

**Global trophic ecology of yellowfin, bigeye, and albacore tunas: understanding predation on  
micronekton communities at ocean-basin scales**

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## Abstract

Predator-prey interactions for three commercially valuable tuna species: yellowfin (*Thunnus albacares*), bigeye (*T. obesus*), and albacore (*T. alalunga*), collected over a 40-year period from the Pacific, Indian, and Atlantic Oceans, were used to quantitatively assess broad, macro-scale trophic patterns in pelagic ecosystems. Analysis of over 14,000 tuna stomachs, using a modified classification tree approach, revealed for the first time the global expanse of pelagic predatory fish diet and global patterns of micronekton diversity. Ommastrephid squids were consistently one of the top prey groups by weight across all tuna species and in most ocean bodies. Interspecific differences in prey were apparent, with epipelagic scombrid and mesopelagic paralepidid fishes globally important for yellowfin and bigeye tunas, respectively, while vertically-migrating euphausiid crustaceans were important for albacore tuna in the Atlantic and Pacific Oceans. Diet diversity showed global and regional patterns among tuna species. In the central and western Pacific Ocean, characterized by low productivity, a high diversity of micronekton prey was consumed while low prey diversity was evident in highly productive coastal waters where upwelling occurs. Spatial patterns of diet diversity were most variable in yellowfin and bigeye tunas while a latitudinal diversity gradient was observed with lower diversity in temperate regions for albacore tuna. Sea-surface temperature was a reasonable predictor of the diets of yellowfin and bigeye tunas, whereas chlorophyll-*a* was the best environmental predictor of albacore diet. These results suggest that the ongoing expansion of warmer, less productive waters in the world's oceans may alter foraging opportunities for tunas due to regional changes in prey abundances and compositions.

**Keywords:** meta-analysis, food webs, ecosystems, inter-ocean comparison, trophic relationships, classification trees, climate changes, macroecology

## 1. Introduction

Examining broad-scale patterns in marine food webs and ecosystems is essential for macroecological understanding that can support ecosystem-based management of ocean resources (Pikitch et al., 2004; Marasco et al., 2007). Improved ecological understanding of dynamic open-ocean systems is becoming increasingly important to guide transboundary and cross jurisdictional management efforts of species, assemblages, and ecosystems in response to the cumulative effects of global climate change, in addition to localized impacts of fishing (Perry et al., 2010). There is growing evidence to suggest that the dynamics of several marine ecosystems have been significantly altered as a result of recent changes in climate (IPPC-AR5, 2013). At the same time, fishery-induced reductions of the biomass of large pelagic predators have been reported to have dramatic ecological consequences (Worm et al., 2009; Blenckner et al., 2015), but are not well understood. Such changes directly affect the community structure and diversity of food webs, as well as the productivity and connectivity of the ecosystem's constituent species (Doney et al., 2012). Declines in phytoplankton species and size composition have been reported in subtropical regions (Polovina and Woodworth, 2012) and the temperate North Atlantic Ocean (Beaugrand et al., 2010). Changes at the bottom of the food web that are tightly coupled to the physical environment propagate through the food web by altering energy and nutritional transfer pathways to higher-level consumers (Blanchard et al., 2012). In contrast, changes at the top of the food web, through top-down trophic effects, can be similarly important by directly and indirectly affecting the abundance and composition of lower trophic level species (Heithaus et al., 2008; Baum and Worm, 2009; Chen et al., 2016).

Studies of stomach contents provide fundamental empirical knowledge of food web dynamics and predator-prey distributions. Predator-prey relationships underpin predator growth and survival and are key variables to predicting patterns in distribution and abundance, especially for highly mobile species. The efficacy and predictive capability of large-scale ecosystem models (Fulton, 2010; Dueri et al., 2012; Christensen et al., 2015; Lehodey et al., 2015) are limited by a lack of understanding of broad-scale spatial and temporal distributions of mid-trophic micronekton communities that support commercially-important pelagic fishes, such as tunas and billfishes (Young et al., 2015a). Due to the difficulty and cost of gathering biological samples in the open ocean, diet studies of top predators are generally spatially and temporally restricted, thus constraining macroecological understanding of food webs. Few comprehensive, large-scale datasets of diets have been compiled, but where they do exist, major changes have been observed in the forage base of some large pelagic species. For example, Olson et al. (2014) noted a decadal shift in the diets of yellowfin tuna (*Thunnus albacares*) in the eastern Pacific Ocean from large, energetically rich, epipelagic prey to smaller, less nutritious, mesopelagic species as well as range

86 expansions for some prey. Expansion of oligotrophic oceanographic provinces is thought to be at least  
87 partly responsible for this diet shift (Olson et al., 2014). Elsewhere, declines in larger phytoplankton  
88 (diatoms), attributed to ocean warming, altered the signature fatty acid profiles of albacore tuna (*Thunnus*  
89 *alalunga*) in the western Pacific Ocean (Parrish et al., 2015; Pethybridge et al., 2015). This increasing  
90 “tropicalization” of tuna habitats sensu Parrish et al. (2015) may impact the response of tuna populations  
91 to fishing and environmental pressures as well as their health benefits to humans. Additionally, Golet et  
92 al. (2015) hypothesized that tunas can exhibit a decline in condition even when prey items are abundant  
93 due to changes in the size structure and nutritional composition of the prey.

94 Predation plays a fundamental role in shaping ecological communities (Mourier et al., 2016) and  
95 maintaining resilience (Bellwood et al., 2004; Llope et al., 2014), although a greater understanding of the  
96 ecosystem-level effects of predation is required. Tunas are widely recognized as opportunistic generalist  
97 (i.e. non-selective) high-trophic level predators that have extensive ranges and move freely between  
98 habitats, transferring energy between otherwise isolated and nutrient-poor food webs (Alverson, 1963;  
99 Sund et al., 1981; Ménard et al., 2006; Potier et al., 2007; Young et al., 2010). Their predation habits can  
100 be used to infer (and monitor) broad community-scale changes in the abundance, availability, and  
101 diversity of poorly studied mid-trophic micronekton prey (fishes, crustaceans, cephalopods, and  
102 gelatinous organisms in the 2-20 cm size range) (Bertrand et al., 2002; Ménard et al., 2006; Nicol et al.,  
103 2012; Staudinger et al., 2013b; Olson et al., 2016) and can elucidate important changes in ecosystem  
104 structure (Olson et al., 2014; Townhill et al., 2015; Yonezaki et al., 2015). Despite apparent generalist  
105 feeding, previous studies have shown that differences in vertical feeding behavior can explain inter- and  
106 intra-specific dietary differences over relatively short distances (Young et al., 2010; Williams et al.,  
107 2015). Yellowfin tuna exhibit repetitive foraging dives into the deep-scattering layer (Carey and Olson,  
108 1982; Schaefer et al., 2007) but primarily occupy the epipelagic zone (Brill et al., 1999; Gunn and Block,  
109 2001), hence exploiting prey resources near the surface (Schaefer et al., 2009). By contrast, bigeye tuna  
110 (*Thunnus obesus*) have physiological capabilities (Holland et al., 1992; Lowe et al., 2000; Brill et al.,  
111 2005) that allow them to dive deep beyond the scattering layer to exploit prey resources in the meso- and  
112 bathypelagic realms (Schaefer and Fuller, 2002; Lam et al., 2014; Fuller et al., 2015). Albacore tuna  
113 undergo large latitudinal migrations related to their life history (Childers et al., 2011; Williams et al.,  
114 2015) and display diverse regionally-specific vertical behaviors (Goñi et al., 2009; Young et al., 2010;  
115 Childers et al., 2011; Cosgrove et al., 2014). In essence, these tunas are “biological samplers” of  
116 micronekton communities in different water bodies. Global and ocean-basin comparison of diets in these  
117 tuna species facilitates a greater understanding of predator-prey distributions over broader spatial

(regional to global) and biological (population to ecosystem-level) scales, thereby increasing our understanding of the effects of tuna predation on the dynamics of pelagic ecosystems.

Under the umbrella of the international program Climate Impacts on Oceanic Top Predators (CLIOTOP) (Maury et al., 2010; Hobday et al., 2015), scientists from research organizations around the world compiled a dietary database of 14,185 tunas sampled in both hemispheres across all major ocean basins. Here we describe the first global inter-oceanic comparison of pelagic-predator diets, with a focus on three commercially important species: yellowfin, bigeye, and albacore tunas. Using these tuna species as biological samplers of prey in different water masses, and a modified classification tree approach, the aims were to: (1) elucidate predator-prey relationships characterizing the trophic ecology of yellowfin, bigeye, and albacore tunas on a global and cross-ocean basin scale; (2) identify spatial and biological patterns in diet composition and diet diversity in our full global diet dataset from 1969-2013; and (3) investigate the potential influence of oceanographic features on the foraging behavior of tunas using a subset of biological and available environmental data from 2003-2011 (n=5532). Two main strengths of this large global-scale diet analysis are clear: (1) it allows for comparisons of the foraging habits and patterns of micronekton diversity of each tuna species across ocean basins where previous studies described regional foraging habits with limited sample sizes; and (2) it identifies major prey guilds on a global scale which can provide insights into system energetics and when ecosystem changes at lower trophic levels may cause bottom-up effects. This analysis also furthers our understanding of the trophic ecology of tunas by applying a relatively new classification tree method for analyzing diet data, allowing for an exploratory and quantitative predictive evaluation of complex relationships between diet composition and a multitude of explanatory variables. Given that future environmental change can be predicted at large scales (IPPC-AR5, 2013), prey-environment relationships will be critical for parameterizing ecosystem models that seek to project future tuna distribution and abundance.

## **2. Materials and methods**

### *2.1 Compilation of stomach-contents data*

Diet data were compiled for 14,185 yellowfin, bigeye, and albacore tunas from the Pacific, Indian, and Atlantic Oceans (Fig. 1) and assembled in a database to apply a meta-analysis and examine broad-scale diet patterns around the world. A description of the data compilation process and the regional studies used to populate the database, both published and unpublished, is documented in Young et al. (2015b). A review of fine-scale analyses of diet data within each ocean region can be found in Olson et al. (2016). To date, this database is the most extensive in spatial and temporal coverage (Table 1), spanning

40 years (1969-2013) and all major ocean basins. However, due to the disparate nature of the stomach collections with little overlap in sampling locations observed over time and differences in sampling regimes, we primarily focused our analysis on broad spatial variability in diet.

## 2.2 Broad diet compositions of yellowfin, bigeye, and albacore tunas

We used a gravimetric index of diet importance to analyze the stomach contents data, because prey weights are appropriate for comparing the bioenergetics importance of a variety of prey to a predator (Chipps and Garvey, 2007) and pertinent for delineating food web dynamics. For each tuna species, we calculated the proportional composition by weight of each prey group per sample and averaged the proportions for each prey group over all non-empty yellowfin, bigeye, and albacore tuna stomach-contents samples (Chipps and Garvey, 2007). For prey weights, we used:

$$MW_i = \frac{1}{P} \sum_{j=1}^P \left( \frac{W_{ij}}{\sum_{i=1}^Q W_{ij}} \right), \quad (1)$$

where  $MW_i$  is mean proportion by weight for prey group  $i$ ,  $W_{ij}$  is the weight of prey group  $i$  in a tuna species,  $j$ ,  $P$  is the number of non-empty stomach samples, and  $Q$  is the number of prey groups in all samples.

Although nearly 300 prey taxa were available in the global stomach-contents dataset, we included only the principal prey groups in our analysis, based on their gravimetric importance. Principal prey groups were determined for each tuna species in all oceans combined and within each ocean basin (i.e. Pacific, Atlantic, and Indian Oceans) (study objective 1). Principal groups are defined as prey taxa that constituted at least 1% wet weight to the overall diet of each tuna species. Prey were identified to the taxonomic level of species in the individual regional studies used to populate our full dataset when possible, but to simplify the global analysis we grouped species into the family level. When identification to family was not possible, coarser resolutions of prey were necessary (e.g. order Stomatopoda). Functional groups were assigned to each prey group based on habitat depth distribution to gain broad understanding of vertical foraging behavior of each tuna species. We defined shallow prey as those residing above 200 m (epipelagic and epicoastal), vertically-migrating prey as those that move between shallow and deep waters (epi-mesopelagic 0-500 m; epi-bathypelagic 0 to >600 m), and deep prey as those that inhabit waters >200 m permanently (mesopelagic, meso-bathypelagic, bathypelagic). Empty stomachs, unidentified prey, and rare prey, i.e. those contributing <1% MW to the overall global diet of each tuna species, were omitted from further analyses.

### 2.3 Exploratory analysis

To determine which predictor variables were appropriate for including in the classification tree analysis of diet data, we performed a thorough exploratory evaluation of available variables. Several predictor variables were considered for our analysis, including spatial (latitude and longitude, Longhurst province and biome (Longhurst, 1998)), temporal (year, quarter, month), gear (surface or deep gear and gear type), and biological (predator fork length (FL), weight, and sex). While we could consider all of these predictor variables in a classification tree analysis, due to the way in which trees are constructed and important variables are identified (see Section 2.5), we believed that a preliminary investigation of predictor variables was necessary to assist with the interpretation of splits arising from the model. For a subset of the diet data, the environmental variables sea-surface temperature (SST), mixed-layer depth (MLD), eddy kinetic energy (EKE), sea-surface chlorophyll-*a* concentration (Chl*a*), and median phytoplankton cell mass ( $M_{B50}$ ) were extracted and/or computed from various sources (see section 2.4: *Environmental data*). Our exploratory analysis of these variables included simple summary statistics of each variable, pair-wise comparisons to investigate collinearity, and spatial summaries to understand how the distribution of the data varied for different categories and values of potential covariates that could be included in the model. Confounding issues with some covariates were observed (e.g. the spatial and temporal variables; tuna stomach samples expanded and contracted over space and time, and we observed little overlap in sample locations through space and time). This disproportion is primarily due to unbalanced sampling design as is common in fisheries-dependent opportunistic sampling and also because several regional studies were combined into a global meta-analysis. As a result, we focused our classification tree analyses on broad-scale spatial variability in diet and omitted time from our models. Additionally we included the categorical variable, biome (Table 2) to group provinces instead of considering a much larger and more complicated categorization such as Longhurst provinces (Longhurst, 1998). Such provinces were incorporated into our classification tree analysis, because they demonstrate the biogeochemical and climatic variability across which the three tuna species were sampled from in this study (Fig. 1). The global oceans are not homogeneous regions with respect to environmental variables, thus understanding how tuna diet relates to regional dynamics (as defined by Longhurst province (Longhurst, 1998)) was necessary, and we grouped the large number of Longhurst provinces into a smaller category, biomes as defined in Longhurst (1998). We selected latitude, longitude, biome, and length as the explanatory variables used in our first classification tree analysis of the full diet dataset

(study objective 2); and latitude, longitude, biome, length, SST, MLD, EKE, Chla, and  $M_{B50}$  in our second classification tree models of a subset of diet data (study objective 3).

