Journal of the Marine Biological Association of the United Kingdom

cambridge.org/mbi

Original Article

Cite this article: Morales-Rincon N, Morteo E, Delfín-Alfonso CA (2019). Influence of artisanal fisheries on the behaviour and social structure of *Tursiops truncatus* in the South-western Gulf of Mexico. *Journal of the Marine Biological Association of the United Kingdom* **99**, 1841–1849. https://doi.org/10.1017/S002531541900078X

Received: 1 June 2018
Revised: 6 August 2019
Accepted: 7 August 2019
First published online: 10 September 2019

Key words:
Age; behaviour; group size; interaction and fishing net

Author for correspondence:
Eduardo Morteo,
E-mail: eduardo.morteo@gmail.com

Influence of artisanal fisheries on the behaviour and social structure of *Tursiops truncatus* in the South-western Gulf of Mexico

Nataly Morales-Rincon[1], Eduardo Morteo[1,2,3] and Christian Alejandro Delfín-Alfonso[1,2]

[1]Marine Mammal Laboratory (LabMMar, IIB-ICIMAP), Universidad Veracruzana. Calle Dr Luis Castelazo Ayala s/n, km 2.5 Carr. Xalapa-Veracruz, Col. Industrial Ánimas, C. P 91190, Xalapa, Veracruz, México; [2]Instituto de Investigaciones Biológicas, Universidad Veracruzana. Calle Dr Luis Castelazo Ayala s/n, km 2.5 Carr. Xalapa-Veracruz, Col. Industrial Ánimas, CP 91190, Xalapa, Veracruz, México and [3]Instituto de Ciencias Marinas y Pesquerías, Universidad Veracruzana. Calle Hidalgo 617, Col. Río Jamapa, CP 94290, Boca del Río, Veracruz, México

Abstract

Behavioural plasticity in animals is tested whenever competitive interactions for space and/or food resources occur between wildlife and human activities. This study uses the concepts of operational and non-operational interactions between bottlenose dolphins (*Tursiops truncatus*) and artisanal fisheries in Alvarado, to search for differences in behaviour, age structure and group size. We conducted 20 surveys between 2015 and 2016, and recorded 64 groups by means of scan sampling from either a research boat or a fixed vantage point. Average dolphin group size was small ($\bar{x} = 3.2$, SD = 2.2 individuals) and fewer individuals were commonly present when interaction with fisheries occurred. Operational interactions were defined within the first 30 m and occurred mainly with lone individuals (54% recorded from the lighthouse and 82% during surveys); this benchmark also accounted for higher frequencies in locomotion and feeding ($\chi^2 = 83.10$; df = 7; $P < 0.001$). We found a higher rate of new behavioural events for dolphin groups furthest from human activities, as well as a decrease in behaviours that imply greater body exposure as dolphins approach the fishing spots. Age structure and dolphin group size were not different during and in the absence of interaction with fisheries, but most interactions involved male dolphins. Behavioural variations in the dolphins' repertoire are likely a strategy to reduce the risk of injuries or death when interacting with human activities; these dolphins seem to have habituated to or at least tolerate fishing activities within the study area, possibly constituting a sex-biased pressure.

Introduction

Animals develop different strategies and modify their behaviour throughout their life history to adapt in response to environmental stimuli (Tinbergen, 1963). These various strategies are deployed and tested during their ecological interactions (Medel *et al.*, 2009); however, with the accelerated expansion of occupied territory for the development of human activities, these processes are constantly being modified and organisms are forced by anthropic factors to quickly change their behaviour in order to survive (Faeth *et al.*, 2005). For instance, agriculture and livestock demand space, and thus continuously alter and modify the landscape, limiting habitat availability as well as food for various species of both herbivores (Lee & Graham, 2006) and carnivores (Amador-Alcalá *et al.*, 2013; Peña-Mondragón & Castillo, 2013). This situation has created long lasting conflicts between humans and wildlife, which have been widely documented, and generate considerable financial losses as well as violent responses towards the species involved, resulting in serious injuries and probably death for many individuals in populations of these species (Goldstein, 2013).

