm. Crustaceans were always present in a constant and small proportion in the diet of bigeye tuna. This latter prey group contributed 20% by wet weight to the diet of small yellowfin tuna (FL < 90 cm; mean size = 76.1 cm). However, the proportion of crustaceans regularly decreased in the larger size classes. Fishes remained the principal food source, especially for yellowfin tuna larger than 110 cm. Overall, the differences in diet composition between bigeye and yellowfin tunas were not great, especially for tunas larger than 130 cm, and we therefore investigated the relationship between prey size and predator size with no further consideration of the 4 prey groups.

Quantile regression parameters and their standard errors were estimated for a range of quantiles between 0.05 and 0.95 for both tuna species. The slope of the relationship between prey size and predator size changed according to the quantile used for prey length distributions (Fig. 2). The 5th and 95th quantiles were selected to estimate the lower and upper bounds of prey size distribution, respectively, for both tuna species. Maximum prey size increased as body size increased for both predator species, whereas minimum prey size did not exhibit a significant trend (Fig. 3). Table 2 shows the equations of the quantile and ordinary least-squares regressions. For both tuna species, the highest slopes were those for the upper boundary (0.127 and 0.091 for bigeye and yellowfin tuna, respectively), and the lowest corresponded to the lower boundary (slightly negative for bigeye tuna and slightly positive for yellowfin tuna). For each species,

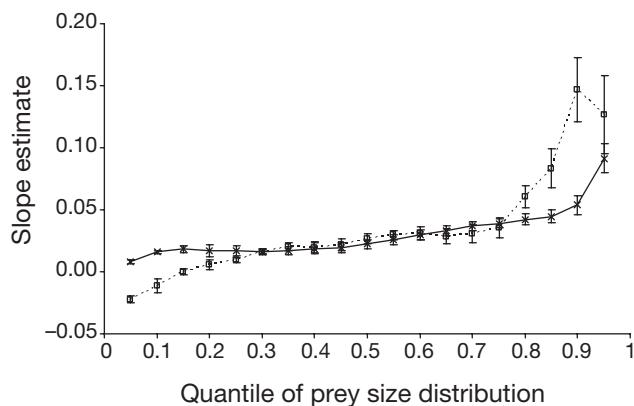


Fig. 2. *Thunnus obesus* and *T. albacares*. Estimates of quantile regression slopes (\pm SE) for range of quantiles varying between 0.05 and 0.95, for *T. obesus* (dashed line) and *T. albacares* (continuous line). These slope coefficients estimate different rates of change in quantiles of distribution of prey length conditional on predator length

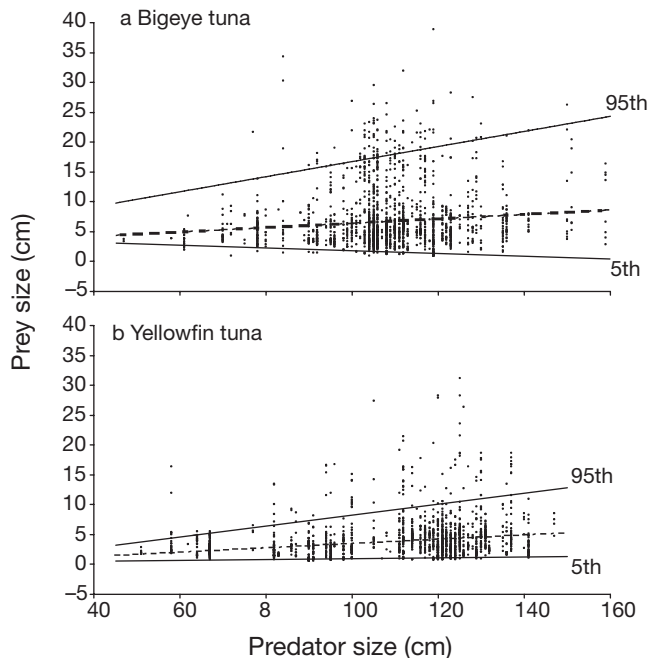


Fig. 3. (a) *Thunnus obesus*, (b) *T. albacares*. Predator-prey size scatter diagrams. Quantile regression lines (continuous lines) indicate upper (95th) and lower (5th) boundaries used to describe predator and prey size relationships. Least-squares regression line (dashed line) estimates rates of change in mean prey size as a function of predator size

