Depredation by Coastal Bottlenose Dolphins (*Tursiops truncatus*) in the Southwestern Gulf of Mexico in Relation to Fishing Techniques

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Abstract

Cetacean-fishery interactions are a recurring problem. These interactions are conflict prone, especially between fishers and those seeking marine mammal conservation. In the southwestern Gulf of Mexico, a large fleet of artisanal fisheries operates using a range of different techniques. We recorded 90 fishing operations in two different fishing areas of Veracruz, Mexico, between 2009-2010 and 2014-2015, assessing whether dolphin interaction negatively affects fish catch and fish gear. These potential impacts were evaluated using three generalized linear models (GLMs) hypothesizing that (1) depredation decreases catch per unit effort (CPUE), (2) the predator presence modifies catch composition, and (3) prey species presence increases the likelihood of depredation. Of the gillnet hauls analyzed, 27 were subject to depredation by bottlenose dolphins, despite conditions and fishing methods varying among sites. Higher CPUE attracts larger pods, but a negative effect by depredation was not detected. We also found that depredation probability increased when there were higher capture volumes, when mackerels and jacks were present, and when operations were most southwesterly. Despite the short distance (< 80 km) between sites, we found that bottlenose dolphins on each site displayed different feeding behaviors towards fishing nets. Regarding conservation, bycatch caused by dolphins does not seem to be problematic. In fact, the increase in boat traffic and declining prey abundances due to overfishing could be the main causes of fishers' economic loss. Dolphin-fishery interactions may not represent an actual challenge for marine conservation managers, but stakeholders, fisheries, and governmental institutions should be aware

that diminishing returns due to overfishing could exacerbate the apparently false notion of dolphins competing for the fish.

Key Words: catch composition, fishing gear, CPUE, interactions, PNSAV-Marine Protected Area, Veracruz

Introduction

Interactions between cetaceans and fisheries are a recurring challenge worldwide (Reeves et al., 2001; Lauriano et al., 2004; Rocklin et al., 2009). These interactions are often conflictive and threaten the interests of fishers while raising concerns among those seeking the conservation of marine mammals in the wild (Lavigne, 2003). Currently, bycatch is regarded as the most important menace to the conservation of small marine mammals such as bottlenose dolphins (Tursiops truncatus) (Santos & Pierce, 2015). On the other hand, cetaceans depredate both commercial and recreational fishing gear, generating annual losses that are estimated in the millions of U.S. dollars (Powell & Wells, 2011). According to the optimum foraging theory, a predator will choose the option that yields the most resources per unit of time, especially considering the opportunity cost due to letting available prev go (MacArthur, 1972). This means that a predator may choose to pursue a certain prey if it is unlikely to catch a better prey item (Hughes, 1980). Depredation on the catch within the fishing nets could take the form of getting hold of some species that are sought-after but difficult to obtain because it yields higher benefits with lower cost (Tixier et al., 2014).

Bottlenose dolphins feeding upon the catches of small-scale (i.e., artisanal) fisheries have been of interest because of the potentially severe economic losses caused by the taking of captured fish or bait (Pennino et al., 2014). Dolphins use the catch from artisanal fishing operations as an advantageous food source due to the relatively easier access to high densities of prey (Rocklin et al., 2009). Thus, dolphins interact intensively with fishing nets, damaging both the catch and fishing gear, but also putting themselves at risk (Reeves et al., 2001; Bearzi et al., 2011; Zappes et al., 2011; Morteo et al., 2012b). Fishers often become aggressive towards the dolphins, harassing, hurting, or even killing them when they come close to the fishing operations (Wells et al., 2008; Powell & Wells, 2011; Morteo et al., 2012b).

Bottlenose dolphins interact with all kinds of fishing gear, but the most frequent are gillnets from which they can feed safely most of the time (Read et al., 2003). The genus *Tursiops* exhibits high behavioral plasticity coupled with a complex cognitive ability, which allows these animals to quickly modify their predatory tactics, even among individuals of the same population (Daura-Jorge et al., 2012). Therefore, while some dolphins may avoid encounters with fishers (Morteo et al., 2012b), some studies suggest that their interactions with the fishing nets is increasing, and they are feeding intensively on trapped fish (Lauriano et al., 2004; Rocklin et al., 2009).