Fishing is another common and worldwide distributed activity with a similar scenario; for instance, non-target species (i.e. accompanying and by-catch fauna such as marine mammals and turtles) are frequently reported as accidentally entangled in nets or even killed by fishers' violent responses; this occurs in both industrial and artisanal fisheries (Bearzi, 2002; Jiménez & Domínguez, 2007; Adimey *et al.*, 2014; Morteo *et al.*, 2017). Particularly in the latter, in which various rustically constructed gear are used (Jiménez & Castro, 2007), marine mammals such as dolphins, especially of the species *Tursiops truncatus* (Montagu, 1821), are the ones with the highest frequency of interaction reports (Reeves *et al.*, 2001; Lauriano *et al.*, 2004; Waples *et al.*, 2013; Morteo *et al.*, 2014). The opportunistic feeding habits of bottlenose dolphins (Hill *et al.*, 2003; Rocklin *et al.* 2009) may play an important role in their frequent interactions with fisheries, as a result of competition for common prey species (Reeves *et al.*, 2001; Lauriano *et al.*, 2004; Waples *et al.*, 2013; Morteo *et al.*, 2014; Rechimont *et al.*, 2018).

These interactions are commonly reported and widely distributed across the world (Rocklin *et al.*, 2009; Powell & Wells, 2011; Jaiteh *et al.*, 2013; Adimey *et al.*, 2014; Morteo *et al.*, 2014);

