



**Abstract**—Demersal sharks and rays are common yet vulnerable components of the bycatch in tropical bottom-trawl fisheries. Little is known about the elasmobranch assemblages associated with most of these fisheries, particularly within the eastern tropical Pacific. This study characterized the elasmobranch assemblage associated with the shrimp trawl fishery along the Pacific coast of Costa Rica. Between August 2008 and August 2012, 346 trawl hauls were conducted at depths of 18–350 m. These hauls resulted in a sample of 4564 elasmobranchs from 25 species and 13 families. The Panamic stingray (*Urotrygon aspidura*), rasptail skate (*Raja velezi*), brown smoothhound (*Mustelus henlei*), and witch guitarfish (*Zapteryx xyster*) accounted for more than 66% of the elasmobranch abundance within the bycatch. Depth was the main factor influencing the elasmobranch assemblage; species richness was significantly higher at depths <100 m than at other depths. Two groups of elasmobranchs were identified: the first was found in shallow waters (<50 m), and the second was observed at depths of 50–350 m. Sex and size segregation patterns are also influenced by depth. Moreover, we documented the shift of the bottom-trawl fishery toward shallow-water resources—a change that could be problematic considering that elasmobranch diversity is higher in shallow waters.

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## Elasmobranch bycatch associated with the shrimp trawl fishery off the Pacific coast of Costa Rica, Central America

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Overfishing and habitat degradation have caused significant declines in elasmobranch abundance (Dulvy et al., 2008; Ferretti et al., 2008; Dulvy et al., 2014). Most of the global elasmobranch catch is incidental and originates from fisheries that target higher-valued teleosts or crustaceans (Stevens et al., 2000; Walker, 2005; Wehrtmann et al., 2012; Worm et al., 2013). In general, elasmobranch bycatch is not regulated or even reported, especially in developing countries (Barker and Schluessel, 2005; Cheung et al., 2005; Walker, 2005). Furthermore, sharks and rays tend to exhibit slow growth rates, late maturity, and low fecundity, and, therefore, they have a low resilience to intense fishing pressures (Cortés, 2000; Dulvy and Reynolds, 2002; Frisk et al., 2005). The severity of this issue increases in the tropics as a result of the interaction between a high

diversity of elasmobranch species and data-deficient fisheries (Barker and Schluessel, 2005; Cheung et al., 2005; White and Sommerville, 2010).

Several studies conducted in the tropics have reported large declines in the abundance of demersal elasmobranchs associated with bottom-trawl fisheries (e.g., Thailand: Stevens et al., 2000; Australia: Graham et al., 2001; Gulf of Mexico: Shepherd and Myers, 2005). Nevertheless, elasmobranch bycatch has been poorly studied in many tropical regions, including the Eastern Tropical Pacific (ETP; from Mexico to Peru), where abundance trends remain unclear (Mejía-Falla and Navia<sup>1</sup>; López-Mar-

<sup>1</sup> Mejía-Falla, P. A., and A. F. Navia (eds.). 2011. Estadísticas pesqueras de tiburones y rayas en el Pacífico Colombiano. Documento técnico Fundación SQUALUS No. FS0111, 70 p. [Available at [website](#).]

tínez et al., 2010; Clarke et al., 2014). The best information available is obtained from the Pacific coast of Colombia, where significant changes in elasmobranch species composition and abundance have been detected since the 1990s (Mejía-Falla and Navia<sup>1</sup>). Other countries, such as Mexico (López-Martínez et al., 2010), have basic information that is limited to species lists and short-term relative abundance. In the remaining countries of the ETP, even this basic information is not available. Scarcity of published data has hindered attempts to estimate the effect of shrimp trawl fisheries on the elasmobranch assemblage in the ETP (Espinoza et al., 2012; Espinoza et al., 2013; Clarke et al., 2014).

The commercial shrimp trawl fishery of Costa Rica operates exclusively along the Pacific coast, in shallow-water and deepwater areas (Wehrtmann and Nielsen-Muñoz, 2009). The shallow-water (<100 m) fishery began in the 1950s, but the rapid depletion of coastal resources forced the fleet to expand their operations toward deeper waters by the 1980s (Wehrtmann and Nielsen-Muñoz, 2009). The shrimp trawl fishery in Costa Rica has elevated bycatch rates of up to 93% of the total biomass catch (Wehrtmann and Nielsen-Muñoz, 2009; Arana et al., 2013). Moreover, the results of a long-term (2004–2012) fishery-independent monitoring program indicate that a shift has occurred in the overall structure of the demersal community of Costa Rica (Wehrtmann and Nielsen-Muñoz, 2009; Hernáez et al., 2011; Wehrtmann et al., 2012; Espinoza et al., 2012, 2013). Changes in elasmobranch abundance associated with this shift remain poorly understood, given that this monitoring program was designed to study deep-water shrimp resources and the crustacean bycatch associated with the fisheries that target them.

Together, the lack of biological information and the unreliability or nonexistence of landing statistics have limited the development of sustainable management practices and conservation strategies for elasmobranchs in Costa Rica. Given the fishery's current management framework is poorly enforced, the sustainability and environmental impacts have become a serious concern. Concern regarding the effect of this fishery culminated in a constitutional judgment (Sentence No. 2013-10540), enacted by the government of Costa Rica and that prohibited the Costa Rican Institute of Fisheries and Aquaculture (INCOPESCA) from granting or renewing commercial shrimp trawl licenses. All current licenses for this fishery are set to expire in 2018, and an ongoing national decision process will eventually define the legal framework requirements for any sustainable shrimp trawling in Costa Rica.

According to the Code of Conduct for Responsible Fisheries, the effects of a fishery on an ecosystem should be accounted for in management policies (FAO, 1995). In data-deficient situations, information on bycatch may provide estimates of a fishery's effects on an ecosystem. We aimed to characterize the relative composition of elasmobranch bycatch associated with the data-poor shrimp trawl fishery of Costa Rica. More specifically, we examined 1) elasmobranch distribution

patterns in relation to geographic position, depth, year, season, and diel period; 2) the relationship between depth and number of elasmobranch species; 3) sex and size segregation patterns of the most common elasmobranch species; 4) the effects of latitude, depth, season, year, and sampling type on elasmobranch species composition; and 5) and a comparison of our results of species composition with those from historical data. This baseline information on the demersal elasmobranch assemblage of Costa Rica will enable an examination of the effects of management strategies to be implemented in the near future.

## Materials and methods

### Study area

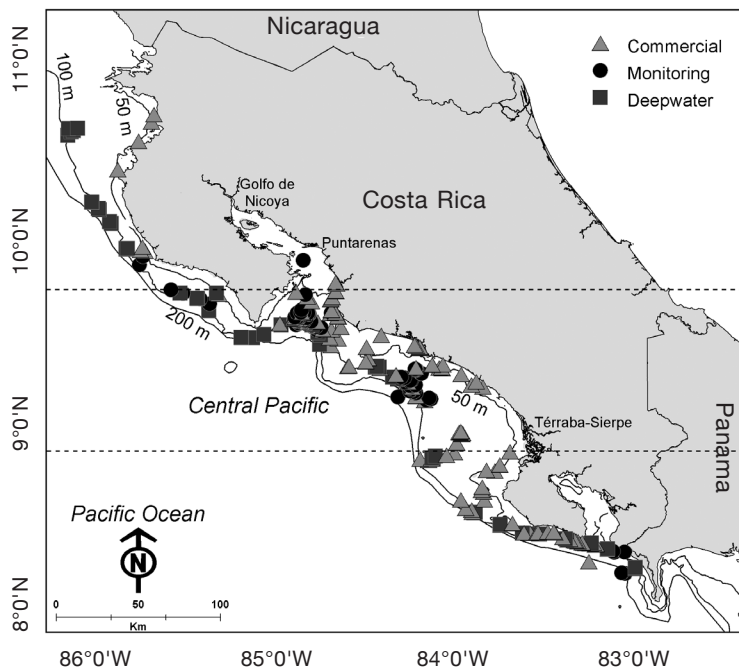
The Pacific coastline of Costa Rica is highly irregular and is approximately 1254 km long, borders 3 large gulfs and a continental shelf that together cover an area of 15,600 km<sup>2</sup> (Fig. 1; Wehrtmann and Cortés, 2009). Costa Rica has pronounced rainy (May–November) and dry (December–April) seasons (Fiedler and Talley, 2006). Although temperature remains relatively constant across seasons (27–30°C), coastal productivity along most of the central and southern Pacific coast increases during the rainy season as a consequence of nutrient input from the largest rivers in this country: the Tempisque, Tárcoles, and Térraba rivers (Fiedler and Talley, 2006; Wehrtmann and Cortés, 2009).

