

Decadal diet shift in yellowfin tuna *Thunnus albacares* suggests broad-scale food web changes in the eastern tropical Pacific Ocean

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ABSTRACT: Widespread climate-induced habitat compression and reductions in biological production are beginning to alter food webs in tropical and subtropical oceans, but the effects on mid-trophic level micronekton communities that support commercially important pelagic fishes are unclear. The predation habits of yellowfin tuna *Thunnus albacares*, a wide-ranging generalist predator with high energy requirements, provide rare insights into the distribution and availability of prey communities in pelagic regions. We used a modified classification tree approach to analyze spatial, temporal, environmental, and biological covariates explaining the predation patterns of 3362 yellowfin sampled across the eastern tropical Pacific Ocean (ETP) during two 2 yr periods occurring a decade apart. Persistent zoogeographical assemblages of prey were important only in relatively small subtropical regions at the extreme northern and southern ranges of the purse-seine fishery for tunas. Prey biomass patterns for the majority of the samples over most of the ETP (6° S to 17° N, coast to 150° W) were best explained by a tree partition distinguishing samples by sampling period, 1992 to 1994 and 2003 to 2005. The classification tree revealed that a major diet shift had transpired in the heart of the ETP. Yellowfin predation had changed from primarily larger epipelagic fish prey in the 1990s to a diverse array of smaller mesopelagic species and a crustacean that apparently had expanded its range in the 2000s. Partial dependence plots from the tree model showed range expansions previously described for some prey and unknown for other prey. Diet analysis of selected marine predators offers a practical means of monitoring prey communities poorly sampled by conventional methods.

KEY WORDS: Classification and regression tree · Diet shift · Eastern Pacific · Food web · Predator–prey interaction · Trophic ecology · Tuna

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INTRODUCTION

Increasing worldwide interest in ecologically based approaches to fisheries management (Pikitch et al. 2004, Marasco et al. 2007) places renewed emphasis on understanding pathways of biomass and energy

flow in exploited ecosystems. Replacing population ecology with community ecology as the fundamental ecological science underlying fisheries (Mangel & Levin 2005) dictates a thorough understanding of the dynamics of community interactions. 'Food webs remain the ecologically flexible scaffolding around

which communities are assembled and structured' (Paine 1996, p. ix). Determining linkages and measuring interaction rates in the food web are prerequisites for gaining insight into the role of predators, commercial fisheries, and the environment in influencing ecosystem structure and dynamics (Watters et al. 2003).

Marine ecologists are challenged by questions about the implications of climate- and fisheries-induced ecosystem changes. Environmental perturbations force ecosystems from the bottom up, while selective removal of large predatory fishes from marine food webs can simultaneously impart top-down changes in trophic structure and stability via trophic cascades (Carpenter et al. 1985, Pace et al. 1999, McClanahan & Arthur 2001, Worm & Myers 2003, Essington & Hansson 2004, Frank et al. 2005). Major reorganizations of food webs have occurred in concert with environmental changes in large marine ecosystems, notably in the Northeast Pacific Ocean (Anderson & Piatt 1999, Conners et al. 2002) during shifts in the Pacific Decadal Oscillation (PDO) (Hare & Mantua 2000). The mechanisms linking climate forcing to changes in food webs are not clear (Johnson & Schindler 2012), and thus comparative and observational approaches using historical data are required (Francis & Hare 1994).

Changes through time in the structure of pelagic, open-ocean food webs are difficult to assess. Fisheries-independent trawl surveys are expensive and pelagic trawls are often biased against larger, active micronekton (Young et al. 2001, Bertrand et al. 2002, Ménard et al. 2006). The foraging patterns of tropical tunas, however, can provide useful information on mid-trophic level communities in pelagic habitats (Lansdell & Young 2007). The yellowfin tuna *Thunnus albacares* is considered an opportunistic predator (Sund et al. 1981, Ménard et al. 2006, Potier et al. 2007, Young et al. 2010), owing to a generalized feeding strategy and high energy requirements in oligotrophic habitats. It is abundant, wide ranging, and an important component of the pelagic ecosystem in the eastern tropical Pacific Ocean (ETP) (Olson & Watters 2003), as it is in all the major oceans. Annual catches of yellowfin in the eastern Pacific averaged in excess of 290 000 metric tons, 91 % by purse seine, during the years of this study (IATTC 2012).

Classification and regression tree (CART) analysis, a non-parametric approach developed by Breiman et al. (1984), has provided insight into the interpretation of a variety of complex ecological data (e.g. Olden & Jackson 2002, Zuur et al. 2007, Massey et al. 2008, Davidson et al. 2009), including foraging ecology (Iverson et al. 1997, Smith et al. 1997, Olson & Galván

Magaña 2002, Griffiths et al. 2009, Rabehagaso et al. 2012, Ménard et al. 2013). Unlike traditional approaches for analyzing diet data, classification trees provide a modeling framework for predicting the prey composition of each predator and can highlight important relationships between explanatory variables and the response (Breiman et al. 1984, Clarke & Pregibon 1992).

Our approach was to examine broad-scale spatial, temporal, environmental, and biological relationships with predator–prey data for yellowfin tuna in the ETP using a modified classification tree approach developed for diet data by Kuhnert et al. (2012). Our objectives were to (1) elucidate the dominant predator–prey patterns characterizing the trophic ecology of the yellowfin population in the ETP, and (2) examine the degree and scale of diet variability on a decadal time frame. This analysis is an essential component for developing improved food web models (e.g. Cox et al. 2002, Olson & Watters 2003) for examining hypotheses of ecosystem effects of fishing over a backdrop of climate variation (Watters et al. 2003).

MATERIALS AND METHODS

Stomach sampling and analysis

Yellowfin were captured in 433 purse-seine sets on dolphins, floating objects, and unassociated schools in the ETP during two 2-year periods separated by a decade. In 'dolphin sets' the net is deployed around a tuna–dolphin aggregation (Scott et al. 2012) after a chase by speedboats, 'floating-object sets' are made by encircling flotsam (commonly fish-aggregating devices) and associated fauna with the purse seine, and 'unassociated sets' are made on schools of tuna that are not associated with either mammals or flotsam (Hall 1998). Dolphin sets and unassociated sets were made fairly uniformly throughout the day, while most floating-object sets were made in the early morning. The sampling locations (Fig. 1) were distributed throughout the region in which yellowfin tuna were caught by purse seine during both sampling periods (see Fig. A-1a in IATTC 2006 for catch locations). Stomachs were collected at sea by Inter-American Tropical Tuna Commission (IATTC) observers on 212 purse-seine fishing trips between June 23, 1992 and September 29, 1994, and between August 11, 2003 and November 16, 2005. Observers recorded the date, time, location, fishing method, cloud cover, Beaufort sea state, and sea surface temperature (SST) for each set sampled. They measured fork length to the nearest

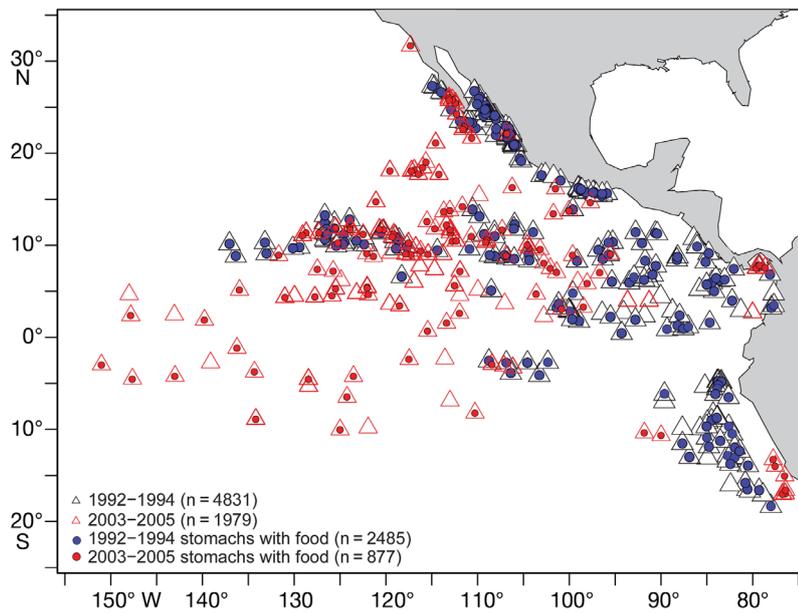


Fig. 1. Sampling locations of yellowfin tuna caught by purse-seine vessels during two 2-year periods in the eastern tropical Pacific Ocean. Sample sizes for all stomachs (open triangles) and for stomachs containing undigested prey remains (i.e. omitting samples that were empty or contained residual hard parts only; filled circles) are shown

millimeter, excised the stomach, and recorded the sex of each fish when sexual maturity was sufficiently advanced. Stomach samples were frozen and later analyzed in the laboratory. Numbers of stomach samples are presented in Table 1 for each sampling period.

Laboratory analyses consisted of thawing the stomachs, identifying the prey to the lowest possible taxon, and quantifying the prey. Prey were weighed to the nearest gram for the samples taken during the 1990s, and to the nearest hundredth of a gram for samples taken during the 2000s, and enumerated when individual prey items were recognizable. When possible, prey fork lengths were measured for the fishes, mantle lengths for the cephalopods, and carapace lengths for the crustaceans, all to the nearest millimeter. Counts of fish otoliths and cephalopod mandibles

were divided by 2 to estimate numbers of individual organisms ingested.

Diet composition

We used gravimetric, numeric, and occurrence indices to examine prey importance. For each individual yellowfin, we calculated the proportional composition by weight and by number of each prey type, and then averaged the proportions for each prey type over all yellowfin with prey remains in the stomachs (Chippis & Garvey 2007). For prey weights:

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

where \bar{W} is mean proportion by weight for prey type i , W_{ij} is the weight of prey type i in yellowfin j , P is the number of yellowfin with food in their stomachs, and Q is the number of prey types in all samples. For prey counts:

$$\bar{N}_i = \frac{1}{P} \sum_{j=1}^P \left(\frac{N_{ij}}{\sum_{i=1}^Q N_{ij}} \right) \quad (2)$$

where \bar{N} is mean proportion by number for prey type i , N_{ij} is the number of individuals of prey type i in yellowfin j , and P and Q are as defined for Eq. (1). Prey counts were not possible for some taxa that were in advanced stages of digestion. For occurrence (O_i):

$$O_i = \frac{J_i}{P} \quad (3)$$

where J_i is the number of yellowfin containing prey i and P is as defined for Eq. (1). We omitted stomachs

Table 1. Numbers of yellowfin tuna sampled onboard tuna purse-seine vessels in the eastern tropical Pacific Ocean, by fishing method and stomach condition, during 2 sampling periods. Residual hard parts are cephalopod mandibles and fish otoliths. Percentages of totals by sampling period are in parentheses

Fishing method	1992–1994				2003–2005			
	Undigested food remains	Stomachs empty	Residual hard parts only	Total	Undigested food remains	Stomachs empty	Residual hard parts only	Total
Dolphin sets	1318 (64)	485 (24)	255 (12)	2058	602 (70)	133 (15)	129 (15)	864
Unassociated tuna sets	1016 (56)	687 (38)	112 (6)	1815	153 (78)	32 (16)	11 (6)	196
Floating-object sets	151 (16)	764 (80)	43 (4)	958	122 (13)	743 (81)	54 (6)	919
All methods	2485 (51)	1936 (40)	410 (9)	4831	877 (44)	908 (46)	194 (10)	1979

that contained only residual hard parts (cephalopod mandibles and fish otoliths) from the \bar{W}_i and \bar{N}_i computations because hard parts accumulate in the stomachs from feeding on an unknown number of previous days. Relatively few prey taxa in the ETP have prominent hard parts that resist digestion (Olson & Galván-Magaña 2002), and treating hard parts the same as undigested soft tissue would over-represent the dietary importance of taxa with digestion-resistant hard parts, especially based on numeric and gravimetric indices (Olson & Galván-Magaña 2002, Chipps & Garvey 2007). We included stomachs that contained only residual hard parts in the O_i computation, however, because that index represents how frequently a particular prey item was consumed, but not the relative importance to the diet.

