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Feeding habits of billfishes (Carangaria: Istiophoriformes) in the Ecuadorian Pacific Ocean

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The feeding habits of *Makaira nigricans, Kajikia audax, Istiophorus platypterus* (Istiophoridae), and *Xiphias gladius* (Xiphiidae) in the southeast Pacific Ocean were examined in Manta and Santa Rosa, Ecuador. This study describes the diets of these billfish species, evaluates dietary differences between species, and assesses seasonal differences in diet. A total of 274 *M. nigricans*, 321 *K. audax*, 267 *I. platypterus*, and 252 *X. gladius* were collected between February 2014 and April 2015. The scombrid *Auxis* spp. was the most important prey for *M. nigricans, K. audax* and *I. platypterus*, while the squid *Dosidicus gigas* was the most important prey for *X. gladius*. The results of the ANOSIM confirmed significant differences in feeding habits between the members of the family Istiophoridae and *X. gladius.* Seasonal differences for *I. platypterus* also were observed. Billfishes are specialist consumers with a narrow niche breadth (B_a: *M. nigricans* and *K. audax*=0.1, *I. platypterus*=0.05, and *X. gladius*=0.04).

Keywords: Feeding strategy, Food partitioning, Istiophoridae, Trophic ecology, Xiphiidae.

Los hábitos alimentarios de *Makaira nigricans, Kajikia audax, Istiophorus platypterus* (Istiophoridae) y *Xiphias gladius* (Xiphiidae) en el Océano Pacífico sudeste se examinaron en Manta y Santa Rosa, Ecuador. Este estudio describe las dietas de estas especies de peces de pico, evalúa las diferencias de la dieta entre especies y las diferencias estacionales en la dieta. Se obtuvo un total de 274 *M. nigricans*, 321 *K. audax*, 267 *I. platypterus* y 252 *X. gladius* entre febrero 2014 y abril 2015. El escómbrido *Auxis* spp. fue la presa más importante para *M. nigricans, K. audax* y *I. platypterus*, mientras que el calamar *Dosidicus gigas* fue la presa más importante para *X. gladius*. Los resultados de ANOSIM confirmaron diferencias significativas en los hábitos alimentarios entre los miembros de la familia Istiophoridae y *X. gladius.* También se observaron diferencias estacionales para *I. platypterus*. Los peces de pico son consumidores especialistas con una amplitud de nicho estrecha (B_a: *M. nigricans* y *K. audax*=0.1, *I. platypterus*=0.05 y *X.gladius*=0.04).

Palabras clave: Ecología trófica, Estrategia alimentaria, Istiophoridae, Repartición alimentaria, Xiphiidae.

Introduction

Commonly known as billfishes, the large fishes of the families Xiphiidae and Istiophoridae are active predators characterized by a protruding upper jaw that extends considerably beyond their lower jaw (Nakamura, 1985). The longline fishery for large pelagic fishes operates year round in Ecuador and billfishes are one of the most important resources for the local artisanal fishery as well (Martínez-Ortíz *et al.*, 2015).

The most tropical billfish species is the blue marlin *Makaira nigricans* Lacépède, 1802, which is commonly found in equatorial waters (Nakamura, 1985). This epipelagic species it is the most oceanic of the istiophorids and is found in coastal waters only where the continental shelf is narrow (Nakamura, 1985; Joseph *et al.*, 1988). The striped marlin *Kajikia audax* (Philippi, 1887) is an epipelagic predator usually found above the thermocline, although the species migrates to deeper waters at night (Nakamura, 1985; Sippel *et al.*, 2011). The sailfish *Istiophorus platypterus* (Shaw, 1792) prefers a coastal habitat (Nakamura, 1985) and is usually found within 50 m of the surface, but undertakes short-duration vertical movements to 150 m depth (Chiang *et al.*, 2011; Kerstetter *et al.*, 2011). The swordfish *Xiphias gladius* Linnaeus, 1758 is the sole member of the family Xiphiidae and exhibits the greatest temperature tolerance among billfishes (Nakamura, 1985), performing vertical migrations to more than 900 m depth (Abascal *et al.*, 2010).

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Habitat partitioning is important as it can lead to the consumption of distinct prey in different areas (Shimose *et al.*, 2010); meanwhile, resource partitioning may reduce the competitive pressure between species (Papastamatiou *et al.*, 2006). Prey availability also can be influenced by changes in the primary productivity as well as other biological and physical variables (Olson *et al.*, 2014) that affect the occurrence of billfishes (Shimose *et al.*, 2008; Shimose *et al.*, 2010).

