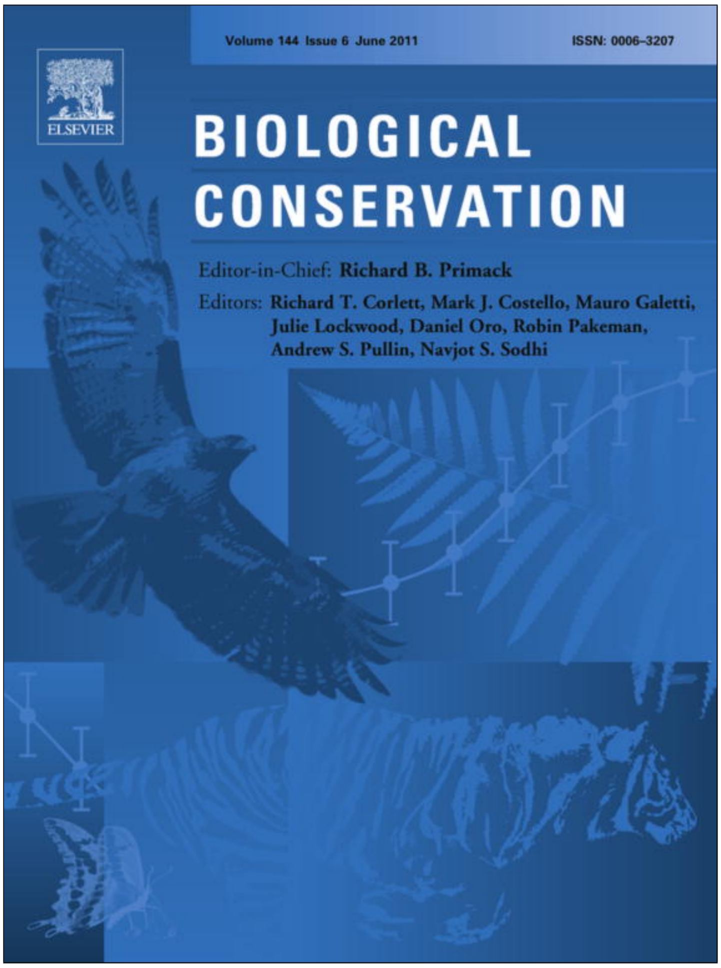
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Potential impacts of emerging mahi-mahi fisheries on sea turtle and elasmobranch bycatch species

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ABSTRACT

Mahi-mahi (*Coryphaena hippurus*) is a resilient pelagic species that could provide long-term highly productive fisheries. Using FAO data we document enormous increases (746%) in reported global mahi-mahi landings since 1950. Detailed mahi-mahi fisheries records are limited, but an observer program monitoring Costa Rica's Pacific mahi-mahi pelagic longline fleet between 1999 and 2008 (n = 217 sets) provided a rare opportunity to quantify bycatch in these fisheries. Several sea turtles and sharks of global conservation concern were caught incidentally: olive ridley turtle (*Lepidochelys olivacea*; n = 1348, mean = 9.05 per 1000 hooks), silky shark (*Carcharhinus falciformis*; n = 402, mean = 2.96 per 1000 hooks), thresher sharks (*Alopias* sp.; n = 158, mean = 1.12 per 1000 hooks), green turtle (*Chelonia mydas*; n = 49, mean = 0.35 per 1000 hooks), and three other threatened sharks in small numbers. Pelagic stingray (*Pteroplatytrygon violacea*; a ray of low conservation concern) was also a common bycatch (n = 625, mean = 4.77 per 1000 hooks). Generalized linear models (GLMs) of catch rates showed increases in olive ridley turtles and decreases in mahi-mahi and silky sharks over the decade examined. The high hooking survival rates of olive ridley and green turtles in observed sets (95% and 96% respectively) suggest that widespread training of the fleet in careful gear removal and turtle release methods could be one effective bycatch mitigation strategy for these species. GLMs also provide evidence that closing the fishery during peak olive ridley nesting times (at least near nesting beaches), in combination with reduced gear soak times, could help minimize the fishery's impacts on threatened bycatch species while still maintaining a productive fishery.

1. Introduction

Declines in traditional food fishes, coupled with ever-rising global demand for seafood products (FAO, 2010), have led many fisheries to shift targets to new species and ecosystems (e.g. Morato et al., 2006). These newly developing fisheries typically outpace scientific knowledge about the fished populations and their broader ecosystem effects, thereby hindering effective management. Fisheries for mahi-mahi are a prime example. These circumtropical and subtropical pelagic fishes (*Coryphaena hippurus*, and a few other less abundant *Coryphaena* species of restricted distribution) should be able to sustain very high fishing mortality rates because of their exceptionally fast growth rates and early maturation (usually in the first year of life; Kraul, 1999; Oxenford, 1999; Schwenke and Buckel, 2008) and thus, in theory, could provide long-term productive fisheries. Globally, however, there is little information about the status of mahi-mahi populations or management of their fisheries (Mahon and Oxenford, 1999). Of conservation concern is the potential for high bycatch levels of marine megafauna in fisheries targeting mahi-mahi with longlines (Lewison et al., 2004a). Reflecting this concern, sustainable seafood guides recommend mahi-mahi caught in the US (where the fleet's bycatch is monitored) or in poll and line fisheries (which have minimal bycatch) as a 'best choice' or 'good alternative', but that consumers should avoid purchasing mahi-mahi caught by international longline fleets due to a lack of management and bycatch issues (Blue Ocean, 2010; Seafood Watch, 2010).

Indeed, many sea turtle and elasmobranch (shark and ray) species are already of conservation concern (Dulvy et al., 2008; IUCN, 2010), at least partially because of bycatch in other pelagic longline fisheries (FAO, 2009; Lewison et al., 2004b; Lewison and Crowder, 2007; Wallace et al., 2010). Sea turtles are often entangled or caught in pelagic longlines (Carranza et al., 2006; Donoso and Dutton, 2010; Lewison et al., 2004a,b; Pinedo and Polacheck, 2004; Watson et al., 2005), and this exploitation is thought to be impeding recovery efforts for leatherback and loggerhead turtles

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(Peckham et al., 2007; Spotila et al., 2000). Pelagic sharks and rays also are commonly caught as bycatch in pelagic longline fisheries (Gilman et al., 2008; Mandelman et al., 2008). Significant declines have been documented for many pelagic shark populations in the Pacific (Ward and Myers, 2005a but see Sibert et al., 2006) and northwest Atlantic Oceans (Baum et al., 2003; Musick et al., 1993; Myers et al., 2007).