the difference between the upper- and lower-boundary slopes was highly significant ($p < 0.0001$ in both F -like tests). Mean prey size-predator size slopes estimated from ordinary least-squares regression were similar for both tuna species and significantly positive (0.037 and 0.036 for bigeye and yellowfin tuna, respectively). They were about 3 times lower than the upper boundaries of the corresponding quantile regressions, indicating that the ontogenetic changes in mean prey sizes were driven primarily by changes in maximum prey size. The higher intercept and slope values of the upper boundary for bigeye tuna indicates that, at equivalent sizes, bigeye tuna feed on prey of larger size than yellowfin tuna, and that the ontogenetic change in maximum prey size is larger for bigeye tuna. The distributions of prey sizes for each tuna size class corroborate this difference between the 2 species (Fig. 4). Larger bigeye tunas tend to feed on larger prey, while a progressive increase in the consumption of larger prey is less pronounced for yellowfin tunas. All these distributions were strongly asymmetrical (log-normal or gamma type), confirming the continued inclusion of small prey in the diet across the whole range of predator sizes.

We used 2 predictor variables for the measure of tuna mouth-gape size: maxillary length (L_m) and inter-maxillary length (L_{im}). Mouth-gape size (cm) increased lin-

Table 2. *Thunnus obesus* and *T. albacares*. Quantile regression equations (95th and 5th upper and lower boundaries, respectively) relating prey size to predator size, and least-squares equation fitted to same prey and predator size data. Standard error estimates of slope coefficients (SE_s) and intercepts (SE_i) are indicated

5th Quantile	95th Quantile	Least-squares
<i>T. obesus</i>		
$y = -0.022x + 4.067$ ($SE_s = 0.006$; $SE_i = 0.610$)	$y = 0.127x + 4.067$ ($SE_s = 0.017$; $SE_i = 1.669$)	$y = 0.037x + 2.746$ ($SE_s = 0.008$; $SE_i = 0.876$)
<i>T. albacares</i>		
$y = 0.008x + 0.140$ ($SE_s = 0.001$; $SE_i = 0.049$)	$y = 0.091x - 0.926$ ($SE_s = 0.018$; $SE_i = 1.529$)	$y = 0.036x - 0.110$ ($SE_s = 0.003$; $SE_i = 0.367$)