We analyzed the distributions of yellowfin tuna size, prey size, and prey–predator size ratios (i.e. actual predator–prey pairs) for both sampling periods to determine whether there were significant differences among distributions. We used a Kolmogorov-Smirnov test (Conover 1971) to test whether predator size, prey size, and prey–predator size ratios were stochastically larger in the 1990s compared with the 2000s. As the p-values calculated for this test were approximate due to tied values, we also constructed a Wilcoxon rank sum test (Bauer 1972) to examine whether the true location shift of predator, prey, and prey–predator sizes across the sampling periods is the same (null hypothesis) or greater than zero (alternative).

Classification tree analysis

We applied CART analysis to yellowfin predation data using the modified approach of Kuhnert et al. (2012) to explore relationships among predictor variables and diet composition. For this application, the diet data were *a priori* arranged into a predator–prey format, where each row characterized a predator–prey combination ($n = 3851$ individual observations), with wet weight prey proportions used as corresponding case weights. Through this simple restructure of the predator–prey data, the CART model is akin to a multinomial model (McCullagh & Nelder 1983), but with more appealing features. The model is easily interpreted and can accommodate missing data for the covariates, variable importance rankings can be computed to identify important covariates, and predictions, as well as classifications, can be formed. CART analysis has been described elsewhere (Breiman et al. 1984), while here we briefly touch on the

method for analyzing diet data (see Kuhnert et al. 2012 for details). CART analysis is a non-parametric approach that recursively partitions data by forming successive splits on covariates at split points deemed important by some criterion (the gini index of diversity for classification problems). Once a large tree has been grown, a pruning method utilizes cross validation to snip off sections of the tree until a smaller, more parsimonious tree with better accuracy in terms of the error rate is identified. Predictions⁴ are made by running observations down the branches of the tree until they reside in a terminal node. Various extensions to the recursive approach have been used to analyze diet data. Kuhnert & Mengersen (2003) developed bootstrap techniques (akin to bagging, Breiman 1996) for examining the uncertainty in terminal nodes of a regression tree, and more recently Kuhnert et al. (2012) extended these methods to accommodate compositional data for predicting the diet composition of each predator and the associated uncertainty at each terminal node of the tree.

We used only the 18 most important prey groups in the classification tree analysis, based on their contribution in \bar{W}_i to the overall diet. These were 3 groups of cephalopods, Argonautidae, *Dosidicus gigas*, and *Sthenoteuthis oualaniensis*; 3 groups of crustaceans, *Pleuroncodes planipes*, Portunidae, and other crustaceans; and 12 groups of fishes (Osteichthyes), *Engraulis ringens*, *Engraulis mordax*, *Vinciguerria luce-tia*, Myctophidae, *Exocoetus* spp., other Exocoetidae, *Oxyporhamphus micropterus*, Carangidae, *Auxis* spp., *Scomber japonicus*, *Cubiceps* spp., and *Lactoria diaphana* (see Table 2 for the phylogenetic affiliations of the prey groups). These principal prey groups ranged in taxonomic level from species (e.g. *Dosidicus gigas*) to subphyla (e.g. other crustaceans) because the taxonomic resolution of prey identifications varied by digestion state and because some rare prey were combined into broader taxa. *Exocoetus* spp., other exocoetids, and *Oxyporhamphus micropterus* were not grouped as ‘flyingfishes’ because they occupy different habitats in the ETP (Pitman et al. 2002). Prey taxa were omitted from the tree analysis if they did not contribute at least 1% wet weight to the overall diet per sampling period. Unidentified prey that could have possibly been a member of another group used in the tree analysis (e.g. unidentified fishes, ‘Osteichthyes’, Table 2) were omitted.

⁴For example, prediction of the diet composition of the ETP yellowfin population for fish of a particular size, at a specific location, during a particular quarter of a particular year, etc., considering all covariates in the model

To explore potential spatial, temporal, environmental, and biological influences on the diet of yellowfin tuna, latitude, longitude, year, quarter-of-year, Pacific Decadal Oscillation (PDO) index (Mantua et al. 1997), and yellowfin size (fork length, mm) were used as covariates in the final classification tree model. Preliminary models included additional covariates, i.e. set type, set time-of-day, and SST, and results were similar to those of the final model, i.e. the most important tree splits were identical. We did not include these 3 potentially important covariates in the final model because they were correlated with one another and with other covariates, and were therefore redundant and captured by other terms in the model. SSTs are correlated with latitude in the ETP, and SST was repeatedly a competing and/or surrogate explanatory variable for splits on latitude in the model summary output. Purse-seine fishing method (set type: dolphin, floating-object, and unassociated), set time-of-day, and yellowfin size were correlated with one another. For instance, floating-object sets were frequently made in the early morning, before 09:00 h, while dolphin and unassociated sets took place throughout the day. Large yellowfin were typically caught in dolphin sets, medium in unassociated sets, and small in floating-object sets (Hall 1998). In addition, purse-seine sets were largely segregated spatially, and spatial segregation varied by sampling period. Yellowfin were caught in dolphin sets made mostly north of the equator, unassociated sets were made closer to the continental coastline, and floating-object sets were often offshore, both north and (primarily) south of the equator (see Fig. A-1a in IATTC 2006). Floating-object sets were more common in the 2000s than the 1990s sampling period. Variable importance rankings indicated that set time-of-day and set type were not influential in predicting diet composition nor were they masked by the spatial variables.

Model diagnostics

We conducted separate analyses to address whether changes in predation patterns could have been due to spatial differences in sample distributions. We investigated whether there was any spatial structure not accounted for by the model by using a spatial version of the bootstrap procedure, as outlined by Kuhnert et al. (2012). We also fitted a separate classification tree model to the data for a subregion in which purse-seine sets made during both sampling periods overlapped in space (15° N to 5° S and 95° W to 135° W).

We investigated the potential for bias due to pseudo-replication (i.e. multiple yellowfin tuna sampled from the same purse-seine set) using the following subsampling approach. We took stratified random subsamples ranging in size ($n_s = 5, 10, 15, 20,$ and 25) for each purse-seine set and within each sampling period. For each subsample, we fitted a classification tree and produced bagged predictions for each predator. We then compared each set of predictions with the observed diet proportions using a Hellinger distance, d_H (Rao 1995), a standard statistical measure of similarity suitable for comparing proportions. The distance metric is defined as:

$$d_H(\mathbf{y}, \hat{\mathbf{y}}) = \left[\frac{1}{2} \sum_{j=1}^J (\sqrt{y_j} - \sqrt{\hat{y}_j})^2 \right]^{\frac{1}{2}} \quad (4)$$

where \mathbf{y} and $\hat{\mathbf{y}}$ represent the observed and predicted vectors of prey proportions, respectively, and J represents the length of each vector comprising the prey proportions. Hellinger distances were computed for the observed and predicted prey proportions for comparison.

RESULTS

Of 6810 yellowfin tuna sampled, 3362 had stomachs that contained quantifiable, partially digested (i.e. recently consumed) prey, and 3448 were either empty or contained only residual hard parts (cephalopod mandibles and fish otoliths), which were presumed to have been consumed on previous days (Table 1). More samples were taken during 1992 to 1994 than during 2003 to 2005, and a greater percentage of the yellowfin sampled were caught in association with floating objects in the later period. For both sampling periods, greater percentages of yellowfin containing partially digested prey were caught in dolphin and unassociated sets than in floating-object sets. Most (85%) of the yellowfin tuna caught in association with floating objects had empty stomachs or contained only residual hard parts (Table 1).

Diet composition

Detailed prey composition data, summarized at several levels of taxonomic resolution, for the 3 diet indices (Eqs. 1 to 3) as percentages are presented by sampling period in Table 2. Given that the spatial range of the yellowfin samples was broad and habitats were varied (Fig. 1), the overall diet was diverse. Fifty families occurred in the stomach contents:

Table 2. Prey taxonomic composition of yellowfin tuna in the eastern tropical Pacific Ocean during 2 sampling periods, in percentages of mean proportion by weight (\bar{W}_i), mean proportion by number for prey type (\bar{N}_i), and occurrence (O_i) (Eqs. 1 to 3). Taxa composing the prey groups in the classification tree analysis (CART) were Arg: Argonautidae, Aux: *Auxis* spp., Car: Carangidae, Cub: *Cubiceps* spp., DG: *Dosidicus gigas*, EM: *Engraulis mordax*, ER: *Engraulis ringens*, Exo: *Exocoetus* spp., LD: *Lactoria diaphana*, Msc: *Myctophidae*, O: Crust: other crustaceans, O: Exo: other exocoetids, OM: *Oxyporhamphus micropterus*, Port: Portunidae, PP: *Pleuroncodes planipes*, S: *Scomber japonicus*, SO: *Sthenoteuthis oualiansis*, and Vluc: *Vinciguerria luctetia*. Trace: trace quantities, i.e. percentages less than 0.01 %