The interactions between dolphins and fisheries have been recorded since the early 1970s (Busnel, 1973); however, most have been described in purely anecdotal terms, particularly along the Mexican coast of the Gulf of Mexico (Morteo et al., 2012b). Therefore, the magnitude of the reciprocal impacts, as well as the conditions in which the interactions occur remain to be analyzed in this area. In the Mexican state of Veracruz on the southwest coast of the Gulf of Mexico, artisanal fisheries operate as an important economic activity, sustaining many families (Jiménez-Badillo & Castro-Gaspar, 2007).

Most artisanal fishing activities take place in coastal waters, river mouths, or reef areas, which are locations preferred by the coastal ecotype of the bottlenose dolphin since these areas provide food, shelter, and refuge from predators (Martínez-Serrano et al., 2011). At southern Veracruz, there are two known resident populations of coastal *T. truncatus*: one in the Veracruz Reef System National Park (PNSAV-Marine Protected Area) and the other in the shallow waters of Alvarado (La Escollera; Ruiz Hernández, 2014), and both populations have been reported to interact with fishing gear and vessels (Morteo et al., 2012a, 2012b; Hernández et al., 2015).

In this study, we evaluated the interaction between bottlenose dolphins and artisanal fisheries in these areas, and whether gillnet depredation by dolphins implies loss of the total catch or produces undesirable changes in catch composition. We hypothesized that the mechanisms underlying the dolphins' choice of feeding from gillnets is linked, through optimal foraging, with possible negative effects on total CPUE due to the fishing procedures (mostly haul operation time) and the catch composition in terms of the species present and their biomass. Our aims were to (1) evaluate differences between fishing operations with and without depredation (negative impact), (2) assess the differences between two fishing areas that are geographically close but quite different in terms of their ecological characteristics, and (3) ascertain if the resident bottlenose dolphins present different feeding patterns.

Methods

Study Area

The surveys included two important fishing communities: (1) La Escollera (18° 46' 3.17" N, 95° 45' 5.46" W) and Mata de Uva (19° 2' 5.08" N, 95° 58' 7.42" W), hereafter referred to as LE and MU, respectively (see Figure 1). The LE area is heavily influenced by the third largest coastal lagoon in the country since it receives the discharge of the strong Papaloapan River (Guentzel et al., 2011). Human presence is relatively high (> 2,000 fishers), and shrimp fisheries are the main activities near the mouth of the lagoon, where most boat traffic occurs (7.8 ± 5.9 vessels/h, mostly small skiffs; Morteo et al., 2012b).

The MU population comprises 18 families (< 200 people) whose whole livelihoods depend on fishing. The artisanal fleet includes 50 boats (counted during a storm day when none were at sea). This area is adjacent to the PNSAV, the most important protected marine area in the state, but also the most impacted by a diverse range of activities (e.g., fishing, tourism, transportation, military, harbor maneuvers, and so on) and high levels of vessel traffic (9.6 with \pm 3.4 vessels h⁻¹; Morteo & Hernández, 2007). This protected area covers 655 km² and is also a RAMSAR site (Number 1346; Figure 1). These abovementioned conditions highlight differences in several features between the sites; however, the climate is similar, with prevailing tropical conditions (annual average temperature 26.4°C and annual rainfall of 2,077.9 mm). There are also three marked seasons: (1) cold northerly fronts (November to February), (2) dry season (March to June), and (3) rainy season (July to October).