Marine predators provide valuable information about prey abundance and composition (Potier *et al.*, 2007; Olson *et al.*, 2014). Stomach content analyses also facilitate the identification of feeding habits as well as competition or resource partitioning between species that occurs in the same region (Baker, 1966; Vaske *et al.*, 2004; Shimose *et al.*, 2010), ecological aspects that are not commonly considered for billfishes. Traditionally, studies on the feeding habits of billfishes in the Pacific Ocean have focused on a single species (Abitia-Cárdenas *et al.*, 1999; Rosas-Alayola *et al.*, 2002; Shimose *et al.*, 2006; Watanabe *et al.*, 2009; Abitia-Cárdenas *et al.*, 2011; Tsai *et al.*, 2015) or prey group (Rosas-Luis *et al.,* 2016).

Despite their ecological and commercial importance, biological information on these fishes remains scarce, particularly for the Southeast Pacific Ocean. The feeding ecology of billfishes in Ecuador was assessed to: (1) quantify the diet of billfishes, (2) evaluate the possible differences in diet between distinct species and seasons, and (3) describe their feeding strategy.

Materials and methods

Study area and sample collection. The study area is located off the coast of Manta (0°56′59″S, 80°42′34″W) and Santa Rosa (02°13′0″ S, 80°58′0″W) (Fig. 1). One of the most important characteristics in this area is the Equatorial Front located between the Galapagos and the Ecuadorian mainland at about 0°-3°, that divide the cold nutrient-rich waters of the Humboldt Current, as well as its extension, the South Equatorial Current, from warmer, nutrient-poor surface waters in the north (Wooster, 1969). Front hydrographic conditions determine the formation of convergence and divergence areas in surface levels that promote primary production, zooplankton biomass and fish stocks (Jiménez, 2008). Fishermen place their longline gear approximately 40 to 200 miles from the coastline, mainly overnight. This gear consists of a mainline with 120-300 branch lines, each separated by 40-60 m. Branch lines are 11-34 m in length and typically hold a J-shaped hook with a curved shank (Martínez-Ortíz *et al.*, 2015).

Billfishes were sampled from the artisanal fishing fleet between February 2014 and April 2015. Samples were collected principally during morning hours, including almost all of the landed specimens. All billfishes were measured (lower jaw-fork length, L_{LJF} in cm) and the stomach contents were stored in a labeled plastic bag and then preserved on ice for transportation to the laboratory. Samples were frozen at -20°C until they could be analyzed.

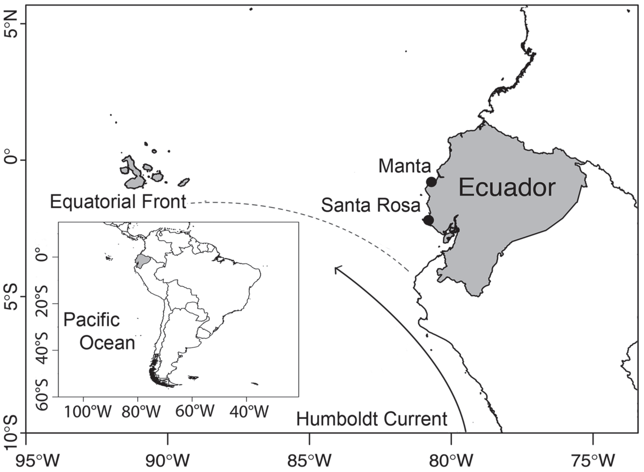

Fig. 1. Map showing the study area. Filled circles represent the sampling localities.

Stomach content analysis. The stomach contents were identified to the lowest taxonomic level, and prey species were counted and weighed to the nearest 0.01 g. Whole fish and cephalopods were identified following Fischer *et al.* (1995a,1995b), and Jereb, Roper (2010). Other prey items were identified based skeletons or beaks through comparison with the project's fish skeleton collection or published identification guides (Clothier, 1950; Clarke, 1962; Iverson, Pinkas, 1971; Wolff, 1984; Clarke, 1986).

Sample size sufficiency. To evaluate if the sample size was sufficient to describe the full diet, a randomized cumulative prey curve was generated using the "vegan" package (Oksanen *et al.*, 2010) in R (R Development Core Team, 2014) based on the lowest taxonomic level identified for each prey (Preti *et al.*, 2012). The mean species accumulation curve (± 2 standard deviations) was plotted from 500 random permutations of the data. The number of samples is assumed to be sufficient to describe the diet when the curve approaches the asymptote (Hurtubia, 1973). When the asymptote was not evident, a straight line to the last four points was fitted and the slope of the line was compared with a line of slope zero, reaching the asymptote when the lines did not differ significantly (Bizzarro *et al.*, 2007).