Pelagic longline fisheries targeting mahi-mahi may be particularly detrimental to sea turtles and epipelagic elasmobranchs because of the high degree of spatial overlap of these species (Gilman et al., 2006, 2008). Mahi-mahi tend to reside in surface waters (Benetti et al., 1995), so longline sets targeting them are typically shallower than those targeting tunas. Previous studies have shown that sea turtles and sharks are both captured at higher rates on shallow pelagic longline sets: near-surface swordfish sets tend to catch far more sea turtles than deep sets targeting tuna (Lewison and Crowder, 2007); in the western and central Pacific, sharks are caught over twice as frequently on shallow longline sets (500,000 sharks/year) than on deep ones (200,000/year) (Molony, 2005); and, like mahi-mahi, the catchability of many epipelagic elasmobranchs declines rapidly with depth (Beverly et al., 2009; Ward and Myers, 2005b).

Despite the potential threats, a paucity of data has limited assessment of bycatch in mahi-mahi fisheries to date. In this paper, we aimed to document recent global trends in mahi-mahi landings and quantify sea turtle and elasmobranch bycatch in these fisheries. Onboard records from most of the world's mahi-mahi fisheries are poor, but Costa Rica's fleet has had an onboard observer program since 1999 (initiated and led by co-author Arauz, 2002, 2004). Data from this program thus provide a rare opportunity to assess bycatch levels in a commercial mahi-mahi longline fishery. Costa Rica's Pacific waters are home to several pelagic shark species, and its shores are host to two of the largest known mass synchronous olive ridley turtle (*Lepidochelys olivacea*) nesting aggregations (hundreds of thousands of turtles) in the world, Nancite in Santa Rosa National Park and the Ostional National Wildlife Refuge (Cornelius, 1986). We examined the observer data for associations between catch rates of the different species and the temporal, spatial, and operational characteristics of the fishery with the goal of identifying fishing strategies that could potentially minimize bycatch while maintaining attractive catch rates of mahi-mahi.

2. Methods

2.1. Global mahi-mahi landings

We first documented trends in mahi-mahi landings within each ocean and globally between 1950 and 2009, using data pooled for all countries from the UN Food and Agriculture Organization's (FAO) Global Capture Production Database (FAO, 2011). We cross-checked the US portion of these data with US imports and landings data from the National Marine Fisheries Service database over the same time period (NOAA-NMFS, 2011). Although we searched for similar information from other countries, including Canada, UK, and Australia, no other data source isolated mahi-mahi in sufficient taxonomic detail for comparison.

2.2. Case study: Costa Rica's mahi-mahi fishery

Costa Rican authorities classify their Pacific pelagic longline vessels as being part of either the "medium scale" or "advanced scale" fleet. Vessels in the "medium scale" fleet ($n = 350$), which is the focus of this paper, usually have only 10–15 ton capacity and iced holds. They typically undertake two-week trips using approximately 18-mile longlines and wire leaders, with 650 hooks per set and 12–16 sets per trip (Table 1). This fleet targets mainly mahi-mahi, but also catch tunas and sailfish, and operates throughout the Exclusive Economic Zone (EEZ). In contrast, "advanced scale" vessels are capable of deploying 150 mile longlines, and operate within and beyond the EEZ targeting swordfish, marlins and tunas (Arauz, 2004; Arauz, pers. obs.). Sharks are considered a complementary catch in both fleets and are typically retained (Rojas et al., 2000). There are currently no spatial or temporal restrictions on longlining in Costa Rica.

Observers began onboard monitoring of a small proportion of the medium-scale fleet in 1999. All observations have been made onboard six vessels owned by Papagayao Seafood S.A., which operates from Playas del Coco. In total, the observer data consist of 217 mahi-mahi targeted fishing sets spanning the years 1999–2008 (Table 1). The highest proportion of observed sets occurred in 1999 (29%), 2003 (33%), and 2006 (12%). Within years, fishing effort typically was highest in December and January because of seasonal increases in mahi-mahi, and observer coverage increased correspondingly, with 20% and 15% of total observed sets in these months, respectively, compared to between 1% and 10% in other months.

Two species of mahi-mahi occur in this area, *C. hippurus* and *C. equiselis*, known as the common and pompano dolphinfish, respectively. *C. hippurus* is thought to comprise the vast majority of the catch (Lasso and Zapatta, 1999). These species are also referred to as dorado, but are generally sold under their Hawaiian name mahi-mahi; herein we refer to them collectively as mahi-mahi.

Bycatch in this fishery includes at least 14 pelagic teleost species, 14 elasmobranch species, and two sea turtles (Table 2). We focused on the latter two groups, because their life history characteristics (e.g. late age at sexual maturity, low fecundity) typically render them more vulnerable to overexploitation than teleost fishes, and modeled the four most commonly caught of these species (Table 2).

2.3. Data analyses

Following initial data checks and exploratory analyses, we plotted maps of the observer data to visualize and compare the spatial distribution of the fishing effort and the catch rates for the target species with those of the most commonly caught sea turtle and elasmobranch species.

We then fitted generalized linear models (GLM) to the observer data for mahi-mahi and for each of our focal bycatch species, using a negative binomial error distribution and a log link. For each species, s, the initial model of the expected mean catch, μ_i on set i is

Table 1
Variables included in initial models of observed sets in Costa Rica's mahi-mahi targeted pelagic longline fishery.

Variable	Class	Description (mean ± 1SD)
Years fished	Continuous	1999, 2002–2008
Day of year fished	Continuous (sines, cosines)	Year-round
Soaktime (h) per set	Continuous	11.03 h ± 1.86
Set period[*]	Categorical	Day ($n = 205$); night ($n = 12$)
Distance from shore	Continuous	143 km ± 112.5
Hooks per set	Continuous, offset	647.7 ± 156.30

[*] Although only 12 sets were fished at night, we included this variable in the models because it has been shown to significantly affect sea turtle and shark catch rates (Watson et al., 2005; Ward and Myers, 2005b).