The northern Pacific coast is characterized by strong, seasonal upwelling between December and February and by a limited freshwater input resulting from the absence of large rivers (Jiménez, 2001; Fiedler, 2002). The coast of the central Pacific region is influenced by 2 large estuarine systems, the Golfo de Nicoya and the Térraba-Sierpe delta; both estuaries have large mangrove forests in close proximity to coral communities or rocky reefs (Quesada-Alpízar and Cortés, 2006). The southern Pacific coast has a very steep continental slope and includes the Golfo Dulce tropical fjord (Quesada-Alpízar and Cortés, 2006).

### Sampling

Sampling effort was concentrated near the main fishing port, Puntarenas, located in the northern Pacific region (Fig. 1). Data for this study were collected from 3 types of surveys: 1) deepwater, 2) monitoring, and 3) commercial (Fig. 1). Sampling depth range was divided into shallow (<50 m), intermediate (50–100 m), and deep (>100 m). Bottom trawls were carried out exclusively on soft sand or mud because of sampling gear limitations.

Deepwater surveys were conducted annually along the entire Pacific coastline of Costa Rica to examine the bycatch associated with the deepwater shrimp trawl fishery. A total of 4 deepwater surveys were conducted, 2 during the rainy season (August 2008 and May 2009) and 2 during the dry season (March 2010



**Figure 1**

Map of the geographic regions and sampling locations for elasmobranch bycatch along the Pacific coast of Costa Rica, Central America, during 2010–2012. Solid lines represent the 50-m, 200-m, and 500-m depth contours. Dotted lines represent the boundaries of the central Pacific region.

and February 2011). These surveys followed a systematic sampling design, in which 15-min trawl hauls were conducted at 3 different depths: 150, 250, and 350 m. Hauls were conducted in areas where shrimp were expected to be caught. Strict grids were not used to determine sampling sites in order to respect marine protected areas but were distributed as evenly as possible along the coast.

Monitoring surveys were part of a program designed to analyze crustacean bycatch and were carried out on a monthly basis between 2010 and 2012; they consisted of one nocturnal and one diurnal set of four 20-min trawl hauls conducted at depths of approximately 100, 140, 180, and 220 m (Fig. 1). The location of each haul was determined by the vessel's captain; therefore, the majority of the sampling effort was concentrated in shrimp fishing grounds in the central Pacific region (Fig. 1). These sampling stations were chosen because of their general proximity to the main port of Puntarenas and their high probability of yielding large catches of shrimps, according to the captain's previous experience.

Commercial sampling was carried out during the same trips as those conducted by the monitoring surveys. Commercial sampling points were not selected on the basis of a systematic grid; instead, sampling occurred at locations where the captain had previously targeted shrimps. Sampling occurred on a monthly basis from April 2010 to August 2012 and includ-

ed trawl hauls conducted at depths of 18–350 m.

Sampling for all 3 surveys was carried out aboard commercial shrimp trawlers (22.5 m), equipped with a 270-hp engine and 2 standard epibenthic nets (20.5 m long; mouth opening of 5.35×0.85 m; mesh size of 4.45 cm; and codend mesh size of 3.0 cm). Trawl speed varied between 2.1 and 5.7 km/h during all surveys. Information recorded for each trawl haul included geographic coordinates (latitude and longitude), depth (measured in meters with an installed sonar), and trawl duration (defined as the time, in minutes, during which the net was on the bottom).

Elasmobranchs were identified, classified according to sex, measured (total length [TL] for sharks and disc width [DW] for rays), and weighed (total weight [TW]) (Bussing and López, 1993; Compagno et al., 2005). Maturity stage was assessed by macroscopic examination of the reproductive tract (Conrath, 2005; Clarke et al., 2014).

#### General abundance and distribution patterns

The effects of depth, latitude, year, diel period (day: 0600–1800; night: 1800–0600), and season (rainy and dry) on elasmobranch abundance were examined by using a delta-lognormal generalized linear model (delta-GLM). This method is commonly applied to zero-inflated fishery data, which tend to violate key assumptions of many statistical techniques (Stefánsson, 1996). The delta-GLM approach comprised 2 stages: 1) elasmobranch presence and absence data were modeled by using a binomial GLM with a logit-link, and 2) the observed positive densities were modeled with a log-transformed positive subset, which was assumed to be Gaussian with an identity link function. Because of the differences in the sampling design between the 3 survey methods, separate delta-GLMs were applied to deepwater, monitoring, and commercial data. Total elasmobranch abundance was standardized to catch per unit of effort (CPUE), defined as the number of individuals per hour of trawling.

For deepwater surveys, the independent variables considered in the analyses were depth, latitude, year, and season. Diel period was excluded from the model for deepwater trips because hauls were carried out only during the day. The independent variables considered in models for monitoring and commercial surveys included depth, latitude, year, season, and diel period. In all 3 models, depth and latitude were treated as continuous variables, and year, diel period, and season were treated as factors. In order to avoid strong interactions between depth and longitude, depth and latitude were used to represent the geographic location of each trawl survey. Interactions between variables could not be considered because of the small size of the available

data sets, although we recognize that they would likely be important to consider should a larger data set become available (Venables and Ripley, 2002).

For each delta-GLM, forward selection was used to select separately the binomial model based on presence and absence data and the lognormal model based on log-transformed data for elasmobranch CPUE. The effects that explained more than 5% of the deviance were considered to have a high explanatory power (Tascheri et al., 2010). Chi-square tests were run for the binomial model, and *F*-tests were run for the lognormal model. The performance of the models was also compared by using Akaike information criterion (AIC). Analyses were conducted with R, vers. 3.0.2 (R Core Team, 2013).

Patterns in species richness related to depth were explored with a nonparametric test, Spearman's rank correlation coefficient ( $\rho$ ), because data did not conform to a normal distribution. In this analysis, the independent variable was depth and the dependent variable was the average number of species per trawl haul ( $\alpha=0.05$ ). Data from all survey methods conducted between 2010 and 2012 were pooled for this analysis. General patterns of sex and size segregation were analyzed in relation to depth and diel period by using pooled data from all types of survey conducted between 2010 and 2012. This analysis was undertaken to determine whether a larger proportion of females and immature individuals was caught in shallow waters. Diel period was included in this analysis to detect changes in activity levels associated with sex and maturity stage. Variations in the proportion of females and immature individuals with depth range (<50 m, 50–100 m, >100 m) and diel period (day and night) were examined with a binomial GLM (logit link) (Venables and Ripley, 2002). Only species with at least 100 individuals were used in this analysis.

### Elasmobranch assemblage

The importance of depth on elasmobranch assemblage was further explored with PRIMER<sup>2</sup>, vers.6.2.1 (PRIMER-E Ltd., Plymouth, UK). We used data from all surveys conducted in the central Pacific region during 2010–2012. A matrix was constructed with the transformed species CPUE per haul in columns (log [(individuals/hour)+1]) and depth ranges in rows. To reduce the influence of extremely abundant species, CPUE was transformed (Clarke and Warwick, 2001). Rare species caught in less than 5 trawl hauls were excluded from our analyses (Clarke and Warwick, 2001). Differences in elasmobranch assemblages among depth ranges were examined by using an analysis of similarity (ANOSIM;  $\alpha=0.05$ ; Clarke and Warwick, 2001). A similarity percentage (SIMPER) analysis was used to identify species that showed the highest contribution

to the dissimilarities among depth ranges (Clarke and Warwick, 2001).

Redundancy analyses (RDAs) were applied to examine the relationship between environmental variables and elasmobranch assemblages (Borcard et al., 2011). An RDA is a constrained ordination technique that combines a multivariate, multiple linear regression with a principal component analysis. We performed RDAs that were based on covariance matrixes to confer a higher weight to the common species in these analyses.

A separate RDA was conducted for each survey type to avoid biases that may have resulted from combining the 3 survey methods. For all analyses, a Hellinger transformation was applied to the species CPUE to minimize the effects of the large number of zeros in the data set (Borcard et al., 2011). Rare species (caught in less than 5 trawl hauls) were excluded from the analysis to prevent strong distorting effects. The environmental variables considered in the RDAs were standardized depth, standardized latitude, year, season, and diel period. The statistical significance of the ordination axes was examined with a Monte Carlo permutation test. Results were plotted on a correlation biplot, in which angles between species and environmental variables represent correlations between variables (Borcard et al., 2011). These analyses were conducted by using the vegan library in R, vers. 3.0.2 (R Core Team, 2013).

