

# Interaction between Coastal and Oceanic Ecosystems of the Western and Central Pacific Ocean through Predator-Prey Relationship Studies

Valerie Allain<sup>1\*</sup>, Emilie Fernandez<sup>1</sup>, Simon D. Hoyle<sup>1</sup>, Sylvain Caillot<sup>1</sup>, Jesus Jurado-Molina<sup>1</sup>, Serge Andréfouët<sup>2</sup>, Simon J. Nicol<sup>1</sup>

**1** Oceanic Fisheries Programme, Secretariat of the Pacific Community, Noumea, New Caledonia, **2** Unité de Recherche 227– CoRéUs, Institut de Recherche pour le Développement, Noumea, New Caledonia

## Abstract

The Western and Central Pacific Ocean sustains the highest tuna production in the world. This province is also characterized by many islands and a complex bathymetry that induces specific current circulation patterns with the potential to create a high degree of interaction between coastal and oceanic ecosystems. Based on a large dataset of oceanic predator stomach contents, our study used generalized linear models to explore the coastal-oceanic system interaction by analyzing predator-prey relationship. We show that reef organisms are a frequent prey of oceanic predators. Predator species such as albacore (*Thunnus alalunga*) and yellowfin tuna (*Thunnus albacares*) frequently consume reef prey with higher probability of consumption closer to land and in the western part of the Pacific Ocean. For surface-caught-predators consuming reef prey, this prey type represents about one third of the diet of predators smaller than 50 cm. The proportion decreases with increasing fish size. For predators caught at depth and consuming reef prey, the proportion varies with predator species but generally represents less than 10%. The annual consumption of reef prey by the yellowfin tuna population was estimated at  $0.8 \pm 0.40CV$  million tonnes or  $2.17 \times 10^{12} \pm 0.40CV$  individuals. This represents  $6.1\% \pm 0.17CV$  in weight of their diet. Our analyses identify some of the patterns of coastal-oceanic ecosystem interactions at a large scale and provides an estimate of annual consumption of reef prey by oceanic predators.

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\* E-mail: ValerieA@spc.int

## Introduction

The tropical area of the Western and Central Pacific Ocean (WCPO) represents a vast area of about 35 million km<sup>2</sup> (120°E–140°W, 15°N–25°S), larger than the Indian and Atlantic Ocean tropical areas. Compared to these oceans and to the Eastern Pacific, the WCPO is uniquely scattered with many atolls, high islands and island groups [1], totaling about 140,000 km of coast (excluding Australia) with diverse habitats including lagoons and reefs. The WCPO is also characterized by complex bathymetry with numerous seamounts [2,3]. This unique topography induces multiple and complex vertical hydrological structures and current circulation patterns (eddies, frontal zones) [1].

The WCPO region is also characterized by tuna fisheries that generate the highest tuna catches in the world (>60% of the global tuna catches) with skipjack, yellowfin, bigeye and albacore tuna annual catches estimated at nearly 2.5 million tonnes in recent years [4]. In 2011 the total estimated landed value of tuna catches in this region exceeded USD 4 billion [4] representing a major economic resource for Pacific Island Countries and Territories [5].

The complex structure of the WCPO coastal system and its spread over such a large area where important oceanic fisheries operate create the opportunity for a high degree of interaction between coastal and oceanic ecosystems. Organisms with an obligate coastal, reef or lagoon life-history phase, named reef prey in our study, drifting in the oceanic domain before coming back to the reef, have a role in transferring energy between the coastal and the oceanic realm and vice versa.

Interactions between coastal and oceanic ecosystems have been explored through predator-prey relationship studies. Reef organisms have been identified as prey of the oceanic predators in a number of diet analyses of large pelagic fish [6–22]. According to the studies considered, their importance in the diet in terms of frequency and quantity varied from minor [6,8,15,22] to major or dominant [9–11,14,16–20]. Proportion in the diet varied according to factors such as the predator species considered (surface feeders tend to consume more reef prey) [7,10,18,21], size of the predators (large fish eat less reef prey) [11,17], and habitats (e.g. near-shore predators eat more reef prey than offshore fish) [9–10,13–14,16–18].

However, most of these studies were based on limited sample size (fewer than 400) collected in restricted areas, in the open ocean less than 100 km from land, close to land or around near-shore fish aggregating devices (FAD) anchored in deep waters. These studies do not offer the possibility to systematically analyze the influence of multiple factors such as distance to land or reef, predator species, or predator length, latitude and longitude so as to properly characterize reef prey consumption by oceanic predators at a large scale. Moreover, to our knowledge, the total amount of reef prey consumed by predator's populations has never been estimated.

Trophic studies conducted by the Secretariat of the Pacific Community (SPC) in the whole WCPO provide a unique opportunity to explore the potential importance of reef prey for the offshore pelagic ecosystem at an ocean basin scale. We examine patterns of interaction between coastal ecosystems and oceanic ecosystems in the WCPO by applying generalized linear models (GLM) to this large dataset of oceanic predator stomach contents data, and present an example of estimating total annual consumption of reef prey by oceanic predators in the WCPO.

## Results

### 1. Description of Reef Prey Consumed

The most important reef prey found in the stomach contents were Acanthuridae (surgeonfish), Balistidae (triggerfish), Chaetodontidae (butterflyfish), Holocentridae (squirrelfish), Monacanthidae (filefish), Pomacanthidae (angelfish), Siganidae (rabbitfish), Synodontidae (lizardfish) larval and juvenile fishes, and Stomatopoda (mantis shrimp), Brachyuran (crabs) and Palinuroidea (lobsters) crustacean larvae (Table S1). Average standard length (SL) and weight ( $\pm$ SE) of larval and juvenile fishes were  $32.9 \pm 0.4$  mm and  $1.85 \pm 0.14$  g (30, 24, 20, 35, 36, 15, 52 mm and 1.26, 1.25, 0.60, 1.59, 1.78, 0.24, 1.88 g respectively for families cited previously except Synodontidae for which no individual measures were available) and average cephalo-thorax length and weight for crustaceans larvae were  $7.5 \pm 0.2$  mm and  $0.27 \pm 0.02$  g (8.4, 4.9 and 14.5 mm and 0.25, 0.13 and 1.13 g respectively for groups cited previously).

### 2. Probability of Consumption or Frequency of Occurrence of Reef Prey by Large Predators

The chosen model for explaining the reef prey occurrence in stomach contents included predator species, distance-to-land and longitude (Table 1, Table S2). At the median longitude and distance-from-land, albacore and yellowfin tuna had the highest probabilities of consuming reef prey ( $>0.6$ ), followed by skipjack, mahi mahi and wahoo which had intermediate probabilities ( $>0.3$

and  $<0.6$ ), while bigeye, rainbow runner and lancetfish had lower probabilities ( $<0.3$ ) of consuming reef prey (Figure 1A). The highest proportions of stomachs containing reef prey were observed closer to land and decreased logarithmically as distance-to-land increased (Figure 1B). The probability that a stomach contained reef prey decreased strongly in the first 100 km from land. The data indicated a clear spatial pattern with higher probabilities of presence of reef prey in the stomach of predators located in the western part of the area (Figure 1C). The probability decreased towards the date line ( $180^\circ$ ) and stabilized at lower values east of the dateline up to the eastern limit of our study area ( $130^\circ$ W).