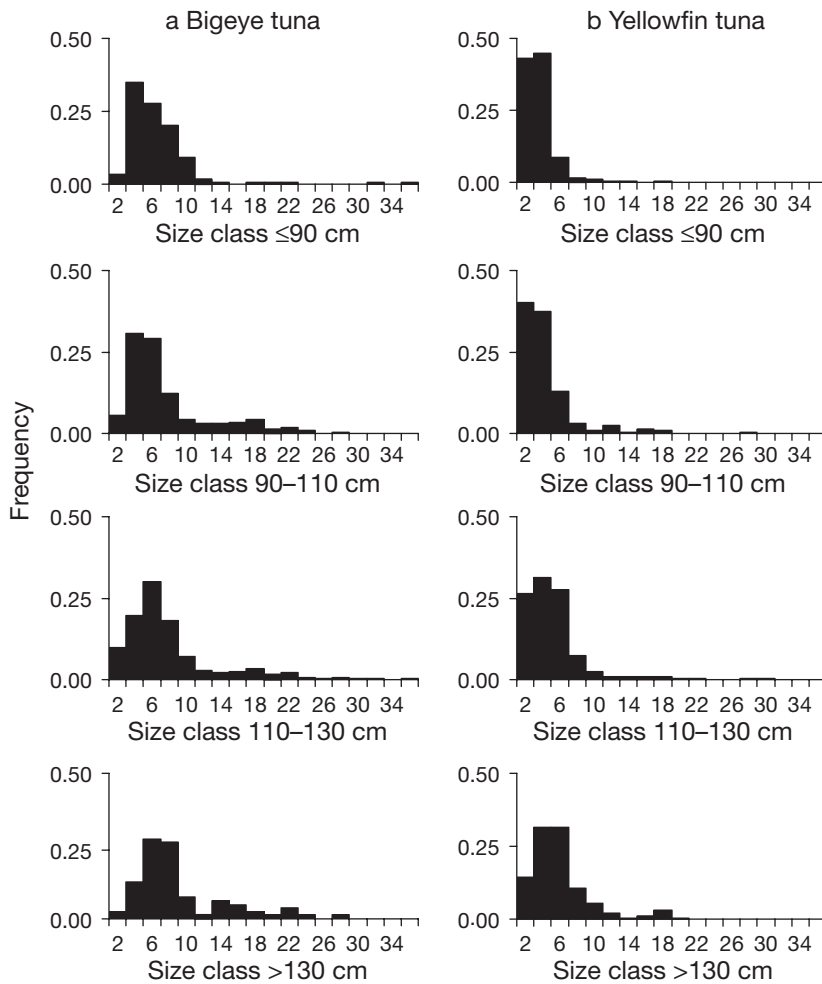


Fig. 4. (a) *Thunnus obesus* and (b) *T. albacares*. Size-frequency (n) distributions of prey (cm) in stomach contents. Tunas are divided into 4 size classes (fork length)

early with increasing tuna fork length: $L_m = 0.0823 FL + 1.758$, $n = 69$, $R^2 = 0.95$; $L_{im} = 0.0860 FL + 0.952$, $n = 126$, $R^2 = 0.83$. These very close slope coefficients can be compared to the slope of the maximum prey body height estimated from the 95th quantile regression of fish prey body height (H) versus tuna length ($H = 0.0246 FL +$

4.603, Fig. 5). Mouth-gape size increased 3 to 4 times faster than the body height of fish prey, even when adopting a conservative hypothesis for the conversion of fish prey length to body height; thus, gape size does not seem to be the limiting factor of maximum prey size consumed by yellowfin and bigeye tuna.

Neither tuna species exhibited a significant ontogenetic change in trophic-niche breadths, estimated from quantile regressions fitted to prey:predator size ratios versus predator sizes (Table 3 & Fig. 6). Tests of equality of slope coefficients between upper (95th quantile) and lower (5th quantile) limits were not significant (F -value = 0.725, $p > 0.395$ for bigeye tuna; F -value = 0.678, $p > 0.411$ for yellowfin tuna). The use of other pairs of quantiles did not modify the results: neither convergence nor divergence was found in the slope coefficients, which were all close to zero.

Fig. 7 & Table 4 compare the size distribution of organisms collected by trawling, and that of prey found in the tuna stomachs. Bigeye tuna fed on prey that were larger than the organisms sampled by trawling, as well as a significant amount of smaller prey, whereas the size distributions of the prey of yellowfin tuna and of trawl samples were very similar (in the range 0.5 to 9 cm). Notwithstanding the selectivity of the trawl, these tuna species did exhibit an apparent difference in the selectivity for large prey compared to the prey available in the environment.

DISCUSSION

Body size is known to play a crucial role in predator-prey interactions, especially in aquatic ecosystems (Sheldon et al. 1977). Previous studies of predation by both marine and freshwater fishes have shown asymmetric prey size distributions and an increase in the range of prey size with increasing predator size (e.g. Mittelbach & Persson 1998, Scharf et al. 2000). To our knowledge, no study has yet dealt specifically with tuna size-based predation in open-sea ecosystems, even though several studies have reported the size distribution or size range of tuna prey. Rancurel (1976)

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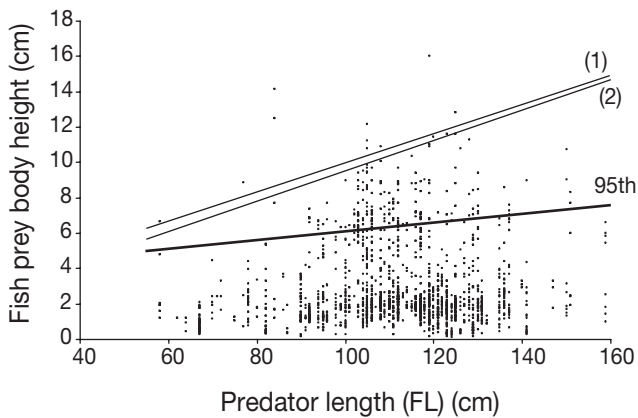