### Results

For this study, data were examined from 346 trawl hauls conducted along the entire Pacific coast of Costa Rica from 2008 to 2012. Of these hauls, 108 were from deep water surveys, 111 were from monitoring surveys, and 127 were from commercial surveys (Fig. 1). Commercial and monitoring sampling efforts were highest in the central Pacific region, where 76% of commercial hauls and 91% of monitoring surveys were conducted (Table 1). Most commercial trawl hauls occurred at depths <100 m, and the majority of monitoring and all deepwater trawl hauls were conducted in deeper waters (Table 1). The average standardized elasmobranch abundance was 9.37 individuals/hour in deep water surveys, 6.96 individuals/hour in monitoring surveys, and 7.92 individuals/hour in commercial surveys.

### Elasmobranch diversity and distribution patterns

During the entire sampling period, 4564 elasmobranchs from 25 species, 13 families, and 6 orders were captured as bycatch (Table 2). Four species represented more than 66% of the entire elasmobranch abundance: Panamic stingray (*Urotrygon aspidura*) accounted for 26%, rasptail skate (*Raja velezi*) contributed 16%, brown smoothhound (*Mustelus henlei*) composed 15%, and witch guitarfish (*Zapteryx xyster*) accounted for 9%. Of the remaining 21 species, 10 were relatively

<sup>2</sup> Mention of trade names or commercial companies is for identification purposes only and does not imply endorsement by the National Marine Fisheries Service, NOAA.

**Table 1**

Sampling effort for surveys of bycatch of elasmobranchs conducted along the Pacific coast of Costa Rica, Central America, in 2008–2012 at 3 depth ranges: shallow (<50 m), intermediate (50–100 m), and deep (>100 m). Number of trawling hours (h) and trawl hauls (Hauls) per geographic area and depth range. The highest sampling effort occurred in the central geographic region at depths <50 m with commercial surveys (underlined).

Region	Depth	2008		2009		2010		2011		2012		Total	
		h	Hauls	h	Hauls	h	Hauls	h	Hauls	h	Hauls	h	Hauls
Commercial sampling													
Northern	<50 m	–	–	–	–	–	–	3.7	2	5.9	1	9.6	3
	50–100 m	–	–	–	–	10.3	2	9.3	3	–	–	24.1	5
Central	<50 m	–	–	–	–	24.6	5	61.8	14	28.6	6	115.0	25
	50–100 m	–	–	–	–	115.2	20	45.1	10	62.9	14	223.1	44
Southern	>100 m	–	–	–	–	29.6	14	18.9	9	6.2	4	54.7	27
	50–100 m	–	–	–	–	–	–	6.1	1	–	–	6.1	1
	>100 m	–	–	–	–	12.5	6	–	–	53.2	16	65.7	22
Monitoring sampling													
Northern	50–100 m	–	–	–	–	6.0	1	–	–	–	–	6.0	1
	> 100 m	–	–	–	–	1.4	4	–	–	–	–	1.4	4
Central	<50 m	–	–	–	–	0.7	2	–	–	–	–	0.7	2
	50–100 m	–	–	–	–	2.7	8	4.0	12	2.2	6	8.9	26
Southern	>100 m	–	–	–	–	6.5	19	11.6	35	6.6	19	24.7	73
	50–100 m	–	–	–	–	0.3	1	–	–	–	–	0.3	1
	>100 m	–	–	–	–	1.5	4	–	–	–	–	1.5	4
Deepwater sampling													
Northern	>100 m	2.1	8	2.1	8	2.1	8	2.6	10	–	–	8.9	34
Central	>100 m	3.2	12	3.1	12	3.0	12	2.7	10	–	–	12.0	46
Southern	>100 m	2.3	8	2.0	8	1.7	7	1.3	5	–	–	7.0	27
Total		12.1	27	7.3	28	218.0	113	167.3	111	165.6	66	570.0	345

common (1–5% of total abundance) and 11 were rare (<1% of total abundance).

Species richness and distribution patterns of elasmobranchs were examined across depths. Overall, 2279 individuals of 24 species were recorded at shallow depths (<50 m), 1642 individuals from 14 species were found at depths between 50 and 100 m, and only 643 individuals from 7 species were observed at depths >100 m (Table 2). The number of species caught per trawl haul varied from 0 through 9. A significant, negative relationship was detected between the average number of species per haul and depth (Spearman's  $\rho = -0.831$ ,  $P < 0.001$ ; Fig. 2).

Body size ranged from 21.8 to 138.0 cm TL for sharks and from 2.6 to 107.7 cm DW for rays (Fig. 3). The large number of small species (<50 cm TL or DW) were mainly from the families of Narcinidae, Urotrygonidae, and Rajidae. The sicklefin smoothhound (*Mustelus lunulatus*), prickly shark (*Echinorhinus cookei*), Pacific angel shark (*Squatina californica*), and long-tail stingray (*Dasyatis longa*) were the largest species recorded; and these species collectively represented nearly 5% of the total elasmobranch abundance. The percentage of species that were small (<50 cm TL) was larger in shallow waters (depths <50 m, Fig. 3A) than at other depths (Fig. 3, B and C). Although most species presented narrow depth ranges, trends in size

were apparent for some species with wide depth distributions (Fig. 3). Large, adult-size brown smoothhound dominated all depth categories. Smaller individuals of the rasptail skate were found in the shallower limit of the depth range for this species: 50–100 m. Likewise, average sizes of the sicklefin smoothhound, Peruvian torpedo (*Torpedo peruana*), and witch guitarfish increased across depth ranges (Fig. 3).

Elasmobranch presence in deepwater surveys was low, given that elasmobranchs were absent from 63% of the trawl hauls. Of the surveys in which elasmobranchs were present, 16.6% had a CPUE of 1–10 individuals/hour and 20.4% had CPUE of 10–152 individuals/hour. The delta-GLM applied to the deepwater survey data revealed that depth had a significant effect on the density of elasmobranch CPUE, and depth and latitude had a significant effect on the proportion of positive trawl hauls (Table 3). In monitoring surveys, we found that elasmobranchs were absent from 65.8% of all trawl hauls. The lognormal submodel of the delta-GLM applied to monitoring data did not detect significant effects. In contrast, the binomial submodel revealed that depth, latitude, and year had significant effects on elasmobranch presence (Table 3). In commercial surveys, 17.8% of trawl hauls did not result in elasmobranch catch. The delta-GLM for commercial data indicated that depth was the only significant factor

**Table 2**

For the elasmobranch species captured as bycatch in the shrimp trawl fisheries of the Pacific coast of Costa Rica, Central America, during 2008–2012, total number of individuals (*N*); percentages of the species sample caught in commercial (C), monitoring (M), and deepwater (D) surveys; percentages of abundance per depth category (<50 m, with 2279 individuals in total; 50–100 m, with 1642 individuals in total; and >100 m, with 643 individuals in total). Data for the most abundant species are presented in bold type.