### 3. Weight Proportion of Reef Prey in Predator's Stomach Consuming Reef Prey

The preferred model for explaining the weight proportion of reef prey in the stomach of the predator consuming reef prey only included fishing gear (Table S3). Predators caught with surface gears contained a higher proportion of reef prey in their stomachs than predators caught with longline gear:  $0.27 \pm 0.01$  vs.  $0.07 \pm 0.04$  respectively (predicted mean and 95% confidence interval). However, samples collected with these two fishing gear types were different in terms of predator species, length, and longitude. Further modeling was conducted separately on surface and longline gears to identify additional determining factors. The preferred model when only considering samples from predators caught by surface gears included the length of the predator (Table S4). The weight proportion of reef prey per stomach was more than 0.3 for small predators (20 to 40–50 cm) and the proportion decreased with the size of the predator (Figure 2). The preferred model when only considering samples from predators caught by longline gears included only predator species (Table S5). Bigeye tuna consumed the lowest weight proportion of reef prey with less than 0.02 (Figure 3). Albacore and yellowfin consumed similar proportions, predicted to be between 0.05 and 0.1. Predicted weight proportions were between 0.09 and 0.19 for other predators (Figure 3), however their confidence intervals were large, most likely due to the small sample size ( $<50$ ) for these predators.

### 4. Reef Prey Consumption Estimate

The yellowfin tuna population, estimated at 1.47 million tonnes in 2009 in the equatorial Western and Central Pacific Ocean between  $20^\circ$ N and  $10^\circ$ S [23], consumed an annual estimate of  $0.818 \pm 0.40$ CV million tonnes of reef prey, representing  $6.1\% \pm 0.17$ CV of the  $13.426 \pm 0.36$ CV million tonnes of preys consumed by this predator. Based on average weight of reef prey crustaceans and fish (cf Results §1) and on reef prey proportions in weight of crustaceans ( $0.67 \pm 0.02$ CV) and fish ( $0.33 \pm 0.04$ CV) consumed by yellowfin tuna, the total number of reef prey consumed by the yellowfin tuna population in the WCPO was estimated to be  $2.17 \times 10^{12} \pm 0.40$ CV individuals ( $2.02 \times 10^{12} \pm 0.41$ CV crustaceans and  $0.15 \times 10^{12} \pm 0.41$ CV fishes).

## Discussion

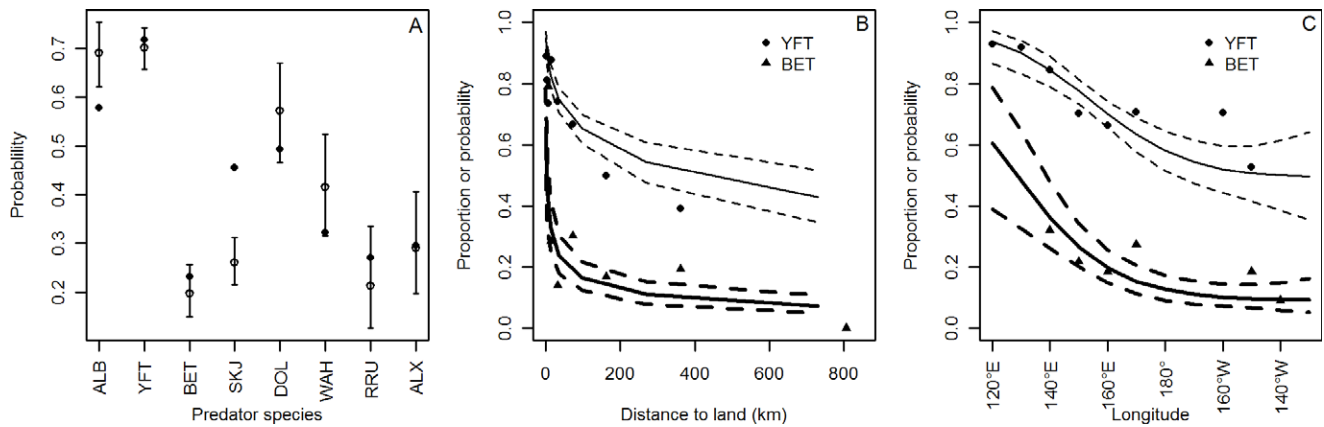
Our analyses suggest that reef organisms are a frequent prey for small oceanic predators in the WCPO. They also suggest that the degree of interaction is affected by the spatial distribution of reef prey: the majority of reef prey is consumed in the western part of the region and at distance-to-land less than 100 km. The predator's behavior also influences the reef prey consumption as small specimens and species foraging at the surface eat more reef prey. A total of 0.8 million tonnes of reef prey (about  $2.2 \times 10^{12}$

**Table 1.** Results of GLM modeling presence-absence of reef prey in stomach contents of predators.

|                         | Df | Chisq | p-value                    | BIC  |
|-------------------------|----|-------|----------------------------|------|
| set_code random effect  |    |       |                            | 5123 |
| + predator              | 7  | 398.7 | $<2.2 \times 10^{-16}$ *** | 4745 |
| + log(dist_land+1)      | 1  | 61.4  | $4.8 \times 10^{-15}$ ***  | 4667 |
| + ns(longitude, df = 2) | 2  | 40.8  | $1.4 \times 10^{-9}$ ***   | 4645 |

Df, degree of freedom; Chisq, Deviance of the final model; p-value from Anova Chi-test; BIC, Bayesian Information Criterion. Significance codes: 0 '\*\*\*' 0.001 '\*\*' 0.01 '\*' 0.05 '.' 0.1 ' ' 1.

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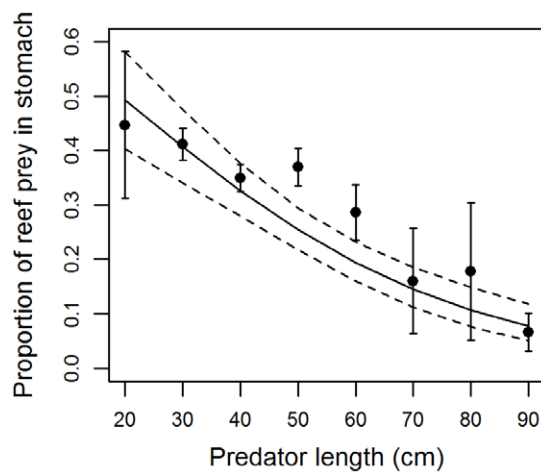


**Figure 1. Observed proportion (frequency of occurrence) and model predicted probability with 95% confidence interval of the number of stomachs containing reef prey for all predators.** A) By predator species, B) by distance-to-land and C) by longitude. Solid dots are observations, open circles with error bars or solid and dashed lines are predicted probabilities and 95% confidence intervals. YFT (solid circles and normal lines) and BET (triangles and bold lines) are shown as examples in B) and C). One variable was predicted at a time from the results of the model by fixing the other variables at median value. In Figure 1A, because the predictions are established for median values of distance-to-land and longitude, some discrepancies between predicted and observed values are apparent, particularly for SKJ, as observed data come from places on average significantly different from median values chosen for predictions. ALB, albacore tuna; YFT, yellowfin tuna; BET, bigeye tuna; SKJ, skipjack; DOL, dolphinfish; WAH, wahoo; RRU, rainbow runner; ALX, lancetfish. doi:10.1371/journal.pone.0036701.g001