Taxon	Prey group for CART	Sampling period						Taxon	Prey group for CART	Sampling period					
		1992-1994 % \bar{W}_i	2003-2005 % \bar{W}_i	1992-2003 % \bar{N}_i	2003-2005 % \bar{N}_i	1992-2003 % O_i	2003-2005 % O_i			1992-2003 % \bar{W}_i	2003-2005 % \bar{W}_i	1992-2003 % \bar{N}_i	2003-2005 % \bar{N}_i	1992-2003 % O_i	2003-2005 % O_i
MOLLUSCA		14.23	17.68	13.27	14.64	49.40	67.79	Mastigoteuthidae		Trace	0.03	7.70	7.19		
BIVALVIA		0.05	0.05	Trace	Trace	Trace	0.28	<i>Mastigoteuthis dentata</i>		Trace	0.03	7.70	7.00		
GASTROPODA		0.18	0.10	0.28	0.32	0.52	0.47	<i>Mastigoteuthis</i> spp.		Trace	0.03	7.70	0.19		
CEPHALOPODA		14.05	17.52	12.99	14.32	49.15	67.79	Loligimidae		0.04	0.55	0.57	0.48		
Vampyromorpha						0.03	0.03	<i>Doryteuthis opalescens</i>		0.04	0.04	0.03	0.38		
Vampyroteuthidae						0.03	0.03	<i>Lolliguncula diomedea</i>		0.23	0.23	0.23	0.56		
<i>Vampyroteuthis infernalis</i>						0.03	0.03	ARTHROPODA		14.64	28.95	15.31	30.44		
Octopoda						22.38	39.12	CRUSTACEA (subphy)	O:Crus	0.40	2.12	0.55	1.97		
Octopodidae		0.35	2.37	0.39	3.10	2.00	2.15	MALACOSTRACA		14.24	26.83	14.76	28.47		
<i>Octopus rubescens</i>		0.14	0.05	0.11	0.16	2.00	1.77	Decapoda	O:Crus	12.41	25.74	12.72	27.40		
<i>Octopus</i> spp.		Trace	Trace	0.11	0.01	2.00	0.19	Galatheidae		6.96	24.90	8.09	26.36		
Argonautidae		0.21	2.31	0.27	2.91	18.48	35.67	<i>Pleuroncodes planipes</i>	PP	6.96	24.90	8.09	26.36		
<i>Argonauta cornutus</i>	Arg	0.92	0.92	1.40	1.40	16.25	16.25	Pennaeidae	O:Crus	0.10	0.23	0.09	0.12		
<i>Argonauta nouryi</i>	Arg	0.05	0.05	0.04	0.04	1.04	1.04	Hippidae		0.09	0.10	0.10	0.14		
<i>Argonauta</i> spp.	Arg	0.16	1.39	0.22	1.52	17.44	19.61	<i>Hippa</i> spp.	O:Crus	0.09	0.10	0.10	0.14		
Bolitaenidae		Trace	Trace	0.01	0.03	6.22	8.87	Portunidae	Port	5.26	0.61	4.44	0.92		
<i>Japetella diaphana</i>		Trace	Trace	0.01	0.03	6.22	8.87	<i>Portunus xantusii</i>	Port	4.16	3.63	4.87	4.87		
Tremoctopodidae						0.59	0.59	<i>Euphyllax robustus</i>	Port	1.10	0.81	1.45	1.45		
<i>Tremoctopus violaceus</i>						0.59	0.59	<i>Callinectes</i> spp.	Port	0.13	0.42	0.42	0.65		
Alloposidae						0.21	0.21	Euphausiacea		0.11	0.11	0.11	0.09		
<i>Alloposus mollis</i>						0.17	0.17	Euphausiidae	O:Crus	0.11	0.11	0.11	0.09		
Vitreledonellidae						0.14	0.09	Amphipoda	O:Crus	0.23	0.23	0.23	0.19		
<i>Vitreledonella richardi</i>						0.14	0.09	Caprellidae	O:Crus	0.11	0.11	0.11	0.09		
Teuthida						44.42	58.73	Isopoda		0.37	0.54	1.45	1.45		
Octopoteuthidae		13.71	15.16	12.61	11.22	0.97	0.09	Cymothoidae	O:Crus	0.37	0.54	1.45	1.45		
<i>Octopoteuthis deletron</i>						0.97	0.09	Mystida	O:Crus	1.46	1.50	1.76	1.76		
<i>Octopoteuthis</i> spp.						0.09	0.09	Stomatopoda	O:Crus	0.63	0.63	0.61	0.75		
Thysanoteuthidae		0.09	0.17	0.10	0.19	2.69	4.76	Squillidae		0.46	0.46	0.46	0.37		
<i>Thysanoteuthis rhombus</i>		0.09	0.17	0.10	0.19	2.66	4.76	<i>Squilla</i> spp.	O:Crus	0.46	0.46	0.46	0.37		
Ancistrocheiridae						0.65	0.65	Hemisquillidae	O:Crus	0.11	0.11	0.11	0.09		
<i>Ancistrocheirus lesueurii</i>						0.65	0.65	CHORDATA	O:Crus	71.13	52.90	68.24	40.33		
Ommastrephidae		12.60	8.13	11.76	6.66	39.90	45.94	CHONDRICHTHYES		0.01	Trace	Trace	0.03		
<i>Dosidicus gigas</i>	DG	9.38	8.02	8.88	6.50	34.72	44.72	Carcharhiniformes		0.01	Trace	Trace	0.03		
<i>Sthenoteuthis oualiansis</i>	SO	3.22	0.11	2.88	0.15	5.84	2.71	Sphyrnidae		0.01	Trace	Trace	0.03		
Onychoteuthidae						1.69	1.21	<i>Sphyrna</i> spp.		0.01	Trace	Trace	0.03		
<i>Onychoteuthis banksii</i>						1.59	1.12	OSTEICHTHYES		71.12	52.90	68.24	40.33		
<i>Onychoteuthis</i> spp.						0.10	0.09	Clupeiformes		5.42	3.52	5.35	2.71		
Pholidoteuthidae						0.59	0.47	Engraulidae		5.42	3.44	5.35	2.64		
<i>Pholidoteuthis boschmani</i>						0.59	0.47	<i>Engraulis ringens</i>	ER	5.42	3.37	2.55	3.17		
Enoploteuthidae		0.03	0.07	0.07	0.07	3.32	0.19	<i>Engraulis mordax</i>	EM	5.42	0.07	0.09	0.09		
<i>Abrialopsis falco</i>		0.01	0.02	0.02	0.02	3.14	0.17	Anchoa spp.		Trace	Trace	Trace	0.03		
<i>Abrialopsis</i> spp.		0.03	0.04	0.04	0.04	0.17	0.19	Clupeidae		Trace	Trace	Trace	0.03		

Table 2. (continued)

Taxon	Prey group for CART	Sampling period						Taxon	Prey group for CART	Sampling period									
		1992-1994	2003-2005	1992-1994	2003-2005	1992-1994	2003-2005			1992-1994	2003-2005	1992-1994	2003-2005	1992-1994	2003-2005				
		% \bar{W}_i	% \bar{W}_i	% \bar{N}_i	% \bar{N}_i	% O_i			% \bar{W}_i	% \bar{W}_i	% \bar{N}_i	% \bar{N}_i	% O_i		% \bar{W}_i	% \bar{W}_i	% \bar{N}_i	% \bar{N}_i	% O_i
<i>Harengula thrissina</i>		0.08	0.07	0.19			<i>Coryphaena equiselis</i>		0.43	0.31	0.10	0.27	0.48	0.28	0.43	0.31	0.10	0.27	0.48
Osmertiformes							Carangidae	Car	7.00	0.43	6.66	0.40	7.70	0.47	7.00	0.43	6.66	0.40	7.70
Bathylagidae							<i>Alectis ciliaris</i>	Car	0.10				0.14		0.10				0.14
<i>Bathylagus</i> spp.							<i>Caranx caballus</i>	Car	0.02	Trace	Trace		0.03		0.02	Trace	Trace		0.03
Stomiiformes							<i>Chloroscombrus orqueta</i>	Car	Trace	Trace	0.01	0.07	0.07		Trace	0.01	0.01	0.07	0.07
Phosichthyidae	Vluc	7.54	11.91	7.74	10.23	7.36	<i>Decapterus</i> spp.	Car	1.25	1.25	1.25	1.73	1.73		1.25	1.25	1.25	1.73	1.73
<i>Vinciguerria lucetia</i>	Vluc	7.22	11.91	7.36	10.23	6.98	<i>Decapterus macrossoma</i>	Car	1.19	1.08	1.08	1.14	1.14		1.19	1.08	1.08	1.14	1.14
Mycetophiformes							<i>Naucrates ductor</i>	Car	0.55	0.47	0.47	0.59	0.59		0.55	0.47	0.47	0.59	0.59
Mycetophidae	Myc	0.47	1.00	0.51	1.02	3.59	<i>Seriola</i> spp.	Car	0.08	0.08	0.06	0.09	0.09		0.08	0.08	0.06	0.09	0.09
<i>Diaphus</i> spp.		0.47	1.00	0.51	1.02	3.59	<i>Seriola lalandi</i>	Car	0.11	0.11	0.11	0.09	0.09		0.11	0.11	0.11	0.09	0.09
<i>Diogenichthys laternatus</i>						0.21	<i>Trachurus symmetricus</i>	Car	2.28	2.28	2.24	2.18	2.18		2.28	2.28	2.24	2.18	2.18
<i>Hygophum</i> spp.						0.14	Bramidae		0.15	0.15	0.17	0.19	0.19		0.15	0.15	0.17	0.19	0.19
<i>Lampadena luminosa</i>						0.21	<i>Brama</i> spp.		0.15	0.15	0.14	0.17	0.17		0.15	0.15	0.14	0.17	0.17
<i>Lampanyctus</i> spp.						0.07	Chaetodontidae		0.02	0.02	0.03	0.07	0.07		0.02	0.02	0.03	0.07	0.07
<i>Lampanyctus parvicauda</i>						0.55	Kyphosidae		Trace	Trace	0.02	0.03	0.03		Trace	0.02	0.02	0.03	0.03
<i>Myctophum aurolatermatum</i>						0.79	<i>Sectator ocyurus</i>		0.01	0.19	0.01	0.17	0.03		0.01	0.19	0.01	0.17	0.03
<i>Myctophum nitidulum</i>						0.17	<i>Gempylus</i> spp.		0.01	0.11	0.01	0.11	0.03		0.01	0.11	0.01	0.11	0.03
<i>Myctophum nitidulum</i>						0.03	<i>Gempylus serpens</i>		0.01	0.11	0.01	0.11	0.03		0.01	0.11	0.01	0.11	0.03
<i>Symbolophorus</i> spp.	Myc	Trace	Trace	0.04	1.02	0.93	Scombridae		24.17	10.22	22.14	8.58	24.15	9.15	24.17	10.22	22.14	8.58	24.15
<i>Benthosema panamense</i>	Myc	0.08	1.00	0.04	1.02	2.52	<i>Auxis thazard</i>	Aux	1.04	1.04	1.04	0.68	0.93		1.04	1.04	1.04	0.68	0.93
Gadiformes						0.52	<i>Auxis</i> spp.	Aux	20.99	7.92	19.15	7.18	20.79	7.19	20.99	7.92	19.15	7.18	20.79
Bregmaceroiidae						0.48	<i>Euthynnus lineatus</i>		0.44	0.44	0.32	0.55	0.55		0.44	0.44	0.32	0.55	0.55
<i>Bregmaceros bathymaster</i>						0.48	<i>Katsuwonus pelamis</i>		0.83	0.27	0.82	0.23	1.00	0.28	0.83	0.27	0.82	0.23	1.00
Merlucciidae						0.03	<i>Scomber japonicus</i>	SJ	1.60	0.63	1.48	0.15	1.62	0.56	1.60	0.63	1.48	0.15	1.62
<i>Merluccius productus</i>						0.03	<i>Thunnus albacares</i>		0.13	0.01	0.20	Trace	0.09		0.13	0.01	0.20	Trace	0.09
Belontiiformes						10.43	<i>Thunnus</i> spp.		0.15	0.11	0.14	0.11	0.24	0.09	0.15	0.11	0.14	0.11	0.24
Exocoetidae	O.Exo	3.77	3.38	3.80	2.25	6.56	Nomeidae		8.58	2.03	8.92	1.98	12.09	2.61	8.58	2.03	8.92	1.98	12.09
<i>Cheilopogon dorsomacula</i>	O.Exo	0.01	0.01	0.01	0.03	0.03	<i>Cubiceps pauciradiatus</i>	Cub	8.27	0.23	8.62	0.23	11.85	1.12	8.27	0.23	8.62	0.23	11.85
<i>Cheilopogon furcatus</i>	O.Exo	0.09	0.10	0.10	0.10	0.10	<i>Cubiceps baxteri</i>	Cub	0.07	0.07	0.08	0.21	0.21		0.07	0.07	0.08	0.21	0.21
<i>Cheilopogon pinnatibarbus</i>	O.Exo	0.04	0.04	0.04	0.03	0.03	<i>Cubiceps</i> spp.	Cub	0.24	1.80	0.22	1.75	0.24	1.49	0.24	1.80	0.22	1.75	0.24
<i>Cheilopogon</i> spp.	O.Exo	0.63	0.11	0.57	0.23	0.90	Tetraodontiformes		8.50	6.33	7.79	5.84	9.19	7.84	8.50	6.33	7.79	5.84	9.19
<i>Cypselurus callopterus</i>	O.Exo	0.01	0.04	0.04	0.04	0.09	Balistidae		0.43	0.31	0.44	0.38	1.14	1.31	0.43	0.31	0.44	0.38	1.14
<i>Exocoetus monocirrus</i>	Exo	0.60	0.04	0.63	0.04	0.97	<i>Balistes polylepsis</i>		0.02	0.24	0.03	0.25	0.10	1.03	0.02	0.24	0.03	0.25	0.10
<i>Exocoetus volitans</i>	Exo	1.49	1.96	1.49	1.13	2.66	<i>Balistes</i> spp.		0.07	0.07	0.07	0.12	0.28		0.07	0.07	0.07	0.12	0.28
<i>Exocoetus volitans</i>	Exo	0.74	0.38	0.76	0.20	1.69	<i>Xanthichthys mento</i>		0.01	0.01	Trace	Trace	0.03		0.01	0.01	Trace	Trace	0.03
<i>Exocoetus</i> spp.	O.Exo	0.02	0.02	0.02	0.03	0.03	Monacanthidae		Trace	Trace	0.01	0.07	0.07		Trace	0.01	0.01	0.07	0.07
<i>Hirundichthys marginatus</i>	O.Exo	0.04	0.04	0.04	0.04	0.03	<i>Aluterus</i> spp.		Trace	Trace	0.01	0.07	0.07		Trace	0.01	0.01	0.07	0.07
<i>Hirundichthys speculiger</i>	O.Exo	0.04	0.04	0.04	0.04	0.03	Ostraciidae		7.91	5.31	7.17	4.77	8.19	5.79	7.91	5.31	7.17	4.77	8.19
<i>Hirundichthys</i> spp.	O.Exo	0.08	0.08	0.08	0.14	0.09	<i>Lactoria diaphana</i>	LD	7.91	5.31	7.17	4.77	8.19	5.79	7.91	5.31	7.17	4.77	8.19
Hemiramphidae		3.61	1.85	3.75	1.89	4.87	Tetraodontidae		0.16	0.71	0.16	0.69	0.31	1.31	0.16	0.71	0.16	0.69	0.31
<i>Oxyporhamphus micropterus</i>	OM	3.61	1.85	3.75	1.89	4.87	<i>Lagocephalus lagocephalus</i>		0.16	0.71	0.16	0.69	0.31	1.31	0.16	0.71	0.16	0.69	0.31
Gasterosteiformes						0.17	Diodontidae		Trace	Trace	0.01	0.01	0.09	0.09	Trace	Trace	0.01	0.01	0.09
Syngnathidae						0.17	<i>Diodon holacanthus</i>		Trace	Trace	0.01	0.01	0.09	0.09	Trace	Trace	0.01	0.01	0.09
<i>Hippocampus ingens</i>						0.10	Unidentified invertebrates		Trace	Trace	0.01	0.01	0.09	0.09	Trace	Trace	0.01	0.01	0.09
Perciformes						42.18	Unidentified organic matter		0.34	0.34	Trace	Trace	0.28		0.34	0.34	Trace	Trace	0.28
Echeneidae						0.03	Inorganic matter		0.12	0.12	0.09	0.09	0.19		0.12	0.12	0.09	0.09	0.19
<i>Coryphaena hippurus</i>						0.03			0.12	0.12	0.09	0.09	0.19		0.12	0.12	0.09	0.09	0.19