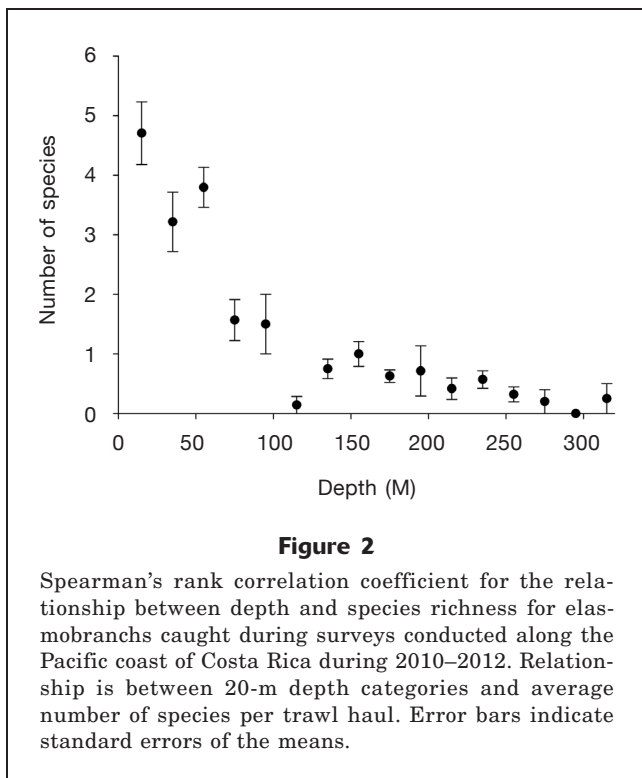
Order and family	Common name (scientific name)	<i>N</i>	Survey type			Depth range		
			C	M	D	<50 m	50–100 m	>100 m
<b>Carcharhiniformes</b>								
Carcharhinidae	Pacific sharpnose shark ( <i>Rhizoprionodon longurio</i> )	6	100	–	–	0.26	–	–
Sphyrnidae	Scalloped hammerhead ( <i>Sphyrna lewini</i> )	4	100	–	–	0.18	–	–
Triakidae	Brown smoothhound ( <i>Mustelus henlei</i> )	<b>696</b>	<b>55.9</b>	<b>21.3</b>	<b>22.8</b>	<b>0.44</b>	<b>23.45</b>	<b>46.81</b>
	Sicklefin smoothhound ( <i>Mustelus lunulatus</i> )	122	99.2	0.8	–	0.26	7	0.16
<b>Squaliformes</b>								
Echinorhinidae	Prickly shark ( <i>Echinorhinus cookei</i> )	11	–	–	100	–	–	1.71
<b>Squatiniiformes</b>								
Squatinae	Pacific angel shark ( <i>Squatina californica</i> )	57	94.7	3.5	1.8	0.04	3.23	0.47
<b>Myliobatiformes</b>								
Dasyatidae	Longtail stingray ( <i>Dasyatis longa</i> )	35	100	–	–	1.14	0.55	–
Myliobatidae	Spotted eagle ray ( <i>Aetobatus laticeps</i> )	2	100	–	–	0.09	–	–
	Golden cownose ray ( <i>Rhinoptera steindachneri</i> )	39	100	–	–	0.13	2.19	–
Urotrygonidae	Panamic stingray ( <i>Urotrygon aspidura</i> )	<b>1178</b>	<b>100</b>	–	–	<b>51.56</b>	<b>0.18</b>	–
	Blotched stingray ( <i>Urotrygon chilensis</i> )	189	100	–	–	7.81	0.67	–
	Denticled roundray <i>Urotrygon cimar</i>	1	100	–	–	0.04	–	–
	Spiny stingray ( <i>Urotrygon munda</i> )	1	100	–	–	0.04	–	–
	Dwarf stingray ( <i>Urotrygon nana</i> )	16	100	–	–	0.7	–	–
	Thorny stingray ( <i>Urotrygon rogersi</i> )	143	100	–	–	6.27	–	–
Gymnuridae	California butterfly ray ( <i>Gymnura marmorata</i> )	1	100	–	–	0.04	–	–
<b>Rajiformes</b>								
Rajidae	Equatorial skate ( <i>Raja equatorialis</i> )	88	100	–	–	1.97	2.62	–
	Rasptail skate ( <i>Raja velezi</i> )	<b>750</b>	<b>89.6</b>	<b>3.6</b>	<b>6.8</b>	<b>0.04</b>	<b>34.65</b>	<b>27.99</b>
	Cortez skate ( <i>Raja cortezensis</i> )	1	100	–	–	0.04	–	–
Rhinobatidae	Whitesnout guitarfish ( <i>Rhinobatos leucorhynchus</i> )	90	100	–	–	3.91	0.06	–
	Witch guitarfish ( <i>Zapteryx xyster</i> )	<b>393</b>	<b>96.4</b>	<b>3.6</b>	–	<b>2.63</b>	<b>19.98</b>	<b>0.78</b>
<b>Torpediniformes</b>								
Narcinidae	Bullseye electric ray ( <i>Diplobatis ommata</i> )	206	100	–	–	8.86	0.24	–
	Giant electric ray ( <i>Narcine entemedor</i> )	152	100	–	–	6.06	0.85	–
	Vermiculate electric ray ( <i>Narcine vermiculatus</i> )	165	100	–	–	7.24	–	–
Torpedinidae	Peruvian torpedo ( <i>Torpedo peruana</i> )	<b>218</b>	<b>59.6</b>	<b>22.9</b>	<b>17.4</b>	<b>0.22</b>	<b>4.32</b>	<b>22.08</b>
Total		4564				100	100	100

in both the lognormal and binomial submodels (Table 3).

Many of the elasmobranch species observed were segregated by sex and maturity stage (Table 4). Binomial GLMs indicated that neither depth nor diel period had a significant effect on sex ratios in the catch of brown smoothhound, sicklefin smoothhound, blotched stingray (*Urotrygon chilensis*), thorny stingray (*U. rogersi*), rasptail skate, witch guitarfish, bullseye electric ray (*Diplobatis ommata*), giant electric ray (*Narcine entemedor*), or vermiculate electric ray (*N. vermiculatus*) (Table 4). Conversely, depth had a significant effect on the sex ratios of the catch of Panamic stingray (Table 4): females of this species dominated at shallow depths (<50 m) but were absent from depths >50 m (Fig. 4).

Diel period had a significant effect on the sex ratios of the catch of Peruvian torpedo; more females were caught during the day than during the night (Table 4). For all depths and diel periods, the proportion of males in the catch of brown smoothhound was higher than the proportion of females. Sex ratios were skewed toward females in the catch of species that were distributed mainly in shallow waters (depths <50 m): namely in the catches of Panamic stingray, thorny stingray, bullseye electric ray, giant electric ray, and vermiculate electric ray (Fig. 4A).

Binomial GLMs indicated that depth and diel period did not influence maturity ratios of the catch of sicklefin smoothhound, blotched stingray, witch guitarfish, bullseye electric ray, vermiculate electric ray, and Peru-



vian torpedo (Table 4). Conversely, depth was a factor that significantly influenced maturity ratios of brown smoothhound, rasptail skate, and giant electric ray. Although mature brown smoothhound were more abundant at all depths, the proportion of immature individuals peaked at the depths of 50–100 m (Fig. 4). For the rasptail skate and giant electric ray, proportions of immature individuals were higher in the shallow limits of these species' depth ranges (50–100 m and <50 m, respectively) (Fig. 4). Maturity ratios in the catch of Panamic stingray and thorny stingray varied significantly among diel periods; proportionally more immature individuals were caught during the day than during the night (Fig. 5). A high proportion (>50%) of immature Peruvian torpedo was recorded across all depths and diel periods. For the witch guitarfish, a high proportion (73%) of immature individuals was found at shallow depths (<50 m), and a high proportion (57%) of mature individuals was found at depths of 50–100 m. A higher abundance of mature round stingrays (*Urotrygon* spp.) was observed at shallow depths than at other depths.

#### Elasmobranch assemblage

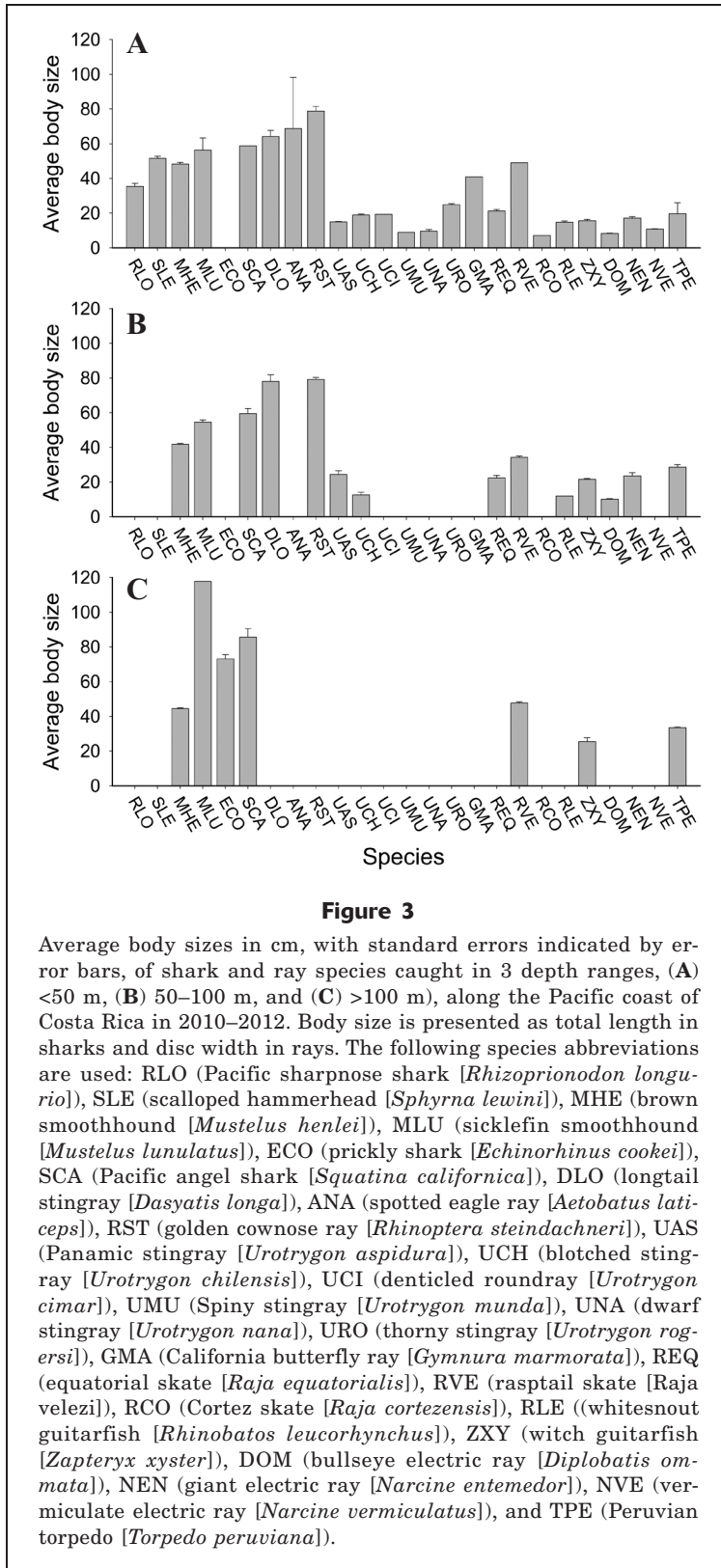
The elasmobranch assemblage varied significantly among depths (ANOSIM  $R=0.710$ ,  $P=0.001$ ). The elasmobranch assemblage in shallow waters differed from the assemblages in intermediate-depth ( $R=0.792$ ,  $P=0.001$ ) and deep ( $R=0.934$ ,  $P=0.001$ ) waters. The shallow-water assemblage was characterized by the