Table 2
Total number recorded, proportion of sets with a catch, and mean catch per 1000 hooks (±1 SD) of the species recorded between 1999 and 2008 by onboard observers in Costa Rica's Pacific mahi-mahi targeted longline fishery ($n = 217$ sets). Species are listed in declining order of frequency caught, with their 2010 IUCN Red List global status (EN = endangered, VU = vulnerable, NT = near threatened, LR/LC = lower risk/least concern, DD = data deficient; IUCN, 2010). Modeled species are in bold.

Species		Total number recorded	Proportion of sets caught on	Mean catch per 1000 hooks (±1 SD)	IUCN status
Common name	Latin name				
Mahi-mahi	***Coryphaena hippurus/C. equiselis***	**6884**	**0.935**	**53.14 ± 72.58**	**LC**
Olive ridley sea turtle	***Lepidochelys olivacea***	**1348**	**0.921**	**9.05 ± 10.11**	**VU**
Pelagic stingray	***Pteroplatytrygon violacea***	**625**	**0.611**	**4.77 ± 6.10**	**LC**
Silky shark	***Carcharhinus falciformis***	**402**	**0.477**	**2.96 ± 5.56**	**NT (VU)**[a]
Yellowfin Tuna	*Thunnus albacares*	337	0.375	2.69 ± 6.81	LR/LC
Indo-Pacific Sailfish	*Istiophorus platypterus*	307	0.601	2.52 ± 4.48	–
Thresher sharks[b]	***Alopias pelagicus, A. vulpinus, A. superciliosus***	**158**	**0.300**	**1.12 ± 3.35**	**VU**
Skipjack Tuna	*Katsuwonus pelamis*	112	0.064	0.86 ± 7.61	–
Rays	*Mobula* sp.	83	0.199	0.56 ± 1.76	NT
Indo-Pacific blue marlin	*Makaira mazara*	64	0.157	0.39 ± 1.10	–
Green sea turtle	*Chelonia mydas*	49	0.185	0.35 ± 0.81	EN
Black marlin	*Makaira indica*	42	0.134	0.32 ± 0.90	–
Blue shark	*Prionace glauca*	41	0.111	0.33 ± 1.18	NT
Wahoo	*Acanthocybium solandri*	38	0.134	0.24 ± 0.66	–
Striped marlin	*Tetrapturus audax*	31	0.092	0.21 ± 0.80	–
Swordfish	*Xiphias gladius*	11	0.037	0.097 ± 0.569	DD
Marlins	*Makaira* sp.	10	0.037	0.091 ± 0.535	multiple
Pacific bluefin tuna	*Thunnus orientalis*	9	0.027	0.061 ± 0.382	–
Ocean sunfish	*Mola mola*	6	0.023	0.043 ± 0.291	–
Scalloped hammerhead	*Sphyrna lewini*	6	0.023	0.041 ± 0.279	EN
Oceanic whitetip shark	*Carcharhinus longimanus*	5	0.023	0.037 ± 0.247	VU
Crocodile shark	*Pseudocarcharias kamoharai*	4	0.018	0.015 ± 0.130	NT
Unidentified dolphin sp.	–	3	0.013	0.028 ± 0.222	–
Bigeye tuna	*Thunnus obesus*	3	0.013	0.026 ± 0.222	VU
Smooth hammerhead	*Sphyrna zygaena*	3	0.013	0.025 ± 0.217	VU
Whitenose shark	*Nasolamia velox*	2	0.004	0.015 ± 0.226	DD
Blacktip shark	*Carcharhinus limbatus*	2	0.009	0.012 ± 0.127	NT
Snake mackerel	*Gempylus serpens*	2	0.009	0.012 ± 0.130	–
Black Skipjack tuna	*Euthynnus lineatus*	1	0.004	0.007 ± 0.113	–
Tiger shark	*Galeocerdo cuvier*	1	0.004	0.005 ± 0.076	NT

[a] Silky shark are listed on the IUCN Red List as Near Threatened globally, but as Vulnerable in the eastern central Pacific.
[b] Thresher shark species were grouped for analysis because of uncertainty in the reliability of species-specific identification.

$$\mu_{s,i} = \beta_0 + \beta_1 \cos(2\pi d_{,i}/365.25) + \beta_2 \sin(2\pi d_{,i}/365.25) + \beta_3 Y_i + \beta_4 D_i + \beta_5 ST_i + \beta_6 P_i + \log(H_i)$$

where the seasonal cycle was estimated by fitting sines and cosines with periods of one year to d_i, the ordinal day of the year that set i occurred on, to allow smooth transitions in catch rates across the year; Y_i is the year; D_i is the distance from shore, measured as the shortest distance between the coastline (coastline values from http://rimmer.ngdc.noaa.gov/coast/) and the average coordinates of the set (calculated as the average of the initial and final longitude and latitude of each set); ST_i is the soaktime, calculated as the length of time between mid-setting and mid-hauling times; P_i is the set period; the βs are the parameters to be estimated; and $H_{,i}$ is the number of hooks, which is a known value that is treated as an 'offset' in the model in order to maintain the probability distribution of the catch data (see Table 1 for details). We did not include hook variables in the models because all hooks used were circle hooks, and little variation existed in hook sizes among sets (all #14, 15, 16, with and without 10° offset; Swimmer et al., 2010). A combination of frozen and fresh squid, skipjack tuna, and shark were used as bait in the fishery depending on availability and price, but lack of set-specific information precluded examination of this variable.

For each species, we employed backwards selection to sequentially remove variables using Akaike Information Criteria (AIC) as the criteria for model comparison, until a model of best fit was obtained (Maunder and Punt, 2004; Murtaugh, 2009). For comparative purposes we also ran the models using forward selection, but found that this led to the same final model for each species. For each species, we report the coefficients and standard errors of each variable included in the final model, as well as the percent deviance (which is analogous to the variance explained in linear regression) explained by the overall final model. We used the final model for each species to predict the number of the species that would be caught based on values of the variables that span the range of the variable within the dataset. Analyses were conducted in R, version 2.6.1 (R development core team, 2007).