16 cephalopod families, 9 crustacean families, and 25 fish families. Only the fishes in aggregate were >50% in \bar{W}_i (Eq. 1) for either sampling period, whereas most individual taxa were somewhat rare overall (Table 2). The ommastrephid squids *Dosidicus gigas* (Humboldt squid) and *Sthenoteuthis oualaniensis* (purpleback flying squid), galatheid crustacean *Pleuroncodes planipes* (red crabs), phosichthyid fish *Vinciguerria lucetia* (lightfishes), and scombrid fishes (primarily bullet and frigate tunas *Auxis* spp.) were particularly important by weight. Taxa with high numeric importance, in general, comprised individuals that are small in size and occur in groups or schools, such as *P. planipes* and *V. lucetia*. The cephalopods showed the greatest occurrence values, due partly to the accumulation of residual hard parts, and *P. planipes*, *V. lucetia*, *Auxis* spp., and nomeid fishes (primarily driftfish *Cubiceps pauciradiatus*) were also important in occurrence.

Overall, cephalopods and crustaceans were more prevalent in the diet by weight, number, and occurrence in the 2000s than in the 1990s (Table 2), while the fishes (Osteichthyes) were more prevalent in the earlier period. Several fish families that were dominant components of the diet in the 1990s, e.g. *Auxis*

spp., Carangidae (jacks), and *Cubiceps pauciradiatus*, decreased in \bar{W}_i by the greatest percentages. Although trends of change were clear, major prey taxa did not disappear from the diet during either period. Only prey families with minor \bar{W}_i were present in 1 of the 2 sampling periods and absent from the other (Table 2).

Classification tree analysis

The classification tree analysis produced a tree with 55 splits, i.e. 56 terminal nodes (Fig. 2). In spite of the complexity of the data, the classification tree predicted yellowfin diet composition well, yielding a cross-validated error rate of 0.376 (SE = 0.010, $\sim R^2 = 62\%$). We labeled the explanatory variables associated with some of the most important splits on the tree diagram (longest branches, Fig. 2), while for visualization purposes we omitted the labels for the split variables in the lower portion of the tree. Details for all internal and terminal nodes are presented in Table S1 in the Supplement at www.int-res.com/articles/suppl/m497p157_supp.pdf. The classification tree (Kuhnert et al. 2012) predicts proportions of all

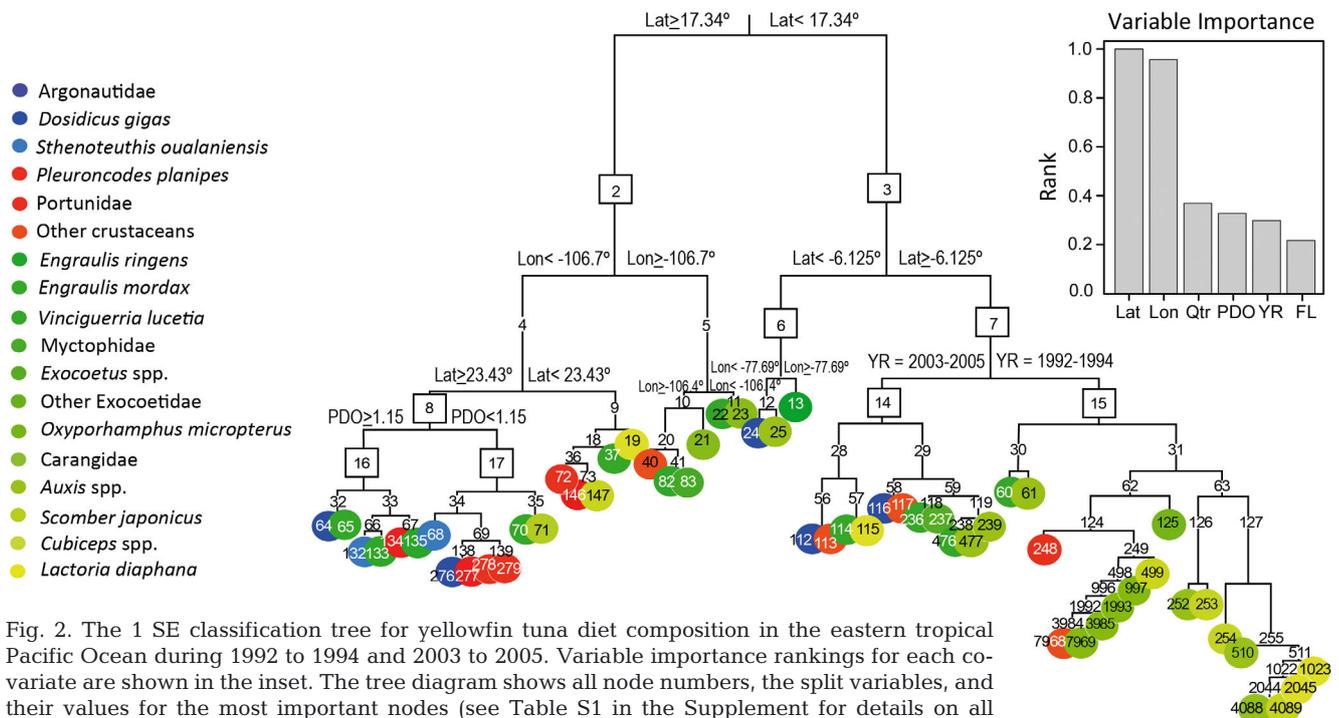


Fig. 2. The 1 SE classification tree for yellowfin tuna diet composition in the eastern tropical Pacific Ocean during 1992 to 1994 and 2003 to 2005. Variable importance rankings for each covariate are shown in the inset. The tree diagram shows all node numbers, the split variables, and their values for the most important nodes (see Table S1 in the Supplement for details on all nodes). Lat: latitude; Lon: longitude; Qtr: quarter-of-year; PDO: Pacific Decadal Oscillation index; YR: year; FL: fork length. The node numbers enclosed in boxes are those discussed in the text and referred to in Figs. 3 & 4. The nodes are labeled according to the naming convention of Breiman et al. (1984), and the prey group comprising the greatest proportion by weight of the diet at each terminal node is displayed by colored circles. The colors signify broad groupings: blues represent cephalopods, reds crustaceans, and greens to yellows fishes

18 principal prey groups for the yellowfin samples at each internal and terminal node. At the terminal nodes, labeled with node numbers according to the naming convention of Breiman et al. (1984), the prey group comprising the greatest proportion of the diet is displayed by colored circles (Fig. 2). The colors signify broad groupings: blues represent cephalopods, reds crustaceans, and greens to yellows fishes. Variable importance rankings for each covariate in the final model were: latitude (rank = 1.00) and longitude (rank = 0.96) followed by quarter-of-year (rank = 0.37), Pacific Decadal Oscillation index (rank = 0.32), year (rank = 0.30), and fork length (rank = 0.21) (Fig. 2).

Two of the most important splits in the tree separated samples taken in a small region in the extreme north of the sample distribution and samples in a narrow band at the extreme south from the majority of the data set. The remaining majority of samples, taken from 65% of the purse-seine sets in the database, were from the large central part of the ETP purse-seine fishery. The most important explanatory variable partitioning the samples in the central re-

gion was year, which distinguished the samples between the 2 decadal periods. These results illustrate a major decadal diet shift in tropical and equatorial surface waters (Fiedler & Talley 2006) in the heart of the purse-seine fishing region, while zoogeography of the prey fauna explained the diet in northern and southern subtropical waters. We expand on these results below.

The first split of the tree (Fig. 2), providing the greatest reduction in deviance over the entire data set, partitioned the diet composition for 1052 yellowfin caught at latitudes $\geq 17.34^\circ\text{N}$ on the left side of the tree (node 2) from the diet composition for 2070 fish from south of latitude 17.34°N on the right side of the tree (node 3). This northern area is small but dynamic (Kessler 2006, Gaxiola-Castro et al. 2010) at the southern terminus of the California Current (Fiedler & Talley 2006). The diet composition of yellowfin in this region was diverse (gini index of diversity 0.729) (Fig. 3a, node 2), comprising a variety of cephalopods, crustaceans, and fishes (see terminal node colors for the principal prey on the left side of the tree, Fig. 2).

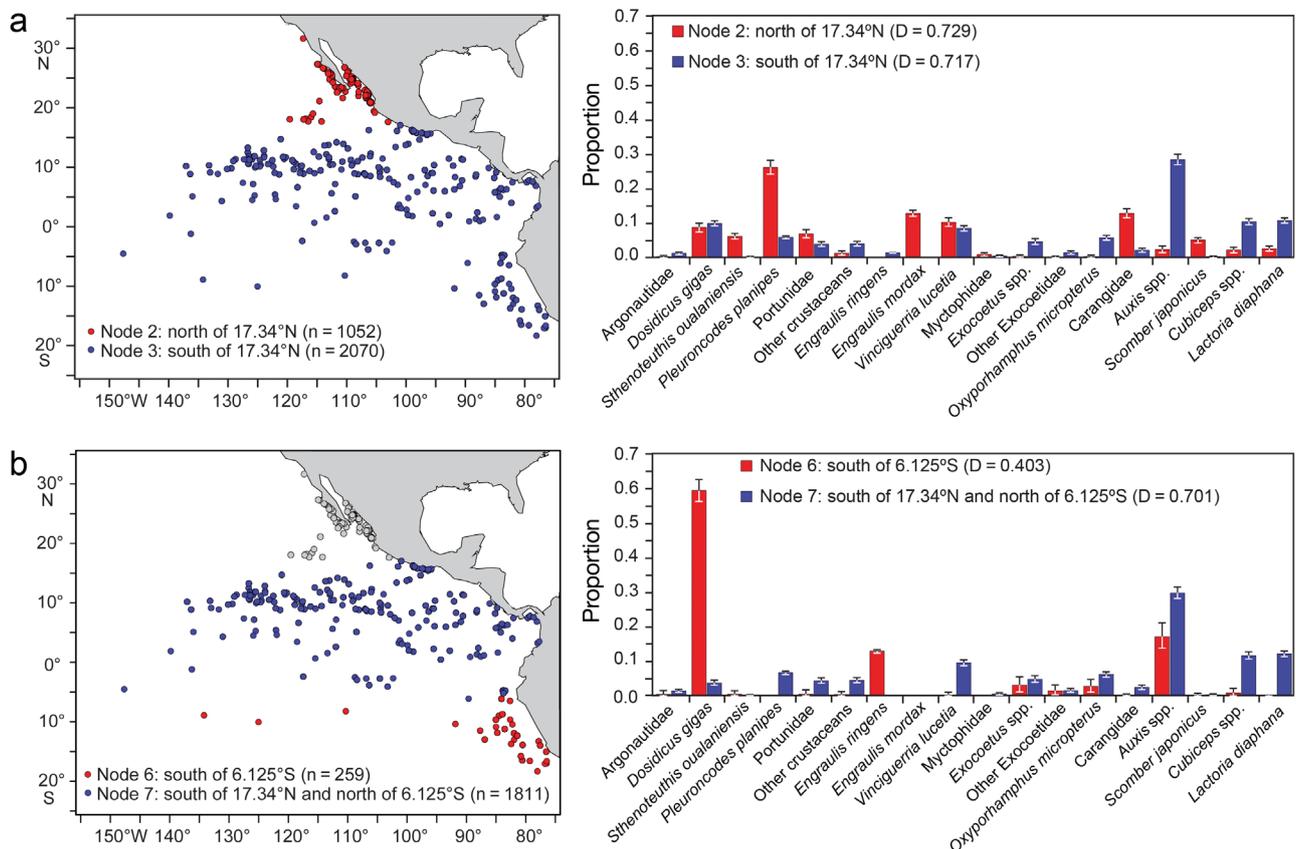


Fig. 3. Details of the first two of the most important splits of the 1 SE classification tree, showing sample locations, sample numbers, and prey compositions (mean proportion by weight) for (a) 3122 yellowfin tuna partitioned by latitude into nodes 2 and 3 and (b) 2070 yellowfin partitioned by latitude into nodes 6 and 7. Node numbers are shown in Fig. 2. D is the gini index of diversity. Grey filled circles in (b) show sample locations that are not included in nodes 6 and 7