Data Collection

Fishing Operations—The study was conducted from August 2009 to January 2010 at LE, and from April 2014 to April 2015 at MU. Data were collected throughout 4 d/mo during normal operational



Figure 1. Study area: Central coast of Veracruz, Mexico. Study sites: Mata de Uva (MU) and La Escollera (LE). Total hauls observed during the study with catch per unit effort (CPUE) harvest in each point.

trips on board < 8 m fishing boats (known locally as pangas), which were equipped with outboard engines of 40 to 60 hp. Since the intention was to document the usual experience of the fishers when interacting with dolphins, we did not develop any sort of experimental treatment design for the operations. Moreover, the distance covered and fishing gear utilized both were entirely at the discretion of the fishers and, thus, reflected normal operations. Data were continuously recorded from the deployment of the fishing gear until its recovery. All sets were considered an independent fishing operation (hereafter referred to as a haul) and were established as the unit of measure for this study (Lauriano et al., 2004). Only net hauls were analyzed since these are more commonly depredated by dolphins (Morteo et al., 2012b).

On-board observers recorded data during each fishing operation following Rocklin et al. (2009). Variables were separated into three groups: (1) operational, (2) interaction, and (3) environmental. The *operational* variables were type of gear, fishing effort (time [h] elapsed from start to end of the haul), mesh size (or distance between knots [m]), net length and width (m), catch composition (species richness), total weight of the catch, geographical position (Garmin GPS 72H), depth (m; measured with a portable Echo Sounder Depth Meter speed tech), and number of vessels (counted within a radius of approximately 1 km).

Dolphin-fishery *interactions* were defined as such when dolphins were observed within a 200-m radius from the fishing gear (see Lauriano et al., 2004; Morteo et al., 2012b). Evidence of depredation by bottlenose dolphins was assessed by direct observation of the animals taking fish from nets, feeding behavior such as diving towards the net, or by the presence of at least one damaged fish in the recorded catches. In addition, damage to the nets, such as holes in the mesh attributed to dolphin attacks, was recorded as possible evidence of depredation in consensus with the fishers after each haul. Whenever dolphins were present, we recorded the time (h) of the interaction and the number of dolphins observed.

The environmental information recorded included the sea-bottom substrate type (e.g., sandy, rocky, or sea grass) and sea conditions (Beaufort scale). Since net size and operation time were widely variable, we standardized catch biomass per unit of effort, defined as weight of the total catch, divided by net length and time of exposure (CPUE = kgm⁻¹ h⁻¹). Taxonomical identification of captured species was carried out to the level of genus, and to species if possible, using taxonomic keys (Froese & Pauly, 2015) at the Functional Ecology Laboratory of the Institute of Ecology A.C. (INECOL). In addition, the Shannon diversity index (H' = $-\Sigma$ p_i ln p_i) was estimated for each haul using the software *Estimates*, Version 9.1.0 (Colwell, 2013). Calculation of the total number of species per haul allowed taxonomic richness as another variable (Peet, 1974).

The distance to the coastline (DTCL) was calculated for each haul by tracing a direct line (in km) perpendicular to shore. This variable was found to be highly correlated with depth but was also easier to estimate by fishers. We mapped the corresponding CPUE for each observed haul (Figure 1) using GIS analysis tools in *ArcMap*[®], Version 9.3 (ESRI, 2014).

Data Analyses

Selection of Relevant Variables—A Principal Component Analysis (PCA) was performed to assess the causes of variability in the dataset and to rank their importance; this tool also allowed for the exploration of relationships among the variables. For each haul, we evaluated the location (latitude, longitude), total CPUE, Shannon diversity index (H'), richness, number of dolphins present, interaction time (h), net length (m), number of vessels, depth (m), and DTCL (km). Visualization of results was enhanced with a biplot using the first two principal components (48% of the variance). Data was also separated into categorical variables (site and fishing gear type) to improve data display.

Modeling CPUE Response, Haul Composition (H'), and Depredation Probability—We evaluated the effect of depredation events and the recorded environmental and operational variables on total CPUE and haul composition (taxonomic diversity

patterns) through generalized linear models (GLMs). Differences between hauls with and without depredation were analyzed in terms of catch biomass and species composition. Thus, total CPUE and H' were modeled as response variables, and depredation events were modeled as a covariate.