#### 2.4 Environmental data

Environmental variables were considered for a subset of our diet data from 2003-2011 (Table 3) with the aim of exploring oceanographic influences on diet composition (study objective 3). The year range chosen coincided with the majority of our tuna samples and availability of environmental data. Global environmental datasets of sufficient spatial and temporal resolution generally are not available prior to the 1990s. Sea-surface temperature ( $^{\circ}\text{C}$ ) data were obtained using a General Circulation Model from National Centers for Environmental Prediction (NCEP) Global Ocean Data Assimilation System (GODAS) (GODAS, 2016) ([http://apdrc.soest.hawaii.edu/datadoc/godas\\_monthly.php](http://apdrc.soest.hawaii.edu/datadoc/godas_monthly.php)). Global-scale annual climatologies were used to extract environmental data for MLD. A monthly climatology of MLD estimated from a fixed threshold on temperature profiles using a criterion of  $0.2^{\circ}\text{C}$  was taken from the IFREMER (IFREMER, 2016) data portal ([http://www.ifremer.fr/cerweb/deboyer/mld/Surface\\_Mixed\\_Layer\\_Depth.php](http://www.ifremer.fr/cerweb/deboyer/mld/Surface_Mixed_Layer_Depth.php)) with a spatial resolution of  $1^{\circ} \times 1^{\circ}$  grid and was averaged over the 12 months to obtain an annual climatology. Satellite-derived EKE values were computed from geostrophic currents derived from the monthly AVISO (AVISO, 2016) Delayed-Time Reference Mean Sea-Level Anomaly (MSLA) product (<http://www.aviso.altimetry.fr/en/data/products/sea-surface-height-products/global/>), combined with the Niiler climatology (Niiler et al., 2003), downloaded from the NOAA Ocean Watch (NOAA, 2016) data portal (<http://oceanwatch.pifsc.noaa.gov/thredds/ncss/>), and computed as  $\text{EKE} = 0.5(U^2 + V^2)$ . Sea-surface chlorophyll-*a* concentration (Chla,  $\text{mg m}^{-3}$ ) was taken from monthly MODIS Aqua ([https://modis.gsfc.nasa.gov/data/dataproduct/chlor\\_a.php](https://modis.gsfc.nasa.gov/data/dataproduct/chlor_a.php)) (NASA, 2016). Median phytoplankton cell mass ( $M_{B50}$ ) was estimated using SST and Chla data and equations based on Barnes et al. (2011):  $M_{B50}(\log_{10} \text{ pg C}) = 1.340 - 0.043(\text{SST}) + 0.929(\text{Log}_{10}(\text{Chla}))$ .

Because of the sparsity of the diet data, environmental data were averaged over a  $1^{\circ} \times 1^{\circ}$  grid by year to identify broad trends. For each  $1^{\circ} \times 1^{\circ}$  grid cell, environmental variables were matched to the corresponding diet data. However, Chla concentration and EKE were used without re-gridding data due to computing constraints. For these two variables each  $1^{\circ} \times 1^{\circ}$  grid cell and date were matched to the closest point and month available in the dataset.

#### 2.5 Classification tree analysis of stomach-contents data



We applied classification tree methodology (Breiman et al., 1984) to yellowfin, bigeye, and albacore tuna predation data separately, to explore relationships among predictor variables and diet composition using the modified approach outlined in Kuhnert et al. (2012) and illustrated in Duffy et al. (2015), Young et al. (2015b) and Olson et al. (2014). The principal prey groups used in the classification tree analysis were those that constituted at least 1% MW to the diet of each tuna species across all oceans combined to identify patterns in diet composition across space. Sample sizes of stomachs and sample locations varied through space and time for each tuna species. Thus, to gain a better representation of the relationship between predictor variables and global diet composition and diversity for each tuna species, we believed it was appropriate to run a separate classification tree for yellowfin, bigeye, and albacore tunas. Furthermore, in a preliminary analysis with all three species in one analysis, predator species was not important and results were less informative. The tree methodology developed for diet data is akin to a multinomial model but is fit non-parametrically to provide an exploratory and predictive framework for identifying complex relationships between predictor variables and diet composition (Kuhnert et al., 2012). Classification trees were developed from rearranging a multivariate response of a predator's diet to a univariate categorical response variable of prey group (class) with observation (case) weights. The Gini index of diversity (D), which is the criterion used to determine optimal splits, was used to estimate diet diversity, where values near 0 indicate low diet diversity and values near 1 represent a highly diverse diet. Once a large tree is grown, the tree is pruned using 10-fold cross-validation and the "1 standard error" ("1 SE") rule (Breiman et al., 1984) to identify the tree that yielded the lowest cross-validated relative error or alternatively, a tree with an error that was within 1 standard error of the minimum. Predictions were formed by partitioning observations down branches of the tree until they resided in a terminal node. The relative importance of each split was represented by the length of the tree branches with longer branches indicating greater importance than shorter branches. Variable importance rankings are also a byproduct of the process of growing and pruning the tree, whereby an importance measure (calculated as a goodness of split from primary and surrogate splits (Breiman et al., 1984)) is calculated to highlight important variables in the model. The prey with the highest gravimetric proportion among a suite of prey in the diet composition was shown at each terminal node of the tree, and prey were color coded according to broad taxonomic groupings. Uncertainty in the predicted prey composition was achieved using a spatial bootstrap approach with 500 iterations, and variable importance rankings were computed for each tuna species to identify and rank important predictor variables (Kuhnert et al., 2012). The spatial bootstrap is akin to the bagging approach by Breiman (1996), where spatial bootstrap samples are drawn from the data and an unpruned tree is constructed for each sample. The spatial bootstrap accounts for spatial dependence in the data which can then be tested by fitting a variogram to the residuals formed from the

bootstrap predictions. The bootstrap is based on a large number of resamples of the data (e.g. 500), from which average prey compositions and corresponding errors can be calculated. This information can be mapped to the original tree to provide a bootstrap estimate of the prey composition and its associated error, giving an idea of the accuracy of the predictions arising from the model. Bagging was originally proposed as a method for overcoming the instability inherent in decision tree models and can be used to explore the uncertainty in the predictions from the classification trees presented here.

Two classification tree analyses were conducted to address our study objectives. The first analysis was conducted on the full dataset to identify spatial and biological patterns in tuna diets (study objectives 1 and 2), and we analyzed the stomach-contents data for 7295 yellowfin, 1208 bigeye and 1804 albacore tunas containing food. The second analysis explored potential oceanographic influences in addition to spatial and biological effects on tuna diets (study objective 3) using the subset with stomach-contents data for 3265 yellowfin, 589 bigeye, and 1678 albacore tunas containing food. This subset of stomach-contents data was selected based on the availability of associated environmental data.

Several visualization tools were used to assist in the interpretation of key splits from the model. These included heat maps to highlight predicted prey composition at terminal nodes of the tree, partial dependence plots produced using the bootstrap method of Kuhnert et al. (2012) to explore the predicted proportion of important prey groups with confidence bands for different predictor variables, and contour maps to examine the variation in tuna diet diversity quantified by the 1 SE classification trees. Contour maps were produced using a generalized additive model fitted to latitude and longitude with smoothing splines in the R mgcv package (Wood, 2006). All tree-based analyses were implemented in R (R Development Core Team, 2013), using the ‘rpart’ package (Therneau et al., 2013).

### 3. Results

#### 3.1 Ocean-basin diet compositions of yellowfin, bigeye, and albacore tunas

Diet composition data for the principal prey groups are summarized by tuna species and ocean basin as percentages of the gravimetric index of diet, (Eq.1:  $MW_i$ ) for the full global diet dataset in Table 4. The diets of yellowfin, bigeye, and albacore tunas in each of the three oceans consisted of a wide range of micronekton fishes, squids, and crustaceans. Across all oceans, a diversity of fish prey was most prevalent in the diets of all tuna species (23.6-37.2% MW), but crustaceans and squids were also important prey for all three tunas. Epipelagic scombrid fishes and epi-mesopelagic ommastrephid squids were most important for yellowfin tuna (11.3% and 10.2% MW, respectively), ommastrephid squids for

bigeye tuna (10.0% MW), and epi-bathypelagic euphausiid crustaceans for albacore tuna (17.0% MW) across all oceans (Table 4).

Tunas did not feed exclusively on one prey group, globally or at the ocean scale. Several families of fishes, squids, and crustaceans were consumed in small amounts by each of the tuna species, with only a few taxa contributing to more than 5% MW within each ocean (Table 4). Regional differences in key prey from each of the three major ocean basins for each tuna species were evident. Of the fish prey, epipelagic scombrids were important prey for yellowfin tuna in all ocean basins while epi-mesopelagic nomeid fishes were a dominant prey for yellowfin tuna in the Indian Ocean. For bigeye tuna, primary fish prey included epicoastal priacanthids and epi-mesopelagic gempylids in the Atlantic Ocean, epi-mesopelagic nomeids and alepisaurids in the Indian Ocean, and mesopelagic paralepidids in both the Indian and Pacific Oceans. Key fishes consumed by albacore tuna in the Atlantic Ocean included epipelagic scomberesocids and engraulids as well as epi-mesopelagic gadids, while albacore tuna in the Indian Ocean fed mostly on epi-mesopelagic alepisaurids and epi-bathypelagic myctophids. Of the squids, ommastrephids were dominant in all regions for all tunas with the exception of albacore in the Pacific and Atlantic Oceans, while epipelagic onychoteuthids were also important in the diets of bigeye and albacore tunas in the Indian Ocean. For yellowfin tuna, key crustacean prey consisted mainly of epipelagic portunids and epicoastal stomatopods in the Indian Ocean and epipelagic galatheids in the Pacific Ocean. Other important crustacean prey included portunids for bigeye tuna in the Indian Ocean and euphausiids for albacore tuna in the Atlantic and Pacific Oceans (Table 4).

### *3.2 Spatial and biological variables explaining diet composition*

#### *3.2.1 Yellowfin tuna*

Distinct geographic regions were identified by the classification tree based on the global diet composition of yellowfin tuna (Fig. 2a, cross-validated error rate =0.76, SE=0.007). Strong longitude and latitude trends were highlighted by longer tree branches and the variable importance ranking whereby longitude and latitude were closely ranked (1.00 and 0.93, respectively), followed by length and biome with shorter tree branches and lower importance (0.49 and 0.38, respectively). Explanatory variables associated with some of the important splits on the tree are labeled (Fig. 2a) while details for all internal and terminal nodes are presented in Table S1. The initial split of the classification tree, which provides the greatest reduction in deviance over the entire dataset, partitioned yellowfin tuna in the western Pacific Ocean (node 2) from yellowfin in other ocean regions (node 3). Diet diversity (D) was similar in both nodes (D=0.754, D=0.792; nodes 2 and 3, respectively), although diet composition differed between the

two nodes (Fig. 3a). Stomatopods (26% MW) were the dominant crustacean prey in yellowfin tuna from the western Pacific Ocean (Fig. 3a, node 2) while ommastrephid squids (20% MW) were important elsewhere (Fig. 3a, node 3). Stomatopods were predicted to be the most important prey for small yellowfin tuna in the western Pacific Ocean relative to other regions based on terminal nodes in the classification tree (Fig. 4a, node 4). Across all regions ommastrephid squids and scombrid fishes (Fig. 4a) were highly important, in particular for yellowfin tuna sampled in the Peru Current along the west coast of South America (node 24, Ommastrephidae) and inshore regions of the eastern Pacific Ocean (node 62, Scombridae). High proportions of other prey taxa were observed for yellowfin tuna in the California Current, along the west coast of North America, nodes 56 (galatheid crustaceans) and 115 (engraulid fishes).

### 3.2.2 Bigeye tuna

Bigeye tuna diet also showed strong spatial patterns in the classification tree analysis, with longitude as the most important variable in explaining diet composition (rank=1.00), followed by latitude, length, and biome (ranks <0.6) (Fig. 2b, cross-validated error rate =0.882, SE=0.015). Longer branches occurred on longitude and biome in the upper portion of the tree further highlighting spatial patterns. The initial split of the classification tree identified regional differences in diet composition for small (<684.5 mm, n=197, node 2) and large ( $\geq$ 684.5 mm, n=1,011, node 3) bigeye tunas. Small bigeye tunas sampled from the western Pacific and Indian Oceans fed primarily on stomatopod crustaceans while those from other regions fed mostly on ommastrephid squids (Fig. 2b, nodes 4 and 5) lending to the lower diet diversity (D=0.691, Fig. 3b node 2). Large bigeye tunas showed high diet diversity (D=0.85) due to an increase in piscivory and consumption of small amounts of different micronekton prey groups (molluscs, crustaceans, and fishes) as compared to smaller conspecifics (Fig. 3b, node 3). Diet composition of bigeye tuna summarized at the terminal nodes of the classification tree showed that bigeye tuna mainly fed upon small amounts of deep-dwelling or vertically-migrating micronekton including ommastrephid squids, alepisaurid, myctophid, and paralepidid fishes with only a few observations of a single prey dominating diet composition (Fig. 4b). Stomatopods (node 4) were a key prey in small bigeye tuna from the western Pacific Ocean while ommastrephids were consumed by small and large bigeye tuna in all regions (nodes 4-15) and were also a dominant prey in the eastern Pacific and Atlantic Oceans (node 5) (Fig. 4b).

### 3.2.3 Albacore tuna

Latitude was the highest-ranking variable (rank=1.00) of the diet of albacore tuna, followed closely by biome and longitude, (rank=0.84 and 0.75, respectively) and lastly length (rank=0.58) (Fig. 2c;

cross-validated error rate = 0.871, SE = 0.014). The longest tree branches were observed for biome and latitude. The initial split of the classification tree identified regional differences in albacore tuna diet among the trade wind and coastal biomes (Atlantic Trade Wind, Indian Ocean Coastal, Indian Ocean Trade Wind, Pacific Coastal, Pacific Trade Wind) and the westerly winds biomes (Antarctic Westerly Winds, Atlantic Westerly Winds, and Pacific Westerly Winds) (Fig. 2c). Albacore consumed small amounts of various micronekton prey (shallow dwellers and vertical migrators) in the trade wind and coastal biomes resulting in a highly diverse diet ( $D=0.901$ , Fig. 3c, node 2). Within the westerly winds biomes, albacore diet diversity was moderate ( $D=0.594$ ) given these tunas fed predominantly on euphausiid crustaceans (40% MW) and scomberesocid (15% MW), engraulid (13% MW), and gadid fishes (11% MW) (Fig. 3c, node 3). Diet composition summarized at the terminal nodes of the classification tree identified ommastrephid squids as a moderately important prey item for albacore tuna in the Atlantic and Indian Oceans (Fig. 4c, node 4) while euphausiid crustaceans were key prey in the Bay of Biscay (France, Spain), Mediterranean Sea and along the coast of New Zealand (Fig. 4c, nodes 14-31).

### 3.3 Spatial trends in tuna diet

Partial dependence plots were used to examine spatial patterns in the predicted proportions of prey composition using latitude and longitude, conditional on all other predictor variables in the model held constant at their respective means (Kuhnert et al., 2012). Ommastrephid squids were predicted as important prey items particularly for yellowfin and bigeye tunas with proportions varying across space (0.1-0.45) (Fig. 5). The highest predicted consumption of ommastrephid squids was in the Peru Current area of the southeastern Pacific Ocean (~0.45) as well as the Indian Ocean (~0.4) for yellowfin tuna (Fig. 5a) and in the Atlantic and Pacific Oceans for bigeye (~0.3) and albacore tunas (~0.2) (Fig. 5b and c, respectively). Galatheid (~0.5) and stomatopod (~0.4) crustaceans were predicted as being prominent in yellowfin tuna diet only off the southern coast of Baja California, Mexico and in the tropical western Pacific Ocean off the coast of Indonesia, respectively (Fig. 5a). Scombrid fishes were also predicted in the stomachs of yellowfin tuna in all oceans with slightly higher proportions in yellowfin tuna from the eastern and central Pacific Ocean (~0.3). Globally, proportions of prey taxa contributing to the diet of bigeye tuna were predicted to be low (primarily <~ 0.2), but onychoteuthid squids and nomeid and paralepidid fishes expressed the highest proportions of the 19 prey taxa (Fig. 5b). The highest proportions of nomeids (~0.4) were predicted in the Indian Ocean, and the highest proportions of paralepidids were predicted in the tropical western Pacific Ocean (~0.4). For albacore tuna, euphausiid crustaceans were predicted in moderate proportions (~0.5-0.6) in the Bay of Biscay, Indian and western Pacific Oceans, scomberesocid fishes (~0.4) in the Northeast Atlantic and engraulid fishes (~0.2) in the eastern and

central Pacific and Atlantic Oceans (Fig. 5c). The remaining prey taxa were predicted in low proportions ( $\leq 0.1$ ) across the globe, highlighting greater diet diversity in albacore tuna relative to yellowfin and bigeye.