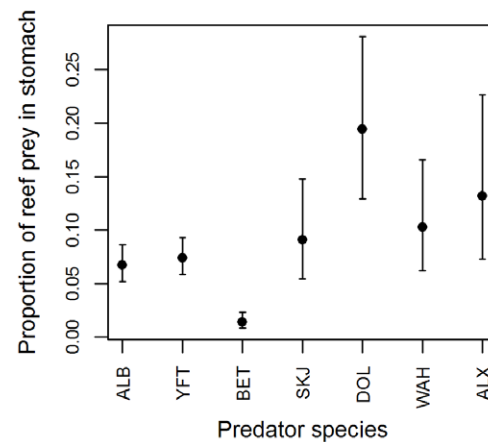
specimens) is estimated to be consumed by the yellowfin tuna population in the region, representing 6.1% in weight of their diet.

We observed that more interaction occurs west of 160°E in the area that encompasses the Western Pacific warm pool ecosystem (e.g. Indonesia, Palau, Papua New Guinea, Federated States of Micronesia and Solomon Islands). The decreasing trend observed from west to east can be explained by the topography and its related oceanography. The western region of the WCPO has more islands, more coast line and higher reef surface area than the eastern region of the studied area (Figure S1). In general the production of reef larvae is positively correlated with the quantity of reef and coastal habitats [24–25] and consequently higher availability of reef prey can be expected in the western region than in the eastern region of our study area. The pelagic phase of reef

larvae can extend up to 1 year [26] for some species and it has been demonstrated that the longer the duration of the pelagic larval phase, the wider the potential dispersion [27]. Duration of the pelagic phase along with dispersion is one of the most important factors influencing the distribution and availability of reef prey and consequently their presence in stomach contents. Late-stage reef larvae are effective swimmers [28–29], but before developing these capabilities, part of the reef prey is assumed to be advected by currents [30]. Large-scale circulation patterns will tend to disperse larval organisms from their spawning site by several hundred kilometers [31–32]. Complex topography with many islands and seamounts disrupts the flow of the main currents and induces the formation of eddies in the lee of the islands in the WCPO [33–34]. These eddies and other oceanographic features act as strong larval retention zones [26,31,35–36]. We observed an



**Figure 2. Proportion by weight of reef prey in stomach content against predator's length, the main explanatory variable, for all predators consuming reef prey and caught with surface fishing gear.** Observed mean (dot) with 95% confidence interval (error bars) and predicted value (solid line) with 95% confidence interval (dashed line). doi:10.1371/journal.pone.0036701.g002



**Figure 3. Proportion by weight of reef prey in stomach content against predator's species, the main explanatory variable, for all predators consuming reef prey and caught with longline gear.** Predicted means with 95% confidence interval. Predator code: see caption of figure 1. No rainbow runner (RRU) was caught with longline gear. doi:10.1371/journal.pone.0036701.g003

association between reef prey presence in predator stomachs and the proximity to land, with a high probability that reef prey are consumed within 0–100 km of land. This trend has been previously noted in other tuna stomach content studies [7,13,17–18] and in fish larvae distribution studies [37,38]. This association is in agreement with larval retention zones occurring around islands. In our model, at the scale of the ocean basin, the proportion of reef prey in stomachs was better explained by proximity to land than proximity to reef which might be linked to the prevalent effect of larval retention associated to land masses over the production effect of reefs. We acknowledge that, at different scales, the results of the model might differ. Reef could be a better predictor than land in areas dominated by atolls such as Tuamotu Archipelago in Central Pacific, as atolls and banks may be characterized by large reef and lagoon areas without land. Conversely, several large islands do not necessarily have reefs around them (Marquesas Islands, Vanuatu Islands). Surface of reef or lagoon around the predator were not included in the model but they are expected to be positively correlated with presence and proportion of reef prey in the stomachs if it is assumed that a larger surface of reef produces more reef prey.

The school type (FAD vs. non-FAD school) did not appear as a significant explanatory variable in our chosen models. However it came forward in models ranked within the 5 best models with lowest BIC (Table S2, Table S3, Table S4). In the WCPO there are large arrays of anchored FADs in Papua-New-Guinea and Solomon Islands particularly and many drifting FADs in the western part of the region. In this region the anchored and drifting FADs are located offshore. Predators were caught on average on anchored FADs, drifting FADs and drifting logs located respectively at  $68 \pm 6$  km (mean  $\pm$  95% confidence interval),  $152 \pm 17$  km and  $103 \pm 22$  km from shore while fish from free schools were caught at  $147 \pm 22$  km from shore. These distances are much larger than in other studies on the impact of FADs on the diet of oceanic predators which are dealing with near-shore anchored FADs less than 30 km from shore [9–11,14,16]. Like floating sargassum, FADs do have associated fauna which is largely composed of reef pre-settlement larvae and juveniles [39–42]. Many studies have suggested that oceanic predators caught in the vicinity of FADs or floating sargassum contained a large proportion of reef prey [10,14,16,43–44]. One study is discordant however as Brock observed that, around Hawaii, reef prey were dominant in non-FAD predators while FAD predator were mainly feeding on deep crustaceans [9]. Results of this particular study might be linked to a specific availability of this shrimp. If our study indicates that FAD associated predators also consumed reef prey, it is not a major explanatory variable in our models because their large distance from shore probably means they aggregate less reef prey than near-shore FADs. It could also be linked to the scale of our study which includes confounding factors: most of the anchored FADs are located in the western part of the region. Studies at smaller spatial scale might reveal the prominence of the FAD effect on the diet.

In the water column reef prey are commonly distributed in the upper 100 to 200 m, with maximum abundance observed between 10 and 100 m for fish and crustaceans larvae [26,31,35]. This vertical distribution matches our observation that predators captured with surface gear consume a higher proportion of reef prey than predators captured at depth by longline. Large oceanic fishes and particularly tuna are considered to be opportunistic predators feeding on any available prey [45–46], but access to this prey depend upon the habitat preferences of predators, particularly the depth range linked to diving possibilities, temperature and oxygen tolerances [47–48]. Bigeye and lancetfish for example are

deep dwellers [49] and will therefore have limited interactions with surface reef prey. Both species show low probability and low proportion of reef prey in their diet as also noted in other studies [7,15,21]. On the other hand, yellowfin, skipjack, dolphinfish and wahoo forage mainly at the surface [48,50] and, in our study as well as in others [7,21], they show higher consumption of reef prey. Albacore appears to be a special case as our data indicated they frequently consume reef prey despite the adults being considered deep dwellers [51–52]. Albacore show a pronounced preference for crustaceans in their diet [7], and in our study they consumed reef crustaceans, crab (Brachyuran), mantis shrimp (Stomatopoda) and lobster larvae (Palinura), more frequently and in larger quantities than reef fish larvae. The forage biology of albacore is highly uncertain, but diel vertical migrations that are common to many tuna species have been observed in albacore, where they migrate to shallower habitats at night and deeper habitats during the day [53].