The prey at node 2 were predicted in low proportions, but with high precision (Fig. 3a). *Pleuroncodes planipes* predominated overall in this northern area, followed by carangid (jacks) and engraulid (anchovies) fishes. This was similar to the diet of yellowfin in this region as well during the late 1950s (Alverson 1963). The diet composition of 2070 yellowfin sampled throughout the ETP south of latitude 17.34° N (node 3, Fig. 3a) was nearly as diverse as that in the small northern area, but consisted of greater proportions of fishes than cephalopods and crustaceans.

The split below node 3 partitioned the diet of 259 yellowfin caught south of latitude 6.125° S (node 6, Figs. 2 & 3b) from 1811 yellowfin caught throughout a large central area of the ETP, between 6.125° S and 17.34° N (node 7). This region at the extreme southern range of the purse-seine fishery (Fig. 1) is influenced by the Peru Current. The upwelling region off coastal Peru is typified by a simple wasp-waist ecosystem (Cury et al. 2000), which explains the low diet diversity index (0.403) for node 6. The diet was dom-

inated by Humboldt squid *Dosidicus gigas*. The diet of yellowfin at node 7 (the 'central area') closely resembled that at node 3 because 87% of the samples at node 3 mapped down the tree to node 7.

Node 7 split into nodes 14 and 15 (Fig. 2), separating the samples taken in the central area by the 2 decadal periods: 1992–1994 samples were classified into the right branch, node 15, and 2003–2005 samples into the left branch, node 14. The diet in the early period was dominated by epipelagic fishes (82% by weight). *Auxis* spp. comprised 34% of the diet, followed by nomeid fishes *Cubiceps* spp. (15%) and the ostraciid *Lactoria diaphana* (boxfish, 15%) (Fig. 4a). During the 2003–2005 period, these prey components were reduced to 16, 1, and 4% of the diet, respectively. Instead, mesopelagic species and the crustacean *Pleuroncodes planipes* increased in importance during 2003 to 2005 by a total of 46% compared with that predicted for the early period (Fig. 4a). The mesopelagic fish *Vinciguerra lucetia* was predicted at 20% of the diet, a 14% increase

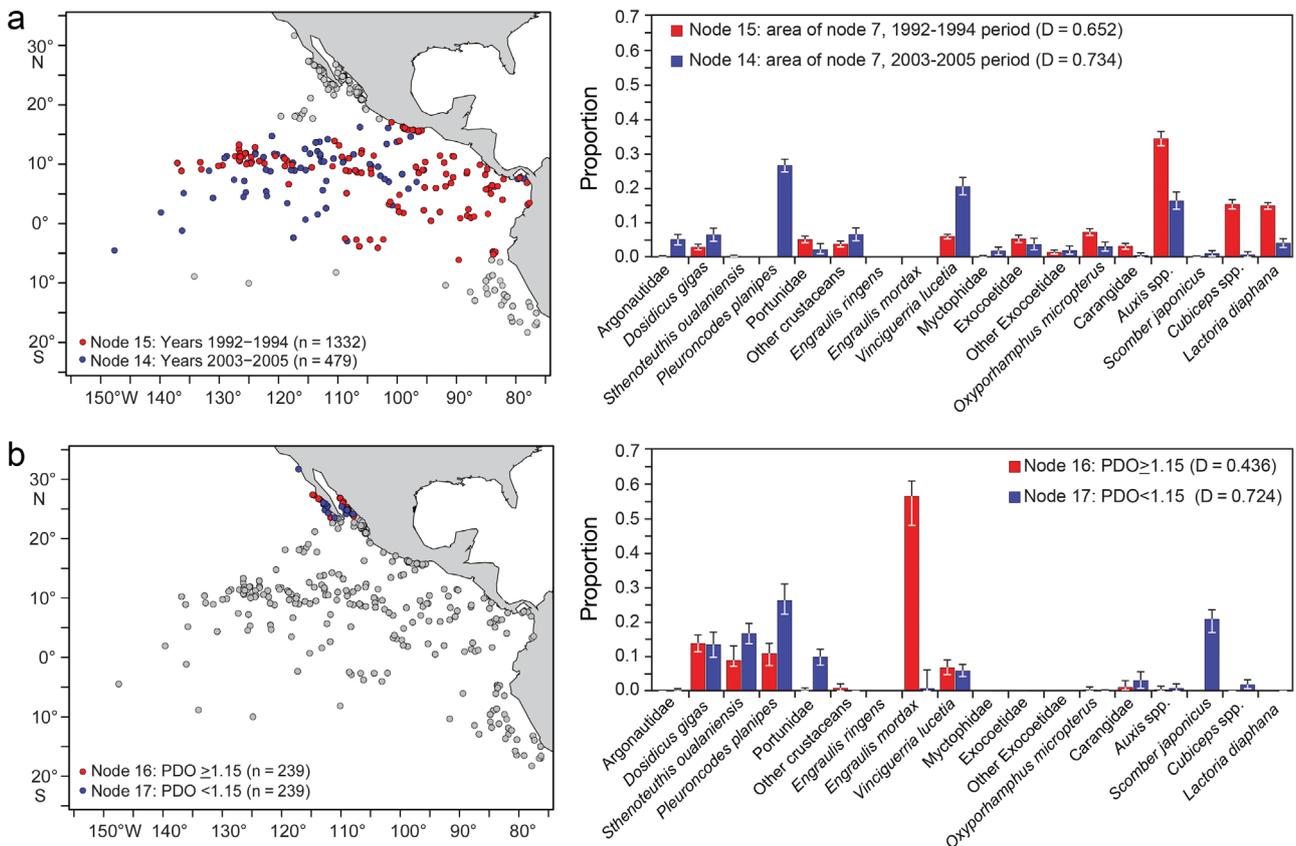


Fig. 4. Details of splits of the 1 SE classification tree, showing sample locations, sample numbers, and prey compositions (mean proportion by weight) for (a) 1811 yellowfin tuna at node 7 partitioned by sample period into nodes 14 and 15, and (b) details of the splits for 478 yellowfin samples at node 8 partitioned by the Pacific Decadal Oscillation (PDO) index into nodes 16 and 17. Node numbers are shown in Fig. 2. D is the gini index of diversity. Grey filled circles in maps show sample locations that are not included in nodes 14, 15, 16, and 17

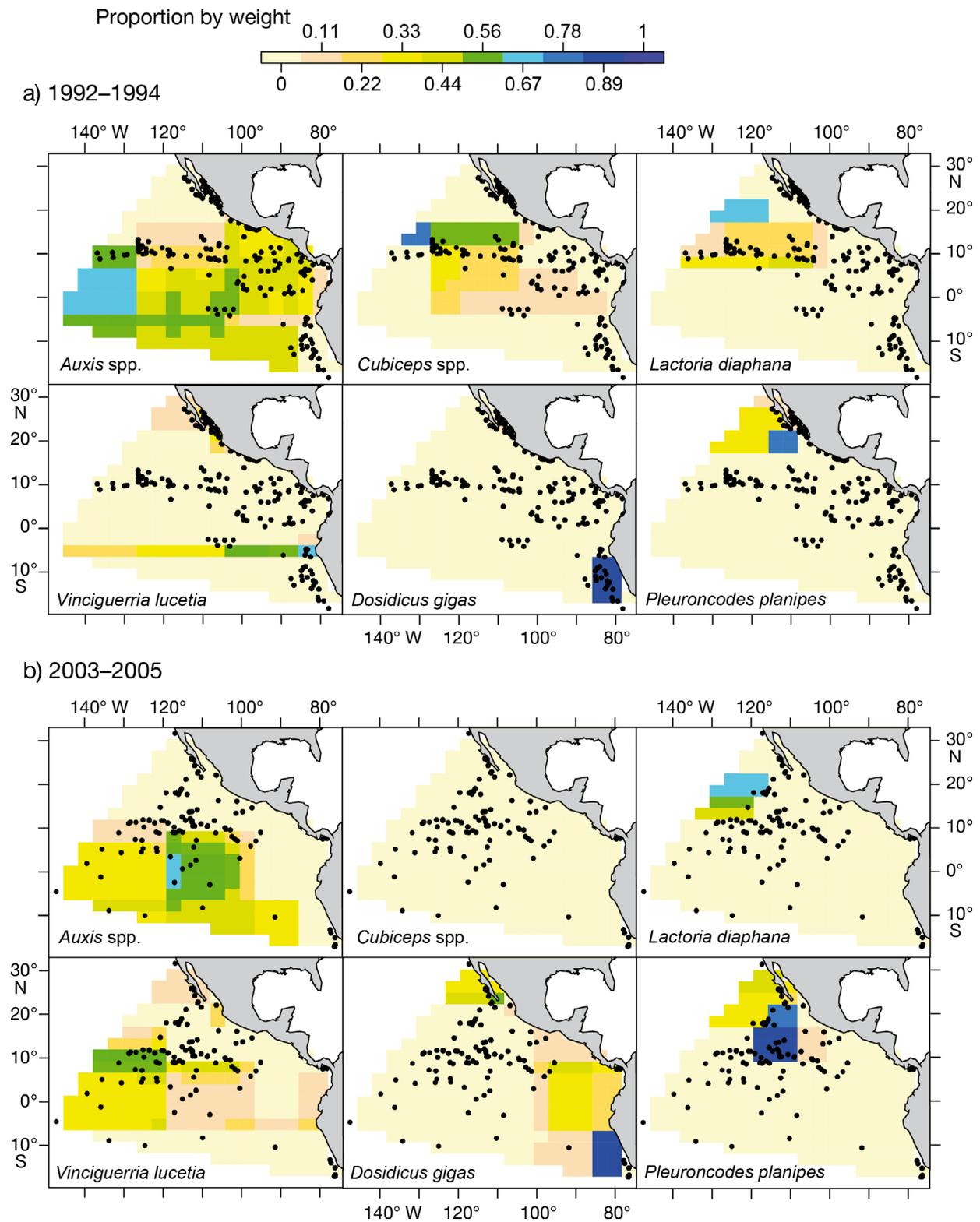


Fig. 5. Partial dependence plots showing relationships between sample locations (latitude and longitude) and predicted proportions by weight of 6 of the principal prey groups in the diet composition of yellowfin tuna during (a) 1992 to 1994 and (b) 2003 to 2005. The shaded areas often extend beyond the spatial extent of the sample locations (black points) due to the mapping routine, and prey-proportion predictions outside of the sample areas should be interpreted with caution. Proportions range from 0 to 1 (scale bar)

over that during 1992 to 1994. Acoustic surveys have also shown an increasing biomass trend of *V. lucetia* in the Peruvian exclusive economic zone after 2000 (Keyl et al. 2008). An assortment of myctophid fishes, an important component of the mesopelagic micro-nekton (Gjøsaeter & Kawaguchi 1980), were predicted at only 2% of the diet, but that amount comprised an increase of nearly 2%, or 9.9 times as much relative to the early period. *Dosidicus gigas*, which occurs at mesopelagic depths during the day and migrates into the epipelagic zone primarily at night (Nigmatullin et al. 2001), was 6% of the diet, a 4% increase, or 2.3 times as much compared with the earlier period. The red crab *P. planipes*, which reproduces in embayments along Baja California (Longhurst 1968), was nearly absent from the yellowfin diet in the central area during 1992 to 1994, but its distribution apparently expanded much farther to the south and offshore during the intervening decade, and it was predicted to have become the most important diet component (27%) in the central area during 2003 to 2005 (Fig 4a).