Global distribution of diet diversity predicted by the 1 SE classification trees were presented on contour maps for each tuna species (Fig. 6). Diet diversity of yellowfin tuna varied regionally with low diversity ( $D \leq 0.4$ ) observed in the Pacific Coastal biome along the coasts of Baja California, Mexico (north of  $20^{\circ}\text{N}$ ) and Peru (south of  $5^{\circ}\text{S}$ ) as well as in the Indian Ocean Coastal biome in the southwest Indian Ocean (south of  $10^{\circ}\text{S}$ ) (Fig. 6a). Yellowfin tuna in the upwelling regions off Baja California, Mexico (terminal node 115 in the classification tree, Fig. 2a) consumed primarily engraulids while those in the Peru Current (terminal node 24, Fig. 2a) fed upon ommastrephid squids. Highest diet diversity for yellowfin tuna ( $D \geq 0.9$ ) was predicted in the south central Pacific Ocean within the Pacific Trade Wind biome between  $5^{\circ}\text{N}$ – $20^{\circ}\text{S}$  and  $150^{\circ}\text{W}$ – $120^{\circ}\text{W}$ . Diet diversity of bigeye tuna also varied regionally. Highest diversity ( $D \geq 0.9$ ) was represented among bigeye tuna within the Indian Ocean Trade Wind biome (including northern areas, north of  $10^{\circ}\text{S}$  and southeastern areas, east of  $75^{\circ}\text{E}$ ) and the Atlantic Trade Wind biome ( $10^{\circ}\text{S}$ , coastal Brazil) (Fig. 6b). Less diverse diets of bigeye tuna ( $D < 0.5$ ) were predicted in the Pacific Trade Wind biome (central eastern Pacific  $125^{\circ}\text{W}$ – $100^{\circ}\text{W}$  and western Pacific  $125^{\circ}\text{E}$ – $150^{\circ}\text{E}$  around Indonesia and Papua New Guinea), Indian Ocean coastal biome (south Africa), and in the Atlantic Westerly Winds biome (northern areas, north of  $20^{\circ}\text{N}$ ) (Fig. 6b) due to the consumption of large amounts of ommastrephid squids and stomatopod crustaceans. Overall, high diversity in albacore tuna diet was predicted in tropical and subtropical regions with the highest diversity ( $D \geq 0.9$ ) in the Pacific (west of  $125^{\circ}\text{W}$  and east of  $150^{\circ}\text{E}$ ) and Atlantic (tropical, near the equator) Trade Wind and the Pacific Coastal biomes (Fig. 6c). Lower diversity ( $D < 0.5$ ) was observed in albacore tuna diets in the temperate sampling locations, including within the Atlantic (Bay of Biscay and Mediterranean Sea) and Pacific Westerly Winds biomes (coastal, western New Zealand) and the Indian Ocean Trade Wind biome (South Africa) (Fig. 6c) based on large amounts of euphausiid crustaceans observed in albacore diets. This pattern in diversity is different from the patterns seen in yellowfin and bigeye tunas and is consistent with the results of the classification tree for albacore tuna, in which latitude was the main factor explaining diet composition.

### *3.4 Exploring the relationship between environmental variables and diet*

Environmental variables were not as important as spatial variables for yellowfin and albacore tunas, but SST was identified as the highest ranked variable influencing the diet of bigeye tunas based on classification tree analyses of the subset of data from 2003–2011 (Fig. 7). For yellowfin tuna, SST was

ranked third in importance, had a similar rank to latitude (rank=0.79 and 0.75, respectively), and was the initial split of the classification tree where stomatopods were a dominant prey predicted in warmer waters of the Pacific and Indian Oceans (Fig. 7a, cross-validated error rate=0.783, SE=0.01). The remaining biological, spatial, and environmental predictor variables had less of an effect on yellowfin tuna diet (variable importance ranking  $\leq 0.3$ , Fig. 7a). Environmental (SST, MLD), biological (length), and spatial (longitude) variables all ranked high in importance for predicting bigeye tuna diet composition (variable importance ranking  $\geq 0.7$ ); long tree branches were observed for length (the initial tree split), longitude, and SST although the cross-validated error rate for this tree was the highest of the three tunas (0.9, SE=0.02) (Fig. 7b). The spatial variables biome, latitude, and longitude were the most important variables affecting albacore diet, and all ranked  $\geq 0.8$  while Chl $a$  and length were identified as moderately important variables ( $\geq 0.5$ ) (Fig. 7c, cross-validated error rate=0.823, SE=0.015). The lowest ranked environmental variables ( $< 0.1$ ) on diet composition were EKE, Chl $a$ , and  $M_{B50}$  for yellowfin and bigeye tunas, and  $M_{B50}$  for albacore tuna.

Predicted prey proportions for the terminal nodes of each 2003-2011 subset classification tree on yellowfin, bigeye, and albacore tunas are summarized in supplemental material Figure S1. In waters with low SSTs ( $< 28^{\circ}\text{C}$ ), galatheid crabs (node 26) and ommastrephid squids (node 12) were dominant prey in the subtropical northeastern Pacific Ocean and in the Pacific and Atlantic Coastal biomes north of  $10^{\circ}\text{N}$ , respectively, while stomatopods (node 2) were observed as a main prey in waters with high SSTs for yellowfin tunas (Fig. S1a). High proportions of stomatopod crustaceans in the tropical western Pacific Ocean (node 4) and ommastrephid squids in the tropical eastern Pacific, Atlantic, and Indian Oceans (node 5) were predicted in small bigeye tunas ( $< 598.5$  mm) while larger bigeye tunas were predicted to have a diverse diet composed of small amounts of various micronekton (molluscs, crustaceans, and fishes, Fig. S1b). High proportions of euphausiid crustaceans were predicted for albacore tunas regionally within the Antarctic Westerly Winds and Atlantic Westerly Winds biomes while those in the coastal and trade wind biomes of the Pacific, Atlantic, and Indian Oceans were predicted to have a diverse diet consisting of various salps, molluscs, crustaceans, and fishes (Fig. S1c).

To further evaluate the relationship between environmental variables and diet, we examined partial dependence plots showing important prey taxa and the highest ranked environmental variables for each tuna species (Fig. 8). Vertically-migrating ommastrephid squids were observed in the diet of yellowfin tunas at all terminal nodes of the tree including regions with warm and cold SSTs but showed a decrease in proportions when SSTs were  $> \sim 22^{\circ}\text{C}$ . The bootstrapped 95% confidence band around these predictions was large indicating considerable error in the relationship between SST and the predicted proportion of ommastrephids (Fig. 8a). Epicoastal stomatopod prey increased with increasing SST, and

epipelagic galatheid crabs showed a slight increase around 25°C before decreasing in the diets of yellowfin tunas, although the confidence bands around the predictions of the latter were also large (Fig. 8a). Epipelagic scombrid fishes were also common prey of yellowfin tunas, but no apparent relationship was observed with SST (Fig. 8a). SST was identified as the highest ranking environmental variable (rank=1.00) influencing the diet of bigeye tunas. Vertically-migrating ommastrephid squids and nomeid and myctophid fishes declined with increasing SST while epipelagic onychoteuthid squids and deep-dwelling paralepidid fishes increased with increasing SST; bootstrapped confidence bands around these predictions were narrow although few points were observed at lower temperatures (Fig. 8b). Stomatopods showed little relationship with SST for bigeye tunas. Ommastrephid and paralepidid prey proportions also showed strong decreasing and increasing patterns with increasing MLD, respectively, while onychoteuthids appeared consistently in small proportions, those of stomatopods varied across MLDs, and nomeids and myctophids reduced around 40 and 45 m, respectively (Fig. 8c). For albacore tunas, vertically-migrating euphausiid crustaceans and gadid fishes increased with increasing Chl $a$  before again decreasing around concentrations at ~0.4 mg m<sup>-3</sup> (Fig. 8c).

#### 4. Discussion

This is the first study to examine the global feeding ecology of three commercially important, wide-ranging tuna species, and to our knowledge the first study of its kind for any fish species at this spatio-temporal scale. We took a macroecological approach to examine abiotic and biological factors driving diet patterns to show explicit differences in micronekton prey composition and corresponding diet diversity of these tuna species using a novel dataset and methodology that was both exploratory and predictive. The predation habits of the tuna species we present here are important particularly because data on offshore pelagic prey are sparse; this information can thus be used to infer (and monitor) broad community-scale changes in the abundance, availability, and diversity of poorly studied mid-trophic micronekton prey. Intraspecific differences in micronekton prey observed spatially support the existing view of generalist feeding habits in these tunas, reinforcing the efficacy of tunas as biological samplers, while observed interspecific differences provides evidence for potential trophic niche separation when species overlap. The linkage between diet diversity and productivity observed in some ocean regions suggests potential trophic effects that may be associated with the expansion of warmer, less productive waters.

##### 4.1 Global and ocean basin characterizations of micronekton communities



In this study, teleost fishes comprised the majority of micronekton in terms of number of species and weight for each of the three tuna species and in all ocean bodies. Two exceptions were Mollusca and Arthropoda, which dominated the diet of albacore tuna in the Indian and Atlantic Oceans, respectively. Our results support the realization that fishes are an important component of mesopelagic micronekton with recent work suggesting that global biomass estimates have been underestimated by an order of magnitude in open ocean ecosystems (Kaartvedt et al., 2012; Irigoien et al., 2014). However, modelling work in the central north Pacific Ocean showed that while fishes represent most of the micronekton biomass, crustaceans account for much more of the micronekton production and along with molluscs, provide the most important direct trophic pathways to top predators (Choy et al., 2016).

Differences in prey groups were noted among ocean basins reflecting regional variation in forage communities. Ommastrephid squids were an important prey particularly for yellowfin and bigeye tunas across all oceans and albacore tuna in the Indian Ocean. Our results are complementary to other recent trophic studies that documented the importance of ommastrephid squids in the diets of tunas (Logan et al., 2013; Ménard et al., 2013; Young et al., 2013; Olson et al., 2014; Teffer et al., 2015; Itoh and Sakai, 2016) and highlight the central role that these squid play as key prey and linkages between upper and lower trophic levels in open ocean ecosystems. Ommastrephid squids are common in pelagic environments (Anderson and Rodhouse, 2001; Rodhouse, 2005; Arkhipkin et al., 2015), and their prevalence in the diets of the three tuna species included in our analysis is likely at least partly due to their ubiquity across the broad spatial region considered in our analysis. The greatest diet proportions of ommastrephid squid were found in the Indian Ocean, consistent with the high abundances of these squid in the region (Ménard et al., 2013). Other important prey taxa in the Indian Ocean were portunid crabs, nomeid fishes, and stomatopod crustaceans for both yellowfin and bigeye tunas, and onychoteuthid squids for both bigeye and albacore tunas. Surface swarms of portunids were reported as a seasonal trophic link in open-ocean ecosystems in the western Indian Ocean (Romanov et al., 2009), while the dominance of mantis shrimp (order Stomatopoda) in tuna diets may reflect their periodic availability that can fluctuate over decadal scales (Romanov et al., 2015). In the Pacific Ocean, galatheid crustaceans and scombrid fishes, paralepidid fishes, and euphausiid crustaceans were prominent prey for yellowfin, bigeye, and albacore tunas, respectively. Paralepidid fishes are typically fast moving species distributed across epipelagic, mesopelagic, and bathypelagic waters in all oceans (Peterson et al., 1999) and are commonly consumed by other top predators in the Pacific Ocean (Choy et al., 2016). In the Atlantic Ocean, important prey taxa included scombrid and nomeid fishes in yellowfin tuna, priacanthid and gempylid fishes in bigeye tuna, and euphausiids (krill), engraulids (anchovies), scomberesocids, and gadids in albacore tuna. Anchovy is an energetically-rich prey (Spitz et al., 2010; Albo-Puigserver et al., this issue)

and likely plays a significant role in albacore tuna energy storage and condition during their summer feeding migration (Goñi and Arrizabalaga, 2010). While documenting dominant prey taxa of these tunas assists in understanding the biomass and biogeography of these micronekton, we should note that some micronekton groups that are known to be important to tunas and other top predators in particular regions of each ocean basin (or at certain times of the year) may have been masked by the global scale of our analysis. For example, gelatinous filter feeders, predatory jellies, and amphipods that are highly abundant in Hawaiian waters and important prey for tuna in this region (Graham et al., 2007) were not well represented in this study.

Clear interspecific differences in the prey taxa consumed by the three tunas were apparent in this study, as has been observed in regional studies (Ménard et al., 2006; Young et al., 2010; Goñi et al., 2011). Across oceans, yellowfin tuna consumed primarily epipelagic and epicoastal prey, such as scombrid fishes and stomatopod crustaceans, representative of the surface layer habitat above the thermocline where yellowfin tuna spends the majority of their time (Schaefer et al., 2009). Bigeye tuna consumed higher proportions of deep-living and vertical-migrating prey than the other tuna species in this study, reflecting its capacity to dive and forage at depths for long periods of time (Holland et al., 1992; Brill et al., 2005; Schaefer and Fuller, 2010). High proportions (>5% MW) of epicoastal priacanthid and epi-mesopelagic gempylid, alepisaurid, and nomeid fishes as well as epipelagic portunid crustaceans and onychoteuthid squid, support the belief that bigeye tuna consume larger amounts of mesopelagic species than yellowfin tuna (Galván-Magaña, 1999; Potier et al., 2004; IATTC, 2013; Olson et al., 2014). Albacore tuna diet consisted of a greater variety of both shallow and deep-living prey taxa, reflecting its broad vertical and horizontal feeding distribution and residency in both tropical and temperate environments (Teffer et al., 2015; Williams et al., 2015). Albacore tuna diet included several prey taxa that were either uncommon (e.g. euphausiids (krill)) or absent (epi-mesopelagic gadid and epipelagic scomberesocid fishes) in yellowfin and bigeye tuna diets, potentially due to a greater sampling range for albacore tuna that included temperate waters. The importance of krill in albacore tuna diets has been noted in temperate parts of the southwest Pacific Ocean (Young et al., 1993) and southern Atlantic Ocean (Goñi et al., 2011), where they occurred in high densities during upwelling events.

#### *4.2 Global patterns in diet diversity linked to productivity*

A clear latitudinal diversity gradient was present for albacore tuna while distinct spatial patterns were found for each tuna species. Few studies have looked at the species diversity of micronekton in the open oceans although a unimodal productivity-diversity relationship for marine phytoplankton has been suggested (Vallina et al., 2014). In a range of open ocean taxa, including zooplankton, squids and krill,

marked peaks of species diversity have been recorded at broad mid-latitudinal bands in all oceans (Rutherford et al., 1999; Tittensor et al., 2010). This pattern also appears to hold for large oceanic predators such as sharks, tunas and billfishes (Worm et al., 2005; Tittensor et al., 2010). High global diet diversity for all tuna species in this study support their generalist feeding habits, resourcefulness given patchy prey distributions, and their high energetic requirements (Olson and Boggs, 1986; Whitlock et al., 2015). The latitudinal gradient of diet diversity and the fact that latitude explained most of the variance for the diet of albacore tuna is consistent with life history traits of this species. Albacore tuna has a large latitudinal distribution and performs long-range summer migrations with important latitudinal displacements between tropical and subtropical wintering regions and temperate summer feeding regions (Williams et al., 2015).