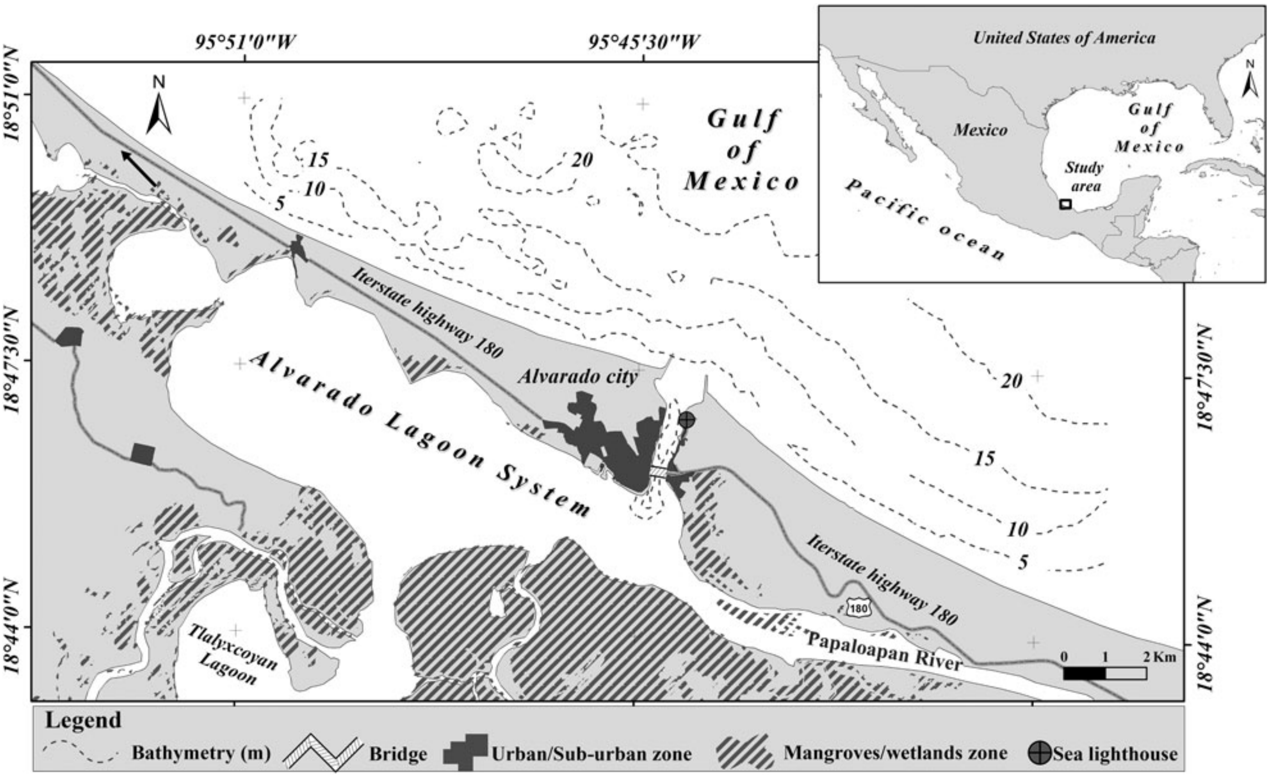

Fig. 1. Study area in Alvarado, located on the central coast of Veracruz, Mexico.

however, there are no studies in Mexico that describe in detail the strategies used by these cetaceans, as well as their behavioural changes in relation to the presence of artisanal fishing activities. Therefore, we studied a bottlenose dolphin population in the coastal waters of the western Gulf of Mexico, where the dolphin–fisheries interactions are well known to cause conflict due to depredation on fishing gear (Morteo *et al.*, 2012, 2014, 2017; Rechimont *et al.*, 2018). Our main goal was to document behavioural variations in relation to dolphin group size and age structure, using their proximity towards the artisanal fishing as an indicator of the types of interactions.

Materials and methods

Study area

The municipality of Alvarado is located within the central coast of the state of Veracruz in the Gulf of Mexico (18°47′47.22″N95° 44′43.77″W; Figure 1). The coastal waters are influenced by one of the largest rivers in the country (Papaloapan River), and the Alvarado Lagoon System (Jiménez *et al.*, 2007); this ecosystem is highly productive, thus this area is of nationwide importance for the abundance of shrimp and coastal fish (López *et al.*, 2011).

Artisanal fisheries support many families in communities along the coastal waters of the Gulf of Mexico, and Alvarado is no exception. Much of its economy depends on artisanal fisheries, mainly for products of commercial importance such as sea bass (*Centropomus parallelus*), mackerels (*Gerres cinereus*, *Scomberomurus regalis*), snappers (*Lutjanus* sp.), mullets (*Mugil curema*), red drums (*Sciaenops ocellatus*) and jacks (*Caranx hipos*) (Morteo, 2011; Rechimont *et al.*, 2018). Fishers generally use 7 m long fibreglass outboard motorboats (40 hp) in fish captures; their implements are diverse and depend on the target species, such as hand lines, long lines and different types of gillnets (Jiménez & Castro, 2007; Morteo & Hernández-Candelario, 2007; Rechimont *et al.*, 2018). The latter are the most frequently deployed in this study area (Morteo *et al.*, 2012, 2014; Rechimont *et al.*, 2018), and are over ~700 m long and 3.5 cm mesh size in average. These nets are not species selective and capture all kinds of pelagic fish (Bjordal, 2002).

Observations from fixed point

From October 2015 to July 2016 we made monthly field observations between 07:00 and 16:00 h from a vantage land point at the top of a 22 m lighthouse (18°46′56.69″N 95°44′44.59″W, Figure 1) located over a lowland tropical dry forest known as 'Monte Simón' at the eastern breakwater of the Alvarado lagoon entrance (Figure 1). Behavioural observations of dolphins were accomplished by means of the continuous recording scanning method (Altmann, 1974).

The most common behaviours with the longest durations were categorized into general states (Villamizar, 2001); these were represented by (1) locomotion, (2) feeding, (3) social, (4) socio-sexual, (5) play and (6) rubbing with objects (Table 1). Most of these observations were carried out in the absence of fisheries, and only the latter were used as control. Behavioural records were also filmed with a high definition digital camera (Panasonic SDR – H80 or Nikon Coolpix p500), in order to reproduce and analyse behavioural displays with higher detail.