Data analysis. To determine the importance of each prey in the diet, the prey-specific index of relative importance (%PSIRI) (Brown *et al.*, 2012) was used according to the equation: $\%PSIRI = 0.5\ \%F_O\ (\%P_{Ni} + \%P_{Wi})$, where $\%F_O$ is the percent frequency of occurrence (the number of stomachs containing prey i divided by the total number of stomachs, n), and $\%P_{Ni}$ and $\%P_{Wi}$ are the prey-specific abundances by number or weight, respectively. Prey-specific abundance was calculated with the equation $\%P_{Ai} = \sum_{j=1}^{n} \%A_{ij}\, n_i^{-1}$, where $\%A_{ij}$ is the abundance (by number $\%P_{Ni}$ or weight $\%P_{Wi}$) of prey i in stomach sample j and n_i is the number of stomachs containing prey i. The %PSIRI is a modification of the index of relative importance (IRI) (Pinkas *et al.*, 1971). The measure accounts for %F_O redundancies in the %IRI, and is additive with respect to taxonomic levels. Thus, the %PSIRI of a family will be equal to the sum of the %PSIRI of all of the species contained in this taxon (Brown *et al.*, 2012). The stomach content index (SCI) was compared between species using the Kruskal-Wallis test; Dunn's test was applied for post hoc comparisons. This index was calculated as SCI = (SCW × 100)/PW, expressing stomach content weight (SCW) as a ratio of the total weight of all stomachs (PW) for each individual billfish to estimate its stomach fullness (Shimose *et al.*, 2006).

The similarity of the diet between different species and seasons (rainy season = December to May; dry season = June to November) was evaluated using analysis of similarities (ANOSIM). Prey were grouped by family in order to reduce the number of prey categories in the samples with zero values, thus increasing the effectiveness of the multivariate analysis (White *et al.*, 2004; Espinoza *et al.*, 2013; Szczepanski, Bengtson, 2014). Data were permutated 999 times for a distribution to determine the *p*-value of the ANOSIM's R statistic (R = 0 is identical, R =−1 or 1 is most divergent). The SIMPER analysis (Clarke, Warwick, 2001) was used as a post-hoc test to identify the prey taxa responsible for the dissimilarities in the diet of different billfish species.

Levin's standardized measure of niche breadth (B_a) (Krebs, 1999) was calculated by applying %PSIRI converted to proportions of the different prey identified. This measure varies from 0 to 1, where values close to 0 reflect a specialized diet and values close to 1 indicate a generalized diet (Krebs, 1999). Feeding strategy was assessed using the graphical analysis proposed by Amundsen *et al.* (1996). This procedure, which is a modification of Costello's (1990) graphical method, provides information about prey importance and the predator's feeding strategy by evaluating a two-dimensional plot of prey-specific abundance (%*Pi*) against %F_O, with %*Pi* = (Σ prey *i* weight/Σ weight of all prey in the stomachs containing prey *i*) × 100.

Results

A sample of 273 *M. nigricans* (119-397 cm L_{LJF}), 321 *K. audax* (102-265 cm L_{LJF}), 267 *I. platypterus* (116-272 cm L_{LJF}), and 252 *X. gladius* (100-331 cm L_{LJF}) were analyzed (Fig. 2). For *M. nigricans,* 84 stomachs contained prey, representing a total of 11 taxa. For *K. audax*, 154 stomachs were found to contain food and a total of 16 taxa were identified. For *I. platypterus*, 100 stomachs containing prey were observed, representing a total of 12 taxa. For *X. gladius*, 108 stomachs were found with food, and a total of 12 taxa were identified. None of the cumulative prey curves for the four billfish species reached the asymptote ($p<0.05$).

Diet composition. For *M. nigricans, K. audax*, and *I. platypterus,* fishes were the most important prey category (90.1, 84.2, and 93.7% PSIRI, respectively). For these species, the scombrid *Auxis* spp. made an important contribution to the diet (Tab. 1). For *X. gladius,* cephalopods were the most important group (89.1% PSIRI), with the squid *Dosidicus gigas* (70.3% PSIRI) being the most representative prey (Tab. 1). The stomach content index (SCI) differed significantly between *M. nigricans* (mean ± SD: 1.2 ± 2.0), *K. audax* (mean ± SD: 0.6 ± 1.1), *I. platypterus* (mean ± SD: 1.0 ± 1.1), and *X. gladius* (mean ± SD: 0.9 ± 1.5) (H=23.44, $p < 0.05$). *K. audax* differed significantly in all comparisons (Dunn's test, $p<0.05$).