We found that diet diversity of all tuna species is linked to ocean productivity with highest diversity in the most oligotrophic offshore regions and lowest diversity in many of the nearshore upwelling regions. Oligotrophic central gyres of oceans are generally characterized by more species-rich and longer food webs than more productive inshore systems, where a few species tend to be predominant (McGowan and Walker, 1985; Venrick, 1990; Rohde, 1992). Low diet diversity (<0.5) values were consistently predicted in areas where primary production is relatively high and coastal upwelling occurs such as in the eastern Pacific Ocean off the coast of Peru and Mexico, coastal areas in the northwest Mediterranean Sea, coastal areas of southern New Zealand, and in the Bay of Biscay (Behrenfeld et al., 2006; Carr et al., 2006). This low diet diversity in productive coastal waters is consistent with the “waist” sensu Rice (1995) or “wasp-waist” (Cury et al., 2000) structure of these food webs in which intermediate trophic levels have low diversity while low and high trophic levels are more diverse. The mid-trophic level species dominating these “wasp-waist” food webs tend to be densely aggregated and of high energetic value (e.g. engraulids (Soriguer et al., 1997; Litz et al., 2010)), characteristics that maximize foraging efficiency for tunas and other top predators. In contrast, for all species, high diet diversity was reported in the tropical central Pacific Ocean where high-nutrient, low-Chl*a* conditions are observed (Morel et al., 2010). Our subset analysis, which included environmental variables, also supported the linkage between albacore tuna diet diversity and productivity with Chl*a* ranked as an important variable. Many of the prey groups identified in these regions have low lipid content (e.g. Salpidae (Doyle et al., 2007), Stomatopoda (Wardiatno et al., 2012)) and lower associated energetic value to tunas. Studies of individual systems have provided evidence of diet diversity in productive upwelling regions (Madigan et al., 2012) and a “wasp-waist” structure in relatively oligotrophic waters (Griffiths et al., 2013), so trophic effects of ocean warming may not always follow the general inversion of prey diversity and productivity observed in most of our global analysis. One anomaly to the linkage between ocean production and diet

diversity was found in bigeye tuna with low diversity predicted in the western parts of the WARM Longhurst province (inside the Pacific Trade Wind biome) (Longhurst, 1998) near Indonesia and Papua New Guinea, typically characterized by low productivity. However, North Pacific thermocline and South Pacific lower thermocline waters merge and produce a small upwelling area in the Halmahera Sea (Susanto et al., 2006). Bigeye tuna have been shown to exhibit a highly-adaptive foraging strategy relative to the fine-scale spatiotemporal variability in the distribution and abundance of prey within their habitat (Fuller et al., 2015).

Little is known about how prey diversity impacts the transfer of energy and matter among trophic levels. Mechanistically, the inverse relationship between tuna diet diversity and productivity shown in this study is likely influenced by various ecosystem processes, mostly trophic transfer dynamics. In waters where production will decline, tuna diet diversity may increase and trophic efficiency may decrease due to patchy prey distributions. Generalist species are expected to be more resilient to climate change than specialists (Harley, 2011; Staudinger et al., 2013a), and the generalist feeding strategy of tunas combined with their highly mobile lifestyles (Polovina, 1996) should allow them to adapt to changes in available prey resources. However, disproportionate impacts on specific life stages (e.g. early life history stages) and the rapid pace of climate change have the potential to exceed the adaptive capacity of many species thus leading to declines (Loarie et al., 2009; Beever et al., 2016). Enhanced resource use efficiency, resulting from diversity-dependent niche partitioning, has also been reported to benefit ecosystem structure and function (Behl et al., 2012). Prey diversity has been shown to influence energy transfer among trophic levels, and in ways that may oppose the influence of consumer diversity on resource utilization in food webs (Hillelbrand and Cardinale, 2004). Long term factors that influence tuna, including ocean productivity (Boyce et al., 2010; Polovina and Woodworth, 2012) and habitat compression (Stramma et al., 2008; Stramma et al., 2010; Stramma et al., 2012) have been reported. For example, shoaling of the oxygen minimum zone can restrict the depth distribution of epipelagic predators (Stramma et al., 2012), potentially narrowing foraging habitat and altering forage communities, but this hypothesis remains untested.

#### *4.3 Key drivers of tuna diet composition*

The best predictor variables of diet composition in the full classification tree analysis were longitude for yellowfin and bigeye tunas and latitude for albacore tuna. These results show that spatial variables may be used as proxies for more dynamic regional-scale features and processes, such as net productivity, which is further supported by the importance of the biome variable in most tuna models. Slight differences in the explanatory power and importance of the geographic variables among tuna

species may reflect their life history; yellowfin and bigeye tunas are strictly tropical tuna species and show more localized movements (Schaefer and Fuller, 2002; Schaefer et al., 2007) while albacore tunas exhibit pronounced latitudinal migrations in their juvenile stage (Childers et al., 2011). Few diet studies of tuna have been undertaken at large enough latitudinal ranges to test spatial and environmental correlates of trophic interactions and prey diversity. In the southwest Pacific Ocean, variations of diet with latitude have been recorded in albacore (Williams et al., 2015), but not bigeye tuna (Young et al., 2010), while in the eastern Pacific Ocean latitudinal differences in yellowfin diet have been observed (Olson et al., 2014).

Regional studies have shown ontogenetic trends in tuna prey species composition and size distribution (Ménard et al., 2006; Graham et al., 2007; Young et al., 2010; Kuhnert et al., 2012; Logan et al., 2013; Teffer et al., 2015), but at the global scale, our analysis suggests that body size is less influential than spatial variables. Tuna body size (fork length) was ranked as a moderately important variable ( $<0.6$ ) in most tuna models. Tunas are generalist predators that consume a diverse array of prey families and a broad spectrum of prey sizes (Olson et al., 2016). Regional analyses of tuna predator-prey size relationships generally show a wedge-shaped pattern in which tunas of all sizes consume small prey and larger individuals consume an increasingly broad range of prey sizes (Ménard et al., 2006; Young et al., 2010; Logan et al., 2013). Given that prey selection generally broadens with tuna size rather than completely changing, tunas of different sizes in a given region would have some dietary overlap with each other as well as other large pelagic predators. The greater relative importance of spatial variables in our global analysis indicates that regional differences in available prey taxa exert a greater effect on tuna diet than subtler body size-based variability and highlights the importance of spatial scale in assessments of tuna trophic ecology.

The subset analysis showed that some environmental factors were reasonable predictors of diet composition, particularly SST for yellowfin and bigeye tunas, MLD for bigeye tuna, and Chl $a$  for albacore tuna. Increasing SSTs seemed to affect the diet of yellowfin and bigeye tunas through decreased proportions of vertically-migrating ommastrephid squids, which have been shown in regional studies to be sensitive to climate (van der Kooij et al., 2016). A similar relationship was found for nomeid fishes consumed by bigeye tuna. In contrast, consumption of epicoastal stomatopod crustaceans and deep-dwelling paralepidid fishes increased in yellowfin and bigeye tunas, respectively, with increasing SSTs. Tittensor et al. (2010) reported that SST was the primary environmental predictor of broad-scale global patterns of diversity across oceanic groups of taxa including tunas and billfishes, sharks, squids, and euphausiids. As MLD increased, ommastrephid squids decreased while paralepidid fishes increased in the diets of bigeye tuna. Reductions in Chl $a$  influenced the diet of albacore tuna by increasing proportions of

vertically-migrating euphausiid crustaceans and gadid fishes. Our results suggest that with predicted climate changes (latitudinal expansion of low Chla, increased stratification, and elevated mean SST) (Polovina et al., 2008), tunas might be impacted by disproportionate responses by their prey groups. However, we note that for all tunas there were high cross-validated error rates and large confidence bands for some prey observed in the subset analyses, reducing our confidence in potential relationships between the environmental variables used in our tree models and diet of tunas. Bottom-up environmental forcing is modulated at each level of the food chain, so tuna and their prey are several steps removed from the driving physical oceanographic changes. Furthermore, life history integration over larger space and time scales means that environmental effects can be complicated. In such cases, additional effort acquiring environmental variables may be misplaced, and instead, information representing the behavior and availability of intermediate prey fields is needed (Hobday and Hartog, 2014).

#### *4.4 Caveats and future research directions*

Various predator-prey and environmental drivers can result in considerable temporal and spatial differences in patterns of predation. For this reason, studies of predation often require large sample sizes and high quality data to overcome uncertainty. Although this study undertook a sophisticated analysis of the largest diet dataset ever compiled for these tuna species, there are several sources of uncertainty. Firstly, the ability to explore global spatial patterns over time is restricted to sample coverage within and among regions. For each study, sampling effort was typically restricted to a specific region (Fig. S2) and time period such that we cannot yet account for known temporal patterns (e.g. seasonality) in predator-prey interactions. Furthermore, disparities in the sample sizes for each ocean region across different time periods as well as fishing method contribute bias to the global summaries of this meta-analysis, because different gear types capture fish at different depths (Bertrand et al., 2002; Potier et al., 2004). A mixture of various sampling procedures (e.g. techniques, gear types, and personnel) used in the field and laboratory analyses are an additional source of uncertainty (Chipps and Garvey, 2007). The environmental data used in the models were obtained from static annual climatologies and from broad temporal scales (e.g. a yearly resolution), which lack the resolution necessary to capture any transient dynamics, especially relevant at highly seasonal latitudes (Vallina et al., 2014). Additionally, most of the environmental variables considered in our subset analysis were surface-related and are challenging to relate to the diet of tuna that forage at depth. Spatial and temporal differences in fishing pressure could also have influenced our global results if predator removals induced trophic cascades (Kitchell et al., 1999; Schindler et al., 2002) although simulated fishery removals of the tuna species included in our analysis do not alter underlying food web structure (Griffiths et al., 2013). Lastly, stomach contents

analysis has inherent sources of uncertainty related to biased estimates of certain prey groups and life-history stages (e.g. larval) and the need for taxonomic expertise (Pierce and Boyle, 1991); this is especially true for tuna species that forage in open-ocean and deep-sea environments where many prey taxa are poorly known.

Future work should focus on assessing temporal (e.g. seasonal and monthly) variation in relative diet composition and diet diversity at regional or ocean-basin scales (Olson et al., 2014). Well-designed, long-term diet studies will allow for a better understanding of tuna diet in relation to environmental variables on finer temporal scales than the broad yearly scales used here to examine potential relationships. Such studies could confirm or refute the patterns described here as they could be affected by a changing climate. Better accounting for sampling uncertainty when interpreting the results of dietary studies (e.g. Bayesian and sensitivity analysis), will be of primary importance. Due to the differences in foraging behavior of the three tuna species analyzed here, information on depth of tuna capture and digestion state of prey will improve knowledge of gear-related effects on diet and may help researchers begin to disentangle possible relationships between ocean dynamics occurring at depth and how they may relate to diet. Prey size information also was not available for the global diet analysis and the upper size range of certain prey species within some of the families represented in the full dataset are outside of the prey-range size of tunas. Future work could include assessing predator-prey size relationships to gain understanding of fine-scale patterns in size compositions across space and time as well as insights into resource sharing and partitioning among other tunas and large pelagic fishes. We encourage similar global-scale analyses using other dietary tracers such as stable isotopes, fatty acids, trace metals, and studies that combine dietary data with tagging, pelagic trawl or acoustic measurements that would allow better understanding of predator-prey interactions.

Insights into the spatial differences in diet are increasingly important given the overlap of commercial fisheries with areas where climate change is predicted to be a critical issue (Hobday, 2010; Polovina et al., 2011). Regional variation in diet and hence production may change subsequent model forecasts. Our diet diversity results could allow ecosystem models to allocate energy flow based on a diet diversity index and allow related parameters to vary regionally. For traditional ecosystem models (such as Ecopath (Christensen et al., 2015) and Atlantis (Fulton, 2010)) diet diversity information could help refine linkages between species and allow these links to vary in space and time. The global diet diversity indices we have described here could also be extracted from ecosystem models, and thus be used in direct comparisons to validate and calibrate ecosystem models over historical periods, which should give greater confidence in future projections.

#### 4.5 Conclusions

Examining global predation patterns in tunas provides key information on the structure and function of marine ecosystems through characterizing micronekton diversity, distribution, and availability. Such information on the opportunistic foraging behavior of tunas is important particularly given that data on offshore pelagic prey are scarce. Global and ocean basin differences were detected within and between each of the three tuna species studied. Spatial patterns in the diet diversity of these tuna species were consistent with theories that predict an inverse relationship between primary productivity and species diversity. Our results collectively suggest that the ongoing expansion of warmer, less productive waters in the world's oceans may alter foraging opportunities of tunas in important upwelling regions as a result of changes in the regional abundance and availability of prey resources. If micronekton communities shift to lower quality species or if the size structure of prey populations are truncated either due to changes in the environment or to fishing pressure, these changes could have consequences for tuna energetics (Golet et al., 2007; Österblom et al., 2008; Golet et al., 2015). The ecological impacts of these changes are not clear, particularly on the biology and population dynamics of the tunas (e.g. growth rates, reproduction), but shifts to less energetically-favorable prey could impact these parameters given the high energetic demands of tuna species (Brill, 1996; Korsmeyer and Dewar, 2001; Olson et al., 2016). Resulting changes in tuna abundance, condition and distribution due to prey variability have notable economic implications as the three focal species in this paper contribute approximately 40% of global tuna catches (FAO, 2010), and are valued at \$5.79-7.5 billion USD per year (Galland et al., 2016). It is critical that broad scale monitoring of tuna feeding ecology should therefore continue and be an integral component of sustainable tuna management strategies into the future.

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Table 1. Summary of data compiled across the globe for the full dataset of yellowfin (*Thunnus albacares*), bigeye (*T. obesus*), and albacore (*T. alalunga*) tunas. Number of non-empty stomachs includes only those with principal prey i.e., prey that constituted at least 1% mean weight to the overall global diet of each tuna species. These data were used in the first classification tree analysis of the entire global diet dataset to identify broad-scale spatial and biological patterns in tuna diets.

Predator	Yellowfin	Bigeye	Albacore
Number of stomachs (non-empty)	9331 (7295)	2127 (1208)	2727 (1804)
Sampling years	1969-2013	1969-2012	1970-2011
Length range, caudal fork length (mm)	119-2140	270-1930	396-1280
Length mean $\pm$ SD (mm)	891 $\pm$ 342	1070 $\pm$ 321	788 $\pm$ 172
Latitude range	37.5°S-39.6°N	36.8°S-41.5°N	44.0°S-51.0°N
Longitude range	179.9°W-178.2°E	179.9°W-179.8°E	178.2°W-178.4°E

Table 2. Biomes used in the classification tree analysis and corresponding Longhurst Biogeographical Provinces (Longhurst 1998) shown in Figure 1.