dominance of Panamic stingray (0.00–138.70 individuals/hour); the remaining species were less abundant (0.01–2.15 individuals/hour). The deepwater assemblage was composed of rasptail skate, brown smoothhound, witch guitarfish, Peruvian torpedo, prickly shark, and Pacific angel shark, of which the first 2 species were most abundant. The elasmobranch assemblage in intermediate-depth waters was characterized by a combination of both shallow-water and deepwater species. Differences in the elasmobranch assemblage between deep and intermediate-depth waters were the smallest ( $R=0.474$ ,  $P=0.001$ ). A SIMPER analysis revealed that Panamic stingray, rasptail skate, brown smoothhound, witch guitarfish, and Peruvian torpedo were also responsible for 49.8–75.8% of the differences in the elasmobranch assemblage between depths.

In the RDA applied to deepwater survey data, depth, latitude, year, and season represented 13% of the variance in species data (Fig. 6A). The biplot that resulted from this analysis displays 97.2% of this variability in its first 2 axes, and all canonical axes were significant (Fig. 6A;  $F=4.224$ ,  $P=0.002$ ). This RDA biplot shows the brown smoothhound, rasptail skate, and Peruvian torpedo as a group. This group was negatively correlated with depth and strongly related to the years 2008 and 2009. The species in this group were separated mainly by latitude: the brown smoothhound was slightly more associated with southern latitudes, and the Peruvian torpedo was slightly more associated with northern latitudes. The prickly shark was placed separately and presented a strong positive correlation with depth.

The RDA for monitoring survey data explained 12% of the variability between environmental variables and species data (Fig. 6B). A biplot captures 91.4% of this variability, and all canonical axes were significant (Fig. 6B;  $F=3.222$ ,  $P=0.002$ ). Although all species are grouped quite closely together in this biplot, the strongest associations were between the witch guitarfish and the rasptail skate. All species had negative correlations with depth and positive associations with the diel period of 0600–1800 and the rainy season. As in the deepwater RDA, the brown smoothhound was more common at the southern limit of the latitudinal range, and the Peruvian torpedo and witch guitarfish were associated with the northern limits of the latitudinal range.

In the RDA applied to commercial survey data, depth, latitude, diel period, season, and year explained 10% of the variance in species data (Fig. 6C). The biplot that resulted from this analysis represents 76.9% of this variance, and all canonical axes were significant (Fig. 6C;  $F=2.772$ ,  $P=0.002$ ). This RDA biplot separates 2 groups of species, mainly according to depth and latitude. The shallow-water assemblage was composed of golden cownose ray (*Rhinoptera steindachneri*), whitesnout guitarfish (*Rhinobatos leucorhynchus*), giant electric ray, bullseye electric ray, vermiculate electric ray, longtail stingray, equatorial skate (*Raja equatorialis*), blotched stingray, thorny stingray, and Panamic stingray. The deepwater assemblage was composed of witch guitarfish, sicklefin smoothhound, brown smoothhound,



Pacific angel shark, and the Peruvian torpedo. Within this group, the Peruvian torpedo had the strongest positive correlation with depth, whereas the witch guitarfish and Pacific angel shark had the strongest negative correlation with depth. The deepwater assemblage was weakly associated with the night, the rainy season, and the years 2010 or 2012.

## Discussion

### Elasmobranch diversity and distribution patterns

The results of our study revealed that elasmobranch bycatch of the shrimp trawl fishery in Costa Rica comprised 25 species, which account for more than 35% of the species richness reported for the Pacific coast of Costa Rica (Bussing and López, 2009). Most of these bycatch species have wide distribution ranges that include the entire ETP. Consequently, the few studies available on elasmobranch bycatch from shrimp fisheries in this region reveal similar species compositions (Gulf of California, Mexico: López-Martínez et al., 2010; Pacific coast of Colombia: Mejía-Falla and Navia<sup>1</sup>) (Table 5). The strong similarity between elasmobranch bycatch in Costa Rica and Colombia (14 species in common) reflects the biogeographic patterns proposed by Robertson and Cramer (2009). Costa Rica and Colombia form part of the Panamic biogeographic province that is composed solely of tropical fishes (Robertson and Cramer, 2009), and the Gulf of California belongs to the Cortez biogeographic province, which is characterized by the convergence of temperate, subtropical, and tropical marine fish fauna (Mora and Robertson, 2005; Rodríguez-Romero et al., 2008).

Our results revealed that the elasmobranch assemblage varies along the Pacific coast of Costa Rica (~1254 km of coastline). This variation is probably due to differences in oceanographic conditions along the coastline, with the north affected by upwelling and the central and South Pacific affected by freshwater inflows. Delta-GLMs indicated that latitude was an important predictor of elasmobranch presence in deepwater and monitoring surveys; however, these differences may reflect the higher sampling efforts in deep waters of the northern and southern Pacific areas. Therefore, the effect of latitude on elasmobranch diversity needs to be interpreted with caution. The uneven sampling effort along the coast was the result of an overall dependence on the presence of commercial shrimp trawl-



**Table 3**

Results of the 3 delta-lognormal generalized linear models (delta-GLMs) applied to abundance (CPUE) of elasmobranchs from deepwater, monitoring, and commercial surveys conducted along the Pacific coast of Costa Rica during 2008–2012: degrees of freedom (df), deviance change (Deviance), residual degrees of freedom (Residual df), residual deviance (Res. dev.), Akaike information criterion (AIC), and the probability ( $P$ ) from the  $F$ -test for lognormal submodels or chi-square test for binomial models.

Model	df	Deviance	Residual df	Res. dev.	AIC	$P$
Deepwater delta-GLM						
Lognormal submodel						
Intercept			39	52.43	128.34	
Depth	1	5.92	38	46.51	125.54	0.03
Binomial submodel						
Intercept	1		107	141.45	143.45	
Depth	1	13.12	106	128.32	132.32	<0.01
Latitude	1	6.10	105	122.22	128.22	0.01
Monitoring delta-GLM						
Lognormal submodel						
Intercept	1		37	62.41	130.69	
Depth	1	4.76	36	57.65	129.68	0.09
Binomial submodel						
Intercept			110	142.65	144.65	
Depth	1	20.33	109	122.32	126.32	<0.01
Latitude	1	6.08	108	116.24	122.24	0.01
Year	2	11.00	106	105.24	115.24	<0.01
Commercial delta-GLM						
Lognormal submodel						
Intercept			103	189.15	361.35	
Depth	1	12.54	102	176.61	356.21	<0.01
Binomial submodel						
Intercept	1		126	120.16	122.16	
Depth	1	18.90	125	101.25	105.25	<0.001

ing vessels. Although sampling depths from monitoring surveys were predefined, the location of sampling stations was chosen by the captain. Consequently, both commercial and monitoring surveys were concentrated in the central Pacific region.

The nonrandom sampling design of both monitoring and commercial surveys may have introduced biases in the estimates of distribution and abundance that must be considered when interpreting the results of our study (e.g., elasmobranch abundance and composition covaries with shrimp abundance). Moreover, it is likely that interactions between environmental variables drive patterns in both species distribution and community structure; however, interactions were not explored because of the small data set. The small sample size may also have limited our ability to detect patterns in elasmobranch diversity across the examined explanatory variables (e.g., depth, latitude, geographic region, year, season, and diel period). This limited ability is the most probable cause of the low percentage of the variance in species abundance data that was explained by the RDAs.