In all models, datasets from both sites (LE and MU) were combined for simultaneous contrast. These models included both site and geographic position (latitude, longitude) as independent variables. In Model 1, CPUE was used as the response variable, with Gaussian family following logarithmic transformation. In Model 2, the Shannon diversity index was fitted as the dependent variable with Gamma family and log-link function. Finally, the presence/absence of interaction was modeled as a binary response variable (Model 3) to assess which factors may influence the likelihood of depredation on nets. Models were produced as follows:

- Model 1 Log (CPUE) ~ latitude + longitude + H' + richness + DTCL + fishing gear type + site + depredation event + haul time + net length + interaction time + number of dolphins
- Model 2 Shannon diversity index (H') ~ CPUE
 + latitude + longitude + DTCL+ fishing gear + site + depredation event + haul time + net length
 + interaction time + number of dolphins
- Model 3 Depredation event ~ CPUE + Atlantic Spanish Mackerel + Jack + Little Tunny + King Mackerel + Blue Runner + latitude + longitude + DTCL + richness + fishing gear + site + haul time + net length + Beaufort scale + sea bottom type

The last model shows the presence of Atlantic Spanish mackerel (*Scomberomorus maculatus*), jacks (*Caranx* sp.), little tunny (*Euthynnus alletteratus*), king mackerel (*Scomberomorus cavalla*), and blue runner (*Caranx crysos*). These species are all known to be preferred prey for bottlenose dolphins in the area (E. Morteo, pers. obs.).

A back-forward selection was performed to find the minimal adequate model using the Akaike information criterion (AIC) and the Deviance information criterion (DIC) to assess fitness (Akaike, 1987; Celeux et al., 2006; Zuur et al., 2009), verifying that the residual deviance was congruent with GLM assumptions. When categorical variables were significant (p < 0.05), post hoc Tukey mean comparisons were performed. The model results showed the effects of statistically significant explanatory variables on response variable prediction. All statistical analyses and plots were carried out in Version 3.1.2 of the *R* environment for statistical computing (R Core Team, 2014).

Site Characterization and Fishing Gear Selectivity

A total of 90 fishing operations were recorded during 2009-2010 (LE = 46 operations) and 2014-2015 (MU = 44 operations), but only 61 used gillnets which were the only ones considered for analysis (37 MU and 24 LE). Dolphin interaction differed in the two locations. From the gillnetting hauls, 19 were depredated in LE and 8 in MU.

Those 19 interactions with bottlenose dolphins at LE were 80% of the operations involving gillnets. This fishing area was characterized by a 45% use of small nets, mostly for shrimps (SHR), followed by rounding gillnetting (RG; locally called *calado*) with 33%. This latter method is fast (average setting time around 35 min) and quite selective, effectively targeting a single species (large Scombrids: mackerels and tunas). Hooks on a long-line (for large fish) were also used but to a lesser extent (5%).

In contrast, the eight dolphin interactions at MU were 20% of the operations recorded. Depredation on the long-line hooks was also observed; in these cases, dolphins removed the bait and even the target fish. The rounding method was also used here, but the main fishing gear in this site was the lying crossed (LC) gillnets which were used 70% of the time (deployed perpendicular to the coastline for an average of almost 2 h). The LC gillnet proved to be an unselective method, presenting higher richness (usually greater than four species per haul) and collecting several other species in the bycatch (Table 1), including sea turtles (*Eretmochelys imbricata* and *Caretta caretta*).

Haul Composition (Species Richness)

A total of 56 species were identified in the hauls. At least 17 of these were economically important as well as potential prey items for bottlenose dolphins. These species included members of the Scombridae (mackerels and tunas), Lutjanidae (snappers), Carangidae (jacks), and Sciaenidae (croakers) families, but there were eight additional species in the bycatch (Table 1).

Relationship Between Variables and Their Effect on the Hauls

The PCA analysis showed a strong spatial pattern where latitude was highly correlated with net length, clearly reflecting the different uses of gear (Figure 2). The expected high correlation between depth and DTCL was readily picked. Total CPUE was positively related to the number of dolphins involved in the interactions and to the duration of such events. Diversity and richness indexes were positively related to haul time but negatively related to CPUE and interactions with the dolphins.