<b>Biome</b>	<b>Biome Abbreviation</b>	<b>Province Abbreviation</b>	<b>Province Definition</b>
Antarctic Westerly Winds Biome	ANTWW	SANT	Subantarctic Water Ring Province
		SSTC	South Subtropical Convergence Province
Atlantic Coastal Biome	AC	GUIN	Guinea Current Coastal Provinces
		NWCS	Northwest Atlantic Shelves Province
Atlantic Trade Wind Biome	ATW	ETRA	Eastern Tropical Atlantic Province
		NATR	North Atlantic Tropical Gyral Province
		SATL	South Atlantic Gyral Province
		WTRA	Western Tropical Atlantic Province
Atlantic Westerly Winds Biome	AWW	GFST	Gulf Stream Province
		MEDI	Mediterranean Sea, Black Sea Province
		NADR	North Atlantic Drift Province
		NASW	North Atlantic Subtropical Gyral Province (West)
		NASE	North Atlantic Subtropical Gyral Province (East)
Indian Ocean Coastal Biome	IOC	ARAB	Northwestern Arabian Coastal Province
		EAFR	Eastern Africa Coastal Province
		INDW	Western Indian Coastal Province
Indian Ocean Trade Wind Biome	IOTW	ISSG	Indian South Subtropical Gyre Province
		MONS	Indian Monsoon Gyres Province
Pacific Coastal Biome	PC	AUSE	East Australian Coastal Province
		CCAL	California Current Province
		CAMR	Central American Coastal Province
		HUMB/CHIL	Humboldt Current Coastal Province
		NEWZ	New Zealand Coastal Province
		SUND	Sunda-Arafura Shelves Province
Pacific Trade Wind Biome	PTW	ARCH	Archipelagic Deep Basins Province
		NPTG	North Pacific Tropical Gyre Province
		PEQD	Pacific Equatorial Divergence Province
		PNEC	North Pacific Equatorial Countercurrent Province
		SPSG	South Pacific Subtropical Gyre Province
		WARM	Western Pacific Warm Pool Province
Pacific Westerly Winds Biome	PWW	TASM	Tasman Sea Province



Table 3. Summary of data for the diet subset from 2003-2011 of yellowfin (*Thunnus albacares*), bigeye (*T. obesus*), and albacore (*T. alalunga*) tunas. Number of non-empty stomachs includes only those with principal prey i.e., prey that constituted at least 1% mean weight to the overall global diet of each tuna species. These data were used in the second classification tree analysis to investigate the potential influence of oceanographic features on tuna foraging behavior. Values for the environmental variables are reported as mean  $\pm$  standard deviation.

Predator	Yellowfin	Bigeye	Albacore
Number of stomachs (non-empty)	4320 (3265)	1227 (589)	2536 (1678)
Length range, caudal fork length (mm)	119-1970	270-1930	396-1280
Length mean (mm) mean $\pm$ SD	773 $\pm$ 352	1070 $\pm$ 321	788 $\pm$ 172
Latitude range	37.47°S-39.6°N	36.8°S-41.5°N	44.0°S-51.0°N
Longitude range	179.9°W-179.8°E	179.9°W-179.8°E	178.2°W-178.4°E
Sea-surface temperature (SST°C)	27.3 $\pm$ 3.0	27.5 $\pm$ .5	20.3 $\pm$ 5.3
Mixed-layer depth (MLD, m)	43.1 $\pm$ 9.3	43.7 $\pm$ 11.9	48.4 $\pm$ 12.4
Eddy kinetic energy (EKE, cm <sup>2</sup> /s <sup>2</sup> )	250.1 $\pm$ 406.7	240.6 $\pm$ 408.6	41.5 $\pm$ 86.2
Chlorophyll <i>a</i> (Chl <i>a</i> , mg m <sup>-3</sup> )	0.3 $\pm$ 1.2	0.1 $\pm$ 0.1	0.2 $\pm$ 0.2
Median phytoplankton cell mass (M <sub>B50</sub> , pgC)	-0.6 $\pm$ 0.3	-0.7 $\pm$ 0.3	-0.2 $\pm$ 0.4

Table 4. Taxonomic composition of the principle prey in the full diet dataset of yellowfin (*Thunnus albacares*), bigeye (*T. obesus*), and albacore (*T. alalunga*) tunas. Principal prey used in the classification tree analysis (CART) are defined as those that constituted at least 1% wet weight to the overall diet of each tuna species in all oceans combined (All) and are represented in column ‘CART Prey’ where <sup>1</sup>=yellowfin, <sup>2</sup>=bigeye, <sup>3</sup>=albacore tunas: M=molluscs, C=crustaceans, S=Salps, F=fishes, respectively. Principal prey are also included for each tuna species in each ocean basin (PO=Pacific, AO=Atlantic, IO=Indian) where the 1% weight limit (above) refers to the overall diet of each tuna species within each ocean basin. Number of tunas (n) with principal prey in the stomachs is provided for each ocean basin and all oceans combined. Values are expressed in percentages of mean proportion by weight  $MW_i$ . When prey could not be identified to family, coarser taxonomic levels are shown (ord=order, infraord=infraorder, subord=suborder). Functional group definitions: Epicoastal=only in the epipelagic domain (from the surface to 100-200m depth), but a coastal/lagoon/reef linked species, Epipelagic=only in the epipelagic domain (from the surface to 100-200 m depth), Epi-mesopelagic=vertical migrators in the epipelagic (from the surface to 100-200 m depth) and the mesopelagic domain (200 to 500 m depth), Epi-bathypelagic=in the epipelagic (from the surface to 100-200 m depth) and the bathypelagic domain during the day (deeper than 500-600 m depth), Mesopelagic=only in the mesopelagic domain (200 to 500 m depth), Meso-bathypelagic=in the mesopelagic (200-500 m depth) and the bathypelagic domain (deeper than 500-600 m depth), and Bathypelagic=only in the bathypelagic domain (deeper than 500-600 m depth). Rare prey are those that contributed <1% wet weight to the overall diet of each tuna species in each ocean basin and all oceans combined.

	CART Prey	Functional Group	Yellowfin				Bigeye				Albacore			
			% $MW_i$				% $MW_i$				% $MW_i$			
			PO n=6,088	AO n=320	IO n=887	All n=7,295	PO n=591	AO n=40	IO n=577	All n=1,208	PO n=863	AO n=859	IO n=82	All n=1,804
<b>Mollusca</b>			<b>12.37</b>	<b>12.23</b>	<b>14.08</b>	<b>12.00</b>	<b>10.00</b>	<b>15.46</b>	<b>22.76</b>	<b>14.33</b>	<b>4.49</b>	<b>3.53</b>	<b>38.85</b>	<b>4.82</b>
Cavoliniidae		Epipelagic						1.03						
Argonautidae	M-Arg <sup>1</sup>	Epi-mesopelagic	2.20			1.82								
Octopodidae		Unassigned											1.83	
Enoploteuthidae	M-Eno <sup>2</sup>	Epi-mesopelagic			1.01			1.03	1.57				2.19	
Histioteuthidae		Meso-bathypelagic										1.24		
Ommastrephidae	M-Omm <sup>1,2,3</sup>	Epi-mesopelagic	10.17	10.37	10.12	10.17	8.16	10.77	12.56	9.97	2.04	2.28	17.70	2.88
Onychoteuthidae	M-Ony <sup>2,3</sup>	Epipelagic			2.95		1.84	1.03	8.63	4.35	2.45		17.14	1.94
Loliginidae		Epicoastal		1.85				1.60						
<b>Arthropoda</b>			<b>14.97</b>	<b>9.00</b>	<b>22.25</b>	<b>15.98</b>	<b>3.21</b>	<b>1.03</b>	<b>17.63</b>	<b>8.45</b>	<b>21.11</b>	<b>29.39</b>	<b>13.96</b>	<b>23.55</b>
Stomatopoda (ord)	C-Stom <sup>1,2,3</sup>	Epicoastal	3.79		7.97	4.14	2.08		4.49	2.87	3.16		2.25	1.69
Odontodactylidae		Epipelagic											1.47	
Decapoda (ord)	C-Dec <sup>1</sup>	Unassigned		4.65		1.05								

			Yellowfin				Bigeye				Albacore			
			% $MW_i$				% $MW_i$				% $MW_i$			
	CART Prey	Functional Group	PO n=6,088	AO n=320	IO n=887	All n=7,295	PO n=591	AO n=40	IO n=577	All n=1,208	PO n=863	AO n=859	IO n=82	All n=1,804
Galatheidae	C-Gal <sup>1</sup>	Epipelagic	5.74			4.60								
Enoplometopidae	C-Eno <sup>3</sup>	Epi-mesopelagic											1.62	
Brachyura (infraord)	C-Bra <sup>1</sup>	Epicoastal	1.67			1.36								
Portunidae	C-Por <sup>1,2</sup>	Epipelagic	1.99		13.08	3.40			6.63	2.56				
Oplophoridae	C-Opl <sup>2</sup>	Meso-bathypelagic			1.20				3.04	1.33			3.11	
Thalassocarididae	C-Thal <sup>1,2,3</sup>	Epipelagic	1.79			1.44	1.12				2.50			1.17
Pasiphaeidae		Epi-bathypelagic										1.38		
Palinura (infraord)	C-Pal <sup>3</sup>	Epicoastal									1.06			
Penaeidae	C-Pen <sup>2</sup>	Epi-bathypelagic							3.47	1.70			1.29	
Euphausiacea (ord)	C-Euph <sup>3</sup>	Epi-bathypelagic		1.13							10.86	24.43		16.96
Amphipoda (ord)	C-Amp <sup>3</sup>	Epi-mesopelagic		3.23								1.82		1.24
Hyperiidea (subord)	C-Hyper <sup>3</sup>	Epi-mesopelagic										1.75	1.94	1.36
Lestrigonidae		Epi-mesopelagic											1.00	
Phronimidae	C-Phro <sup>3</sup>	Epi-mesopelagic									1.80			
Phrosinidae	C-Phros <sup>3</sup>	Epi-mesopelagic									1.74			1.13
Platyscelidae		Epi-mesopelagic						1.03					1.28	
<b>Chordata</b>			<b>39.55</b>	<b>30.21</b>	<b>39.50</b>	<b>37.21</b>	<b>18.48</b>	<b>33.82</b>	<b>42.63</b>	<b>27.41</b>	<b>9.11</b>	<b>43.10</b>	<b>32.46</b>	<b>23.56</b>
Salpidae	S-Sal <sup>3</sup>	Epi-mesopelagic									3.03			1.71
Exocoetidae	F-Exo <sup>1</sup>	Epipelagic	2.20	1.74	3.87	2.40								
Hemiramphidae	F-Hem <sup>1</sup>	Epipelagic	1.74			1.46								
Scomberesocidae	F-Scomb <sup>1,3</sup>	Epipelagic									1.74	11.66	1.95	6.58
Diretmidae		Bathypelagic						1.63						
Syngnathidae		Epicoastal										1.70		

	CART Prey	Functional Group	Yellowfin				Bigeye				Albacore			
			% $MW_i$				% $MW_i$				% $MW_i$			
			PO n=6,088	AO n=320	IO n=887	All n=7,295	PO n=591	AO n=40	IO n=577	All n=1,208	PO n=863	AO n=859	IO n=82	All n=1,804
Bramidae	F-Bra <sup>2,3</sup>	Epi-mesopelagic			2.14		1.93		1.48	1.65	1.31		2.86	
Carangidae	F-Car <sup>1</sup>	Epicoastal	4.07	2.90	3.49	3.92			1.05			1.38	1.00	
Priacanthidae		Epicoastal		2.94				12.37						
Gempylidae	F-Gem <sup>2</sup>	Epi-mesopelagic			2.57			6.61	3.68	2.21			1.69	
Scombridae	F-Scom <sup>1,2</sup>	Epipelagic	12.30	9.19	6.57	11.33		2.74	4.10	2.27				
Nomeidae	F-Nom <sup>1,2</sup>	Epi-mesopelagic	4.28	6.04	9.05	5.04	2.74	4.30	5.90	4.02			3.09	
Chiasmodontidae	F-Chi <sup>2</sup>	Epi-bathypelagic			1.07				2.33	1.23			1.61	
Dactylopteridae		Epicoastal		2.69										
Balistidae	F-Bal <sup>1</sup>	Epicoastal	1.54			1.35								
Molidae		Epipelagic											1.00	
Monacanthidae		Epicoastal		1.17										
Ostraciidae	F-Ost <sup>1</sup>	Epicoastal	3.88			3.20								
Clupeidae		Epicoastal		1.55				1.03						
Engraulidae	F-Eng <sup>1,3</sup>	Epipelagic	4.03		3.12	3.66						12.32	2.00	6.46
Alepisauridae	F-Ale <sup>2,3</sup>	Epi-mesopelagic			3.26		2.15		9.94	4.95	1.15		4.81	
Omosudidae	F-Omo <sup>2</sup>	Mesopelagic							2.04				2.17	
Paralepididae	F-Par <sup>2,3</sup>	Mesopelagic			2.32		5.16	2.63	8.74	6.36	1.89	1.14	2.41	1.55
Scopelarchidae	F-Sco <sup>2</sup>	Bathypelagic											1.07	
Trachipteridae	F-Trach <sup>3</sup>	Meso-bathypelagic										3.27		1.60
Gadidae	F-Gad <sup>3</sup>	Epi-mesopelagic										11.64		5.66
Myctophidae	F-Myc <sup>1,2,3</sup>	Epi-bathypelagic	1.14		2.04	1.23	3.90	2.50	3.38	3.62			5.01	
Sternoptychidae	F-Ste <sup>2</sup>	Epi-bathypelagic					1.49			1.09			1.80	

	CART Prey	Functional Group	Yellowfin				Bigeye				Albacore			
			% $MW_i$				% $MW_i$				% $MW_i$			
			PO n=6,088	AO n=320	IO n=887	All n=7,295	PO n=591	AO n=40	IO n=577	All n=1,208	PO n=863	AO n=859	IO n=82	All n=1,804
Phosichthyidae	F-Pho <sup>1</sup>	Epi-mesopelagic	4.35	1.99		3.62	1.10							
		Rare prey	12.46	10.80	14.59	14.62	13.93	2.82	8.96	13.36	16.06	6.80	7.08	16.36
		Unidentified prey	20.65	37.77	9.58	20.20	54.38	46.87	8.01	36.45	49.22	17.18	7.65	31.71
		Number of rare prey taxa	167	63	92	203	113	17	56	128	123	43	25	142

## Figure captions:

**Figure 1** Map of sample locations for yellowfin, bigeye, and albacore tunas in the compiled global data base. Longhurst Provinces (Longhurst 1998) for corresponding biomes used in the classification tree analysis (Figure 2) are displayed. Abbreviations are defined in Table 2.

**Figure 2** Classification tree for (a) yellowfin, (b) bigeye, and (c) albacore tuna diet composition from the analysis of the full dataset. The tree diagram shows all node numbers, the split variables, and their values for (b) bigeye and (c) albacore tunas. For (a) yellowfin tuna, the split variables and their values are shown for the most important nodes (see Table S1 in the Supplement for details on all nodes). Lon: longitude; Lat: latitude; Len: length; Biome: see Table 2 for description. To facilitate interpretation of the graphs, additional information on the location of the samples is provided in italics below the spatial split variables (longitudes or biomes): WPO=Western Pacific Ocean, EPO=Eastern Pacific Ocean; CPO=Central Pacific Ocean; IO=Indian Ocean; AO=Atlantic Ocean; MS= Mediterranean Sea; BB=Bay of Biscay (France, Spain); NZ=New Zealand. The prey taxon with the highest proportion weight among a suite of prey in the diet composition is shown at the terminal nodes (see Table 4 for prey abbreviations). Broad prey groups are *S*=salps (tan), *M*=molluscs (blue), *C*=crustaceans (red – orange), and *F*=fishes (green – yellow). Node numbers are labeled according to the naming convention of (Breiman et al., 1984). Variable importance rankings for each covariate are shown in the inset.

**Figure 3** Details of the top split (nodes 2 and 3) of the 1 SE classification tree for (a) yellowfin tuna partitioned by longitude (Fig. 2a), (b) bigeye tuna partitioned by length (Fig. 2b), and (c) albacore tuna partitioned by Biome (Fig. 2c), showing sample locations, sample numbers, and prey compositions (mean proportion by weight). For all plots, D is the Gini index of diversity. *S*-, *M*-, *C*-, and *F*-: Salps, molluscs, crustaceans, and fishes, respectively.