Distances between dolphins and human activities (either fishing gear or boats) were calculated by means of a theodolite (Sokkia Mod. FOIF-DT 205), recording the horizontal and vertical angles relative to the height of the lighthouse. Such distances (m) were estimated at the centre of each group and these were categorized using the limits proposed by Morales-Rincon (2016); therefore all dolphin sightings were divided following Nadeau (2013) in: (1) operational interactions (<30 m from nets), (2) non-operational interactions (31–150 m from the net) and (3) no interactions (>150 m or no fishing gear).

Surveys

During the same months, we also carried out monthly boat-based surveys between 07:00 and 16:00 h during the normal operations

https://doi.org/10.1017/S002531541900078X Published online by Cambridge University Press

Table 1. Behavioural description for bottlenose dolphins in the coastal waters off the Alvarado Lagoon according to Morales-Rincon (2016)

State	Definition
Locomotion	Variety of behaviours related to the movement or continuous change in location with a determined speed and direction (García-Vital, 2012). These activities may be developed freely or around fishing gear.
Feeding	Behaviours associated with the search, pursuit and capture of food, with constant changes in direction and speed (Chilvers & Corkeron, 2001) in the presence and absence of fishing gear.
Social	Variable displays of behaviours such as rubbing, approaching, or swimming synchronously that involve the interaction of the dolphins less than a body-length away from each other (Chilvers & Corkeron, 2001), with and without the presence of artisanal fishing activity.
Socio-sexual	Behaviour performed by individuals of different or the same sex, such as rubbing, transport of objects in pairs, or copulating without the sole purpose of reproduction (Murillo & Díaz, 1995).
Play	Individuals display their motor skills, as a 'game' in a repetitive way, including leaps, chases and acrobatic manoeuvres (Petryna & Bavera, 2002).
Rubbing with objects	Displays associated with the friction of the totality or parts of the dolphin's body on the surface of aquatic plants or other objects found in their environment (Dudzinski *et al.*, 2012).

of the artisanal fishers of Alvarado. Behavioural recordings used the same sampling method as on land, and through the information provided by the control observations, all states were then partitioned into different events related to instantaneous and sporadic movements according to their proximity to fishing activities (*sensu* Nadeau, 2013).

The activities were based on the ethogram developed by Morales-Rincon (2016) specifically for the dolphin population inhabiting the study area (available at: http://eduardo.morteo.mx/WebPage/PDF/Morales_2016.pdf).

Due to the proximity of target objects (i.e. gear, boats and dolphin groups), estimates from the survey boat usually had sufficient precision, as these were made by experienced crew and based on well-established references (e.g. GPS distance to the coast, dimensions of known fishing gear, nearby boats and coastal landmarks) (Morteo & Hernández-Candelario, 2007; Morteo *et al.*, 2012, 2014; Morales-Rincon, 2016; Rechimont *et al.*, 2018). However, these were also calibrated regularly during the fixed point observations by means of the theodolite as described earlier (Cox *et al.*, 2003).

Also, all behavioural records were divided by platform (i.e. fixed point or surveys) and compared to determine the extent of observer bias.

Behaviour in the presence and absence of fisheries interaction

Behavioural observations categorized as events were used to construct discovery curves (Fisher *et al.*, 1943); these were used to measure the rate of appearance for new behavioural events throughout the sampling effort. The variety of these events over time was classified according to the presence and the distance towards fishing activities by means of linear regressions.