Assessing the Importance of Dolphin Depredation

Negative Effect on Total CPUE-Variation in the total CPUE of the hauls seems to be influenced by interactions between the location (as indicated by latitude; Figure 3a) and haul time, fishing gear type, net length, and number of dolphins (Table 2). Latitude negatively influenced the predicted CPUE (Table 2), and, therefore, their interaction was significant and reflected differences in gear usage (Figure 3b). Conversely, the number of dolphins was positively related to CPUE (Figure 3c); thus, larger groups of dolphins approached the nets when the harvests were greater. Rounding fishing gear had a positive effect on captures with the highest CPUE values. Post-hoc tests showed that this gear differs significantly from the LC gillnet method but not from shrimp netting (Figure 3d). It is important to note that no significant direct effect of the depredation event (as a covariate) was found under current conditions in the study area.

Haul Species Composition—Model 2 evaluated whether dolphin interactions (direct or indirect) affected the composition of hauls more than the environmental and operational variables. The fitted model showed that there was no significant effect of dolphin presence on catch diversity (Table 2). However, significant effects were found for DTCL, net length, fishing gear, and season. Greater DTCL and longitude (i.e., more distance from the coast) had negative effects on catch diversity (Figure 4a & b). On the other hand, longer nets (> 400 m), LC gear, and the season of northerly cold fronts positively affected the diversity index (Figure 4c & d).

Factors Influence the Likelihood of Depredation—The third model also supported the spatial patterns found for depredation probability and CPUE (Figure 2). However, total CPUE and the presence of Atlantic Spanish mackerel had the highest positive effect on increasing depredation probability (Figure 5a-c). Conversely, high densities of vessels in the fishing area, the presence of jacks, and the use of vessels from the northern area (MU) seemed to decrease the presence of bottlenose dolphins during fishing operations (Figure 5b, d & e; Table 2c).

Table 1. List of species captured in hauls during the study. The site indicates where each species was captured. Status points out whether the species is commercialized in harbors (CI), only consumed locally (LC), or if they are bait (B) or bycatch product (Y). * = reported as prey of bottlenose dolphins.