**Figure 4** Prey proportions by weight for (a) yellowfin (b) bigeye, and (c) albacore tunas predicted at the terminal nodes of the 1 SE classification trees of the full diet dataset. Terminal node labels, ordered bottom to top, correspond to the terminal node labels on the trees in Fig. 2, ordered left to right. The bold black line represents the first split of the trees, while dotted lines represent the second split on each side of the trees in Fig. 2. *S*-, *M*-, *C*-, and *F*-: Salps, molluscs, crustaceans, and fishes, respectively. See Table 1 for description of Biomes.

**Figure 5** Spatial partial dependence plots showing the relationship between the spatial variables (latitude and longitude) and the predicted proportions by weight of four principal prey in the diet composition of (a) yellowfin, (b) bigeye, and (c) albacore tunas in the full global dataset. Proportions range from 0 to 1 (scale bar). Predictions are based on averaging across all other variables in the classification tree model. *S*-, *M*-, *C*-, and *F*-: Salps, molluscs, crustaceans, and fishes, respectively.

**Figure 6** Spatial trends in diet diversity on contour maps, ranging between 0 and 1, predicted by the 1SE classification trees of (a) yellowfin, (b) bigeye, and (c) albacore tunas for the full diet dataset. Values of the Gini index of diversity were smoothed with a generalized additive model. Black points represent sample locations of each tuna species.

**Figure 7** Classification tree for (a) yellowfin, (b) bigeye, and (c) albacore tuna diet composition from the analysis of the subset of data from 2003-2011. The tree diagram shows all node numbers, the split variables, and their values. Lon: longitude; Lat: latitude; Len: length; Biome: see Table 2 for description; SST: sea-surface temperature; MLD: mixed layer depth; eke: eddy kinetic energy; chl: chlorophyll-*a* concentration,  $M_{B50}$ : median phytoplankton cell mass. To facilitate interpretation of the graphs, additional information on the location of the samples is provided in italics below the spatial split variables (longitudes or biomes) and the SST splits: WPO=Western Pacific Ocean, EPO=Eastern Pacific Ocean; CPO=Central Pacific Ocean; IO=Indian Ocean; AO=Atlantic Ocean; MS= Mediterranean Sea; BB=Bay of Biscay (France, Spain); NZ=New Zealand. The prey taxon with the highest proportion weight among a suite of prey in the diet composition is shown at the terminal nodes (see Table 4 for definitions of prey abbreviations). Broad prey groups are *S*=salps (tan), *M*=molluscs (blue), *C*=crustaceans (red – orange), and *F*=fishes (green – yellow). Node numbers are labeled according to the naming convention of (Breiman et al., 1984). Variable importance rankings for each covariate are shown in the inset.

**Figure 8** Partial dependence plots constructed on the subset of data from 2003-2011 for (a) yellowfin, (b,c) bigeye, and (d) albacore tunas showing the relationship between sea-surface temperature ((a,b); SST°C), mixed layer depth ((c); MLD, m), and chlorophyll-*a* concentration ((d); chl, mg m<sup>-3</sup>). A rug plot is shown beneath each plot to indicate the distribution of the measurements.

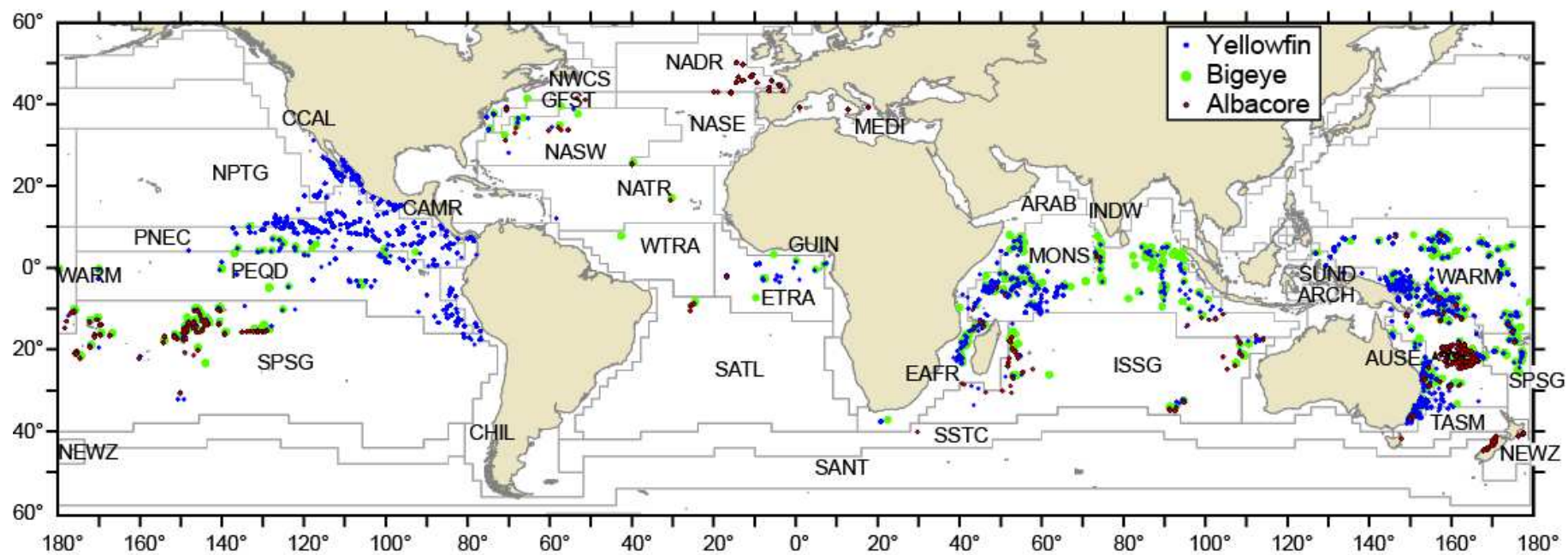
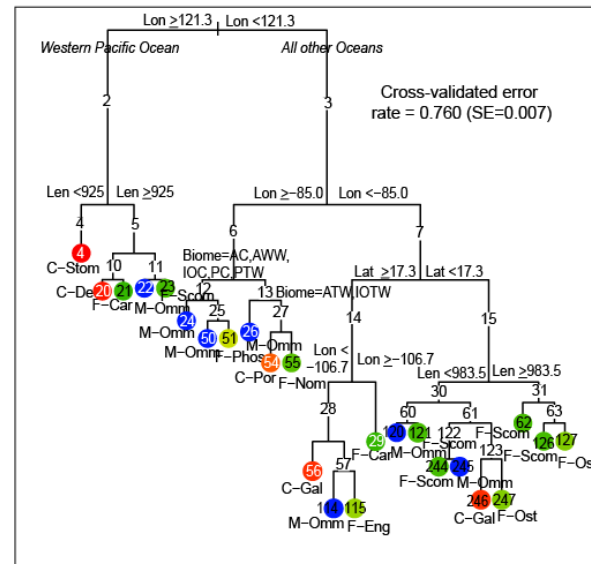


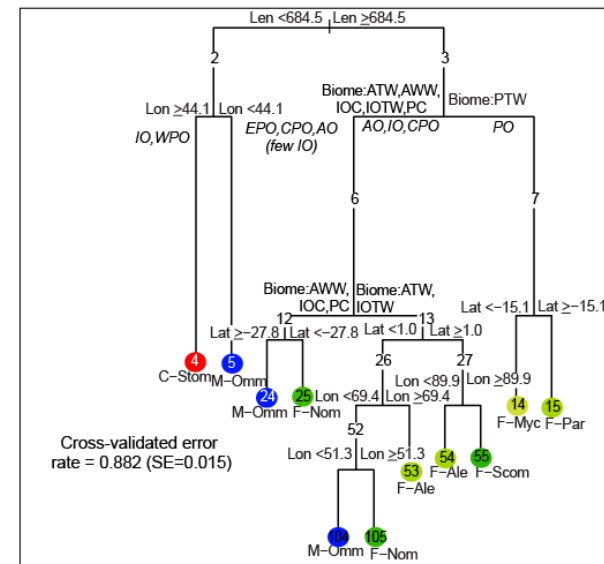
Figure 1



(a) Yellowfin



(b) Bigeye



(c) Albacore

- S-Salpidae
- M-Ommastrephidae
- C-Stomatopoda
- C-Decapoda
- C-Galatheidae
- C-Portunidae
- C-Thalassocarididae
- C-Euphausiacea
- F-Scomberesocidae
- F-Carangidae
- F-Scombridae
- F-Nomeidae
- F-Ostraciidae
- F-Engraulidae
- F-Alepisauridae
- F-Paralepididae
- F-Gadidae
- F-Myctophidae
- F-Phosichthyidae

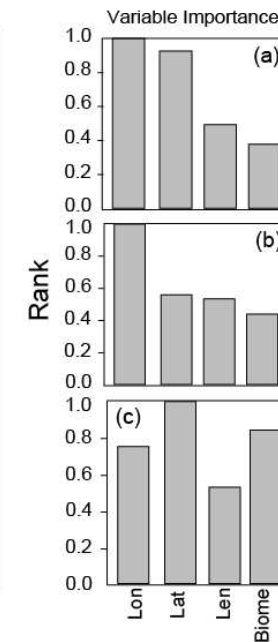
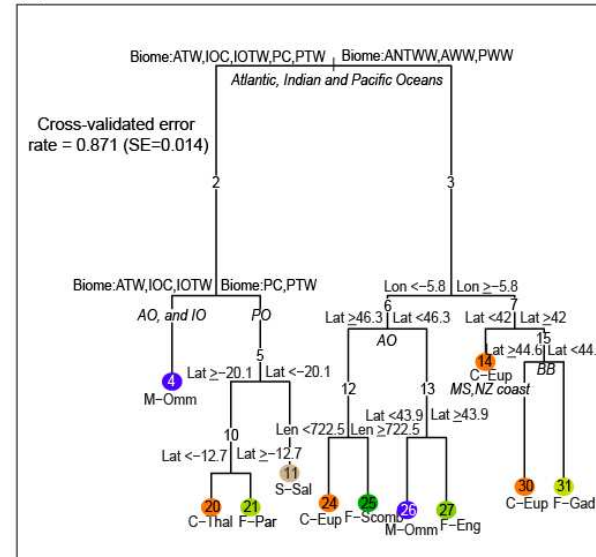