The size ratios between predator and prey also influence the consumption of reef prey. Our analyses suggested that the diet contribution of reef prey, smaller than non-reef prey on average (35 vs. 78 mm SL for fish prey), was higher for predators smaller than 40–50 cm caught at the surface than for larger predators. Graham [11] and Nakamura [17] also observed this trend mainly due to a decrease of the consumption of reef crustaceans' larvae when predator's size increased. In Graham's study [11], the consumption of reef fish larvae increased with the size of the predator but did not compensate the decrease of crustaceans inducing an overall decrease of reef prey. We also found that very large species such as shark and billfish did not consume reef prey. This observed higher consumption of small reef prey by small predators matches the previously observed trend of increased mean prey size with increasing predator size in fish communities [46, 54–55].

The estimated annual amount of prey (reef and oceanic) consumed by the yellowfin population in the WCPO (13.4 million tonnes or  $0.39$  tonnes/y/km<sup>2</sup>) is in the same order than previous estimates for yellowfin tuna in the same region [56] (10.7 million tonnes or  $0.31$  tonnes/y/km<sup>2</sup>), in the Eastern Pacific Ocean [57] ( $0.25$  tonnes/y/km<sup>2</sup>), for *Thunnus tonggol* in Australian waters [58] ( $0.37$  tonnes/y/km<sup>2</sup>) and for *Euthynnus affinis* in eastern Australia [59] ( $0.15$  tonnes/y/km<sup>2</sup>). To our knowledge, our study provided for the first time an estimate of reef prey consumed by oceanic fish predation ( $0.818$  million tonnes  $\pm$   $0.4$ CV-  $2.17 \times 10^{12} \pm 0.40$ CV individuals  $-6.1\% \pm 0.17$ CV in yellowfin tuna population diet) which indicate their importance in the diet of top predators and highlight the role of pelagic predators on mortality of coastal organisms during their pelagic offshore phase. However it is difficult to estimate if the impact of this type of predation on the recruitment rate of reef larvae to the reef. Moreover it likely does not have influence on abundance of juvenile and adult reef organisms at the reef as it was suggested that post-recruitment mortality had much greater effect on abundance than recruitment rate [60].

Our study showed the important interactions between coastal and oceanic domains in the WCPO; the question of reciprocal subsidies between these 2 ecosystems remains unanswered. According to our study  $0.8$  million tonnes of reef prey are consumed by the yellowfin tuna population alone. However this biomass cannot be considered as direct subsidy from coastal to oceanic ecosystem as reef prey left the reefs and lagoons as eggs or at a very early life-stage representing a very small biomass. The energy necessary for eggs and small larvae to develop up to a late larval stage and juvenile consumed by oceanic predators was taken from the oceanic environment. Hence most of the biomass of reef

prey consumed by pelagic predators comes from the oceanic ecosystem itself and is not subsidized by the coastal ecosystem. In return the coastal ecosystem is benefiting from the biomass of juvenile reef fish produced in the oceanic ecosystem and coming back to the reef. However it is not possible to estimate how much the oceanic ecosystem is subsidizing the coastal system as it is very difficult to estimate the amount of reef prey coming back to the reef. Their survival once at the reef is poor [60] which will have an impact on their adult's population abundance, however by being consumed by predators on the reef they do enter the coastal food web and contribute to the coastal ecosystem.

Exploration of multiple models highlighted a specific issue linked to the opportunistic sampling programme used in this study. Our sampling programme relied on fishing operations with surface and longline fisheries, which operate in very different ways and catch fish of different size (small versus large respectively), different species (skipjack versus albacore for example), different school types (FAD and non-FAD versus non-FAD) and different locations (equator versus subtropical), with limited overlap between these factors. Location, FAD schools and distance-to-land are also related parameters as FAD are preferentially anchored in the western part of the region (Papua New Guinea and Solomon Islands). Despite the number of stomachs examined, the large number of co-variables makes it difficult to explore the influence of each covariate independently as the degrees of freedom in the analyses were insufficient to explore all relationships. Close relationships between some of the parameters are apparent when testing all the possible models, as the 4 or 5 best models usually highlighted the importance of related factors (Tables S2, Table S3, Table S4, Table S5). We chose the best model based on the BIC which identified clear trends in the dataset; however some of the parameters not selected in the final model also had support in other models. Moreover, the distribution of the samples through time did not permit exploration of annual and seasonal changes, but temporal variability is likely to be important in our area which undergoes strong interannual variation such as El Niño Southern Oscillation (ENSO) and perceptible seasonality in the subtropical areas. Further analyses are also needed to quantify the contribution of reef prey to the total energy budget of oceanic ecosystem to fully understand the subsidy provided by coastal ecosystems. Nevertheless our analyses based on a robust statistical method, applied to a large dataset and covering a vast area clearly identify some of the patterns in the relationship between coastal and oceanic ecosystems at a large scale and gives for the first time an estimate of the annual consumption of reef prey by oceanic predators.

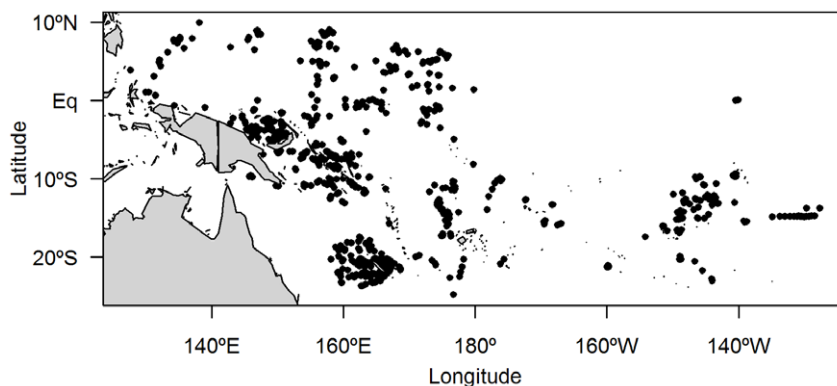
## Materials and Methods

### Sampling Programme

A total of 7633 stomachs of pelagic predators were collected between January 2001 and April 2011 in the Western and Central Pacific Ocean (9°N - 27°S and 127°E - 132°W) (Figure 4). All samples came from commercial fisheries and were already dead when provided to the sampler, no permission was required. Among the 5444 non-empty stomachs, 585 were removed from the dataset due to missing information such as predator length or spatial data. A total of 58 species were sampled with 1 to 1598 non-empty stomachs per species (Table S6). The analysis was conducted on the 4286 non-empty stomachs of the 8 species with more than 100 samples. Samples were collected by fisheries observers and scientists onboard fishing vessels during 812 different sets. Between 1 and 34 predators were collected per set. Fishing gear (longline, purse-seine, pole-and-line, trolling, handline), school association (free school, anchored FAD, drifting FAD, drifting log, seamount, whale and whale shark), predator species, fish length, date, time, position of the catch (position of the beginning of the set for longline gear and trolling for which catch occur when the boat is underway; position of the boat for purse-seine, pole-and-line and handline for which catch occur when the boat is stationary), were recorded on logsheets. Samples were frozen onboard.