Site	Species	Spanish common name	Family	Status	Potential prey
Both	Caranx latus	Jurel Carangidae		CI	*
Both	Scomberomorus cavalla	Peto	Scombridae	CI	*
Both	Scomberomorus maculatus mamaculatus	Sierra	Scombridae	CI	*
MU	Oligoplites altus	Quiebra cuchillos	Carangidae	CI	
MU	Ariopsis felis	Bagre	Ariidae	CI	
Both	Conondon nobilis	Ronco	Haemulidae	CI	*
MU	Aurolineatum sp.	Jiniguaro/Charchis	Haemulidae	В	
MU	Menticirrhus littoralis	Ratón	Scianidae	LC	
MU	Prionatus sp.	Pájaro	Triglidae	LC	
Both	Lutjanus synagris	Villajaiba	Lutjanidae	CI	*
MU	Chloroscombrus chrysurus	Chicharra/Casabe	Carangidae	LC	
MU	Oligoplites saurus	Chapeta	Carangidae	LC	
Both	Caranx crysos	Cojinuda	Carangidae	CI	*
MU	Brevoortia patronus	Sardina lacha	Clupeidae	В	
MU	Citharichthys abbotti	San Pedro	Paralichthyidae	LC	
MU	Harengula jaguana	Sardina escamuda	Clupeidae	В	
MU	Sardinella aurita	Sardina común	Clupeidae	В	
Both	Lutjanus vivanus	Huachinango cola amarilla	Lutjanidae	CI	*
Both	Lutianus campechanus	Huachinango común	Lutianidae	CI	*
Both	Euthynnus alletteratus	Bonito	Scombridae	LC	*
MU	Strongylura notata notata	Pico de aguia	Belonidae	LC	
Both	Trachinotus carolinus	Pampano amarillo	Carangidae	CI	*
Both	Ocvurus chrysurus	Rubia	Lutianidae	CI	*
MU	Seriola dumerili	Medregal amarillo/Pez limón	Carangidae	CI	
MU	Anisotremus surinamensis	Burriquete	Haemulidae	CI	*
MU	Cephalopholis cruentata	Cabrilla	Serranidae	CI	
MU	Sarda sarda	Carito	Scombridae	CI	*
MU	Mugil curema	Lebrancha	Mugilidae	CI	*
MU	Mycteroperca honaci	Mero negrillo	Serranidae	CI	*
MU	Aluterus monoceros	Cochino	Monacanthidae	CI	*
MU	Synodus foetens	Chile vaquero	Synodontidae	LC	
MU	Onsanus beta	Sano	Batrachoididae	LC	
MU	Micropogonias furnieri	Doradilla	Sciaenidae	LC	
MU	Conoscion arenarius	Corvina arenera	Sciaenidae	LC	*
Both	Umbring coroides	Trucha	Sciaenidae	LC	*
MU	Decepterus punctatus	Qiudo	Carangidae	B	
MU	Lagocaphalus lagoinatus	Pascagio	Tetraodontidae	IC	
MU	Balistas capriscus	Cochino ²	Religidae		
MU	Sphyraena barracuda	Borracuda	Sphyroepidee		
MU	Opisthonema oplinum	Sardina	Churaidaa	P	
MU	Salana setaninnis	Jorobada	Caranaidaa	ц Д	
Dath	Diantomia aunatu-	Mojomo	Caraligidae	D CI	*
Boin	Diapierus auraius	Mojarra	Democidae	CI	
LE	Farjaniepenaeus aziecus	Camaron care	Penaeidae	CI	
	Luopenaeus setijerus	Camaron blanco	Penaeidae	U V	
MU D-d	Spnyrna tiburo	Tiburon martillo	Spnyrnidae.	ľ V	
Both	Carcharninus leucas	Liburon toro	Carcharhinidae	Y	
Both	Dasyatis americana	Raya latigo blanca	Dasyatidae	Y	
MU	Dasyatis sabina	Raya latigo de espina	Dasyatidae	Y	
MU	Gymnura micrura	Raya mariposa	Gymnuridae	Y	
Both	Rhinoptera steindachneri	Raya tecolote	Myliobatidae	Y	
MU	Eretmochelys imbricata	Tortuga carey	Chelonidae	Y	
MU	Caretta caretta	Tortuga caguama	Chelonidae	Y	



Figure 2. Principal component analysis (PCA) grouping points by fishing gear and labeled by site

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Parameter	Value	SE	df	t value	<i>p</i> value
Intercept	19.40123	9.65556	60	2.009	0.0495
Latitude	-1.05484	0.50881	60	-2.073	0.0429
Haul time	-13.21363	5.97378	60	2.212	0.0312
Fishing gear	0.64292	0.12540	60	5.127	< 0.0001
Net long	1.02911	0.37822	60	2.721	0.00879
No. of dolphins	0.09171	0.03534	60	2.595	0.01222
Lat:Haul time	0.69374	0.31431	60	2.207	0.0316

Table 2a. Coefficient estimated by Model 1 for CPUE

Best fit model chosen after stepwise analysis: AIC = $131.14 - D^2 = 65\%$.

Parameter	Value	SE	df	t value	p value
Intercept	0.816037	0.059884	60	13.627	< 0.0001
Longitude	0.232391	0.137350	60	1.692	0.09653
DTCL	-0.013244	0.005584	60	-2.372	0.02130
Fishing gear	-0.108549	0.060116	60	-1.806	0.07654
Net long	0.131168	0.046581	60	2.816	0.00678
Season	0.145515	0.049702	60	2.928	0.00499

Best fit model chosen after stepwise analysis: AIC = $-49.642 - D^2 = 48\%$.

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Parameter	Value	SE	df	t value	p value
Intercept	4.7487	3.1163	60	1.524	0.1276
Total CPUE	21.5753	12.2910	60	1.755	0.0792.
Jurel	-8.4062	4.8664	60	-1.727	0.0841 .
Sierra	1.9772	1.0688	60	1.850	0.0643 .
No. of vessels	-0.7769	0.5097	60	-1.524	0.1275
Site	-6.9167	2.7617	60	-2.504	0.0123*

c. Coefficient estimated by Model 3 for depredation event

Best fit model chosen after stepwise analysis: AIC = $-40.272 - D^2 = 66\%$.