To further evaluate the scale of the apparent diet shift, we examined partial dependence plots showing the interaction between the spatial covariates (latitude and longitude) and sampling period. The spatial ranges of the diet trends described in the

previous paragraph are illustrated for 6 of 18 prey taxa in Fig. 5. The shaded areas in Fig. 5 often extend beyond the spatial extent of the sample locations (black points, Fig. 5) due to the mapping routine, and prey-proportion predictions outside of the sample areas should be interpreted with caution. *Auxis* spp., *Cubiceps* spp., and *Lactoria diaphana* are 3 of the prey taxa that declined over the decade between sampling periods. *Auxis* spp. were predicted to have been an important, but variable component of the diet over most of the region during 1992 to 1994 (Fig. 5a), but over considerably less of the region during 2003 to 2005 (Fig 5b). The spatial extent over which *Auxis* spp. comprised $\geq 50\%$ of the diet greatly contracted from the early to the late period. *Cubiceps* spp. were predicted to have been especially important diet components toward the north during 1992 to 1994, but uniformly very low in the diet during 2003 to 2005. *L. diaphana* were also predicted in greater proportions over a greater spatial scale in the early than the later period. Of the prey taxa that increased in importance during the later sampling period, *Vinciguerria lucetia* was predicted to have occurred in yellowfin stomachs over a much larger area and in higher proportions offshore west of 120° W in the 2003–2005 sampling period (Fig. 5b) than during the 1992–1994 period

(Fig. 5a). In the 1990s, *Dosidicus gigas* was important in the yellowfin diet only off the coast of Peru (Fig. 5a), whereas a decade later *D. gigas* appeared in the diet over the entire region east of 100° W, and also off coastal Baja California. This is consistent with the well-documented range expansion of *D. gigas*, most noticeable north into waters off the west coast of the USA and Canada and to the south to southern Chile (Cosgrove 2005, Acuña et al. 2007, Zeidberg &

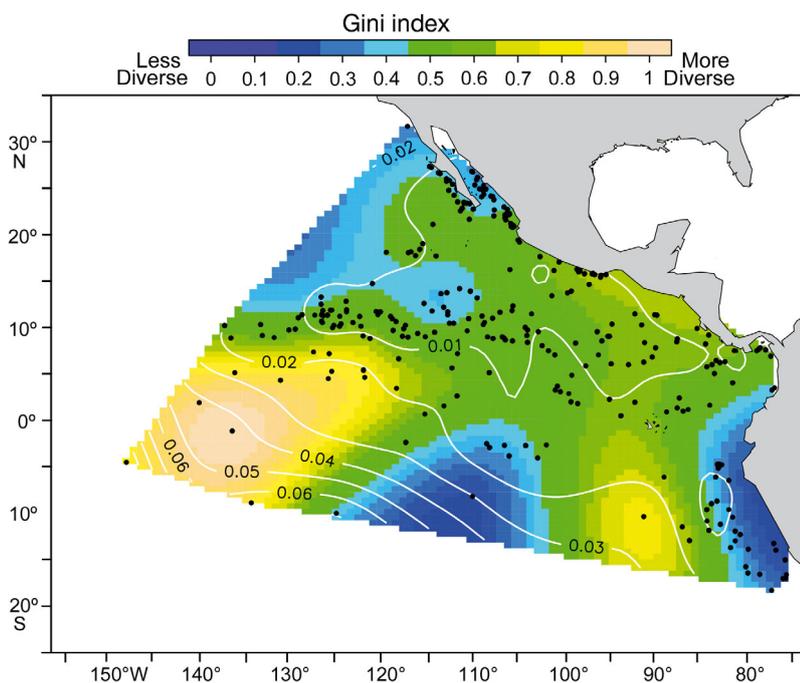


Fig. 6. Spatial trends in diet diversity predicted by the 1 SE classification tree. Values of the gini index of diversity were smoothed with a generalized additive model. Black points represent yellowfin tuna sample locations and white lines represent SE contours

Table 3. Hellinger distances (d_H) computed between the observed (y) and predicted (\hat{y}) prey proportions for each sampling scenario investigated

Subsample (n_s)	$d_H(y, \hat{y})$
5	0.410
10	0.403
15	0.398
20	0.395
25	0.394
All data	0.395

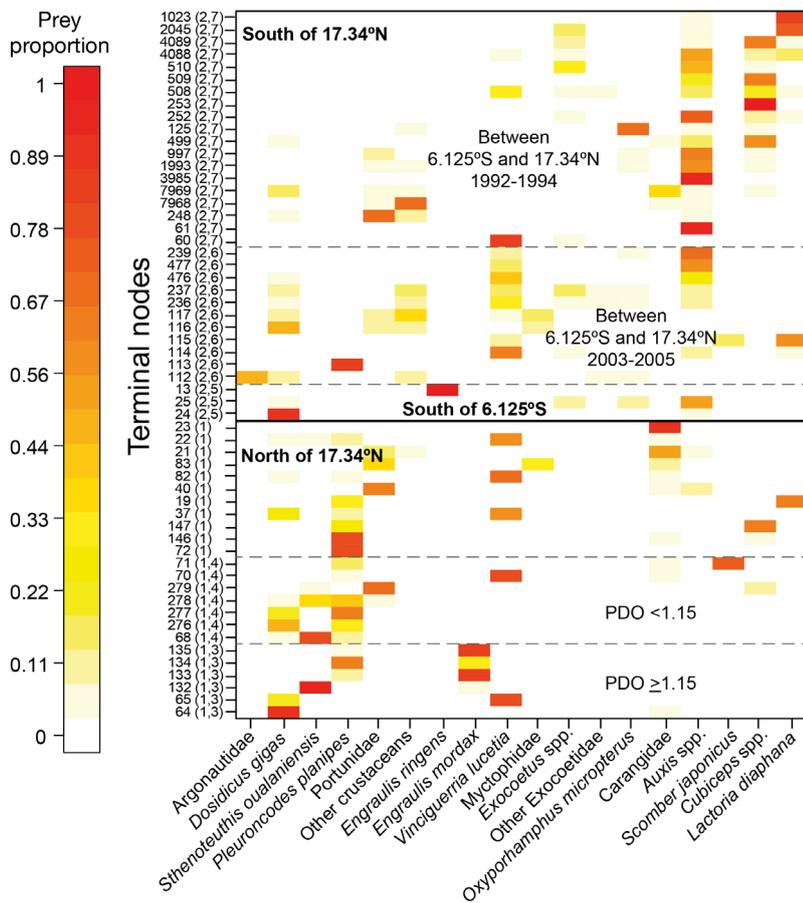


Fig. 7. Prey proportions by weight for yellowfin tuna predicted at the terminal nodes of the 1 SE classification tree. Terminal node labels, ordered bottom to top, correspond to the terminal node labels on the tree in Fig. 2, ordered left to right. Numbers in parentheses — 1: terminal nodes 64 to 23 on left side of tree below internal node 2 (yellowfin sampled north of 17.34°N); 2: terminal nodes 24 to 1023 on right side of tree below internal node 3 (yellowfin sampled south of 17.34°N); 3: terminal nodes 64 to 135 below internal node 16 (Pacific Decadal Oscillation (PDO) index ≥ 1.15); 4: terminal nodes 68 to 71 below internal node 17 (PDO index < 1.15); 5: terminal nodes 24 to 13 on right side of tree below internal node 6 (yellowfin sampled south of 6.125°S); 6: terminal nodes 112 to 239 below internal node 14 (yellowfin sampled during 2003 to 2005); 7: terminal nodes 60 to 1023 below internal node 15 (yellowfin sampled during 1992 to 1994). Prey proportions range from 0 to 1 (scale bar)

Robison 2007, Keyl et al. 2008). *Pleuroncodes planipes* also expanded its range over time according to tuna predation habits. *P. planipes* occurred in the diet mostly off coastal Baja California in 1992 to 1994, but a decade later proportions were predicted to be high south of Baja California down to 10°N .

Spatial trends in diversity based on the 1 SE classification tree are presented by set location and smoothed with a generalized additive model (Wood 2006) (Fig. 6). In nearshore parts of the extreme northern ($>17.34^{\circ}\text{N}$) and southern ($<6.125^{\circ}\text{S}$) areas, which were partitioned near the top of the tree, the

diet was medium to low in diversity (Fig. 6). The samples farthest offshore, however, contained the greatest diet diversity. These overall spatial trends are consistent with broad-scale patterns of biogeography described for the region (see 'Yellowfin tuna as samplers of forage communities' in 'Discussion').

Diet proportions predicted at the tree's terminal nodes are summarized in Fig. 7. The terminal node labels in Fig. 7, ordered bottom to top, correspond to the terminal node labels on the tree (Fig. 2), left to right. The color patterns in Figs. 2 & 7 show greater proportions of cephalopods, crustaceans, *Engraulis mordax*, and *Vinciguerra lucetia* at the left side of the tree (lower left, Fig. 7) and more fishes at the right side, especially nodes 60 to 1023 (upper right, Fig. 7).

Model diagnostics

A spatial version of the bootstrap procedure (Kuhnert et al. 2012) showed that, apart from a nugget effect (representing small-scale or measurement error), spatial dependence was negligible and ordinary bootstrapping methods for examining the error in predictions were considered sufficient for this study.

Fitting a separate classification tree model to the data for a subregion in which purse-seine sets made during both sampling periods overlapped in space (15°N to 5°S and 95°W to 135°W) provided results nearly identical to the splits below node 7 on the right side of the tree for the full data set.

This indicated that the decadal diet shift we observed is not biased by an unequal sample distribution for the 2 periods.

The subsampling approach we used to investigate the potential for bias due to pseudo-replication showed similar Hellinger distances for all subsample sizes investigated (Table 3), indicating similarity between the bagged predictions based on subsamples and observed species compositions. This showed that pseudo-replication was not an issue for this data set.

Prey–predator size relationships

We analyzed the size composition of prey in the stomach contents of yellowfin during the 2 sampling periods by computing ratios of prey size:predator size for each prey that was measured. Only the yellowfin that mapped down the tree to node 7 were included in the computations to determine whether the decadal diet shift involved changes in prey sizes. Since prey–predator size ratios alone are inconclusive to determine whether differences in distributions are due to changes in prey size or predator size, we also analyzed the size compositions of yellowfin tuna and the prey items separately. The results of the Kolmogorov-Smirnov test indicated a significant difference in predator sizes ($D = 0.4032$, $p < 0.001$), prey sizes ($D = 0.4955$, $p < 0.001$), and prey–predator size ratios ($D = 0.3507$, $p < 0.001$) between the 2 sampling periods, with the 1990s data exhibiting larger predator and prey sizes and prey–predator size ratios than the 2000s. The Wilcoxon rank sum test statistic indicated a significant location shift for predator sizes ($W = 251\,809$, $p < 0.001$), prey sizes ($W = 273\,528$, $p < 0.001$), and prey–predator size ratios ($W = 250\,477$, $p < 0.001$), therefore supporting the initial proposition that predator, prey, and prey–predator size ratios were indeed greater in the 1990s compared with the 2000s sampling period.