### Stomach Content Examination

Stomachs were considered empty when containing only digestive fluids. For non-empty stomachs, prey were identified to the lowest taxonomic level possible. Identification keys used for prey identification were, for fish: Smith & Heemstra [61] and Carpenter & Niem [62], for crustaceans: Poore [63], for cephalopods: Young et al [64], for invertebrates: Wrobel & Mills [65], and for zooplankton: Boltovskoy [66]. For each prey taxon the total weight in grams and the number of specimens were determined; the weight and length of individual specimens were measured when possible according to their digestion stage. Reef or oceanic origin of the prey was determined based on bibliographic information. However, due to their advanced stage of digestion, 22% (in weight) of the prey were not identified to a taxonomic level sufficient to determine their origin. These were grouped with oceanic prey, which were the most numerous; the analysis could therefore underestimate the proportion of reef prey.



**Figure 4. Locations of the 812 sets where samples were collected.**  
doi:10.1371/journal.pone.0036701.g004

## Response Variable

Quantitative analysis of stomach contents can be achieved in different ways [67]. In this study only two prey items were considered: reef prey and oceanic prey, and were expressed as proportions of weights per stomach. Proportion in weight of reef prey was used as the response variable.

## Co-variates

The explanatory variables included in the model were predator's species (*pred\_code*), predator's length (*pred\_L*), latitude (*lat\_dec*) and longitude (*lon\_dec*) of catch, gear code (*gr\_code*), school code (*sch\_code*) and distance to closest land (*dist\_land*) or closest reef (*dist\_reef*). Surface of reef or lagoon in a 100-nautical miles-diameter-circle around the predator were also included in preliminary models, however considering that these data were not available for about 20% of the samples, these variables were not included in the model. Considering the opportunistic nature of the sampling, the number of samples per year or month did not allow taking into account temporal variability. Fishing gears were grouped into longline (catching fish from the surface down to approximately 400 meters depth) and surface gears (pole-and-line, trolling, purse-seine, handline, catching fish at the surface). School associations were grouped into FAD (anchored FAD, drifting FAD, drifting log, whale and whale shark) and non-FAD schools (free school, seamounts). Distance between the sampled predator and the closest land was calculated based on predator's position and land information established by the National Geospatial Intelligence (NGA) World Vector Shoreline (WVS) (<http://shoreline.noaa.gov/data/datasheets/wvs.html>). Distance between the sampled predator and the closest reef was calculated based on predator's position and reef data from the Millennium Coral Reef Mapping Project (MCRMP) [68] and the lower resolution United Nations Environment Programme (UNEP) -World Conservation Monitoring Centre (WCMC) Global Coral Reef distribution (2010) ([www.unep-wcmc.org](http://www.unep-wcmc.org)) for locations where MCRMP was not available (Fiji, Philippines, Indonesia, and North Papua New Guinea).

## Statistical Models

The frequency distribution of reef prey weight in pelagic predator stomachs exhibits skewness and a spike at zero (2780 zero, i.e. 52% of the values). To account for this data structure we analyzed the data in two parts using a delta generalized linear models (GLM) by modelling occurrence separately from the quantity observed [69]. In the first model, the response variable was defined as presence of reef prey in the sample. These data were analyzed using a generalized linear mixed model fitted using the Laplace approximation, with a binomial response and logit link function, with a random effect applied to fishing set as predators caught in the same set were not considered to be independent. In the second approach only the samples containing reef prey were analyzed using the reef prey by weight as a proportion of the total prey. The statistical distribution of this variable was markedly non-normal. We normalized its distribution by transforming it using a logit function. Samples that contained 100% of reef prey (7% of the predator samples) were omitted (as  $\text{logit}(1) = \text{Inf.}$ ). Data were analyzed using a generalized linear mixed model with a Gaussian response and identity link function, with a random effect applied to fishing set. Both analyses used the function `lmer` in the package `lme4` in R version 2.12.1 [70]. In each case, the complete range of models from Model 1 to Model 2 (below) with all the possible combinations of co-variates was explored.

Model1: response variable  $\sim (1 | \text{set})$ .

Model2: response variable  $\sim \text{pred\_code} + \text{pred\_L} + \text{sch\_code} + \text{ns}(\text{lon\_dec}, \text{df} = 2) + \text{ns}(\text{lat\_dec}, \text{df} = 2) + \text{gr\_code} + \text{log}(\text{dist\_land} + 1)$  or  $(\text{dist\_reef} + 1) + (1 | \text{set})$ . where  $(1 | \text{set})$  represents the random effect for fishing set.

Due to their high degree of correlation, co-variates distance-to-land and distance-to-reef were evaluated in separate models. Log transformation and splines with various degrees of freedom were explored for continuous co-variates longitude, latitude, distance-to-land and distance-to-reef. Model fits were compared using the BIC Bayesian Information Criterion [71] and models with lower BIC were preferred. Anova type II tests (Chi-square statistic test) were performed to identify the degree of significance of the covariates.

For the model of occurrence, the chosen model was preferred to the model with the smallest BIC since the BICs were almost equal and the chosen model was simpler with 3 explanatory variables instead of 5 (Table S2). The expected frequency of occurrence or probability-of-consuming-reef-prey  $p$  by a predator of species  $i$ , caught at longitude  $j$  and distance-to-land  $k$  is defined as follow:

$$p_{i,j,k} = \text{inv.logit} \left( \alpha_i^{\text{pred\_code}} + f(j) + \alpha^{\text{dist\_land}} \cdot \log(k) + C_1 \right)$$

where the alphas are estimated model parameters, the function  $f$  is a cubic spline estimated with two degrees of freedom and  $C_1$  is a constant calculated in the model.

Correlation between distance-to-land and longitude was statistically significant ( $\text{cor} = 0.42$ ,  $p\text{-value} < 2.2 \times 10^{-16}$ ); but including both variables rather than only one significantly improved the model. Despite the correlation these 2 variables affect  $p$  independently and should be conserved into the model.

For the model of proportion, the preferred model only included fishing gear (Table S3). Further modeling was conducted separately on surface and longline gears (Table S4 and S5). The predicted proportion-of-reef-prey-given-that-reef-prey-was-consumed  $q$  by a predator of species  $i$ , of length  $m$  and caught by fishing gear  $g$  is defined below:

$$q_{g=ps,m} = \text{inv.logit} \left( \alpha^{\text{pred\_Length}} \cdot m + C_2 \right)$$

where  $g$  indicates purse seine (ps)-caught fish, and

$$q_{g=ll,i} = \text{inv.logit} \left( \alpha_i^{\text{pred\_code}} + C_3 \right)$$

where  $g$  indicates longline (ll)-caught fish. The alphas are estimated model parameters and  $C_2$  and  $C_3$  are constants calculated in the models.