Figure 2

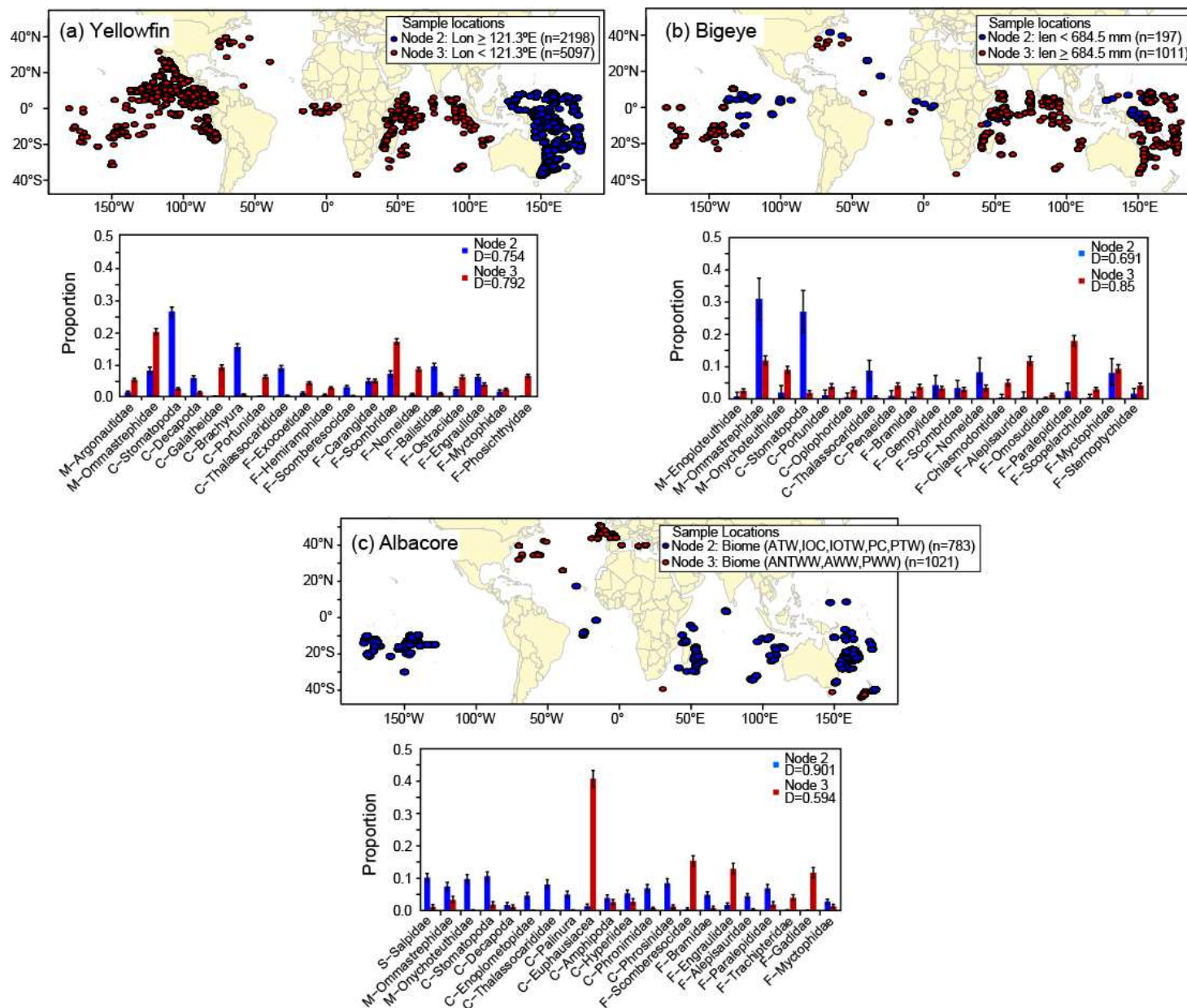


Figure 3

## Predicted prey composition at terminal nodes

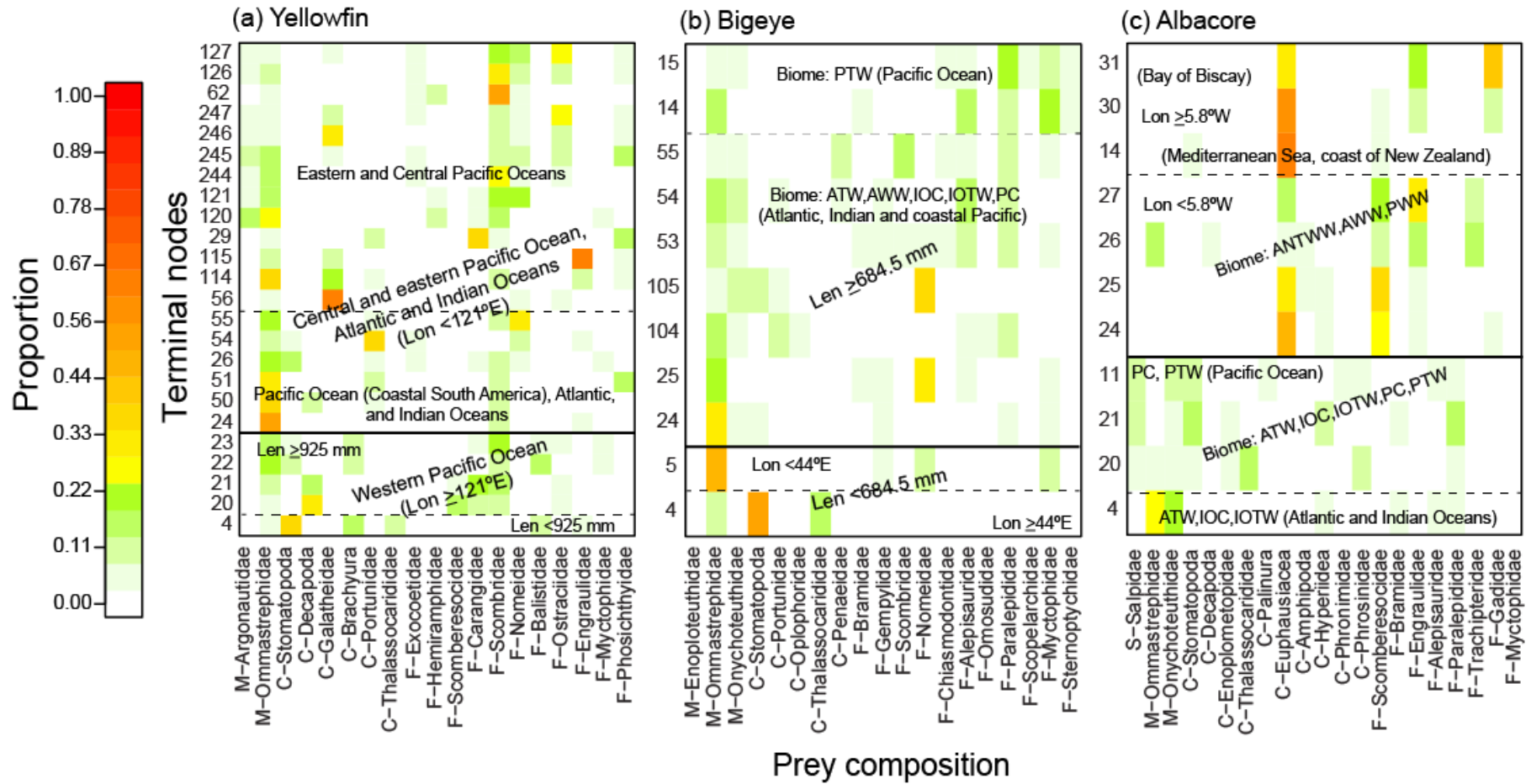


Figure 4



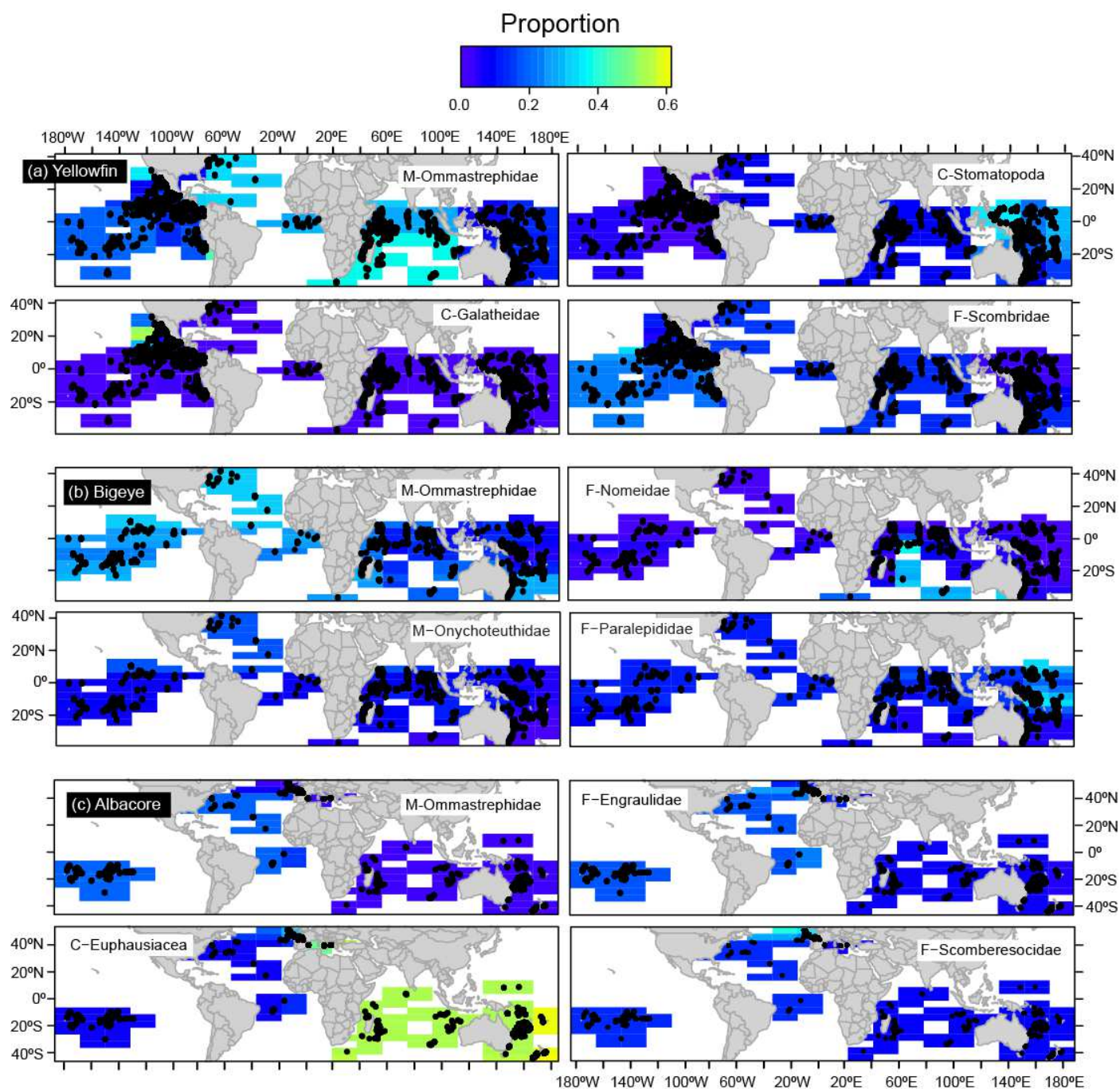
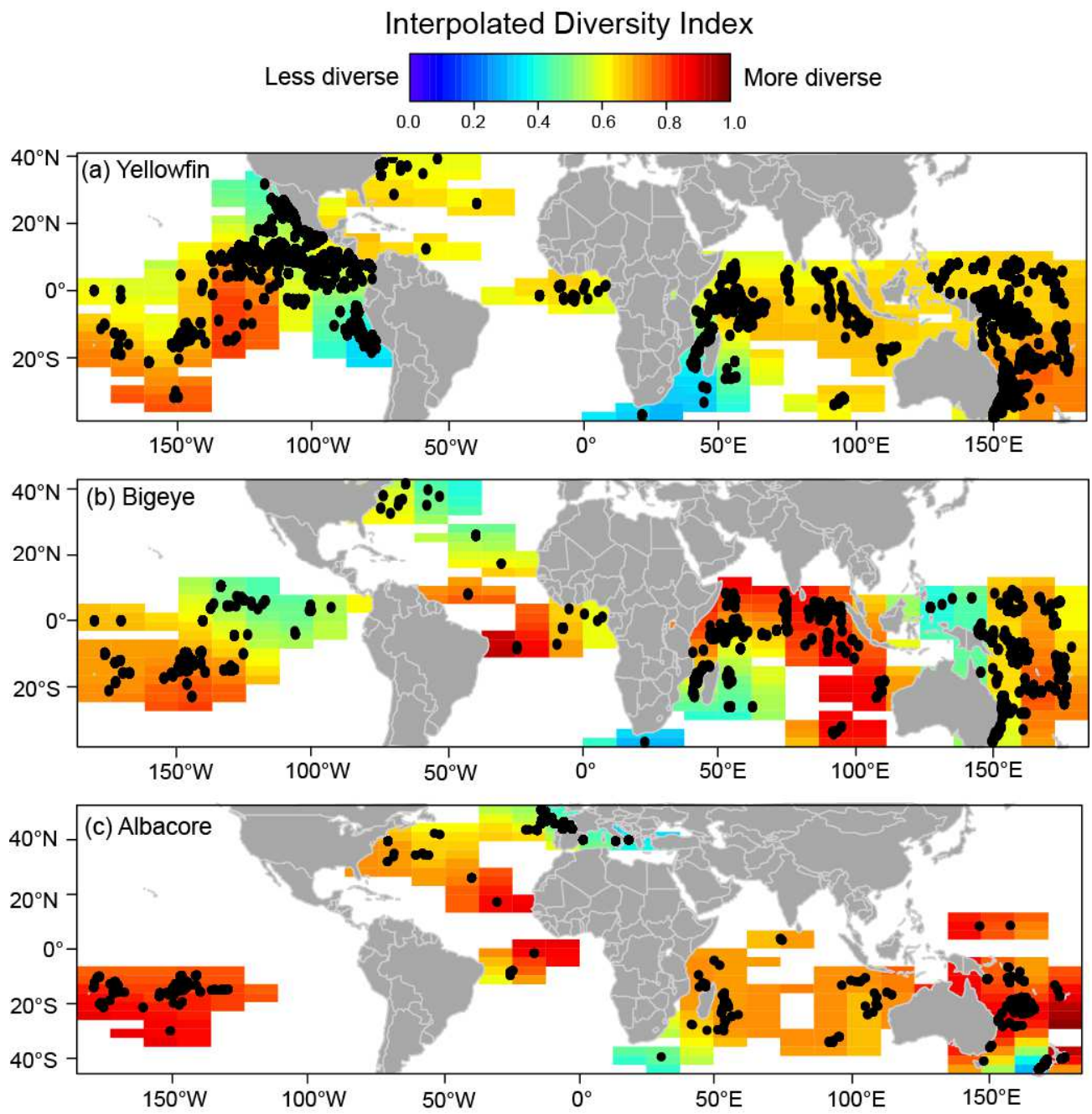
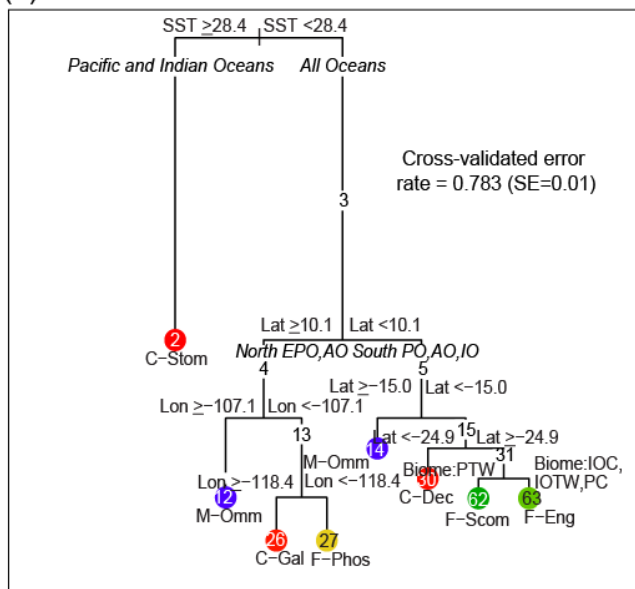


Figure 5

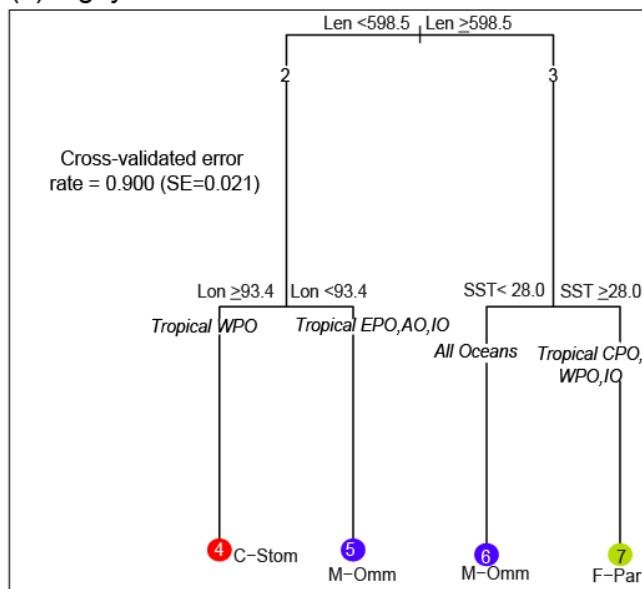


**Figure 6**

(a) Yellowfin



(b) Bigeye



(c) Albacore

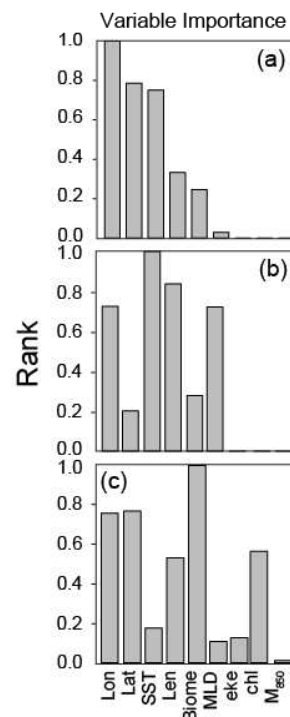
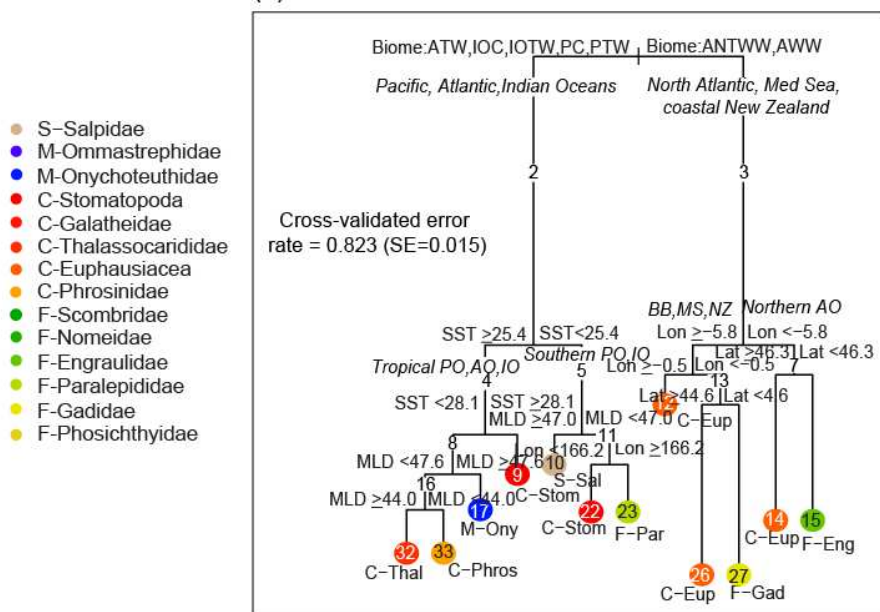
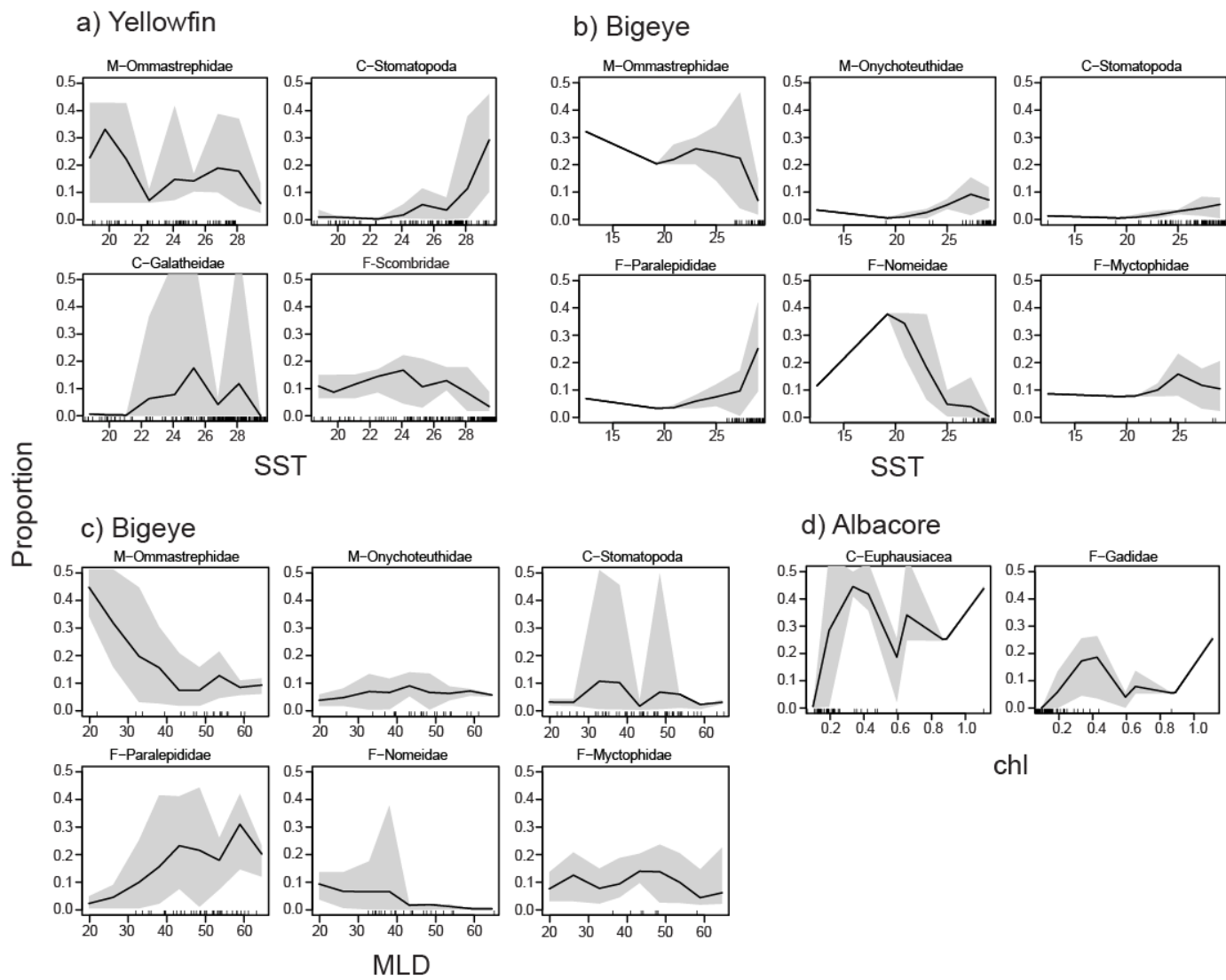