Likewise, the frequency of occurrence for the behavioural state of each sighting was calculated, as well as their local rate; the latter defined as the intensity, measured as the frequency per unit of time of each behaviour (Lopéz-Rull, 2013). Since the behaviour and location of dolphin groups was variable across the observation period, the frequency with which individuals approached the gillnet was calculated, using only one session per group; the session was randomly selected from the records in order to reduce any bias due to pseudo-replication (Hurlbert, 1984). A session consisted of every sighting period registered per group with and without fishing interaction, which had an average duration of 1.8 min. Consequently, differences in frequencies and local rates were also assessed according to the presence and distance towards fishing activities using the three categories (*sensu* Nadeau, 2013) by means of contingency tables (χ^2).

Variations in group size

Our definition of a group followed the chain rule, in which dolphins were considered associated if they remained within two body lengths from each other, usually but not always moving in the same direction and engaged in similar behaviour (Shane, 1990; García-Vital, 2012). As mentioned earlier, the distance between these dolphin groups and fishing activities were estimated from the boat, and were calibrated regularly.

Again, only one observation session per group was randomly selected to reduce the bias from pseudo-replication (Hurlbert, 1984). Likewise, the number of individuals involved in each of the three categories of interaction (i.e. operational, non-operational and without interaction) was estimated and graphed according to the distance from the fisheries activity.

Differences by age class

All sighted individual dolphins were categorized by age (Bearzi, 2002); taking into account the knowledge of the crew and the experience of fishers, and considering that all boats that are commonly used in the artisanal fisheries are about the same size (~ 7 m length), we used them as scale for the estimation of age classes (Read *et al.*, 1993; García-Vital, 2012; La Fauci, 2017), such that: (1) adults were individuals over 2.5 m; (2) juvenile dolphins had an approximate length of two-thirds of an adult, and (3) calves were one-third the size of an adult.

Frequencies of behavioural events were computed for each age class combination (i.e. adults, juveniles and calves), during both interaction categories and in the absence of interaction with fisheries. Once again, only one observation session per group was randomly selected (Hurlbert, 1984). The computed frequencies were divided by the number of individuals involved in the sighting, in order to determine the divergence of the group towards any behavioural state and then averaged this index for each condition (interaction and non-interaction). This divergence index was compared for each age class, as well as in the absence and the presence of fishing interactions, both operational and non-operational, using an ANOVA ($P < 0.05$).

Results

Sampling effort and group size

We conducted 20 field trips in both the mobile platform and the fixed point, and all occurred during the normal activities of the fishers. In total 64 dolphin groups were sighted from which 30 h of recording were obtained for behaviour classification.

https://doi.org/10.1017/S002531541900078X Published online by Cambridge University Press