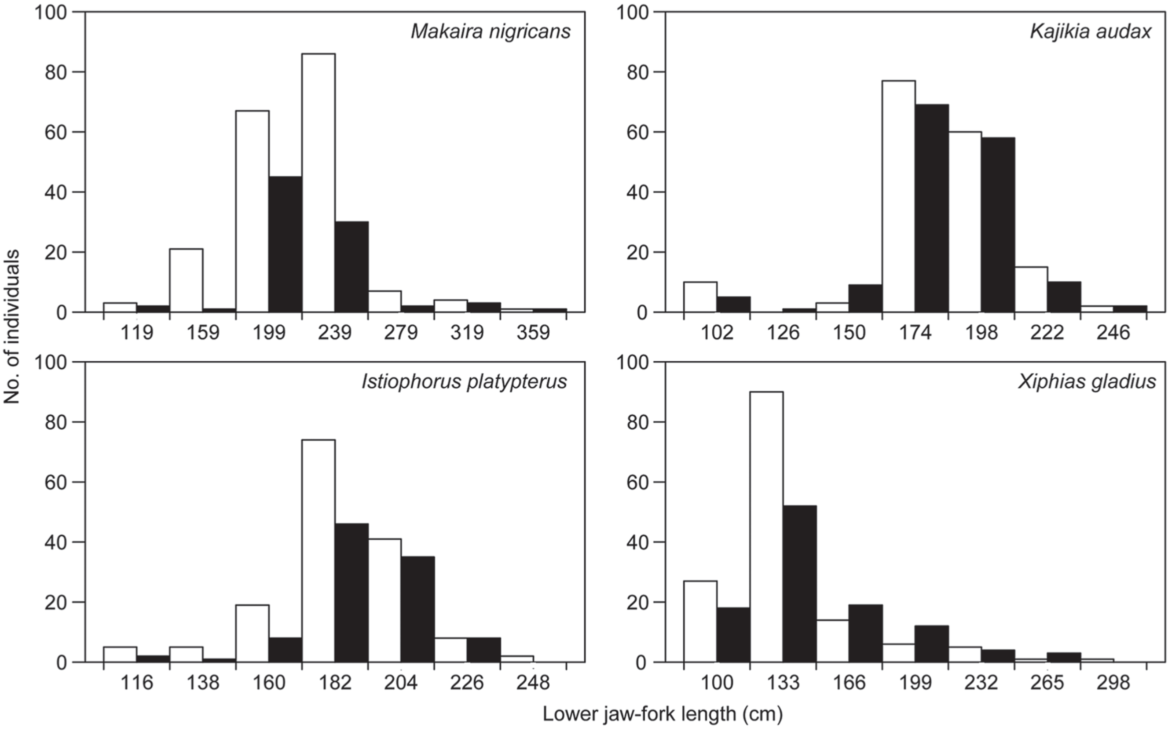

Fig. 2. Combined length-frequency distribution of empty stomachs (white bars) and stomachs containing prey (black bars).

Tab. 1. Diet composition of *Makaira nigricans, Kajikia audax, Istiophorus platypterus and Xiphias gladius* by frequency of occurrence (%F_O), per cent prey- specific abundance (%P_{Ni}), per cent number (%N), prey-specific weight (%P_{Wi}) per cent weight (%W), and prey-specific index of relative importance (%PSIRI). *observed only during dry season, **observed only during rainy season.