Fig. 5. Scatter diagram of predator (*Thunnus* spp.) size versus body height of prey estimated by conservative hypothesis (see 'Materials and methods'). Predator and prey data for *Thunnus obesus* and *T. albacares* are pooled. Lines (1) and (2) represent least-squares regressions of mouth-gape size versus predator size with gape size estimated from (1) maxillary length and (2) inter-maxillary length. Quantile regression line (thick line) indicates upper (95th) boundary used to describe relationship between predator size and body height of prey. FL: fork length

studied the size distribution of cephalopods consumed by tunas caught by longline, and showed that tunas did not systematically seek prey of a specific size. Our results indicate that the maximum size of the prey consumed by tunas tends to increase with increasing tuna body length, while the minimum prey size remains fairly stable. This is evidenced by the asymmetric prey size distributions that are roughly log-normally distributed. Thus, large tunas continue to consume large proportions of small prey. The slope coefficients of the upper bounds estimated by quantile regressions in Scharf et al. (2000) for 18 marine fish predators from continental shelf waters ranged from 0.077 to 0.894 (e.g. 0.435 for Atlantic cod *Gadus morhua*, for which body size varied between 21 and 150 cm; 0.462 for bluefish *Pomatomus saltatrix*, a pelagic species in the

Table 3. *Thunnus obesus* and *T. albacares*. Quantile regression equations (95th and 5th for upper and lower boundaries, respectively) fitted to prey:predator size ratios to track potential changes in trophic-niche breadth. Standard error estimates of slope coefficients (SE_s) and intercepts (SE_i) are indicated

5th Quantile	95th Quantile
<i>T. obesus</i>	
$y = -0.0005x + 0.071$ ($SE_s = 0.00005$; $SE_i = 0.0054$)	$y = -0.0003x + 0.199$ ($SE_s = 0.0002$; $SE_i = 0.0239$)
<i>T. albacares</i>	
$y = -0.00001x + 0.01064$ ($SE_s = 0.00001$; $SE_i = 0.00069$)	$y = 0.00015x + 0.06731$ ($SE_s = 0.00019$; $SE_i = 0.01873$)

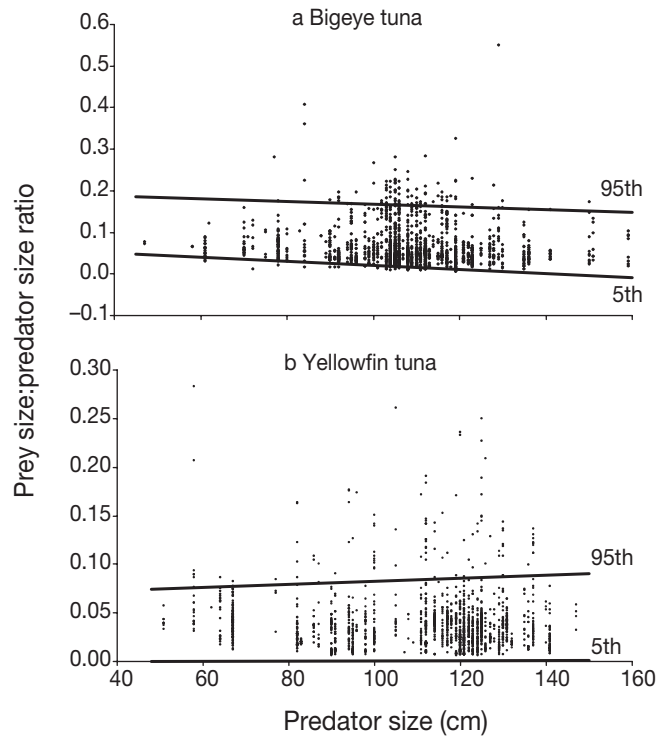


Fig. 6. *Thunnus obesus* and *T. albacares*. Scatter diagrams of relative prey size (prey:predator size ratio) as a function of predator size. Quantile regression lines (95th and 5th for upper and lower boundaries, respectively) indicate potential changes in trophic-niche breadth