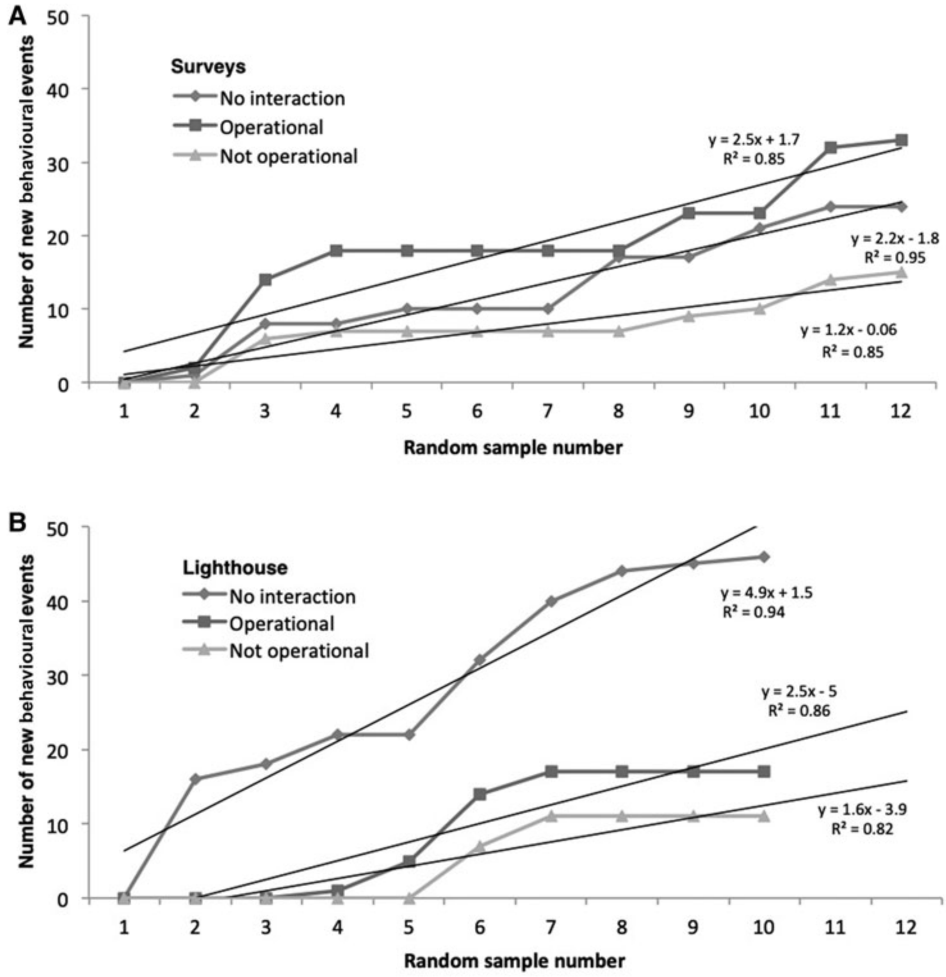

Fig. 2. Discovery curves for behavioural events in bottlenose dolphin sightings recorded by survey sample. Black lines show the linear regression with their respective equations and determination coefficient according to the type of interactions with fisheries.

From these sightings, 28 groups were recorded around fishing activities and the remaining 36 were not. Average dolphin group size was 3.2 ± 2.2 individuals, where trios were the most frequent (41%). Group size was variable and fewer individuals were present when interaction with fisheries occurred (1–7 individuals), compared with the absence of interactions (1 to 16 individuals), but this was not significant ($P > 0.05$).

Behaviour in the presence and absence of fisheries interactions

A total of 110 different behavioural events were recorded during the observations (74 from fixed point and 72 from surveys; where 32 and 36 were exclusive for each platform, respectively). In total, 53 occurred in the absence of fishing interaction, 36 during operational interaction and 21 in the non-operational condition. The discovery curves showed a linear trend throughout the sampling period in all cases; however, the slope was different for each case and also for each platform. A marked difference in the appearance of new behaviours was observed during the absence of fishing activity when these were observed from land. In contrast, new behaviours were constant for the three conditions when recorded from the boat, and the rate of appearance was higher for the operational interaction (Figure 2). Locomotion was the most common behaviour during all the sightings in the three conditions (Figure 3A–C). Feeding was also recorded regardless of the interaction with fisheries, but it was more frequently observed during the operational interaction when measured from the boat (Figure 3A). Conversely, in the non-operational interaction this behaviour was displayed only a few times; but, from fixed point observations, its intensity (i.e. local rate) was higher (Figure 3D). The behaviours associated with socio-sexual, play and rubbing also showed low occurrences in the different conditions and platforms (Figure 3A, C); however, they presented the highest intensity rates (Figure 3B, D). Social behaviour was only present in the absence of fishing interactions with the second highest local rate (Figure 3A–D). Significant differences were found in the frequency of the behavioural states, in relation to the platforms during the three conditions (operational $\chi^2 = 50.33$, df = 7; $P < 0.001$; non-operational $\chi^2 = 21.73$, df = 7; $P < 0.002$; No interaction $\chi^2 = 39.88$, df = 7; $P < 0.001$). Local rates also showed differences in frequency of behaviours in the operational and non-operational distances ($\chi^2 = 41.80$, df = 5; $P < 0.001$; $\chi^2 = 29.28$, df = 4; $P < 0.001$) but not in the absence of interaction with fisheries ($\chi^2 = 12.85$, df = 7; $P < 0.075$).