	Makaira nigricans						*Kajikia audax*						*Istiophorus platypterus*						*Xiphias gladius*					
	%F_O	%P_{Ni}	%N	%P_{Wi}	%W	% PSIRI	%F_O	%P_{Ni}	%N	%P_{Wi}	%W	% PSIRI	%F_O	%P_{Ni}	%N	%P_{Wi}	%W	% PSIRI	%F_O	%P_{Ni}	%N	%P_{Wi}	%W	% PSIRI
Osteichthyes																								
Aluterus monoceros	1.2	100	1.2	100	1.2	1.2*	0.6	100	0.6	100	0.6	0.6*												
Auxis spp.	57.1	92.1	52.7	91	52	52.3	51.3	85.6	43.9	85	43.6	43.7	75.0	88.8	66.6	89.0	66.8	66.7	2.8	75.0	2.1	70.4	2.0	2.0
Auxis thazard							0.6	100	0.6	100	0.6	0.6	1.0	100	1.0	100	1.0	1.0						
Balistes polylepis							1.3	75.0	1.0	69.1	0.9	0.9*												
Belonidae							1.3	100	1.3	100	1.3	1.3**	3.0	59.6	1.8	56.7	1.7	1.7						
Coryphaena hippurus	1.2	100	1.2	100	1.2	1.2*																		
Decapterus macrosoma							1.3	75.0	1.0	67.6	0.9	0.9												
Etrumeus teres													3.0	32.9	1.0	38.8	1.2	1.1*	1.9	14.6	0.3	6.3	0.1	0.2*
Katsuwonus pelamis	7.1	87.5	6.3	93.5	6.7	6.5	1.9	100	1.9	100	1.9	1.9							1.9	41.7	0.8	34.6	0.6	0.7
Lagocephalus lagocephalus	7.1	86.7	6.2	85.2	6.1	6.1	10.4	59.5	6.2	57.3	6.00	6.1	19.0	64.6	12.3	65.5	12.4	12.4	6.5	74.3	4.8	70.8	4.6	4.7
Merluccius gayi							1.9	86.7	1.7	89.4	1.7	1.7	3.0	76.9	2.3	60.5	1.8	2.1	1.9	53.1	1.0	44.3	0.8	0.9*
Mugil cephalus	6.0	93.3	5.6	95.6	5.7	5.6	1.9	100	1.9	100	1.9	1.9*							1.9	66.7	1.2	61.4	1.1	1.2*
Opisthonema libertate													1.0	100	1.0	100	1.0	1.0*						
Pristigenys serrula	1.2	16.7	0.2	3.8	<0.1	0.1**	1.3	62.5	0.8	91.9	1.2	1.0												
Scombridae	1.2	100	1.2	100	1.2	1.2	0.6	50	0.3	64.8	0.4	0.4	1.0	33.3	0.3	15.0	0.2	0.2						
Scomber japonicus													2.0	22.5	0.5	40.1	0.8	0.6						
Thunnus albacares							1.3	57.1	0.7	99.6	1.3	1.0												
Uninditified osteichthyes	17.9	90.2	16.1	87.4	15.6	15.9	26.0	84.2	21.9	84.3	21.9	21.9	9.0	71.8	6.5	73.4	7.3	6.9	3.7	37.5	1.4	29.1	1.1	1.2
Cephalopoda																								
Ancistrocheirus lesueurii	1.2	100	1.2	100	1.2	1.2*																		
Argonauta spp.							0.6	50.0	0.3	34.5	0.2	0.3							0.9	50.0	0.5	25.0	0.2	0.3**
Dosidicus gigas	8.3	56.5	4.7	67	5.6	5.1	16.2	66.7	10.8	65.6	10.6	10.7	8.0	49.0	3.9	52.1	4.2	4.0	78.7	89.5	70.4	89.2	70.2	70.3
Hyaloteuthis pelagica																			0.9	22.2	0.2	23.6	0.2	0.2
Liocranchia reinhardti													1.0	12.5	0.1	5.4	0.1	0.1						
Loligo sp.													2.0	58.3	1.2	21.7	0.4	0.8**						
Onychoteuthidae	1.2	100	1.2	100	1.2	1.2*													1.9	8.5	0.2	6.1	0.1	0.1**
Sthenoteuthis oualaniensis							0.6	100	0.6	100	0.6	0.6							2.8	86.7	2.4	86.7	2.4	2.4
Thysanoteuthis rhombus																			10.2	57.4	5.8	61.1	6.2	6.0**
Uninditified cephalopoda	2.4	100	2.4	100	2.4	2.4	5.8	72.6	4.2	70.6	4.1	4.2	3.0	52.8	1.6	38.9	1.2	1.4	13.9	64.6	9.0	69.2	10.2	9.6

Based on the results of the ANOSIM, there was a significant difference in dietary composition between billfish species (R=0.31, *p*=0.001). The SIMPER analysis showed that *Auxis* spp. and *D. gigas* were the prey most responsible for differences in the dietary compositions of *X. gladius* and the members of the family Istiophoridae. *M. nigricans* ingested greater amounts of *Auxis* spp. than *K. audax*, while *I. platypterus* consumed more *Auxis* spp. than *M. nigricans* and *K. audax*. *Xiphias gladius* ingested greater amounts of *D. gigas* in all comparisons.