Figure 3. Effects of linear predictors on predicted CPUE by Model 1. For categorical variables: quartiles (box), mean (middle line), standard error (SE) (vertical lines), and *post-hoc* Tukey test results show different letters for significant contrasts: (a) for net length (m) and (b) for fishing gear. For numerical variables: tendency (black line) and 95% confidence interval (CI) for prediction (grey shadow) for (c) number of dolphins and (d) haul time and latitude interaction.

Discussion

Interactions between cetaceans and fisheries are controversial, and detailed mechanisms underlying this complex process remain unknown; however, optimum foraging seems to be an important element modulating dolphin behavior. This study represents the first attempt to assess depredation by *Tursiops* *truncatus* in small-scale fleets in Mexico. Our results show that the presence of an intense interaction between bottlenose dolphins and fishers in the southwestern Gulf of Mexico may represent an important challenge for marine resource managers. This work is especially important since most efforts in researching depredation events have focused on large fleets of artisanal fisheries in developed countries.



Figure 4. Effects of linear predictors on predicted Shannon diversity index (H') by Model 2. For continuous variables: fitting (black line) and 95% CI for prediction (grey shadow) for (a) longitude (°W) and distance to coast line (km); for categorical variables: quartiles (box), mean (middle line), and SE (vertical lines) for (b) net long (m), (c) fishing gear, and (d) season. *Post hoc* Tukey test results. LC = lying crossed, RG = rounding gillnetting, and SHR = shrimp net.



Figure 5. Effects of linear predictors on probability of depredation event predicted by Model 3. For numerical variables: tendency (black line) and 95% CI for prediction (grey shadow) for (a) number of vessels, (b) total CPUE, (c) presence of jacks (Spanish common name *Jurel*), and (d) presence of Atlantic Spanish mackerel (Spanish common name *Sierra*). For categorical variables: quartiles (box), mean (middle line), SE (vertical lines), and *post-hoc* Tukey test results show different letters for significant contrasts: (e) site.

Most coastal fisheries on the central coast of Veracruz are unspecific, unregulated, and practiced mostly for self-sustenance (Jiménez-Badillo & Gaspar-Castro, 2007); thus, most boats work with different gear and target different species throughout the year. Gillnets are the most frequently used and, therefore, are most frequently encountered by the bottlenose dolphins (Morteo et al., 2012b). Our data showed a high rate of depredation events associated with the use of gillnets (44.3%), which exceeds other data reported around the world (Lauriano et al., 2004; Hernandez-Milian et al., 2008; Rocklin et al., 2009; Goetz et al., 2014; Pennino et al., 2014). Because of the strong spatial stratification and based on behavioral differences (Morteo et al., 2015) and the very low (< 1.2%) interchange of dolphins between LE and MU (Ruiz-Hernández, 2014), we suggest that each site should be distinguished as a specific unit. The discrepancy in depredation rates, therefore, appears to provide additional support for the social differentiation of these dolphins.

MU is close to a coral reef; therefore, the yields are quite variable and influenced by many environmental factors, which favors multispecies fisheries. Conversely, LE is highly influenced by a coastal lagoon and river discharges, especially during the rainy season. These factors make this a particularly highly productive site (Morteo et al., 2012b). As the geomorphological and ecological characteristics of each area may largely explain the highlighted differences found in this study, other cultural and economic factors are deemed fundamental for gear selection at each site (McClanahan et al., 2008). LC nets are frequently used in MU, although they yield lower captures. This choice could be dictated by the proximity of MU to the PNSAV, but it is mostly due to tradition. Dolphins interacted less frequently with this gear, but when they did, they often caused damage to the nets. In contrast, LE is characterized by the frequent practice of shrimp netting and use of rounding gear. The latter fishing method catches great volumes of large-size fish of a single species (i.e., mackerel and tuna) while reducing the effort (and, thus, the economic cost). However, the most effective deployment requires a diver in the water to close the net (there are few diving fishers in MU). It is the most profitable method in the region, but it is also highly correlated with depredation.