Our findings indicate that depth is a major factor influencing elasmobranch assemblages along the Pacific

coast of Costa Rica. Both species richness and abundance peaked in shallow waters and decreased with the increasing depth. This feature is common and has been reported previously for both demersal (MacPheron, 2003; Massuti and Moranta, 2003; Gouraguine et al., 2011) and pelagic (Smith and Brown, 2002) elasmobranch species. Nearshore environments are very heterogeneous and tend to concentrate a large number of species with small depth ranges, whereas a small number of species with large depth ranges inhabit homogeneous deepwater environments (Smith and Brown, 2002; Knip et al., 2010; Mejía-Falla and Navia<sup>1</sup>). Depth-related changes in environmental factors, such as temperature and productivity, may partially explain observed trends in species richness (Levinton, 1995).

Temperature is known to be an important factor influencing species richness, given that it may affect speciation rates (Allen et al., 2002). Productivity can also influence species richness; for example, areas with higher primary productivity tend to have species with high trophic levels, large body sizes, and high energetic requirements (Smith and Brown, 2002; Leathwick et al., 2006; Knip et al., 2010), including sharks and rays (Priede et al., 2006).

**Table 4**

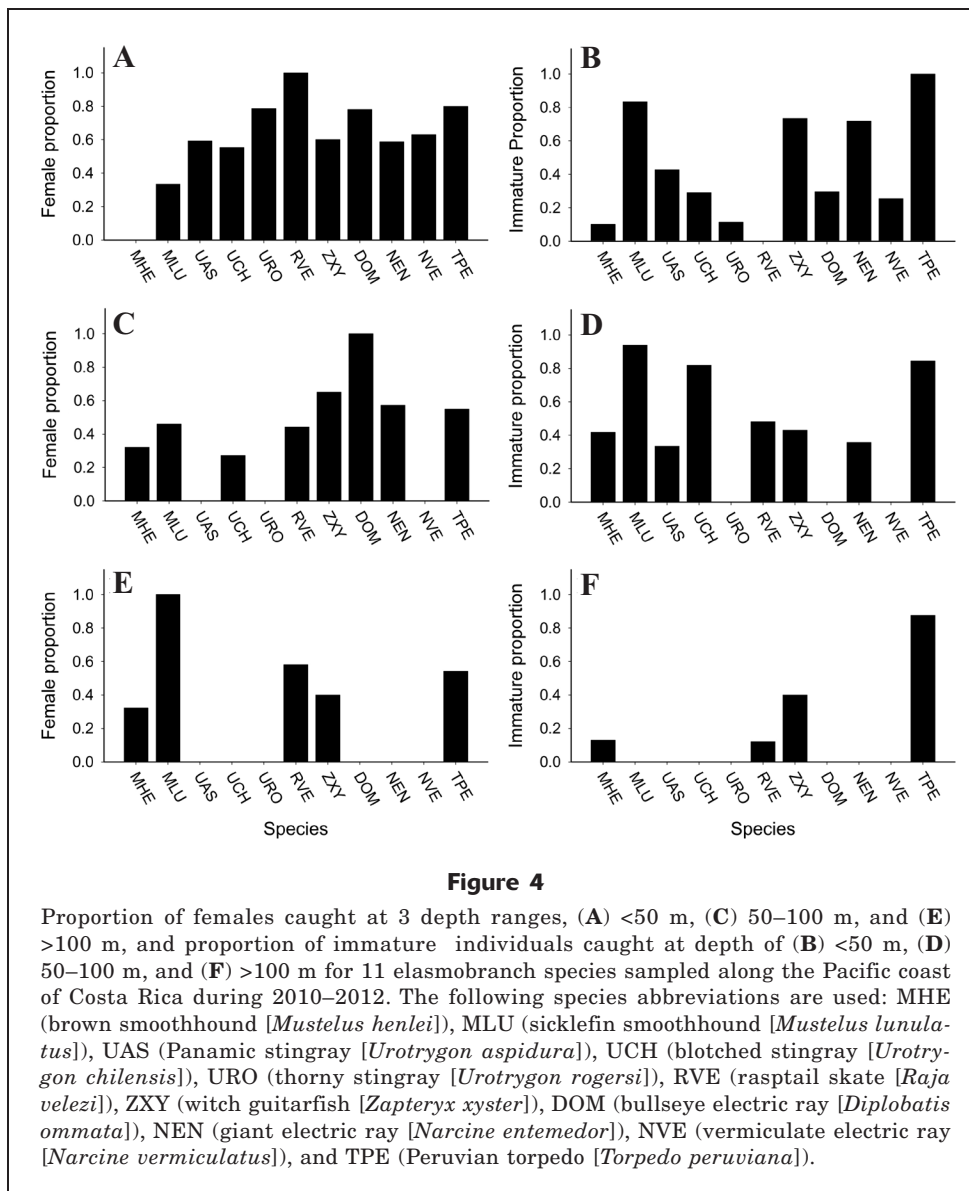
Spatial distribution for sex and maturity ratios of the elasmobranch assemblage, by depth range (<50 m, 50–100 m, or >100 m) and diel period (day or night), along the Pacific coast of Costa Rica, Central America, in 2010–2012. The degrees of freedom (df), deviance, residual deviance (Res. dev), and probability (*P*) of the binomial generalized linear models (GLMs) applied to both maturity and sex ratios of the most abundant elasmobranch species. Significant *P*-values are in bold ( $\alpha=0.05$ ). The following species abbreviations are used: MHE (brown smoothhound [*Mustelus henlei*]), MLU (sicklefin smoothhound [*Mustelus lunulatus*]), UAS (Panamic stingray [*Urotrygon aspidura*]), UCH (blotched stingray [*Urotrygon chilensis*]), URO (thorny stingray [*Urotrygon rogersi*]), RVE (rasptail skate [*Raja velezi*]), ZXY (witch guitarfish [*Zapteryx xyster*]), DOM (bullseye electric ray [*Diplobatis ommata*]), NEN (giant electric ray [*Narcine entemedor*]), NVE (vermiculate electric ray [*Narcine vermiculatus*]), and TPE (Peruvian torpedo [*Torpedo peruviana*]).

Species	Factors	Sex ratios				Maturity ratios			
		df	Deviance	Res. dev.	<i>P</i>	df	Deviance	Res. dev.	<i>P</i>
MHE	Intercept	1	358.0			1	612.1		
	Depth	2	7.7	350.4	0.43	2	50.0	562.1	<b>0.04</b>
	Diel period	1	9.7	340.7	0.15	1	16.5	545.6	0.14
MLU	Intercept	1	24.2			1	53.5		
	Depth	2	2.0	22.3	0.41	2	6.1	47.5	0.56
	Diel period	1	0.0	22.3	0.95	1	0.0	47.5	0.98
UAS	Intercept	1	25.4			1	74.9		
	Depth	1	5.4	20.0	<b>0.04</b>	1	0.1	74.8	0.83
	Diel period	1	1.5	18.6	0.27	1	29.0	45.8	<b>0.00</b>
UCH	Intercept	1	35.0			1	43.4		
	Depth	1	3.3	31.7	0.47	1	12.3	31.1	0.20
	Diel period	1	3.2	28.4	0.47	1	1.8	29.3	0.59
URO	Intercept	1	8.7			1	21.3		
	Diel period	2	0.0	8.6	0.99	1	18.3	3.0	<b>0.01</b>
RVE	Intercept	1	196.1			1	538.0		
	Depth	2	10.4	185.7	0.16	2	70.3	467.7	<b>0.01</b>
	Diel period	1	0.2	185.6	0.80	1	2.1	465.5	0.58
ZXY	Intercept	1	118.8			1	222.6		
	Depth	2	1.8	117.1	0.69	2	19.3	203.2	0.09
	Diel period	1	0.3	116.8	0.74	1	6.9	196.3	0.19
DOM	Intercept	1	23.5			1	12.5		
	Depth	1	1.9	21.6	0.47	1	2.8	9.8	0.20
	Diel period	1	1.6	19.9	0.51	1	1.8	8.0	0.29
NEN	Intercept	1	31			1	34.2		
	Depth	1	0.0	31.0	0.92	1	7.0	27.2	<b>0.02</b>
	Diel period	1	1.2	29.8	0.34	1	2.1	1.8	0.19
NVE	Intercept	1	40.9			1	40.9		
	Diel period	1	19.4	21.5	0.10	1	1.2	21.5	0.10
TPE	Intercept	1	105.5			1	77.3		
	Depth	2	1.4	104.0	0.54	2	1.8	75.5	0.51
	Diel period	1	7.0	97.1	<b>0.02</b>	1	0.4	75.2	0.60

The elasmobranch assemblages caught by the shrimp trawl fishery were slightly influenced by diel period. Most elasmobranch species display higher activity levels during the night—a characteristic mainly related to foraging or social refuging behaviors (Wearmouth and Sims, 2008; Jacoby et al., 2012; Espinoza et al., 2011). Catch of elasmobranchs in trawl hauls, therefore, is expected to be higher during the day than at night; however, very few studies have addressed diel periodicity of bycatch (Molina and Cooke, 2012). The results of this

study support the assumption that elasmobranch catch is higher during the day than at night.