Interaction distance vs *group size*

Most of the recorded interactions were classified as operational since the cumulative curve showed that over half of the randomly selected records (54% in land based and 82% in surveys) occurred between 0 and 30 m of the gear (Figure 4A, B, right axis), and were carried out mainly individually (Figure 4A, B, left axis). Non-operational interactions (>30 m) involved the participation of more group members, although in a smaller proportion ($\Sigma = 26\%$ and $\Sigma = 7\%$).

Differences by age class

Groups composed exclusively of adult animals were the most common during and in the absence of fishing interactions (64%

https://doi.org/10.1017/S002531541900078X Published online by Cambridge University Press

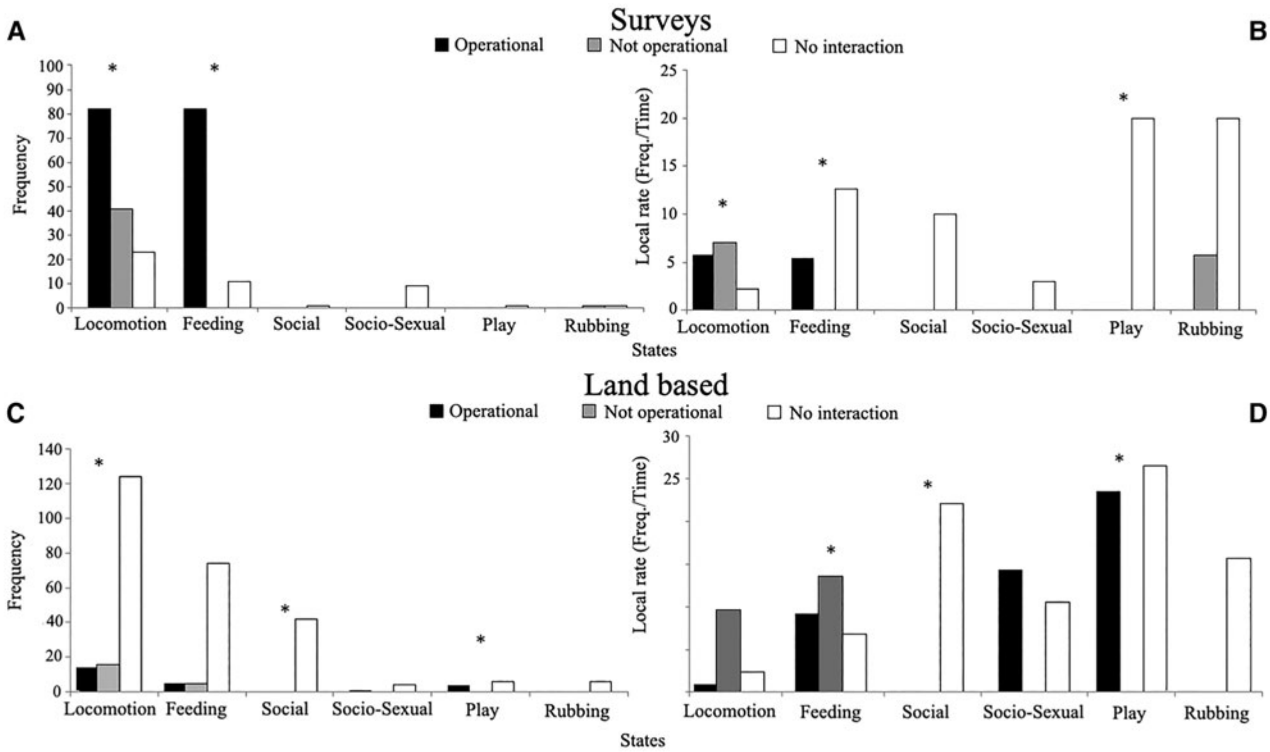

Fig. 3. Histograms of behavioural records for bottlenose dolphins in the study area in the absence and presence of fisheries interactions (operational and not operational) in two platforms. (A) Behavioural frequencies in surveys; (B) Intensity rates in surveys; (C) Behavioural frequencies from the lighthouse; (D) Intensity rates from the lighthouse (N = 64 sightings). Asterisks show statistical differences ($P < 0.05$).