Figure 7



**Figure 8**

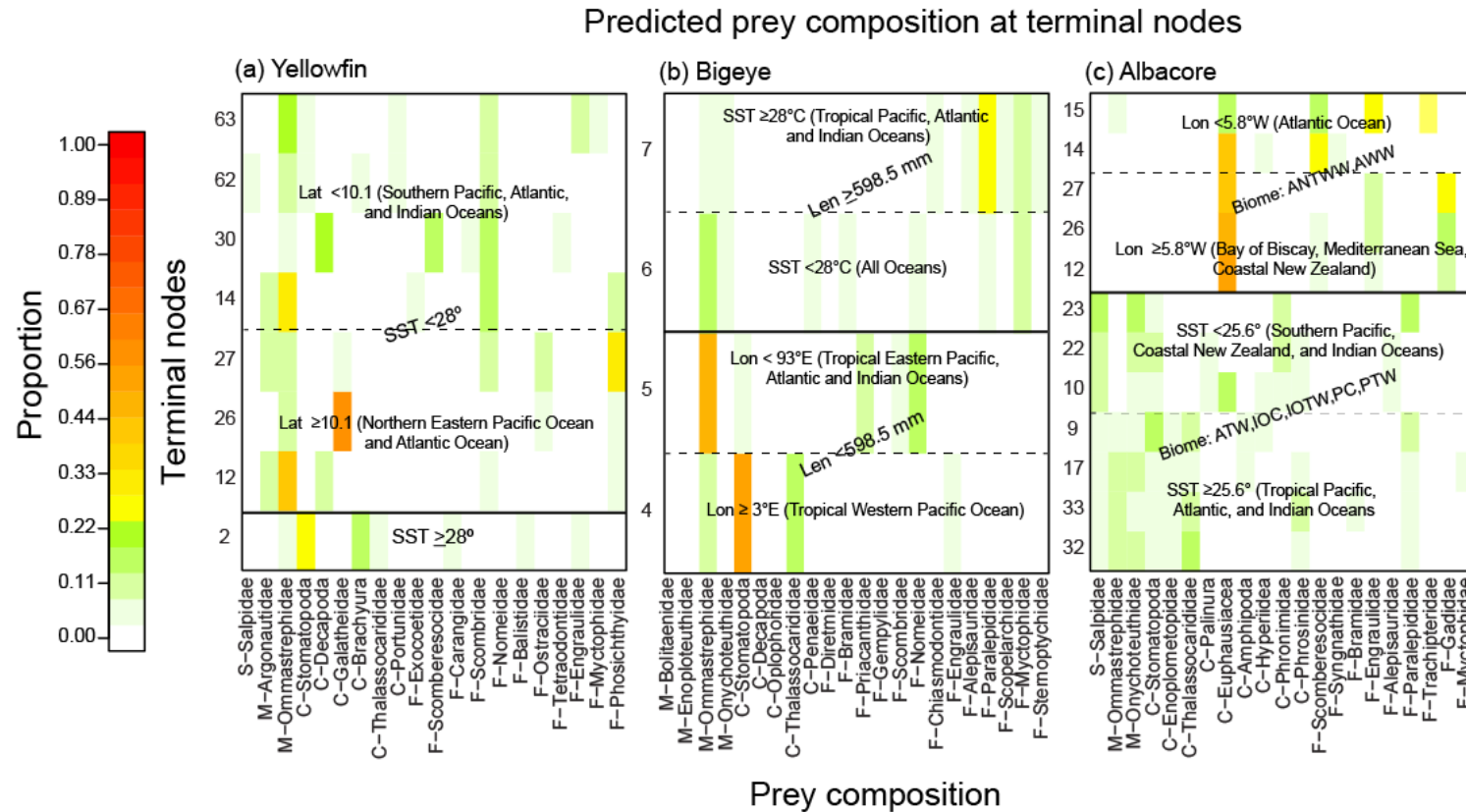


**Table S1.** Summary of splits for all internal and terminal nodes in the tree model. 'Parent node' = node number, using the criteria of Breiman et al. (1984), split into left and right child nodes; 'YFT' = number of yellowfin tuna (*Thunnus albacares*) whose diet data are partitioned at each node; 'Diversity' = diversity index ranging from 0 to 1; 'Split' = the covariate and its value splitting to the left side of each parent node, where longitude and latitude measured in degrees, biome assigned from Longhurst provinces (Longhurst 1998), length measured in mm, and <leaf> = terminal node; 'Pclass' = the predicted prey class comprising the greatest mean proportion weight among all prey in the diet composition of yellowfin at each node (prey abbreviations defined in Table 4; M=molluscs, C=crustaceans, F=fishes, respectively), 'Left child' = node number resulting from parent node split to the left, 'Right child' = node number resulting from parent node split to the right.

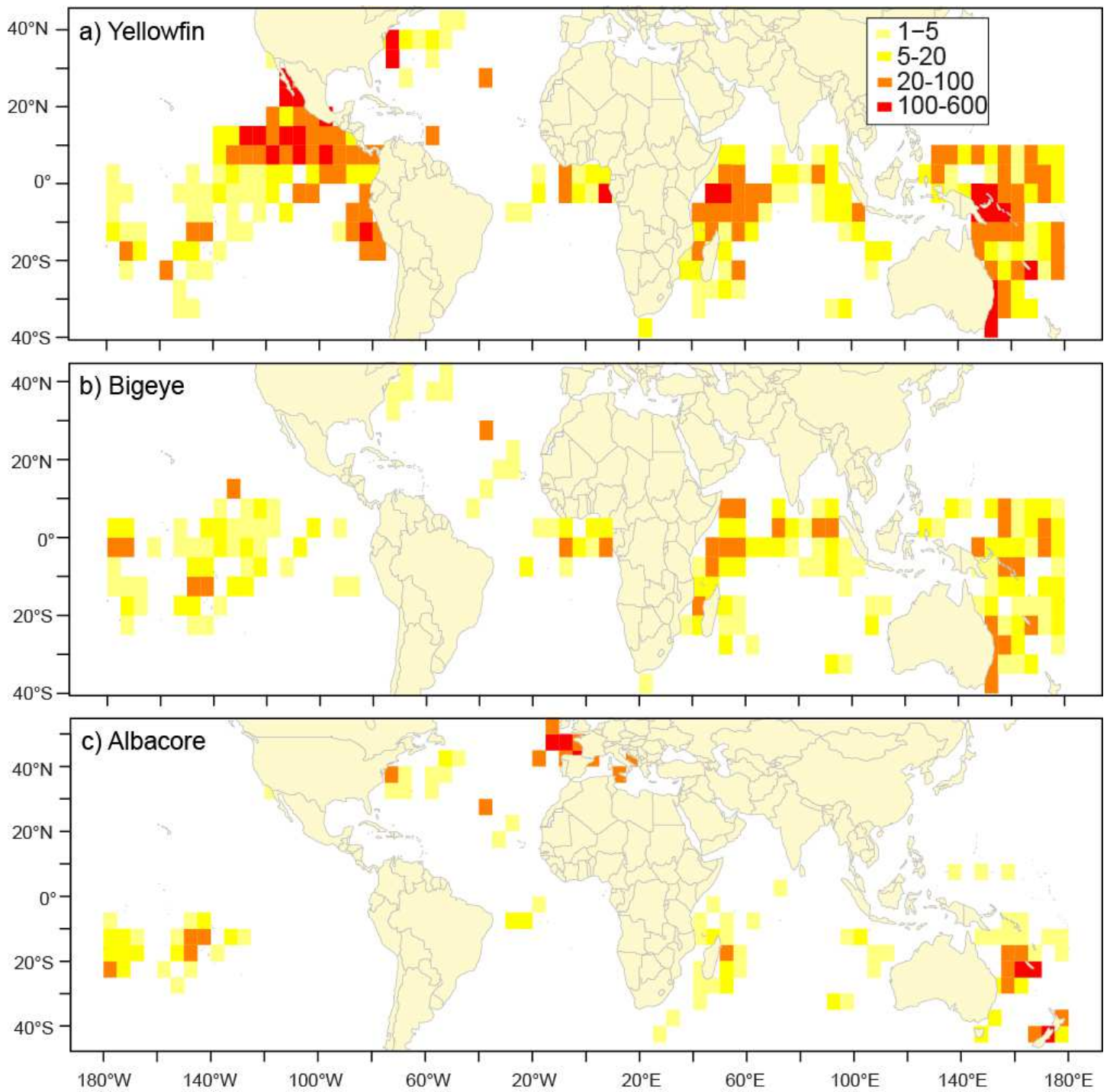
Parent node	YFT	Diversity	Split (to left)	Pclass	Left child	Right child
1	7295	0.83	Longitude $\geq 121.3^{\circ}\text{E}$	M-Omm	2	3
2	2198	0.75	Length < 925 mm	C-Stom	4	5
3	5097	0.79	Longitude $\geq -85.0^{\circ}\text{W}$	M-Omm	6	7
4	1384	0.63	<leaf>	C-Stom	--	--
5	814	0.83	Latitude < $-22.6^{\circ}\text{S}$	F-Scom	10	11
6	1712	0.68	Biome splits as AC, AWW, IOC, PC, PTW	M-Omm	12	13
7	3385	0.80	Latitude $\geq 17.3^{\circ}\text{N}$	F-Scom	14	15
10	472	0.73	Longitude < $154.0^{\circ}\text{E}$	C-Dec	20	21
11	342	0.81	Latitude $\geq -10.79^{\circ}\text{S}$	M-Omm	22	23
12	829	0.55	Latitude < $-5.4^{\circ}\text{S}$	M-Omm	24	25
13	883	0.81	Length < 1185 mm	M-Omm	26	27
14	1107	0.74	Longitude < $-106.7^{\circ}\text{W}$	C-Gal	28	29
15	2278	0.73	Length < 983 mm	F-Scom	30	31
20	283	0.65	<leaf>	C-Dec	--	--
21	189	0.72	<leaf>	F-Car	--	--
22	127	0.74	<leaf>	M-Omm	--	--
23	215	0.77	<leaf>	F-Scom	--	--
24	335	0.33	<leaf>	M-Omm	--	--
25	494	0.70	Latitude $\geq 7.2^{\circ}\text{N}$	M-Omm	50	51
26	330	0.76	<leaf>	M-Omm	--	--
27	553	0.71	Longitude < $57.5^{\circ}\text{E}$	C-Por	54	55
28	791	0.65	Latitude < $23.4^{\circ}\text{N}$	C-Gal	56	57
29	316	0.59	<leaf>	F-Car	--	--
30	1273	0.81	Longitude $\geq -103.8^{\circ}\text{W}$	M-Omm	60	61
31	1005	0.60	Longitude $\geq -101.4^{\circ}\text{W}$	F-Scom	62	63
50	340	0.61	<leaf>	M-Omm	--	--
51	154	0.64	<leaf>	F-Phos	--	--
54	363	0.60	<leaf>	C-Por	--	--
55	190	0.60	<leaf>	F-Nom	--	--
56	291	0.37	<leaf>	C-Gal	--	--
57	500	0.69	Length $\geq 667.5$ mm	M-Omm	114	115
60	495	0.74	Latitude $\geq 8.7^{\circ}\text{N}$	M-Omm	120	121
61	778	0.86	Longitude < $-115.1^{\circ}\text{W}$	F-Scom	122	123
62	318	0.41	<leaf>	F-Scom	--	--
63	687	0.69	Latitude < $11.8^{\circ}\text{N}$	F-Scom	126	127



Parent node	YFT	Diversity	Split (to left)	Pclass	Left child	Right child
114	348	0.61	<leaf>	M-Omm	--	--
115	152	0.36	<leaf>	F-Eng	--	--
120	308	0.68	<leaf>	M-Omm	--	--
121	187	0.72	<leaf>	F-Scom	--	--
122	425	0.79	Longitude < -125.8°W	M-Omm	244	245
123	353	0.72	Latitude $\geq 9.7^\circ\text{N}$	C-Gal	246	247
126	557	0.64	<leaf>	F-Scom	--	--
127	130	0.59	<leaf>	F-Ost	--	--
244	154	0.71	<leaf>	F-Scom	--	--
245	271	0.78	<leaf>	M-Omm	--	--
246	215	0.54	<leaf>	C-Gal	--	--
247	138	0.38	<leaf>	F-Ost	--	--



**Figure S1** Prey proportions by weight for (a) yellowfin (*Thunnus albacares*), (b) bigeye (*T. obesus*), and (c) albacore (*T. alalunga*) tuna predicted at the terminal nodes of the 1 SE classification trees for the subset of diet data from 2003-2011. Terminal node labels, ordered bottom to top, correspond to the terminal node labels on the trees in Fig. 7, ordered left to right. The bold black line represents the first split of the trees, while dotted lines represent the second split on each side of the trees in Fig. 7. S-, M-, C-, and F-: Salps, molluscs, crustaceans, and fishes, respectively. See Table 2 for description of Biomes.



**Figure S2** Number of tunas sampled from 1969-2013 in 5° x 5° areas for (a) yellowfin (*Thunnus albacares*), (b) bigeye (*T. obesus*), and (c) albacore (*T. alalunga*) tunas.