3. Results

3.1. Growth in mahi-mahi fisheries

According to FAO data, mahi-mahi landings have increased globally from 7103 in 1950 to 53,011 tonnes in 2009 (746%), with a peak in 2008 of 57,104 tonnes and an average annual growth of 5.6% (Fig. 1a). Japan and Taiwan dominated global landings throughout this period. Costa Rica, the focus of this study, ranked fifth globally in mahi-mahi landings over the past decade, with a total of 47,922 tonnes and an annual average of 4792 tonnes. Overall, six times as many countries ($n = 52$) reported mahi-mahi landings in the past decade than in the 1950s. Most catches occurred in the Pacific Ocean (45.6% in 2009; Fig. 1a), where landings rose from 5500 tonnes in 1950 to peak at 45,804 tonnes in the early 1990s. Whereas only two or three countries reported mahi-mahi landings from the Pacific in the 1950s, in the past decade 19 countries did. The same general trends are seen in the Atlantic and Indian Oceans (Fig. 1b), as well as in the Mediterranean, but on smaller scales. These substantial increases could still be underestimates because some countries may not report their mahi-mahi catches, and some countries report fisheries catches in aggregated taxonomic units leaving specific landings of mahi-mahi unknown. US national records of mahi-mahi landings closely matched the FAO records

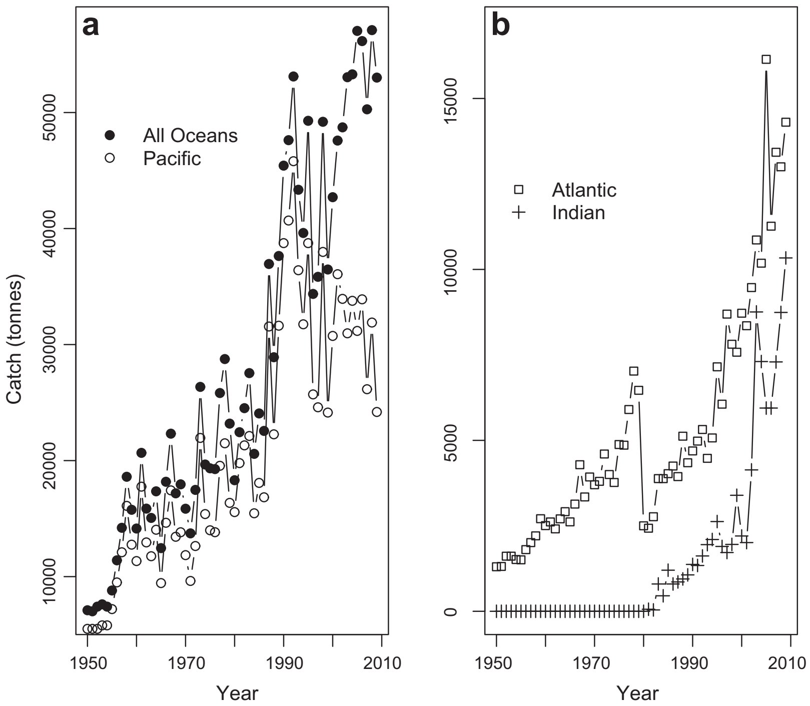

Fig. 1. Mahi-mahi catches between 1950 and 2009 according to the UN Food and Agriculture Organization: (a) globally and in the Pacific Ocean and (b) in the Atlantic and Indian Oceans.

(e.g. 1304 tonnes vs. 1308 tonnes in 2009, respectively) over the entire 60-year timeframe. The US, however, likely keeps more detailed landings records than many other countries, and it was not possible to cross-validate the FAO database more broadly.

3.2. Case study: Costa Rica's mahi-mahi fishery

3.2.1. Nominal catch rates and fishing effort

Observers recorded a total of 6884 mahi-mahi, with an average of 53 caught per 1000 hooks, and captures on almost all sets (Table 2). The next most commonly caught species was the olive ridley turtle (1/5th as common as mahi-mahi), which was taken on 92% of observed sets (Table 2). In contrast, green turtles (*Chelonia mydas*) were seldom caught (and hence were not modeled; Table 2), and no leatherback (*Dermochelys coriacea*) or loggerhead (*Caretta caretta*) turtles were reported. Pelagic stingray (*Pteroplatytrygon violacea*; 1/11th as common as mahi-mahi), silky shark (only 1/17th as common) and thresher sharks were the most commonly caught elasmobranchs (Table 2). Whereas mortality of olive ridley and green turtles was very low on observed sets (hooking survival rates were 95% and 96% respectively; 65% and 69% were released respectively, with the fate of the remaining turtles unrecorded), that of sharks was high, since they were usually retained for their fins, meat, or as bait (84% of all silky sharks retained, and 90% of thresher sharks for which the outcome was recorded ($n = 122$)). Fishermen involved in the observer program released small silky sharks that were alive at the time of capture, but given that the fins of small sharks were still worth $10/kg and there were no size restrictions, it is unlikely that this practice was widespread in the fleet. The fates of pelagic stingrays were only recorded about 30% of the time, and these were all discarded.

Fishing effort was concentrated within the northern half of Costa Rica's Pacific EEZ (range: 19.5 and 596.2 km offshore; Table 1; Fig. 2). The highest catches of mahi-mahi, however, occurred offshore and outside the EEZ; a second cluster of high catches occurred just outside the 1000 m isobath in northern Costa Rica

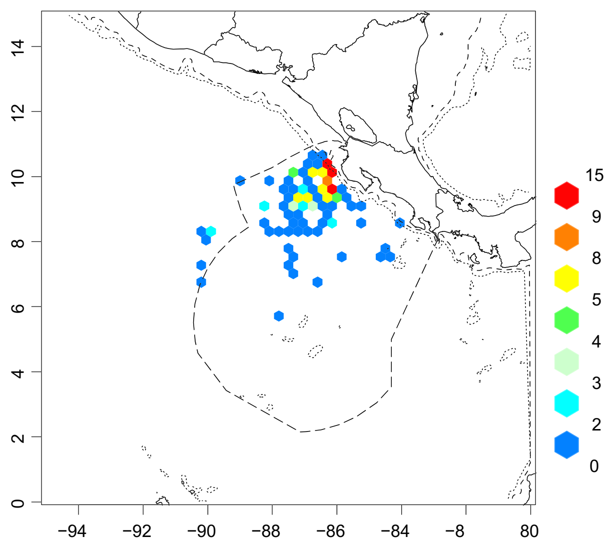

Fig. 2. Observed mahi-mahi targeted pelagic longline fishing effort off Costa Rica's Pacific coast, measured in number of sets, as recorded by observers on 217 sets between 1999 and 2008. The dashed and dotted lines represent the 200 m and 1000 m isobaths, respectively. The outer dashed line represents Costa Rica's EEZ.