## Reef Prey Consumption Estimate

The annual consumption of reef prey by yellowfin tuna population in 2009 in the Western and Central Pacific Ocean (110°E to 150°W and 20°N to 10°S) was estimated by combining probability of reef prey occurrence, proportion of reef prey given reef prey was consumed, number of predators and predator's daily ration. The area was divided into 1/10 degree cells and the longitude and the distance to land of the center of the cell were determined. Probability and proportion were determined by the statistical models as shown above. Numbers of yellowfin tuna at age and per quarter were extracted from the 2011 yellowfin stock

assessment for the year 2009 [23]; we assumed the tuna population was evenly distributed throughout the area considered. Daily ration was adapted from the yellowfin daily ration at length determined by Maldeniya [72] using weight and length at age data from the stock assessment [23].

According to model results above and considering yellowfin tuna catches by longline represent only about 12% of the catches in the equatorial area [23] and only concern large specimens consuming minor quantities of reef preys, we took into account only the purse seine model of reef prey proportion to calculate the annual consumption of reef prey by yellowfin tuna population according to the equation:

$$\text{Consumption} = \sum_{b=1}^n \left\{ p_{i=YFT,j,k} \times \sum_{a=1}^{28} \left[ q_{g=ps,m} \times \sum_{t=1}^4 \left( N_{a,b,t} \times R_a \times W_a \times \frac{365}{4} \right) \right] \right\}$$

where Consumption is the annual reef prey consumption,  $b$  represents the number of cells of 1/10 degree square with  $n = 277436$ ,  $p_{i,j,k}$  is the probability of consuming reef prey as defined above by species  $i$  which is yellowfin (YFT) in this case and for each cell  $b$  defined by its longitude  $j$  and the distance-to-land  $k$  of its center,  $a$  represents the predator age class (1 to 28 quarters),  $q_{g,m}$  is the proportion of reef prey consumed given that reef prey was consumed as defined above with gear  $g$  equals to purse seine (ps) and  $m$  length of the fish,  $t$  represents the quarter of the year,  $N$  is the number of yellowfin tuna of age  $a$  in cell  $b$  at quarter  $t$ ,  $R$  is the predator daily ration at age  $a$  expressed in proportion of predator's weight,  $W$  is the average weight of the predator at age  $a$ .

Uncertainty around the annual consumption estimate was calculated using a randomization method ( $n = 1000$ ) to combine the uncertainty estimates for each of the main input values. Uncertainties around the probability and proportion estimates were determined from the statistical models detailed in results. For the daily ration no uncertainty was provided by Maldeniya [72], so a coefficient of variation of 20% was assumed. In making this judgment we considered several alternative estimates of daily ration [57,73–74], which were similar to Maldeniya. Uncertainty in the number of predators was determined by aggregating three sources of uncertainty. The stock assessment [23] estimated parameter uncertainty in biomass of 7%, and structural uncertainty of 18%. These are minimum estimates since they are based on assuming that the model is correct. Other factors that cannot be estimated, such as the fact that biomass is not evenly distributed throughout the area, were assumed to contribute substantial additional uncertainty, leading to a summary CV of 30%.

## References

1. Longhurst AR (2007) Ecological geography of the sea. San Diego: Academic Press. 542 p.
2. Allain V, Kerandel J-A, Andréfouët S, Magron F, Clark M, et al. (2008) Enhanced seamount location database for the western and central Pacific Ocean: screening and cross-checking of 20 existing datasets. Deep Sea Res I 55: 1035–1047.
3. Morato T, Hoyle SD, Allain V, Nicol SJ (2010) Seamounts are hotspots of pelagic biodiversity in the open ocean. Proc Natl Acad Sci USA 107(21): 9707–9711.
4. Williams P, Terawasi P (2011) Overview of tuna fisheries in the western and central Pacific Oceanic, including economic conditions. Pohnpei, Federated States of Micronesia: Western and Central Pacific Fisheries Commission, Scientific Committee, 7<sup>th</sup> Regular Session. Available: <http://www.wcpfc.int/system/files/documents/meetings/sc7-2011-GN-WP-01%20%5BOverview%20of%20WCPO%20fisheries%20%E2%80%93202010%5D.pdf>. Accessed 2012 Apr 19.

Uncertainties around the average weight of individual reef crustacean and fish preys, and around the proportion of crustaceans and fish in yellowfin tuna diet was based on diet data used in this study.

## Supporting Information

**Figure S1** Quantification of island and reef coverage per longitudinal band in the western and central Pacific. Within the 15°N to the 25°S latitudinal band and excluding Australia. (TIF)

**Table S1** Species composition, raw value and percentages of the cumulated weight (W), number (N) and frequency (F) of the reef preys in the diet of the main pelagic predators. (DOCX)

**Table S2** Results of the five second-best models of reef prey occurrence in stomach content. (DOCX)

**Table S3** Results of the five best models of reef prey proportion in stomach containing reef prey. (DOCX)

**Table S4** Results of the five best models of reef prey proportion in stomach containing reef prey for predators caught with surface fishing gears. (DOCX)

**Table S5** Results of the five best models of reef prey proportion in stomach containing reef prey for predators caught with longline fishing gear. (DOCX)

**Table S6** Number of non-empty stomachs examined for the 58 species collected. (DOCX)

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## Author Contributions

Conceived and designed the experiments: VA SDH SJN. Analyzed the data: VA EF SDH SJN. Contributed reagents/materials/analysis tools: VA EF SDH SC JJM. Wrote the paper: VA EF SA SJN.

5. Bell JD, Reid C, Batty MJ, Allison EH, Lehodey P, et al. (2011) Implications of climate change for contributions by fisheries and aquaculture to economic development, government revenue, food security and livelihoods in the Pacific Community. In Bell JD, Johnson JE, Hobday AJ (eds) Vulnerability of Tropical Pacific Fisheries and Aquaculture to Climate Change, Secretariat of the Pacific Community, Noumea, New Caledonia. Available at: <http://cdn.spc.int/climate-change/fisheries/assessment/chapters/12-Chapter12.pdf>. Accessed 2012 Apr 19.
6. Alverson F (1963) The food of yellowfin and skipjack tunas in the eastern tropical Pacific Ocean. IATTC Bull 7: 295–396.
7. Bertrand A, Bard F-X, Josse E (2002) Tuna food habits related to the micronekton distribution in French Polynesia. Mar Biol 140: 1023–1037.
8. Borodulina OD (1974) The feeding of the bigeye tuna (*Thunnus obesus*) in the Gulf of Guinea and its place in the trophic system of the pelagic zone. J Ichthyol 14: 765–775.