The results of the ANOSIM showed no differences in the diet among seasons for *M. nigricans* (n_{dry} = 42, n_{rainy} = 42, R= 0, *p*=0.55), *K. audax* (n_{dry} = 50, n_{rainy} = 104, R= 0.03, *p*=0.08), and *X. gladius* (n_{dry} = 57, n_{rainy} = 51, R=0.03, *p*= 0.11) diets; however, significant seasonal differences were observed for *I. platypterus* (n_{dry} = 42, n_{rainy} = 58, R= 0.08, *p*=0.004).

Feeding strategy. The Amundsen graphical analysis suggests that these billfish species are specialist consumers with *Auxis* spp. being the dominant prey for *M. nigricans*, *K. audax*, and *I. platypterus,* while *D. gigas* is the main prey of *X. gladius*. Several prey are located in the upper left corner of the diagram, suggesting a high between-phenotype contribution to the niche width, with these prey being consumed by a few specialized individuals (Fig. 3). The niche breadths calculated for *M. nigricans, K. audax, I. platypterus*, and *X. gladius* were narrow (B_a=0.1, 0.1, 0.05, and 0.04, respectively).

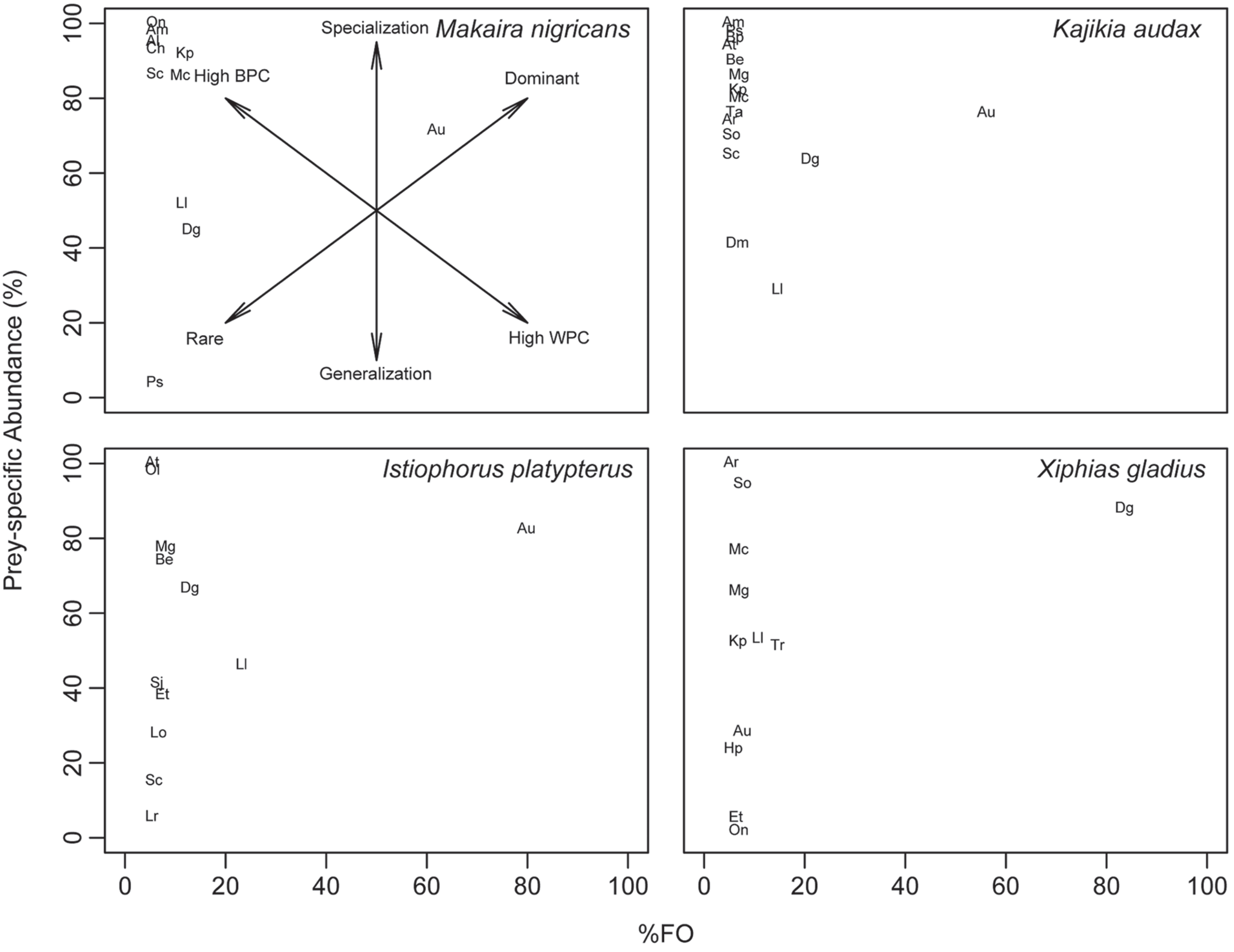

Fig. 3. Prey-specific abundance plotted against frequency of occurrence of prey species. Explanatory axes for foraging patterns are those of Costello (1990) as modified from Amundsen *et al.* (1996). The two diagonal axes represent the importance of prey (dominant *vs.* rare) and the contribution to the niche width (high between-phenotype *vs.* high within-phenotype contribution); the vertical axis defines the predator feeding strategy (specialist *vs.* generalist). Al, *Ancistrocheirus lesueurii*; Am, *Aluterus monoceros*; Ar, *Argonauta* spp.; At, *Auxis thazard*; Au, *Auxis* spp.; Be, Belonidae; Bp, *Balistes polylepis*; Ch, *Coryphaena hippurus*; Dg, *Dosidicus gigas*; Dm, *Decapterus macrosoma*; Et, *Etrumeus teres*; Hp, *Hyaloteuthis pelagica*; Kp, *Katsuwonus pelamis*, Ll, *Lagocephalus lagocephalus*; Lo, *Loligo* sp.; Lr, *Liocranchia reinhardti*; Mc, *Mugil cephalus*; Mg, *Merluccius gayi*; Ol, *Opisthonema libertate*; On, Onychoteuthidae; Ps, *Pristigenys serrula*; Sc, Scombridae; Sj, *Scomber japonicus*; So, *Sthenoteuthis oualaniensis*; Ta, *Thunnus albacares*; Tr, *Thysanoteuthis rhombus*.

Discussion