Although the small sample size prevented us from detecting clear patterns for most species, a higher proportion of female Peruvian torpedo and immature round stingrays were found during the day than at night. The higher abundance of Peruvian torpedo during the day may be a result of its feeding behavior. The Pacific electric ray (*Torpedo californica*) is a bottom ambush predator during the day and actively for-



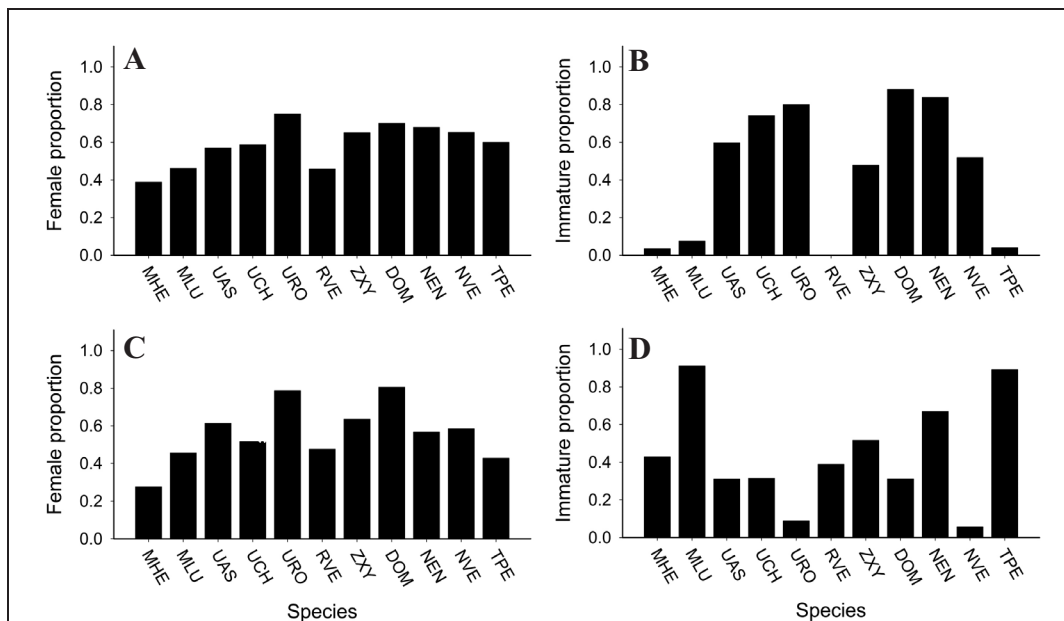
ages in the water column during the night (Lowe et al., 1994). If feeding habits of the Peruvian torpedo are similar to those of the Pacific electric ray, they would explain the higher catch rates for this species observed during the daytime.

Elasmobranch distribution patterns varied intraspecifically, according to sex and size. Sexual segregation has been documented widely in elasmobranchs (Wearmouth and Sims, 2008) and tends to occur more often in adult populations, although it is not restricted to them (Carlisle et al., 2007; Wearmouth and Sims, 2008). Our study showed that small ray species, such as the Panamic stingray and thorny stingray, formed large aggregations dominated by mature females in shallow waters. In the case of these small rays, sexual segregation in shallow waters may reduce intraspecific competition for food resources (Carlisle et al., 2007; Espinoza

et al., 2012). In contrast, some species like the brown smoothhound had a male-biased sex ratio; male brown smoothhound occurred in deep habitats (depths >100 m) and gravid females were more abundant in warmer (>20°C), shallow, coastal habitats. Gravid females are thought to use warmer habitats that may offer thermal reproductive advantages, such as increased growth rates of embryos (Hight and Lowe, 2007; Pereyra et al., 2008; Speed et al., 2012).

#### Elasmobranch assemblages

The elasmobranch assemblages were characterized by the presence of 5 dominant species (i.e., rasptail skate, Panamic stingray, brown smoothhound, witch guitarfish, and Peruvian torpedo), a group that accounted for more than 75% of the total abundance of



**Figure 5**

Proportion of females caught during (A) the day and (B) the night and proportion of immature individuals caught during (C) the day and (D) the night for 11 elasmobranch species sampled along the Pacific coast of Costa Rica during 2010–2012. The following species abbreviations are used: MHE (brown smoothhound [*Mustelus henlei*]), MLU (sicklefin smoothhound [*Mustelus lunulatus*]), UAS (Panamic stingray [*Urotrygon aspidura*]), UCH (blotched stingray [*Urotrygon chilensis*]), URO (thorny stingray [*Urotrygon rogersi*]), RVE (rasptail skate [*Raja velezi*]), ZXY (witch guitarfish [*Zapteryx xyster*]), DOM (bullseye electric ray [*Diplobatis ommata*]), NEN (giant electric ray [*Narcine entemedor*]), NVE (vermiculate electric ray [*Narcine vermiculatus*]), and TPE (Peruvian torpedo [*Torpedo peruviana*]).

**Table 5**

Comparison of elasmobranch species in bycatch of shrimp trawl fisheries in various countries of the eastern tropical Pacific, based on results from previous studies (noted in the reference column) and from this study

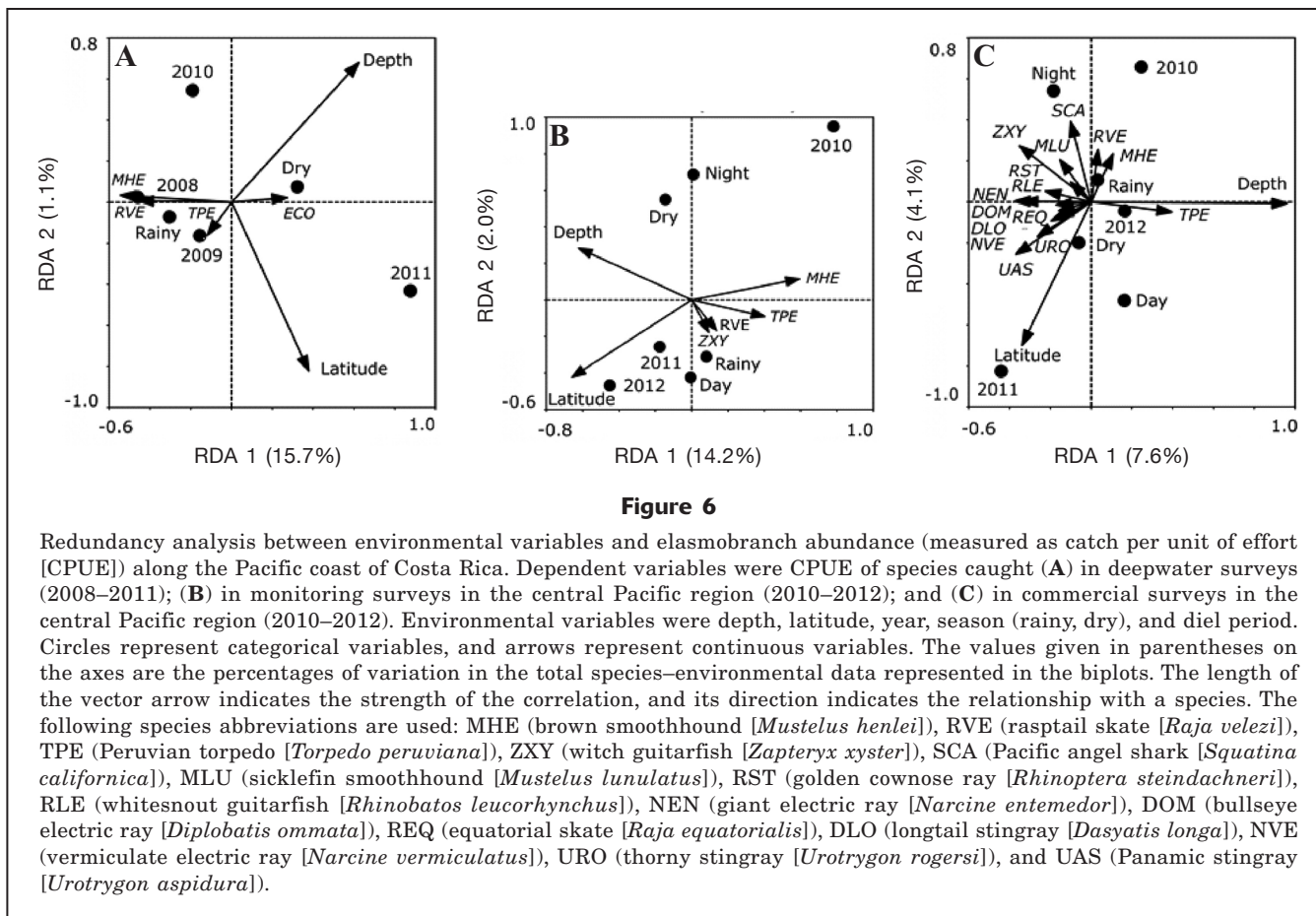
Location	Study period	Depth range (m)	Number of species			Reference
			Sharks	Rays	Species in common with this study	
Gulf of California, Mexico	2004–2005	4–137	3	16	8	López-Martínez et al. <sup>1</sup>
Guatemala	1996–1998	10–100	–	13	11	Ixquiac-Cabrera et al. <sup>2</sup>
Costa Rica	2008–2012	25–350	6	19	–	This study
Costa Rica	1983–1984	10–100	4	13	12	Campos <sup>3</sup>
Colombia	1993–1994, 1995–2007	10–360	11	13	14	Puentes et al. <sup>4</sup>