(Fig. 3a). Olive ridley bycatch was widespread with some of the highest observed catches occurring close to the northwestern shore where two massive nesting sites are located (Cornelius, 1986; Fig. 3b). Elasmobranch catches also were highly variable, although silky shark showed a tendency to increase with distance from shore (Fig. 3c–e).

3.2.2. Modeled catch rates

Both temporal and spatial factors significantly affected mahi-mahi catch rates (Table 3). Significantly more mahi-mahi were caught between October and February, with a peak in December

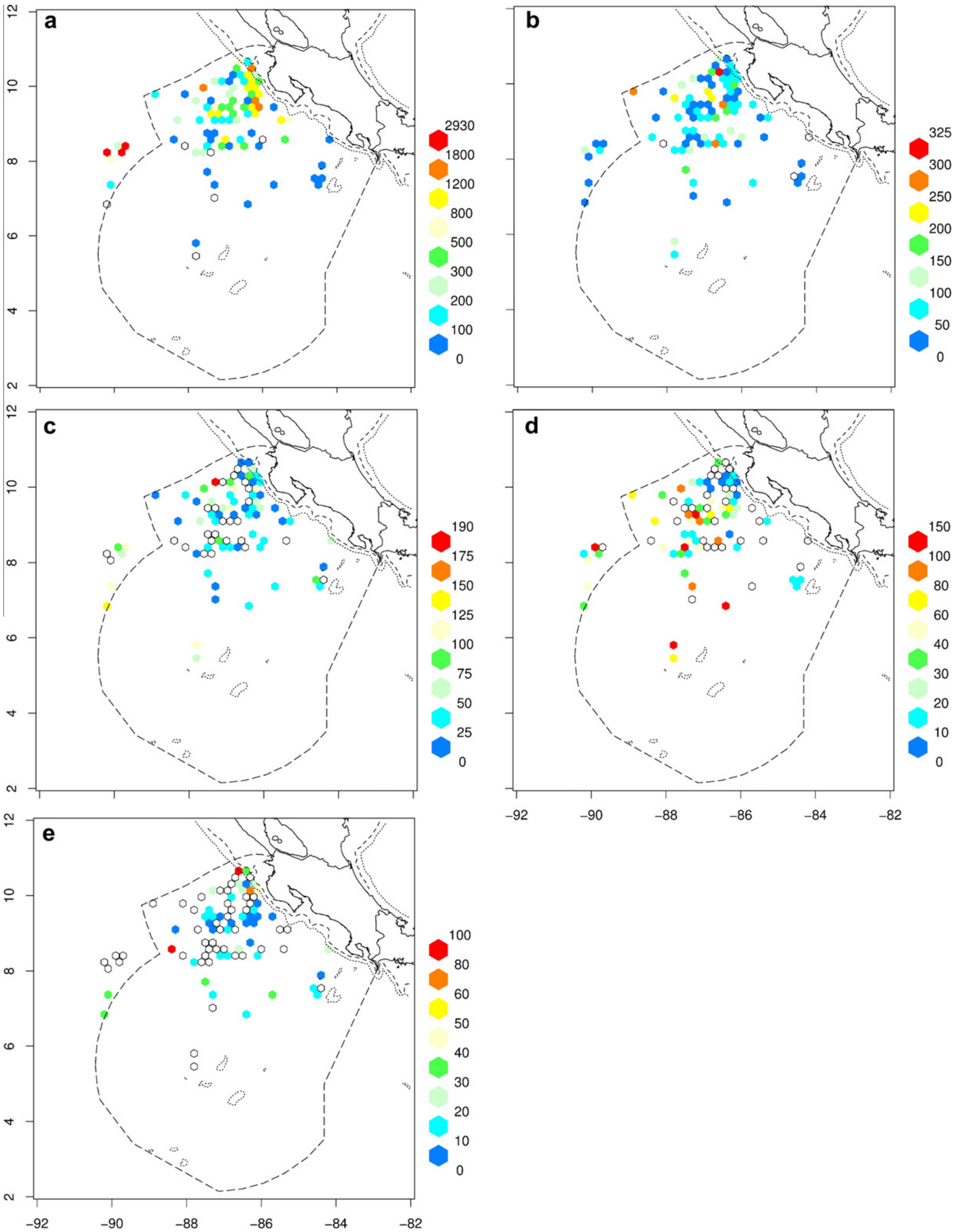

Fig. 3. Catch per 10,000 hooks of: (a) mahi-mahi, (b) olive ridley turtle, (c) pelagic stingray, (d) silky shark, and (e) thresher sharks. The dashed and dotted lines represent the 200 m and 1000 m isobaths, respectively. The outer dashed line represents Costa Rica's EEZ.

and January (Fig. 4): the final model predicted an increase from 3 mahi-mahi caught per 1000 hooks in the low months to 122 at the peak. Mahi-mahi catches also were greater during day than night sets (31 caught per 1000 hooks vs. 16, respectively), during the early years of the study (50 caught per 1000 hooks in 1999 decreasing to 16 in 2008), and offshore (166 caught per 1000 hooks at distances of 600 km from shore compared to 19 at 10 km from shore) (see Table 4).