We did not find evidence to support that CPUE is directly affected by dolphins' depredation, but large catches attract more dolphins. On the other hand, the effort (i.e., time) is directly influenced by the fishing gear utilized. Since larger hauling times negatively affect the catch, we can assume that larger sets indicate LC netting (as above noted) produced the smallest harvests.

We found that dolphins' depredation had no significant effects on haul composition and that higher diversity values corresponded to shallow waters. Trends in species diversity were evident, particularly due to operational (fishing gear and net length) and environmental (depth and season) variables. This could be associated with local processes such as currents and substrate types but may be mostly influenced by the proximity to the coral reefs (Mora et al., 2003) and the use of different fishing gear types. During the rainy season in the Gulf of Mexico, estuarine zones are highly influenced by river discharges and associated processes, causing peaks in the diversity of coastal fish communities (Yáñez-Arancibia et al., 1988; Castillo-Rivera et al., 2002). Nevertheless, the El Niño/Southern Oscillation (ENSO) event that occurred during 2015 (National Oceanic and Atmospheric Administration [NOAA], 2015) might have interfered with observations of this pattern in the fish community.

We propose that the presence of certain fish species increases the chances of haul depredation. When large stocks of migratory fish (mackerel and tuna) arrive (during March and April), most of the fishing effort is focused on capturing these schools since these are commercially important species (fetching around 5 USD/kg in 2012). We also found that depredation events depend mostly on the choice of fishing method and that round netting, which is aimed mostly towards Atlantic Spanish mackerel, presents a higher probability of depredation (Zollett & Read, 2006). When approaching this type of net, dolphins are more likely to become entangled (Read et al., 2003), but we did not record these kinds of events.

The presence of Atlantic Spanish mackerel has a positive effect on depredation events, but the presence of *Caranx latus* (jacks) decreases the likelihood of such interactions. We believe this could be because Carangid fish (such as jacks) move alone, especially while foraging (Silvano, 2001), while Atlantic Spanish mackerel typically form large groups (Begg, 1998); therefore, noise produced by entangled prey may be better heard by dolphins when fish are grouped in large numbers (Gannon et al., 2005).

The risk of bycatch in protected species, such as marine mammals, is a major concern for biodiversity conservation, with gillnet fisheries representing the main source of threat (Read et al., 2006; Read, 2008). However, in contrast with reports by Morteo et al. (2012b), this was not observed during this study. Nevertheless, higher densities of vessels have a negative effect on depredation because they can change the acoustic landscape (Buckstaff, 2004) and, therefore, alter feeding behavior (Dans et al., 2008) and habitat use (Constantine et al., 2004). Dolphins avoid these undesirable interactions. Thus, when large numbers of vessels are fishing in each area, dolphins may use alternative locations, even when large amounts of prey are most likely available at the fishing site (Morteo et al., 2012b).

Conclusions

• Of a total of 56 species of fish, at least 17 species were economically important and potential prey items for bottlenose dolphins. They include the Scombridae (mackerels and

tunas), Lutjanidae (snappers), Carangidae (jacks), and Sciaenidae (croakers) families.

- LE and MU should be distinguished as two specific units due to the strong spatial stratification, behavioral differences, and very low (< 1.2%) interchange of dolphins between them.
- We did not find evidence to support that CPUE is directly affected by dolphins' depredation, but large catches attract more dolphins.
- We found that dolphins' depredation had no significant effects on haul composition and that higher diversity values corresponded to shallow waters.
- We propose that the choice of fishing method and the presence of certain fish species (such as mackerel and tuna) increase the chances of haul depredation.
- There is a high interaction rate (> 40% of sets), but this did not affect CPUE or the composition of the hauls. The perception of harm may be much greater than it represents in economic terms.
- During the study, we did not observe a single occurrence of incidental catch. This suggests that the perception of the damage of the fisheries by the dolphins could be exaggerated.

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