Smaller prey, in general, occupy lower trophic levels than larger prey, and our results imply that yellowfin were feeding on lower-level prey during the early 2000s than the early 1990s.

DISCUSSION

We used a novel classification tree approach to analyze the trophic ecology of yellowfin tuna in the ETP based on data for two 2 yr periods separated by a decade. One of the most important splits in the classification tree model identified a major shift in prey composition that occurred during the intervening decade. Epipelagic fishes, including frigate and bullet tunas *Auxis* spp., declined from 82 to 31% of the diet in the central region (Fig. 4a) over the decade. *A. thazard* and *A. rochei* are known to be abundant (Olson & Boggs 1986) and important prey species for much of the apex predator guild in the ETP (Olson & Watters 2003, Hunsicker et al. 2012). Earlier in the development of the purse-seine fishery (1970 to 1972), *Auxis* spp. comprised ~53% of the overall yellowfin tuna diet in a comparable central part of the ETP (Olson & Boggs 1986), declining to 34% in 1992

to 1994 and to 16% in 2003 to 2005 (Fig. 4a). Mesopelagic fishes and squids increased from 9 to 29% of the diet over the 1990s to 2000s decade, and an abundant crustacean *Pleuoncodes planipes* apparently expanded its distribution offshore and to the south, changing from <0.01 to 27% of the diet in the central region.

We questioned whether changes in predation patterns over time were a reflection of ecosystem-scale changes in prey availability and abundance, or were due to other factors, such as spatial differences in sample distributions. We addressed the latter concern in 2 ways: (1) by investigating whether there was any spatial structure not accounted for by the model, using a spatial version of the bootstrap as outlined by Kuhnert et al. (2012); and (2) by fitting a separate classification tree model to the data for a subregion in which purse-seine sets made during both sampling periods overlapped in space (15° N to 5° S and 95° W to 135° W). We found that spatial dependence was negligible and that the decadal diet shift we observed was not biased by an unequal sample distribution for the 2 periods (see 'Model diagnostics' in 'Results'). Instead, we advocate that the predation patterns of yellowfin tuna, a wide-ranging generalist predator, provide valuable insight on ecosystem-scale prey availability and distribution (e.g. Alverson 1963). If this assumption is justified (see 'Yellowfin tuna as samplers of forage communities' below), then evidence suggests that the ETP has undergone fundamental changes in the mid-trophic level micronekton communities. First, we offer evidence from peer-reviewed literature that large-scale changes in biological production and habitat have resulted from physical forcing in the subtropical and tropical Pacific Ocean. We follow this with information supporting the concept of yellowfin as an effective sampler of the forage populations, linking ecosystem change to yellowfin predation. We conclude with discussion of the efficacy of classification trees for teasing apart the complexity of ecological data, in particular predation data, and several caveats that may pertain to yellowfin tuna predation.

Changes in productivity

Evidence of linkage between biological production and physical forcing in the Pacific Ocean (and elsewhere) is strong. Primary production has declined over vast oceanic regions in the recent decade(s) (Behrenfeld et al. 2006, Polovina et al.

2008, Stramma et al. 2008, Polovina & Woodworth 2012) and yellowfin tuna production appears to have declined in the eastern Pacific Ocean since 2003 (Aires-da-Silva & Maunder 2012). Polovina et al. (2008) used a 9 yr time series of Sea-viewing Wide Field-of-view Sensor (SeaWiFS) remotely sensed ocean color data to examine temporal trends in the areal expanse of oligotrophic surface waters in the major oceans. In the North and South Pacific, the most oligotrophic surface waters have increased in area by 2.2 and 1.4% yr⁻¹ between 1998 and 2006, respectively. These statistically significant increases in the oligotrophic gyres occurred concurrently with significant increases in mean SSTs (Polovina et al. 2008). In the North Pacific, the direction of expansion was northeast, reaching well into the eastern Pacific to ~120°W and as far south as ~15°N, i.e. the edge of our sampling region. According to Behrenfeld et al. (2006), net primary productivity has also declined in the tropical and subtropical oceans since 1999. The mechanism is recognized as increased upper-ocean temperature and vertical stratification, influencing the availability of nutrients for phytoplankton growth (Behrenfeld et al. 2006, Polovina et al. 2008).

Recent assessments of the eastern Pacific yellowfin tuna stock indicate a shift to lower levels of recruitment since 2003 (Aires-da-Silva & Maunder 2012), suggesting the possibility of a lower productivity regime. This and a modeling study indicate that changes in primary production have the potential to cascade up the food web to affect the upper trophic levels in the ETP (Watters et al. 2003). It is conceivable that a long-term reduction in primary production in the ETP could be partly responsible for the diet shift we observed in yellowfin tuna.

Changes in phytoplankton size composition

Evidence is also strong that primary producers have changed in community composition and size structure in recent decades. Phytoplankton cell size is relevant to predation dynamics of tunas because food webs that have small picophytoplankton at their base require more trophic steps to reach predators of a given size than do food webs that begin with larger phytoplankton (e.g. diatoms) (Seki & Polovina 2001). Energy transfer efficiency is lower for picophytoplankton-based food webs than for nanophytoplankton-based food webs, i.e. for a given amount of primary production less energy will reach a yellowfin tuna of given size in the former than in

the latter because mean annual trophic transfer efficiency at each step is relatively constant (Barnes et al. 2010b). Polovina & Woodworth (2012) used satellite remotely sensed SSTs and chlorophyll *a* concentrations in a relationship developed by Barnes et al. (2010a) to estimate the monthly size composition of phytoplankton communities during 1998 to 2007. With the seasonal component removed, the median phytoplankton cell size estimated for the subtropical 10 to 30° North and South Pacific declined by 2.2 and 2.3%, respectively, over the 9 yr period. Given that our yellowfin tuna samples were from these regions, long-term changes in the phytoplankton size composition could have influenced the diet shift we observed between the early 1990s and the early 2000s.

Changes in the oxygen minimum zone

Expansion of the oxygen minimum zone (OMZ) is a third factor that demonstrates ecosystem change on a scale capable of affecting prey communities. The OMZ is a thick low-oxygen layer at intermediate depths, which is largely suboxic (less than about 10 µmol kg⁻¹) in the ETP (Stramma et al. 2008). According to Knauss (1963, p. 244), the OMZ in the ETP 'includes a greater body of almost oxygen-free water than any other region in the world's oceans'. Time series of dissolved oxygen concentration at depth from 1960 to 2008 revealed a vertical expansion and intensification of the OMZ in the central and eastern tropical Pacific and Atlantic oceans (Stramma et al. 2008). The OMZ expansion in the ETP occurred mostly after our early 1990s sampling period. Potential biological consequences of an expanding OMZ are numerous (Stramma et al. 2010, 2012), but for the epipelagic tunas, habitat compression can have profound implications. Shoaling of the OMZ restricts the depth distribution of these and other pelagic fishes into a narrower surface layer, compressing their foraging habitat and altering forage communities. Enhanced foraging opportunities for all epipelagic predators could alter trophic pathways and affect prey species composition. In addition, with a shoaled OMZ, mesopelagic vertically migrating prey, such as phosichthyid (i.e. *Vinciguerria lucetia*) and myctophid fishes and ommastrephid squids, would likely occur at shallower daytime depths and become more vulnerable to epipelagic predators (Stramma et al. 2010). These are some of the taxa that increased most in the yellowfin diet in the ETP between 1992–1994 and 2003–2005.

Physical forcing

The El Niño-Southern Oscillation (ENSO) is a well-known interannual climate perturbation that affects the physics and biology of the ETP (Barber & Chavez 1983, Chavez et al. 1999). We incorporated an ENSO index in a preliminary version of the CART model, but the results were unclear and not instructive. In subsequent model versions, we employed the Pacific Decadal Oscillation (PDO) index to explore a climate driver of ecosystem change on a decadal scale. The PDO index tracks climate variability primarily in the North Pacific Ocean (Mantua et al. 1997), but secondary signatures of the PDO exist in the tropical Pacific (Hare & Mantua 2000). The PDO index was in a positive phase during most of our 1992–1994 sampling period, including peak values >2.0 during May to August 1993 and negative values during only the last 2 mo of the 1990s sampling period. During the 2003–2005 sampling period, the PDO index was also moderately positive except for 2 brief 3 mo periods, October to December 2004 and September to November 2005, during which time the index was slightly to moderately negative. In the intervening decade between the 2 sampling periods, however, the PDO index was in a negative phase during July 1998 to July 2002.

The PDO index was the fourth most important explanatory variable in the tree model, and there were 3 splits for which the PDO index was the primary explanatory variable. All 3 of these splits occurred for samples at the subtropical extreme north of the sample distribution (left branch of the tree), in a small area that included samples from both the 1990s and 2000s. For all 3 PDO splits, diet diversity was predicted to be low during neutral to high PDO phases and more diverse during the cooler PDO phases. For example, at node 8, 478 yellowfin in a small region north of 23.43° N on both sides of the Baja California Peninsula split at PDO index 1.15 into nodes 16 and 17 (Figs. 2 & 4b). In the warmer PDO phase, ≥ 1.15 , prey diversity was low (0.436) and the dominant prey class, *Engraulis mordax* (northern anchovy), comprised 57% of the diet. In the cooler PDO phase, the diet was more diverse (0.724), with 5 prey classes comprising 10% or more of the diet, and crustaceans increasing in importance.

Yellowfin tuna as samplers of forage communities

Yellowfin tuna predation patterns provide valuable information for detecting trends in prey communi-

ties. Stomach-contents analysis is well known as a reliable method for documenting the distribution and ecology of prey species (Boyd et al. 2006). Researchers have noted for many years that yellowfin tuna is an opportunistic predator (Alverson 1963, Sund et al. 1981, Ménard et al. 2006, Potier et al. 2007), owing to high prey diversity and, in general, low abundance of each prey type in the diet. Yellowfin is a Type A generalist, in that all individuals take a wide range of prey types, as opposed to Type B generalists whose individuals each specialize on a different prey type (Van Valen 1965). The ETP is resource limited (Fernández-Álamo & Färber-Lorda 2006), with patchy distributions of forage (Blackburn 1968), yet yellowfin tuna have high energy requirements (Olson & Boggs 1986) owing to high metabolic rates (Brill 1979, Stevens & Dizon 1982), obligate continuous swimming activity (Magnuson 1978), and high rates of somatic and gonadal growth, digestion, and recovery from exhaustive exercise (Brill 1996). A non-selective broad diet is necessary when energy-consuming processes combine with an energetically expensive life style.

Our results showed a reduction in importance of *Auxis* spp. as the principal prey between the early 1990s and early 2000s. Further analysis showed consistency between the stomach contents and a declining trend in incidental catches of *Auxis* spp. by the purse-seine fishery in the ETP for 1996 to 2010 (see the Supplement at www.int-res.com/articles/suppl/m497p157_supp.pdf). However, the possibility that cumulative effects of the fishery itself could partially explain this trend requires consideration. No abundance estimates for *Auxis* spp. exist for the ETP, but the relative impact of the purse-seine fisheries on *Auxis* spp. in the ETP can be evaluated by comparing estimates of catch and predation. Annual catches of *Auxis* spp. during 1993 to 2010 were small (1424 ± 810 SD metric tons), averaging only 0.6 and 0.7% of the annual catches of yellowfin and skipjack tunas, respectively. The amount of *Auxis* spp. consumed was much larger than the *Auxis* spp. bycatch. Early quantitative predation estimates of yellowfin tuna on *Auxis* spp. in the ETP (Olson & Boggs 1986) averaged about 10 times the average annual catches of yellowfin tuna during 1970 to 1972. In summary, coincidentally declining trends in predation of yellowfin on *Auxis* spp. and in the bycatch per set of *Auxis* spp. (Fig. S1 in the Supplement) lends support to the hypothesis that yellowfin is an effective biological sampler of the forage populations. Much earlier, Alverson (1963) showed a remarkable consistency between the areas in which yellowfin consumed 3

species of pelagic crabs and the distributions of the crabs according to the literature.