Temporal, spatial, and operational factors affected olive ridley turtle catch rates (Table 3). High olive ridley catches occurred between late July and November, with a peak in September and October (Fig. 4; predicted 22 turtles per 1000 hooks during peak months versus 3 in low months). About half as many turtles were caught on night sets than day sets. In contrast to mahi-mahi, olive ridley catches increased over time (2 per 1000 hooks in 1999 increasing to 39 in 2008) and decreased with distance offshore

Table 3
Fits of generalized linear models to Costa Rica mahi-mahi pelagic longline observer data indicated using the change in Akaike's information criterion (ΔAIC) (0: model with most support in bold; <2: substantial support in italics; 4–7: considerably less support). Predictors are sine and cosine of Julian day (to model the seasonal effect), year, the distance of the fishing set from shore, the set period (night vs. day), and the soak time of the gear. For each species, fits are shown for the model with most support (that with lowest AIC, which was selected by both the forward- and backward-selection procedure), for all other models from the stepwise selection procedures, and for models with each variable alone for comparison. Also shown is the %deviance explained by the final model for each species.

Model	Mahi-mahi	Olive ridley	Silky	Thresher	Pelagic stingray
			ΔAIC		
Intercept only	149	77	53.6	23.4	42.2
Sine	147	79	38.2	24.8	12.7
Cos	56.4	55.6	55.1	7.8	44.1
Year	147	49	42.3	25.2	23.3
Distance	149	75.4	35.2	23.7	42.7
Period	141	75.3	55.4	7.3	37.9
Soak time	151	79	50	24.6	42.9
Sine, period	–	–	–	–	5.8
Sine, year	–	7	–	–	–
Cos, distance	14.8	–	–	–	–
Cos, period	–	–	–	**0**	–
Year, distance	–	–	8.33	–	–
Sine, year, distance	–	2.7	–	–	–
Sine, cos, period	–	–	–	*0.21*	–
Sine, period, distance	–	–	–	–	*1.1*
Cos, year, distance	*1.1*	–	**0**	–	–
Sine, year, distance, period	–	*0.5*	–	–	–
Sine, cos, distance, period	–	–	–	*0.55*	**0**
Cos, year, distance, period	**0**	–	*1*	–	–
Sine, year, distance, period, soak time	–	**0**	–	–	–
Sine, cos, year, distance, period	*1.1*	–	–	–	*1.61*
Sine, cos, distance, period, soak time	–	–	–	2.16	–
Cos, year, distance, period, soak time	–	–	2.45	–	–
Sine, cos, year, distance, period, soak time	2.5	*1*	4.4	3.7	3.3
	%Deviance explained by final model (AIC = 0)				
	47.3	32.13	27.55	17.82	20.87

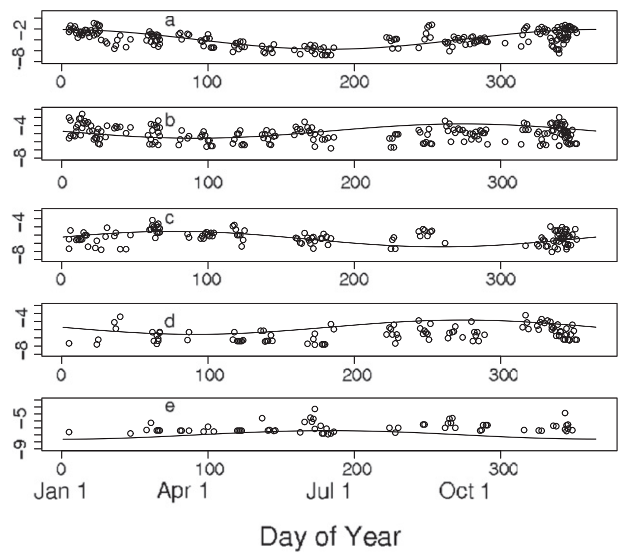

Fig. 4. Seasonal variation in catch rates of: (a) mahi-mahi, (b) olive ridley turtle, (c) pelagic stingray, (d) silky shark, and (e) thresher shark in Costa Rica's mahi-mahi fishery; raw data plotted as ln catch per 1000 hooks (open circles) and predicted catch rates plotted using coefficients for sine and cos from the GLMs of best fit (black line).

(11 per 1000 hooks inshore (10 km) versus 4 offshore (600 km)). Predicted turtle catch rates increased from 7 to 21 per 1000 hooks as soak time increased from 7 to 26 h (Table 3).

Silky shark catch rates were highest from July to November with a peak in September and October (Fig. 4), and predicted catch rates ranging as high as 2.6 and as low as 0.86 per 1000 hooks. As with mahi-mahi, silky shark catch rates declined over time, from a predicted mean of 4.7 per 1000 hooks in 1999 to <1 in 2008, and with proximity to shore, from a predicted mean of <1 caught per 1000 hooks within 10 km of shore up to 56 per 1000 hooks at 600 km from shore.

Thresher shark catch rates were only influenced significantly by temporal variables. Catch rates were highest between April and September, peaking in June and July (Fig. 4), with predicted catches of <1 per 1000 hooks during the low months and 1.6 during peak months. Thresher shark catch rates also were higher at night (3.6 per 1000 hooks) than during the day (<1 per 1000 hooks; Table 3).

Pelagic stingrays were frequently caught from January to May, with peaks in March and April (Fig. 4) and predicted catch rates as low as 1.5 per 1000 hooks and as high as 10 per 1000 hooks. Like mahi-mahi, more pelagic stingrays were caught during the day than at night (4 per 1000 hooks vs. 1.4 respectively) and catch rates increased with distance from shore (with around 3 rays per 1000 hooks predicted at 10 km from shore and 12 at 600 km from shore; Table 3).

4. Discussion

4.1. Growth in mahi-mahi fisheries

Reported global mahi-mahi landings have grown enormously since the 1950s, especially in the past two decades. Despite some year-to-year variation, landings data from all regions showed large overall increases. Although we cannot determine to what extent this trend reflects greater reporting, it strongly suggests that there has been a substantial increase in actual mahi-mahi landings globally, likely reflecting a combination of increased retention and targeting. US records also indicate an associated rise in the species' economic importance (NOAA-NMFS, 2011). A potential factor driving this growth, in addition to increased global demand for seafood (FAO, 2010), is increased abundance of mahi-mahi populations, which is thought to have occurred over the past half century in response to declines of higher trophic level pelagic fishes (Polovina et al., 2009; Ward and Myers, 2005a). Growth in mahi-mahi exploitation has, however, not been matched by management efforts to ensure that the species is not over-fished (Mahon and Oxenford, 1999) and threatened bycatch species are not significantly impacted. With mahi-mahi fisheries presumably still in the developing phase, managers are in the fortunate position of being able to act before population collapses occur, and it behooves them to develop responsible management measures for these fishes and associated bycatch.