The number of different prey species identified for all billfishes examined in this study was lower than that reported for other areas of the Pacific Ocean (Abitia-Cárdenas *et al.*, 1997; Abitia-Cárdenas *et al.*, 1999; Arizmendi-Rodríguez *et al.*, 2006; Letelier *et al.*, 2009), where these predators include other taxa, like crustaceans, in their diet (Shimose *et al.*, 2006; Watanabe *et al.*, 2009; Abitia-Cárdenas *et al.*, 2011). These billfish species exploit a smaller group of feeding resources in the Ecuadorian Pacific Ocean coinciding with their narrow niche breadth. In the eastern Pacific Ocean, *M. nigricans*, *K. audax*, *I. platypterus* and *Tetrapturus angustirostris* prey are scarcer near the equator, which may be related to lower productivity (Shimose *et al.*, 2010).

The asymptote was not reached in any of the species accumulation curves despite the large sample size; a number of factors contributed to this, including differential digestion rates, regurgitation of the stomach contents as the result of being caught during fishing (Chase, 2002; Hernández-Aguilar *et al.*, 2013), and the daily periodicity of feeding (Shimose *et al.*, 2006). The low SCI values suggest that these billfishes do not feed actively before dawn or at night in this area. Off the coast of Japan, Shimose *et al.* (2006) observed that the frequency of empty stomachs among *M. nigricans* tended to be higher in the early morning than at any other time of day, suggesting a daily periodicity in feeding. Furthermore, these low values also may be related to the prey availability in our study area, as prey items varies by area in the Pacific Ocean (Shimose *et al.*, 2010).

Fishes were the main prey group for *M. nigricans*, *K. audax* and *I. platypterus* in our study area; similar results have been reported by other authors in the North Pacific (Abitia-Cárdenas *et al.*, 2002; Shimose *et al.*, 2006), off the coast of Taiwan (Tsai *et al.*, 2015), and in the Ecuadorian Pacific Ocean (Rosas-Luis *et al.*, 2016). *Auxis* spp. has been reported as an abundant prey in the eastern Pacific Ocean (Olson, Boggs, 1986; Olson *et al.*, 2014); the importance of *Auxis* spp. for billfishes previously was demonstrated off the coast of Cabo San Lucas, Mexico, for *M. nigricans* (Abitia-Cárdenas *et al.*, 1999), and off Acapulco, Mexico, for *I. platypterus* (Hernández-Aguilar *et al.*, 2013). Scombrid fishes, including *Auxis thazard* and *Auxis rochei* also have been reported as the most abundant prey group for *I. platypterus*, *M. nigricans*, and *K. audax* in the eastern North Pacific Ocean (Shimose *et al.*, 2010).