9. Brock R (1985) Preliminary Study of the Feeding Habits of Pelagic Fish around Hawaiian Fish Aggregation Devices or Can Fish Aggregation Devices Enhance Local Fisheries Productivity? *Bull Mar Sci* 37: 40–49.
10. Buckley TW, Miller BS (1994) Feeding Habits of Yellowfin Tuna Associated with Fish Aggregation Devices in American Samoa. *Bull Mar Sci* 55: 445–459.
11. Graham BS, Grubbs D, Holland KN, Popp BN (2006) A rapid ontogenetic shift in the diet of juvenile yellowfin tuna from Hawaii. *Mar Biol* 150: 647–658.
12. Grandperrin R, Roger C (1976) Pelagic food webs in the tropical Pacific. *Limnol Oceanogr* 21(5): 731–735.
13. Hida TS (1973) Food of tunas and dolphins (Pisces: Scombridae and Coryphaenidae) with emphasis on the distribution and biology of their prey *Stolephorus buccaneeri* (Engraulidae). *Fish. Bull., U.S.* 71: 135–143.
14. Jacquemet S, Potier M, Ménard F (2011) Do drifting and anchored fish aggregating devices (FADs) similarly influence tuna feeding habits? A case study from the western Indian Ocean. *Fish Res* 107(1–3): 283–290.
15. Jong-Bin K, Dae-Yeon M, Jung-No K, Tae-Ik K, Hyun-Su J (1997) Diets of bigeye and yellowfin tunas in the western tropical Pacific. *J Kor Fish Soc* 30: 719–729.
16. Lehodey P (1990) Comparaison des contenus stomacaux de thonidés pêchés sous et hors D.C.P. (Résultats préliminaires). *22ème Conférence Technique Régionale sur les Pêches, CPS, Nouméa, Nouvelle-Calédonie, 6–10 août 1990 CPS/Pêches* 22/WP 43: 1–6.
17. Nakamura EL (1965) Food and feeding habits of skipjack tuna (*Katsuwonus pelamis*) from the Marquesas and Tuamotu Islands. *Am Fish Soc* 94(3): 236–243.
18. Reintjes JW, King JE (1953) Food of yellowfin tuna in the central Pacific. *Fish Bull Fish Wild Serv* 54: 91–109.
19. Ronquillo IA (1953) Food habits of tunas and dolphins based upon the examination of their stomach contents. *The Philipp J Fish* 2: 71–81.
20. Tester AL, Nakamura EL (1957) Catch rate, size, sex, and food of tunas and other pelagic fishes taken by trolling off Oahu, Hawaii, 1951–55. *US Fish Wild Serv Spec Scien Rep - Fish* 250: 16–25.
21. Watanabe H (1958) On the difference of the stomach contents of the yellowfin and bigeye tunas from the western equatorial Pacific. *Rep Nankai Reg Fish Res Lab* 7: 72–81.
22. Young J, Lansdell M, Campbell R, Cooper S, Juanes F, et al. (2010) Feeding ecology and niche segregation in oceanic top predators off eastern Australia. *Mar Biol* 157: 2347–2368.
23. Langley A, Hoyle S, Hampton J Stock assessment of yellowfin tuna in the western and central Pacific Ocean. Pohnpei, Federated States of Micronesia: Western and Central Pacific Fisheries Commission, Scientific Committee, 7<sup>th</sup> Regular Session. Available: <http://www.wcpfc.int/doc/sa-wp-03/stock-assessment-yellowfin-tuna-western-and-central-pacific-ocean..>
24. Ramírez-Mella JT, García-Sais JR (2003) Offshore dispersal of Caribbean reef fish larvae: how far is it? *Bull Mar Sci* 72(3): 997–1017.
25. Young PC, Leis JM, Hausfeld HF (1986) Seasonal and spatial distribution of fish larvae in waters over the North West Continental Shelf of Western Australia. *Mar Ecol Prog Ser* 31: 209–222.
26. Polovina JJ, Moffitt RB (1995) Spatial and temporal distribution of the phyllosoma of the spiny lobster, *Panulirus marginatus* in the Northwestern Hawaiian Islands. *Fish Bull* 56(2): 406–417.
27. Lester SE, Ruttenberg BI (2005) The relationship between pelagic larval duration and range size in tropical reef fishes: a synthetic analysis. *Proc R Soc B* 272: 585–591.
28. Stobutzki IC, Bellwood DR (1997) Sustained swimming abilities of the late pelagic stages of coral reef fishes. *Mar Ecol Prog Ser* 149: 35–41.
29. Leis JM, Sweatman HPA, Reader SE (1996) What the pelagic stages of coral reef fishes are doing out in blue water: Daytime field observations of larval behavioral capabilities. *Mar Freshw Res* 47: 401–411.
30. James MK, Armsworth PR, Mason LB, Bode L (2002) The structure of reef fish metapopulations: modeling larval dispersal and retention patterns. *Proc R Soc Lond B* 269: 2079–2086.
31. Cowen RK (2002) Oceanographic influences on larval dispersal and retention and their consequences for population connectivity In Sale PF, editor. *Coral Reef Fishes: Dynamics and Diversity in a Complex Ecosystem*. San Diego: Academic Press. pp 149–170.
32. Limouzy-Paris CB, Graber HC, Jones DL, Röpke AW, Richards WJ (1997) Translocation of larval coral reef fishes via sub-mesoscale spin-off eddies from the Florida Current. *Bull Mar Sci* 60(3): 966–983.
33. Coutis PF, Middleton JH (1999) Flow topography interaction in the vicinity of an isolated, deep ocean island. *Deep-Sea Res Part I* 46(9): 1633–1652.
34. Seki M, Lumpkin R, Flament P (2002) Hawaiian cyclonic eddies and blue marlin catches: the case study of the 1995 Hawaiian international billfish tournament. *J Oceanogr* 58: 739–745(7).
35. Lobel PS, Robinson AR (1986) Transport and entrapment of fish larvae by ocean mesoscale eddies and currents in Hawaiian waters. *Deep Sea Res* 33(4): 483–500.
36. Boehlert GW, Watson W, Sun LC (1992) Horizontal and vertical distributions of larval fishes around an isolated oceanic island in the tropical Pacific. *Deep Sea Res* 39(3–4): 439–466.
37. Leis JM (1993) Larval fish assemblages near Indo-Pacific coral reefs. *Bull Mar Sci* 53(2): 362–392.
38. Cowen RK, Lwiza, KMM, Sponaugle S, Paris CB, Olson DB (2000) Connectivity of marine populations: open or closed? *Science* 287: 857–859.
39. Liddelow MJ, Kingsford MJ (2006) The attraction of presettlement reef fish to FADs with live and dead coral. *Proc 10th Int Coral Reef Symp* 403–408.
40. Castro JJ, Santiago JA, Santana-Ortega AT (2002) A general theory on fish aggregation to floating objects: An alternative to the meeting point hypothesis. *Rev Fish Biol Fish* 11: 255–277.
41. Hunter JR, Mitchell CT (1967) Association of fishes with floats in the offshore waters of Central America. *Fish Bull* 66: 13–29.
42. Kingsford MJ (1993) Biotic and abiotic structure in the pelagic environment: importance to small fishes. *Bull Mar Sci* 53: 393–415.
43. Moteki M, Arai M, Tsuchiya K, Okamoto H (2001) Composition of piscine prey in the diet of large pelagic fish in the eastern tropical Pacific Ocean. *Fish Sci* 67: 063–1074.
44. Rudershausen PJ, Buckel JA, Edwards J, Gannon DP, Butler CM, et al. (2010) Feeding Ecology of Blue Marlin, Dolphinfin, Yellowfin Tuna, and Wahoos from the North Atlantic Ocean and Comparisons with Other Oceans. *Trans Amer. Fish. Soc* 139: 1335–1359.
45. Sund PN, Blackburn M, Williams F (1981) Tunas and their environment in the Pacific Ocean: a review. *Oceanogr Mar Biol Annu Rev* 19: 443–512.
46. Ménard F, Labruno C, Shin YJ, Asine AS, Bard FX (2006) Opportunistic predation in tuna: a size-based approach. *Mar Ecol Prog Ser* 323: 223–231.
47. Sharp GD (1978) Behavioral and physiological properties of tunas and their effects on vulnerability to fishing gear. GD In Sharp, AE Dizon, eds. editors. *The physiological ecology of tunas*. San Diego: Academic Press. pp 397–449.
48. Brill RW, Block BA, Boggs CH, Bigelow KA, Freund EV, et al. (1999) Horizontal movements and depth distribution of large adult yellowfin tuna (*Thunnus albacares*) near the Hawaiian Islands, recorded using ultrasonic telemetry: implications for the physiological ecology of pelagic fishes. *Mar Biol* 133: 395–408.
49. Brill RW (1994) A review of temperature and oxygen tolerance studies of tunas pertinent to fisheries oceanography, movement models and stock assessments. *Fish Oceanogr* 3: 204–216.
50. Mugo R, Saitoh SI, Nihira A, Kuroyama T (2010) Habitat characteristics of skipjack tuna (*Katsuwonus pelamis*) in the western North Pacific: a remote sensing perspective. *Fish Oceanogr* 19:5 382–396.
51. Saito S, Ishii K, Yoneta K (1970) Swimming depths of large sized albacore in the South Pacific Ocean. *Bull. Jap. Soc. Fish. Oceanogr.* 36: 578–584.
52. Grandperrin R, Legand M (1971) Overview of the vertical distribution of albacore in the tropical South Pacific: new guidelines for Japanese and experimental fisheries. *Cahiers ORSTOM, Ser Oceanogr* 9(2): 197–202.
53. Domokos R, Seki MP, Polovina JJ, Hawn DR (2007) Oceanographic investigation of the American Samoa albacore (*Thunnus alalunga*) habitat and longline fishing grounds. *Fish Oceanogr* 16(6): 555–572.
54. Scharf FS, Juanes F, Rountree RA (2000) Predator size–prey size relationships of marine fish predators: interspecific variation and effects of ontogeny and body size on trophic niche breadth. *Mar Ecol Prog Ser* 208: 229–248.
55. Olson RJ, Galvan-Magaña F (2002) Food habits and consumption rates of common dolphinfish (*Coryphaena hippurus*) in the eastern Pacific Ocean. *Fish Bull* 100: 279–298.
56. Kirby DS (2005) Prey consumption estimates for tunas in the western and central Pacific Ocean. Nouméa, New Caledonia: Western and Central Pacific Fisheries Commission, Scientific Committee, 1<sup>st</sup> Regular Session. Available: <http://www.wcpfc.int/doc/eb-wp-%C3%A2%E2%82%AC%E2%80%9C4/prey-consumption-estimates-tunas-wcpo>. Accessed 2012 Apr 19.
57. Essington TE, Schindler DE, Olson RJ, Kitchell JF, Boggs CH, et al. (2002) Alternatives fisheries and the predation rate of yellowfin tuna in the eastern Pacific Ocean. *Ecol Appl* 12(3): 724–734.
58. Griffiths SP, Fry GC, Manson FJ, Pillans RD (2007) Feeding dynamics, consumption rates and daily ration of longtail tuna (*Thunnus tonggol*) in Australian waters, with emphasis on the consumption of commercially important prawns. *Mar Freshw Res* 58: 376–397.
59. Griffiths SP, Kuhnert PM, Fry GF, Manson J (2009) Temporal and size-related variation in the diet, consumption rate, and daily ration of mackerel tuna (*Euthynnus affinis*) in neritic waters of eastern Australia. *ICES J Mar Sci* 66: 720–733.
60. Shulman MJ, Ogden JC (1987) What controls tropical reef fish populations: recruitment or benthic mortality? An example in the Caribbean reef fish *Haemulon flavolineatum*. *Mar Ecol Prog Ser* 39: 233–242.
61. Smith M, Heemstra P, eds (1986) *Smith's sea fishes*. Berlin, Germany: Springer-Verlag. 1047 p.
62. Carpenter K, Niem V, eds (1999) *FAO species identification guide for fishery purposes*. Rome: FAO. 6 vol.
63. Poore G (2004) *Marine decapod crustacean of Southern Australia. A guide to identification*. Collingwood: CSIRO Publishing. 574 p.
64. Young R, Michael E, Vecchione I, Mangold KM (2008) *Decapodiformes Leach, 1817. Squids, cuttlefishes and their relatives (1922–2003)*, version 21 April 2008. Available: <http://tolweb.org/Decapodiformes/19404/2008.04.21> Accessed 2012 Apr 19. in *The Tree of Life Web Project*, <http://tolweb.org/> Accessed 2012 Apr 19.
65. Wrobel D, Mills C (1998) *Pacific coast pelagic invertebrates. A guide to the common gelatinous animals*. Monterey, CA, USA: Sea Challengers, Monterey Bay Aquarium. 108 p.
66. Boltovskoy D, eds (1999) *South Atlantic Zooplankton*. Leiden: Backhuys Publishers. 2 Vol.