4.2. Sea turtle and elasmobranch bycatch

In the case of Costa Rica's mahi-mahi longline fishery, there is significant bycatch including olive ridley and green turtles, silky shark, and thresher sharks, all of which are of international conservation concern (Table 2).

Sea turtle bycatch rates in this fishery were very high (mean 9.4 per 1000 hooks) compared to that of other pelagic longline fisheries. Lewison and Crowder's (2007) review of pelagic longline fisheries targeting tuna, billfish, and sharks in 19 different countries showed that sea turtle bycatch was typically less than 2 per 1000 hooks; turtle bycatch was highest in Costa Rica (up to 14 turtles

Table 4
Results of the final generalized linear model (GLM) based on AIC, including coefficients and their standard errors for each variable, for each species. Variables are sine and cosine of Julian day (to model the seasonal effect), year, the distance of the fishing set from shore, the set period (night vs. day), and the soak time of the gear. NA indicates variables that were removed from the final model.

	Mahi-mahi	Olive ridley	Silky	Thresher	Pelagic stingray
Sine	NA	−0.8781 ± 0.1217	NA	NA	0.9253 ± 0.1332
Cos	1.817 ± 0.1116	NA	0.5507 ± 0.1780	−0.6041 ± 0.1993	0.2417 ± 0.1312
Year	−0.1221 ± 0.0277	0.2901 ± 0.0314	−0.2517 ± 0.0454	NA	NA
Distance	0.0037 ± 0.0006	−0.0016 ± 0.0005	0.0076 ± 0.0009	NA	0.0023 ± 0.0008
Period	−0.6095 ± 0.3361	−0.5938 ± 0.2776	NA	1.5571 ± 0.5232	−1.0971 ± 0.5030
Soak time	NA	0.0561 ± 0.0315	NA	NA	NA

per 1000 hooks). Almost all turtles in our study were olive ridleys, which had a mean catch rate of 9.05 per 1000 hooks compared to only 0.38 and 0.098 per 1000 hooks as reported for the Gulf of Guinea and India in two of the only other studies to present bycatch rates for this species (Carranza et al., 2006; Varghese et al., 2010). The high bycatch rate in our study likely reflects the fishery's proximity to two of the largest mass synchronous olive ridley nesting sites in the world, known as *arribadas*, which are found on the northwest coast of Costa Rica (Cornelius, 1986; Eguchi et al., 2007). In Costa Rica, *arribada* nesting events, which are unique to the genus *Lepidochelys*, usually occur for 5–8 nights each month, with major events involving hundreds of thousands of turtles (Cornelius, 1986; Hughes and Richard, 1974; Richard and Hughes, 1972). Encouragingly, olive ridley catch rates increased over the decade monitored by observers, which may reflect the population is recovering (Chaloupka et al., 2004). Almost all observed sea turtles also were released alive; if this practice is widespread in the fleet, population level effects of the fishery on sea turtles may be minimal.

Silky and thresher shark bycatch rates were comparable to those reported from other pelagic longline fisheries (3.16–5.38 silky sharks per 1000 hooks in the northwest Atlantic, Beerkircher et al., 2002; 0.2–1.2 thresher sharks per 1000 hooks in the Pacific, Molony, 2005; 0.24 thresher sharks per 1000 hooks in the northwest Atlantic, Baum and Blanchard, 2010). Unlike sea turtles, however, the fishery clearly increased shark mortality rates since few sharks were released. The high value of shark fins relative to shark meat (Parry-Jones, 1996) has provided a strong incentive for fishermen in this and other fleets to fin sharks (i.e. cutting off the fins and discarding the carcass). Implementation and enforcement of a true shark finning ban in Costa Rica could provide strong incentive to fishermen to reduce shark bycatch and release captured sharks (Gilman et al., 2008). Although Costa Rica moved towards this in 2005 with the approval of a new fisheries law mandating that sharks can only be landed as whole carcasses with the fins attached (Ley de Pesca y Acuicultura #8436), the law does not ban shark finning per se (only the landing of fins) and has been ill enforced such that shark mortality is believed to still be high (EcoAmericas, 2010; Pretoma, 2010). Silky sharks showed a significant negative trend in catch rates over the decade monitored, which may reflect declines.

4.3. Potential bycatch mitigation measures

4.3.1. Area and seasonal closures

Designation and enforcement of a large no-take marine protected area (MPA) extending from Costa Rica's two olive ridley *arribada* nesting sites offshore to the area surrounding the highest sea turtle catches (87°W longitude, Fig. 3b) could be an effective means of reducing olive ridley bycatch in this mahi-mahi fishery; it might also help reduce sea turtle bycatch in Costa Rica's inshore shrimp trawl and artisanal fisheries (Arauz et al., 1998; Pretoma, 2010). Although the olive ridley turtle has recently been downgraded from Endangered to Vulnerable on the IUCN Red List (IUCN, 2010), its recovery from decades of direct harvest (Chaloupka et al., 2004) could be jeopardized by bycatch in these and numerous other fisheries globally (Eguchi et al., 2007). From a conservation perspective therefore, protecting Costa Rica's *arribadas*, which are among the largest in the world, should be a high priority. Such an MPA would, however, involve a significant trade-off between conservation benefits and fishery catches since it would encompass an area with fairly high mahi-mahi catch rates (Fig. 3a). Thus, a seasonal closure of this area may be a more commercially viable option. Olive ridley turtles nest year-round (Plotkin et al., 1995), and therefore there will always be some bycatch because there is no way to completely temporally separate the fishery from the turtles. Peak nesting events in Costa Rica are, however, reported to occur from August to February (Cornelius, 1986; Hughes and Richard, 1974), and our analysis showed peak bycatch rates within this time frame, in September and October. Closing the medium-scale pelagic longline fishery for these 2 months thus could benefit olive ridleys, while having minimal impacts on mahi-mahi catches, which peaked later, in December and January.