size range 11 to 88 cm). The upper-boundary slopes we estimated for bigeye and yellowfin tuna were 0.127 and 0.091, respectively. Compared with the values estimated by Scharf et al. (2000), both tuna species are within the category of predators that feed on prey with the smallest relative size. The trophic-niche breadth of bigeye and yellowfin tuna did not increase with increasing predator size: the prey size:predator size ratios did not change during ontogeny across the tuna size ranges considered in the present study. The absence of bias due to the increase of prey numbers with increasing predator size was checked—Spearman correlation coefficients were not significant ($p = 0.315$ and 0.110 for bigeye and yellowfin tuna, respectively). The lack of significant changes in trophic-niche breadth is consistent with results of previous studies, which focused either on larval and juvenile stages (Pearre 1986, Munk 1997) or on both juvenile and adult fishes (Scharf et al. 2000). We also observed that the largest prey did not necessarily occur in the stomach contents of the largest tunas, but the small number of large tunas in our data set make this observation tentative. The ratio minimum:maximum tuna size in our data set was ca. 3 for both species (Table 1).

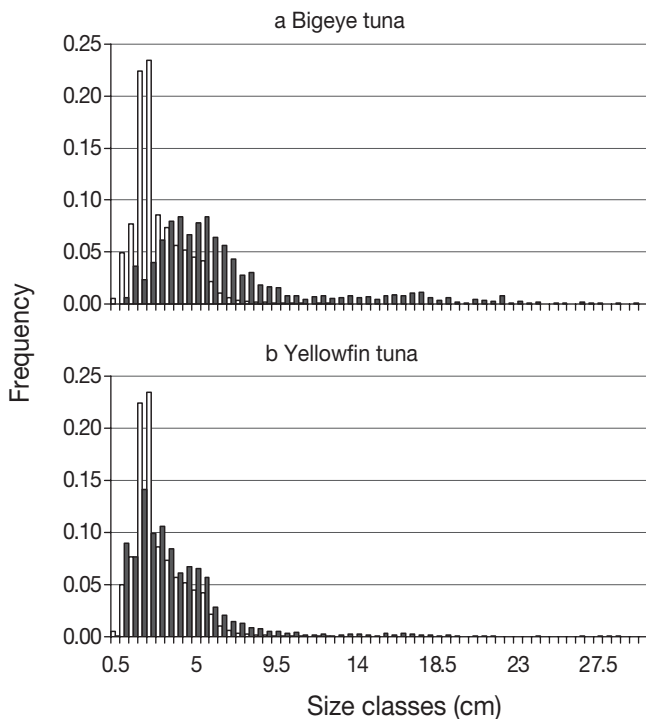


Fig. 7. (a) *Thunnus obesus* and (b) *T. albacares*. Size-frequency (n) distributions of organisms collected by trawling (white columns) and of prey found in stomach contents (black columns)

Table 4. Size (cm) of organisms collected by trawling and of prey recovered from stomach contents of *Thunnus obesus* and *T. albacares*

Size range	Trawl organisms	<i>T. obesus</i> prey	<i>T. albacares</i> prey
Min.	0.5	0.9	0.5
Max.	35.5	71.0	31.2
Mean	3.1	6.7	3.8
Median	2.5	5.2	3.0

Samples of very small tunas were lacking, since specimens of <50 cm are generally caught by purse seiners. We complemented our longline samples with trolling catches, which allowed us to study several small specimens of both species (<90 cm) but were not sufficient to cover a larger size range that would have enabled us to reinforce our interpretation of changes throughout their ontogeny. Furthermore, maturity may influence tuna diet. The gonadosomatic indexes (GSI) of females of both tuna species were recorded during the ECO-TAP programme (Abbes & Bard 1999). High values of GSI were observed for some of the bigeye tunas caught in the NE section of the French Polynesian EEZ during the first 2 quarters of the year, whereas low GSI values

were always recorded for yellowfin tunas. The study area (4 to 20° S; 134 to 154° W) does not appear to be a main spawning area for either species. Thus, the influence of gonad development on diet was not considered.