Our study showed that yellowfin diet composition and spatial patterns of diversity are consistent with previous findings. Vilchis et al. (2009) reported that the largest of 3 oceanic ichthyoplankton assemblages in the ETP comprised 9 taxa, 4 of which were the most dominant in their 13 yr study. In our study, 5 of those 9 taxa were important prey of yellowfin. Yellowfin diet diversity (Fig. 6) was very low in the Peruvian coastal upwelling region, where the highest chlorophyll concentrations in the ETP are recorded (Pennington et al. 2006). Diet diversity was also low in the Baja California area and inside the Gulf of California, where the California Current generates coastal upwelling. Conversely, yellowfin diets were the most diverse in a large offshore region (Fig. 6) that is relatively oligotrophic (Pennington et al. 2006), and the thermocline is much deeper (Vilchis et al. 2009) due to reduced upwelling. It is well known that the oligotrophic central gyres of oceans are characterized by more species-rich and complex food webs than more productive inshore systems (McGowan & Walker 1985, Venrick 1990, Rohde 1992). This pattern appears to also hold for the prey of yellowfin, as evidenced by high diet diversity in the most oligotrophic offshore region and low diet diversity in nearshore upwelling regions (Fig. 6). Vilchis et al. (2009), on the other hand, found ichthyoplankton species diversity to peak at medium chlorophyll concentrations (~ 20 mg chl a m^{-2} , at $\sim 90^\circ$ W longitude), and decline at chlorophyll values below and above that value (i.e. to the west and east of $\sim 90^\circ$ W). Thus, ETP ichthyoplankton diversity did not peak offshore in the area in which yellowfin prey diversity peaked.

Classification tree analysis

The classification tree method proved to be a useful approach for interpreting a complex data set of predator-prey relationships for a ubiquitous predator. This is the first large-scale application of this novel method and the R-based diet package. The method provides a framework for exploratory analysis through visual inspection of important nodes of the tree, provides predictions with estimates of uncertainty at terminal nodes, and explores relationships between explanatory variables and predicted prey composition. Furthermore, the classification tree method provides a summary of the diversity of prey consumed at the nodes of the tree, which has ecological significance.

Many of the modeling assumptions of CART analysis are well suited to diet data. However, there are some instances for which further investigation of the appropriateness of the model is warranted. For example, pseudo-replication has the potential to bias predictions from a model based on multiple fish samples from the same purse-seine set. Given that our yellowfin sample sizes ranged from 1 to 27 per set across both sampling periods, we investigated the potential for bias due to pseudo-replication using a subsampling approach described in 'Materials and methods'. The results from this analysis (Table 3) showed that pseudo-replication was not an issue for this data set (see 'Model diagnostics' in 'Results').

Multivariate regression tree (MRT) analysis is an alternative method used for analyzing compositional data (De'ath 2002, Larsen & Speckman 2004, Griffiths et al. 2009). MRTs are non-parametric, exploratory, and visual; they can deal with missing data and accommodate different data types, and they can be applied to a dissimilarity matrix. However, for large compositional datasets, MRT analysis can be computationally intensive due to the distance calculations that need to be performed. Furthermore, the distance-based implementation is difficult to interpret, particularly if a predicted composition is required, although Griffiths et al. (2009) attempted to resolve this issue by examining the diet proportions at terminal nodes of a tree built on a dissimilarity matrix. In addition, obtaining uncertainty estimates on the predicted proportions through bagging cannot be performed easily or efficiently. As a result, Kuhnert et al. (2012) extended the classification tree approach proposed by Breiman et al. (1984) to develop a model that is akin to a multinomial model as the preferred method for exploring, predicting, and quantifying the uncertainties in prediction for diet compositional data. Nevertheless, we conducted preliminary analyses that included a comparison between MRT and CART models, and both methods produced similar results, i.e. the top, most important splits in the trees were identical.

Caveats

Additional factors not included in our classification tree model (see 'Classification tree analysis' in 'Materials and methods' for justification) may partly influence the predation characteristics of yellowfin tuna in the ETP, and thus require consideration.

Diel feeding periodicity

In preliminary models, feeding periodicity was unimportant in explaining diet variability due to the fact that no tree splits occurred on the set time-of-day variable, and that variable was rarely a competing or surrogate explanatory variable for tree splits. Scott et al. (2012) examined trends in feeding times of yellowfin tuna and 2 species of dolphins (genus *Stenella*) caught while associated ('dolphin sets') in the ETP, using data on prey digestion state and stomach fullness. Yellowfin tuna showed clear signs of recent feeding and 'full' stomachs throughout the daytime, and empty stomachs occurred most frequently in yellowfin caught in the early morning (06:00 to 08:59 h) and early afternoon (12:00 to 14:59 h).

In our study, some of the diet differences between the early and late sampling periods could have been due to diel feeding periodicity, given that a greater proportion of our samples were derived from floating-object sets in the early 2000s than in the early 1990s. The yellowfin tuna that were associated with floating objects, which were primarily small fish from sets in the early morning, showed much greater percentages of empty stomachs and those containing only residual hard parts (84 to 87%, Table 1) than yellowfin associated with dolphins, indicating a low incidence of nighttime feeding at floating objects. While the stomach contents of yellowfin tuna indicate that, in general, some feeding takes place at night (e.g. low incidence of squid tissue in conjunction with high incidence of digestion-resistant squid mandibles with no soft tissue attached), nighttime feeding is inadequately represented in our samples because purse-seine sets were made only during daylight hours. Some common prey species of yellowfin tuna (most notably, Humboldt squid *Dosidicus gigas* and lightfish *Vinciguerria lucetia*) are known to migrate vertically from the mesopelagic zone into the epipelagic zone, primarily at night, while many other prey species are epipelagic during the day and night (Scott et al. 2012, Table 2). Both of those prey species occurred most frequently in the later sampling period (Table 2, % O_i).

Prey availability

Prey availability may differ by tuna aggregation type. The small fishes that associate with floating objects are not typically prey of small tunas or other abundant predators that closely associate with floating objects (Buckley & Miller 1994, Ménard et al.

2000, Taquet et al. 2007). Tunas typically feed away from floating objects during the day while aggregating primarily at night. Ménard et al. (2000) reported that floating objects in the Atlantic Ocean do not have a 'trophic function' for small tunas. Yellowfin tuna caught in association with dolphins and in unassociated schools, however, often had been feeding more recently than those caught on floating objects, i.e. they had more freshly eaten prey in their stomachs (Table 1). The presence of dolphins, however, does not likely affect the prey abundance and feeding behavior of yellowfin tuna prior to capture because dolphins feed primarily at night, rarely during the daytime when purse-seine sets are made (Scott et al. 2012).

Fishing practices

Distributions of purse-seine sets of the 3 types described above changed between the early 1990s and early 2000s sampling periods. Floating-object sets proliferated during the interim period, primarily south of 10° N and in the area west of 110° W. We addressed whether spatial differences in sample distributions influenced our results by using a spatial bootstrap procedure and by fitting a classification tree model to the data for a subregion in which sets made during both sampling periods overlapped in space. We concluded that the decadal diet shift we described was not biased by unequal sample distributions (details in 'Model diagnostics' in 'Results').

Spatial and seasonal fishery closures also did not likely bias our results. There were no closures due to fishery management measures during the entire 1990s sampling period and in 2003. Seasonal closures during August 1 to September 11 and November 20 to December 31, 2004 and 2005 had the potential to bias our results, but quarter-of-year, the third most important variable, showed no seasonal trends. During the 2004 and 2005 seasonal closures, 3 sets were sampled, and all yellowfin stomachs were empty.

The use of technologies that allowed purse-seine vessels to better locate schools of yellowfin tuna, such as high-resolution radar and helicopters, increased slightly between the early 1990s and the early 2000s in the ETP tuna fishery (Lennert-Cody et al. 2001). These technologies increased the capacity of searching for tuna-dolphin schools and unassociated tuna schools, but were not relevant to the collection of diet data.

Bioenergetics

As previously established, information on food web linkages and interaction rates are required for understanding biomass and energy flow in pelagic ecosystems. We have elucidated qualitative and quantitative aspects of changing predation patterns of yellowfin tuna, but we have not considered the bioenergetics implications of a diet shift for yellowfin. A thorough analysis of daily energy consumption estimated from stomach contents and gastric evacuation rates is beyond the scope of this study. However, preliminary calculations using established methodology (Olson & Boggs 1986, Olson & Mullen 1986) suggested that yellowfin sampled during 2003 to 2005 consumed lower daily rations (percent of body weight per day) than those sampled during 1992 to 1994. In addition to changes in prey abundance, changes in prey quality can affect upper trophic level predators. Golet et al. (2007) demonstrated a decadal-scale decline in the somatic condition of Atlantic bluefin tuna *Thunnus thynnus* in the Gulf of Maine, USA, and hypothesized that the decline could be due to a coincident decline in the condition of Atlantic herring *Clupea harengus*, an important prey.

CONCLUSIONS

A modified classification tree approach (Kuhnert et al. 2012) was effective for analyzing predator-prey data for more than 3300 yellowfin tuna sampled over nearly the entire ETP during 2 time periods separated by a decade. Zoogeographical differences in prey assemblages, irrespective of sampling period, were important features of the diet in relatively small subtropical areas at the extreme northern and southern ranges of the purse-seine fishery. For the majority of the yellowfin population in the ETP, however, a major diet shift between 1992–1994 and 2003–2005 was predicted by the classification tree model.

Altered prey composition and predation patterns suggest that broad-scale changes in the pelagic food web occurred in the ETP. This result was not due to a biased sample distribution among the 2 time periods. Fishes were more gravimetrically abundant in the overall diet during the early 1990s, while cephalopods and crustaceans predominated a decade later. As a group, epipelagic fishes declined from 82 to 31% of the diet, while mesopelagic species increased from 9 to 29% over the decade. Assuming yellowfin predation patterns represent prey distributions, spatial partial dependence plots (Fig. 5) revealed range

expansions by *Vinciguerria lucetia*, *Dosidicus gigas*, and *Pleuroncodes planipes*, range contractions by *Auxis* spp. and *Lactoria diaphana*, and a near disappearance of *Cubiceps* spp. from the diet. Our study provides evidence from predation rates that biomasses of the abundant mesopelagic fish *V. lucetia* and Humboldt squid *D. gigas* have increased in the first half of the 2000s (Keyl et al. 2008) and that the distribution of Humboldt squid apparently expanded both offshore and poleward.

Circumstantial evidence of simultaneous broad-scale reductions in biological production and phytoplankton size composition, and a vertical expansion of the hypoxic OMZ in the central and eastern tropical Pacific, point to ecosystem change on a scale thought to be capable of altering prey communities. However, no fisheries-independent evidence of changing prey abundance is available for comparison with yellowfin diet trends. A feature consistent with our result of declining predation rates on frigate and bullet tunas *Auxis* spp. was found in the incidental catch rates of the tuna purse-seine fishery in the ETP. The catch per set of *Auxis* spp. declined during 1996 to 2010 (see the Supplement) in parallel with their reduction in the diet of yellowfin.

Novel methods of sampling mid-trophic level micro-nekton organisms in the pelagic open ocean are needed. The micronekton prey of upper trophic level predators comprise one of the lesser known components of pelagic ecosystems (Olson & Watters 2003). A modest historical time series is provided by dipnet surveys (Pitman et al. 2002) of the Southwest Fisheries Science Center, La Jolla, California (US National Oceanic and Atmospheric Administration (NOAA) Fisheries). Automated acoustic methods, although technologically challenging, may hold promise. A project to develop a mid-trophic automatic acoustic sampler (MAAS) is being promoted by the Integrated Marine Biochemistry and Ecosystem Research's (IMBER) regional program 'Climate Impacts on Oceanic Top Predators' (CLIOTOP) (Handegard et al. 2013). Until new methods are developed, we advocate that low-level, systematic sampling programs of stomach contents from yellowfin or other pelagic fishes be adopted for continuous monitoring of mid-trophic level communities in pelagic ecosystems (Nicol et al. 2013).

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