Identifying area or time-area closures that benefit pelagic elasmobranchs without significantly impacting pelagic fisheries catches is generally challenging (Watson et al., 2009) because the spatial distribution of their catches typically overlaps substantially with that of the targeted pelagic fishes. In Costa Rica, a large no-take MPA (as described above) would be unlikely to benefit elasmobranchs since their catch rates were spatially diffuse, and that of silky shark was greatest farther offshore (Table 3; Fig. 3). Closing inshore areas to protect olive ridley's could in fact inadvertently increase bycatch of these elasmobranchs if fishing effort is merely displaced offshore (Baum et al., 2003; Gilman et al., 2007). However, because peak silky shark catch rates occurred during the same months (September and October) as olive ridleys, a time area closure that includes offshore areas could provide some protection for this threatened shark. Thresher sharks could be afforded some protection by a fishery closure in June and July, when its catch rates are at their peak but those of mahi-mahi are relatively low.

4.3.2. Improved handling practices

Fleet-wide implementation of careful gear removal and bycatch release could be an effective bycatch mitigation strategy for many species in this mahi-mahi fishery. Extremely high hooking survival rates were observed for olive ridley and green turtles in this study, and a recent tagging study indicated that post-release mortality of olive ridleys was low when individuals were only lightly hooked and handled properly (Swimmer et al., 2006). Pelagic sharks often are alive at the time of capture in pelagic longline fisheries and, if handled properly, post-release survival can be high (Gilman et al., 2008). Thus, if fishermen were releasing sharks, improved handling practices could further reduce impacts on these species. Although pelagic stingray is of low conservation concern (IUCN, 2010), it also could benefit significantly from training the crew in improved handling practices. This non-commercial species is usually caught alive and released, but current post-release mortality is expected to be high because of the rough treatment it receives: fishermen typically slam stingrays on the deck and rip their mouths open to remove the hook because they are afraid of their stingers.

4.3.3. Operational changes

Limiting the longline gear's soak time also could be a win–win opportunity, providing conservation benefits both to sea turtles and sharks while minimizing the loss of mahi-mahi catches. In our analyses, olive ridley turtle bycatch rates increased significantly with the duration of sets; silky and thresher sharks also showed a tendency for greater bycatch rates with increased soak time (although the relationships were non-significant). Similar trends have been noted for loggerhead turtles in the Northwest Atlantic Ocean (Watson et al., 2005), and for silky and thresher sharks in other pelagic longline fisheries in the Pacific (Ward and Myers, 2004). Greater shark catch rates could result from attraction to, and predation of, prey species that have already been caught on the longline. Such depredation was reported in 53% of sets in the US Atlantic pelagic longline fishery between 1992 and 2006 (MacNeil et al., 2009), and in Chilean longline fisheries an average of six mahi-mahi were damaged by sharks per set (Gilman et al., 2008). In contrast, mahi-mahi catch rates tended to decline as soak time increased, although the relationship was not significant (perhaps because our dataset was not large enough to tease out this relationship). An analysis of six other pelagic longline fisheries also found mahi-mahi catch rates tended to show the opposite pattern to sea turtle and sharks, decreasing as soaktime increased (Ward and Myers, 2004). This decrease could be the result of depredation, or mahi-mahi may typically be caught during haul in and haul out, such that the amount of time the line is in the water is of little significance. Either way, it appears that there would be little loss of mahi-mahi catches by soaking the longline gear for shorter periods.

It is unclear at present whether additional changes to the fishing operation could further reduce sea turtle and shark bycatch. The use of circle hooks instead of J-hooks and fish instead of squid bait can reduce sea turtle bycatch rates and/or hooking mortality (Gilman et al., 2006, 2007; Read, 2007; Watson et al., 2005), but with most studies focusing on leatherback and loggerhead turtles the effects on olive ridley and green turtles are poorly known. For sharks, fish bait has been shown to reduce catch rates of some species, while studies examining the effects of hook and leader types have often had non-significant results or mixed results depending on the species (Baum and Blanchard, 2010; Branstetter and Musick, 1993; Gilman et al., 2007, 2008; Kaplan et al., 2007; Watson et al., 2005; Yokota et al., 2006). There has been little information on the effects of these aspects of the gear on silky or thresher sharks, but a recent experiment suggested that the use of nylon leaders could reduce catch rates of these species (Ward et al., 2008). We lacked data to examine these operational components of the fishery in detail; improved gear recording by observers or gear experiments in this fishery could provide insight into operational changes that would further reduce bycatch. Finally, increasing the depth of longline sets to avoid shallow sea turtles, silky shark, and pelagic stingray would be infeasible in this fishery because it would greatly reduce the catchability of mahi-mahi (Polovina et al., 2003; Ward and Myers, 2005b).

5. Conclusions and conservation recommendations

Multiple mitigation measures will be necessary to significantly reduce bycatch of all species of conservation concern in mahi-mahi fisheries, and as in other non-selective commercial fisheries, the challenge will be to minimize the trade-off between conservation benefits and fisheries catches. Success in Costa Rica could be achieved through a combination of designating and enforcing a fishery closure in September and October of each year (at least near the olive ridley *arribada* nesting sites), a more stringent shark finning ban, improved gear removal and release practices for turtles and elasmobranchs, and limiting the soak time of the gear. Additional research is needed to determine if switching to fish bait and nylon leaders could also reduce bycatch significantly. We also recommend increased observer coverage and more detailed observer records in this and other mahi-mahi fisheries in order to better understand the spatial, temporal, and operational factors driving bycatch mahi-mahi interactions, and to monitor temporal trends in relative abundance of the target and bycatch species. Given the number of other fisheries, including Costa Rica's advanced fleet and shrimp fleet, and several international pelagic longline and purse seine fleets, capturing sea turtles and sharks in the eastern tropical Pacific (IATTC, 2010; Pretoma, 2010), the mahi-mahi fishery in our study likely constitutes only a minor source of their fishing mortality. Thus, the benefits to these threatened species of reducing bycatch in this fishery could be minimal if other fleets do not also implement and enforce effective bycatch mitigation strategies.

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