<sup>1</sup> López-Martínez, J., E. Herrera-Valdivia, J. Rodríguez-Romero, and S. Hernández-Vázquez. 2010. Peces de la fauna de acompañamiento en la pesca industrial de camarón en el Golfo de California, México. *Rev. Biol. Trop.* 58:925–942.

<sup>2</sup> Ixquiac-Cabrera, M., I. Franco, J. Lemus, S. Méndez, and A. López-Roulet. 2010. Identificación, abundancia, distribución espacial de batoideos (rayas) en el Pacífico Guatemalteco. Proyecto FONDECYT No. 34-2006, 79 p. [Available at website.]

<sup>3</sup> Campos, J. A. 1986. Fauna de acompañamiento del camarón en el Pacífico de Costa Rica. *Rev. Biol. Trop.* 34:185–197.

<sup>4</sup> Puentes, V., N. Madrid, and L. A. Zapata. 2007. Catch composition of the deep sea shrimp fishery (*Solenocera agassizi* Faxon, 1893; *Farfantepenaeus californiensis* Holmes, 1900 and *Farfantepenaeus brevivirostris* Kingsley, 1878), in the Colombian Pacific Ocean. *Gayana* 71:84–95. [Article](#)



elasmobranchs in this study. Similar observations have been documented for other tropical shrimp fisheries in Costa Rica (Campos, 1986), Australia (Stobutzki et al., 2001), and Mexico (López-Martínez et al., 2010). Elasmobranch bycatch from bottom-trawl fisheries is assumed to reflect the composition of demersal species; however, it is important to consider that trawling gear is designed for soft and sandy bottoms. Therefore, species that use reef or hardbottom habitats are likely to be underrepresented in bottom-trawl fisheries (López-Martínez et al., 2010). Similarly, fast-swimming or pelagic elasmobranchs (e.g., spotted eagle ray [*Aetobatus laticeps*], golden cownose ray, and scalloped hammerhead [*Sphyrna lewini*]) are less likely to be caught by bottom trawls.

The assemblage of shallow-water elasmobranchs (depths <50 m) comprised 22 species, among which the Panamic stingray was the most abundant. High abundances of small rays also have been reported for shallow-water bycatch in Colombia (Mejía-Falla and Navia<sup>1</sup>) and the Gulf of California (Rábago-Quiroz et al., 2011). In our study, patchy distributions and large aggregations were observed for many small round stingrays (*Urotrygon* spp.) and electric rays (*Narcine* spp.), possibly as a result of high food availability (Vianna and Vooren, 2009; Knip et al.,

2010) or reproductive behavior (Vianna and Vooren, 2009).

Elasmobranch bycatch associated with the shrimp fishery in Costa Rica was first described by Campos (1986). Differences in sampling methods, however, prevent direct comparisons with our study. For example, we examined the total catch of elasmobranchs, but Campos (1986) analyzed only a small subsample of that catch in 1983–1984. Moreover, Campos (1986) surveyed a smaller depth range (<100 m), and reported only 9 batoids (skates and rays), 4 sharks, and 4 unidentified batoid species. Our study revealed the occurrence of 17 batoid and 5 shark species at similar depths. The dominant species observed by Campos (1986) in 1983–1984 were rasptail skate, witch guitarfish, and giant electric ray, but only those first 2 species were abundant in our study.

Contrary to our results, the brown smoothhound and Panamic stingray were absent or present in very low abundances during the study by Campos (1986). These results support reports based on the traditional ecological knowledge of fishermen that large aggregations of the Panamic stingray are part of recently observed shifts in the demersal assemblages off the Pacific coast of Costa Rica (senior author, personal observ.). Moreover, 11 species of batoids were found in our survey

that were absent in the study conducted during 1983–1984 (Campos, 1986). Conversely, the whitenose shark (*Nasolamia velox*) and scalloped bonnethead (*Sphyrna corona*) were caught during 1983–1984 but were absent in our surveys. The overall lower abundance of elasmobranchs reported by Campos (1986) may be related to differences in the sample size or to actual changes in demersal elasmobranch diversity, changes that probably were due to the loss of top predatory fishes (Dulvy et al., 2014; Stevens et al., 2000).

The elasmobranch assemblage at depths of 100–350 m comprised only 6 species, among which the most abundant were the rasptail skate, brown smoothhound, and Peruvian torpedo. The prickly shark, which inhabits depths up to 1100 m, was the only true deepwater elasmobranch in this assemblage (Compagno et al., 2005). Only one previous study has examined deepwater elasmobranchs within the ETP (Puentes et al., 2007), and that study reported 8 elasmobranch species at depths between 72 and 360 m in Colombia. Additional studies are necessary to broaden our knowledge about deepwater communities of elasmobranchs in this region and about their relation to physical and biological features.

Because of the inherently slow growth of deepwater elasmobranchs, future studies should also focus on the interaction between deepwater species and fisheries (Simpfendorfer and Kyne, 2009). These emergent deepwater fisheries are rarely subjected to management or scientific monitoring. In Costa Rica, shrimp trawl fisheries expanded into deeper waters in the 1980s. As the deepwater shrimp stocks became rapidly depleted, the fishing fleet shifted operations to shallow waters, where they now target several economically important teleosts, such as the Pacific bearded brotula (*Brotula clarkae*) (senior author, unpubl. data). This change is problematic; for example, one of the main findings in our study was the high species richness of elasmobranchs associated with shallow waters. This shift in the target species of shrimp fisheries may increase the effects of this fishery on coastal demersal ecosystems.

A few elasmobranch bycatch species, including smoothhounds (*Mustelus* spp.) and the longtail stingray, are commonly retained in Costa Rica because of their commercial value. The sicklefin smoothhound is an important source of affordable protein in local markets in Costa Rica, and there is a growing demand for longtail stingray in both Mexico and Costa Rica (Rojas et al., 2000). In addition to noting that these species are caught by shrimp trawlers, López Garro et al. (2009) reported that the sicklefin smoothhound and longtail stingray composed 16.7% and 3.5%, respectively, of the landings of elasmobranchs in the artisanal fishery of Tárcoles, in the central Pacific region of Costa Rica during 2006–2007. Although current records are insufficient for an evaluation of long-term trends in abundance of elasmobranchs in Costa Rica, catch data from Colombian commercial shrimp fisheries indicate that abundances of the sicklefin smoothhound and longtail stingray have declined consider-

ably since the 1990s.<sup>1</sup> Therefore, it seems advisable to closely monitor trends in the relative abundance of these 2 species.

Our results indicate that a large number of elasmobranchs interact with the demersal trawl fishery of Costa Rica and, therefore, may be vulnerable to high levels of exploitation. Comparisons with historical data (Campos, 1986) revealed that the species composition of elasmobranchs might have changed since the 1980s. Yet, given the lack of continuous sampling throughout the period 1980–2010, it is difficult to identify the drivers behind these changes.

The creation of independent observer programs would allow monitoring and assessment of long-term trends of bycatch, as well as prediction of potential changes in fish assemblages. In addition, knowledge of the feeding ecology and trophic interactions of elasmobranchs is critical to understanding food web dynamics and trophic cascades that may occur as a result of the loss of top predatory fishes from coastal ecosystems (Ferretti et al., 2008; Heithaus et al., 2008). This information is also essential for defining the role of mesopredators in demersal ecosystems and for developing ecosystem-based management strategies (Espinoza et al., 2015). Future research on the life history traits of these species is also necessary and will allow us to identify vulnerable species and redirect conservation efforts. The interaction between the shrimp trawl fishery and the elasmobranch assemblage may be comparable within the different countries of Central America (López-Martínez et al., 2010; Clarke et al., 2014). Therefore, the results of this study may serve as biological information that can support the development of management strategies in Central America.

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