The stomach content analyses were performed on deep-dwelling tunas caught by longline sets at great depths (Bach et al. 2003). The study of the diet of shallower tunas caught by surface purse-seine fishery might give different results. Indeed, several analyses have revealed symmetrical distribution in the prey size of shallow-water tunas. This difference in prey size distributions in tuna stomachs might be due to differences in prey size distributions in the tunas' environment. For example, Bard et al. (2002) showed that large yellowfin tuna caught by purse seiners in the equatorial Atlantic fed on monospecific concentrations of juvenile *Cubiceps pauciradiatus* belonging to the same size class. Ménard & Marchal (2003) studied the foraging behaviour of tunas feeding on small schooling *Vinciguerria nimbaria* in the surface layer of the equatorial Atlantic. In both cases, concentrations of the schooling prey were dominant in the surface layer where tunas may seek their prey.

The body height of the prey as well as the mouth gape of the predator can limit the size of the prey consumed (Dennerline & Van Den Avyle 2000, Scharf et al. 2000). In our study, only body length measurements of prey were available, and the largest prey eaten by both tuna species were mainly fishes. Therefore, we adopted a conservative hypothesis for the conversion of fish prey length to body height by using a published body height:body length relationship that certainly overestimated the height of the fish prey from our data set. Despite this conservative approach, maximum prey sizes were below those predicted by tuna mouth-gape size. Our results provide important evidence that size-based feeding strategies of tunas may be related to limiting factors other than mouth-gape morphology, such as prey availability and behavioural differences of both predators and prey.

A slight difference was revealed between bigeye and yellowfin tunas, with bigeye tuna feeding on prey of larger relative sizes. This may be attributable to the different vertical distributions of the 2 tuna species arising from their respective physiological abilities (Brill 1994, Swimmer et al. 2004). Results of electronic tagging have shown that adult bigeye tuna are able to reach very deep layers, and that they usually make successive vertical, U-shape dives (e.g. Dagorn et al. 2000, Musyl et al. 2003). They can thus feed on organisms that remain at depth during the night, and forage in depth layers between 200 and 550 m during the day (Dagorn et al. 2000). On the other hand, adult yellowfin tuna spend most of their time in the surface layer, and

consequently their diet is mainly composed of organisms present in the upper 100 m (Bertrand et al. 2002a). Thus both species have distinct foraging strategies, with bigeye tuna foraging over a wider area than the yellowfin tuna. We thus believe that bigeye tuna have access to a larger size range of prey in the environment. Bertrand et al. (2002a) have pointed out that bigeye tuna prey on myctophid aggregations as well as targeting the predators of myctophids, i.e. piscivorous fishes of larger size than myctophids. However, precise information on size distribution of the prey available in the environment is required to examine the selection of prey based upon predator size–prey size relationships. We used pelagic trawls for sampling the prey. The selectivity of the trawl on small organisms was probably not biased, whereas the frequency distribution of the larger sizes was flawed due to the escape behaviour of the large organisms (Fig. 7). Therefore, trawling data cannot reflect the full assemblage of prey in the environment, and it is thus difficult to separate the effects of prey type availability in the environment and active size selection by a predator. Bertrand et al (2002a) compared the proportions (by weight and by number) of various functional prey groups observed in trawls and in tuna stomachs, and interpreted the differences as differences in 'sampling efficiency'. Squid are in fact difficult to collect by nets, and cephalopod predators capture larger specimens and a greater diversity of species than does sampling gear (Rodhouse 1990, Cherel et al. 2004). In our trawl samples, squid were small and numerically fewest, whereas they contributed significantly to the diet of bigeye and yellowfin tunas. However, we believe that comparison of size data of prey from the stomach contents of predators and from pelagic trawls provides a reliable reflection of size-selection of prey by deep-dwelling tunas. Figs. 4 & 7 show that yellowfin tuna preyed on organisms in the same size range as those taken in the pelagic trawls, whereas bigeye tuna selected larger prey than yellowfin tuna, probably from deeper layers. Our results provide some evidence that tunas adopt opportunistic foraging behaviour, although there is an interspecific difference, with bigeye tuna selecting large prey when these are available.

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