The most important prey in the billfishes diet varies by geographic location (Shimose *et al.*, 2010). Thus, for *M. nigricans* off the coast of southwestern Japan, *Katsuwonus pelamis* was important and was consumed mainly during the day (Shimose *et al.*, 2006). *Scomber japonicus* was the most abundant prey for *K. audax* off the coast of Cabo San Lucas, Mexico (Abitia-Cárdenas *et al.*, 1997), while the Humboldt squid *D. gigas* was the prey most commonly consumed prey by *I. platypterus* off Mazatlán, Mexico, (Arizmendi-Rodríguez *et al.*, 2006). Our results demonstrate that *Auxis* spp. is an important feeding resource in the Ecuadorian Pacific. The Humboldt squid *D. gigas* was reported previously as a representative prey in the diet of *X. gladius* in the Pacific Ocean (Ibáñez *et al.*, 2004; Castillo *et al.*, 2007; Letelier *et al.*, 2009). This feeding strategy is related to the abundance of this prey species (Nigmatullin *et al.*, 2001) and to the vertical migrations undertaken by both species. During the day, *X. gladius* prey on *D. gigas* in deep waters (Watanabe *et al.*, 2009), whereas at night they consume the same species on the surface when *D. gigas* migrates there in pursuit of its own prey (Rosas-Luis *et al.*, 2011).

A low trophic overlap was observed between *X. gladius* and the istiophorid fishes, which may be the result of differences in their horizontal distributions. *X. gladius* is found in deeper waters than members of the family Istiophoridae, allowing it to exploit other areas as well as shallower waters where it is is found at night (Abascal *et al.*, 2010; Abecassis *et al.*, 2012). Furthermore, horizontal movements in this area (Abascal *et al.*, 2010) as well as the importance of *D. gigas* in the diet may suggest a close prey-predator relationship.

Although istiophorid fishes consume similar diets throughout the Ecuadorian Pacific, there is low trophic overlap between *I. platypterus*, *M. nigricans*, *Tetrapturus angustirostris* and *K. audax* in the eastern North Pacific Ocean where the prey consumed varies by zone and size (Shimose *et al.*, 2010). While stomach content analyses indicate that *M. nigricans* and *K. audax* consume similar diets in the southern Gulf of California, Mexico, stable isotope analyses show significant differences, suggesting niche segregation (Torres-Rojas *et al.*, 2013).

In the Ecuadorian Pacific Ocean, *M. nigricans*, *K. audax*, and *X. gladius* consume distinct prey species during different seasons; however, we did not observe significant differences in our study. In the northern hemisphere off the coast of Cabo San Lucas, Mexico, the number of food components recorded for *M. nigricans* varies between summer and fall (Abitia-Cárdenas *et al.*, 1999). Off the coast of Mexico, *K. audax* shows seasonal and size-related differences in feeding (Abitia-Cárdenas *et al.*, 2011) wherein cephalopods are the most important prey in the summer, but fishes are the primary prey consumed during spring and fall (Abitia-Cárdenas *et al.*, 1997).

The diet of *I. platypterus* varied seasonally; this contrasts with the results reported for this species off Acapulco, Mexico, where no seasonal differences have been observed in diet (Hernández-Aguilar *et al.*, 2013). This seasonal variation may be influenced by the coastal habitat of this species and the seasonal availability of different prey in the area. In the Ecuadorian Pacific, *I. platypterus* consumes clupeid fishes like *Ophistonema libertate* and *Etrumeus teres* only during the dry season. *Ophistonema libertate* is abundant in the central region of Ecuador (Patterson, Santos, 1992) and *E. teres* is mainly distributed inshore, coinciding with the coastal habitat preferences of *I. platypterus* (Nakamura, 1985). *Ophistonema libertate* catches increase at lower temperatures (Patterson, Santos, 1992); thus, the seasonal preference for this prey may be explained by its greater abundance in cooler waters and the opportunistic feeding strategy employed by *I. platypterus* (Rosas-Alayola *et al.*, 2002; Varghese *et al.*, 2013; Tsai *et al.*, 2015).

In conclusion, these specialist predators consume fewer prey species in the Ecuadorian Pacific than do their counterparts in other regions of the Pacific Ocean. Moreover, resource partitioning occurs between members of the family Istiophoridae and *X. gladius.* As an opportunistic predator, *I. platypterus* varies its diet based on prey availability during different seasons.

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