67. Chipps SR, Garvey JE (2006) Assessment of food habits and feeding patterns. *The Am Fish Soc* 11: 1–42.
68. Andréfouët S, Muller-Karger FE, Robinson JA, Kranenburg CJ, Torres-Pulliza D, et al. (2006) Global assessment of modern coral reef extent and diversity for regional science and management applications: a view from space. In *Proceedings of the 10<sup>th</sup> International Coral Reef Symposium, Okinawa, Japan, 1732–1745*.
69. Stefánsson G, Pálsson ÓK (1997) Statistical evaluation and modeling of the stomach contents of Icelandic cod (*Gadus morhua*). *Can J Fish Aquat Sci* 54: 169–181.
70. R Development Core Team (2010) R: A language and environment for statistical computing. R Foundation for Statistical Computing, Vienna, Austria. ISBN 3-900051-07-0, URL <http://www.R-project.org/>. Accessed 2012 Apr 19.
71. Schwarz GE (1978) Estimating the dimension of a model. *Ann Stat* 6(2): 461–464.
72. Maldeniya R (1996) Food consumption of yellowfin tuna, *Thunnus albacares*, in Sri Lankan waters. *Env Biol Fish* 47: 101–107.
73. Barut NC (1988) Food and feeding habits of yellowfin tuna *Thunnus albacares* (Bonnaterre, 1788), caught by handline around payao in the Moro Gulf. *Indo-Pacific Tuna Development and Management Prog IPTP/ 88*: 1–39.
74. Olson RJ, Boggs CH (1986) Apex predation by yellowfin tuna (*Thunnus albacares*): independent estimates from gastric evaluation and stomach contents, bioenergetics, and cesium concentrations. *Can J Fish Aquat Sci* 43: 1760–1775.