and 75%, respectively). The number of behavioural events in relation to group size and age structure (i.e. divergence index) showed that adult groups were more variable independently of their interaction with fisheries (Figure 5), followed by groups with juveniles and calves; however, these differences were not significant ($\chi^2 = 2.96$, df = 4, $P < 0.56$).

Discussion

Sampling effort

Observation time (N = 30 h) was lower compared with similar studies ($\bar{x} = 80$ h; Chilvers & Corkeron, 2001; Neumann & Orams, 2005; Miller *et al.*, 2010); the latter was due to the persistence of cold northern fronts that limited our sampling efforts in the study area. However, the number of sightings was sufficient to detect significant differences in some cases. This may be attributed to the fact that, unlike most of the studies focused on behaviour that use descriptions from other populations (e.g. Shane, 1990), we used an ethogram developed specifically for the dolphins present in our study area (Morales-Rincon, 2016). Therefore, we deem likely that our samples are representative for the study period and the individuals involved. Also, the use of two platforms (fixed and mobile) allowed behaviour classification from two perspectives, with direct (surveys) and indirect (land based) presence of the researchers. This led to significant differences between the platforms in terms of the frequency of behavioural states and their local rates for dolphin sightings, recording and quantifying both the behavioural responses of dolphins *in situ*, and also the observer bias (Simultea & Lomac-MacNair, 2016). It has been argued that from elevated platforms, the larger field of vision provides a better context and accurate readings; whereas during navigation, the field of vision is more limited, but the superficial observations may be more detailed (Würsig *et al.*, 1998; Yin, 1999). However, we believe that, as shown by our data, the differences found in dolphin behaviour are more related to the effect of the presence and distance of the survey boat (i.e. a local fishing skiff), possibly due to the anticipation of antagonistic responses by fishers posing risk for the dolphin population, as have been described for the study area (Morteo *et al.*, 2012, 2017; Rechimont *et al.*, 2018).

Behaviour in the presence and absence of fishery interaction

The discovery curves for recorded behavioural events showed a linear trend for our three categories of distances towards the fisheries; the latter indicates that not all the behavioural variants of the studied population were documented throughout the study. However, there were differences in the rate of appearance of all these new events (see Figure 3); therefore, the distance towards the fisheries seems to affect the variety of activities that dolphins may perform. This has been widely documented, and has different impacts on the health of dolphin populations, according to the type, frequency and level of interactions, causing stress, feeding deficiencies and even incidental deaths (Shane *et al.*, 1986; Owen *et al.*, 2002; Brotons *et al.*, 2008; Rocklin *et al.*, 2009; Adimey *et al.*, 2014).

Locomotion and feeding were the most frequent behaviours regardless of the distance to the fisheries, and their intrinsic relation is explained by the daily and seasonal shifts in the abundance and distribution of prey (Neumann & Orams, 2005), causing the dolphins to move continuously between the locations with available food. The latter also evidences the opportunistic nature of the bottlenose dolphin, since both these activities were especially recorded around fishing gear, which captures fish that are part of their diet (Jaiteh *et al.*, 2013; Chávez-Martínez, 2017), and also the importance of this site as a feeding ground (Morteo *et al.*, 2012, 2014, 2017; Rechimont *et al.*, 2018).

The most frequent interactions were operational (within the first 30 m from the fishing gear), where the extraction of fish was

https://doi.org/10.1017/S002531541900078X Published online by Cambridge University Press

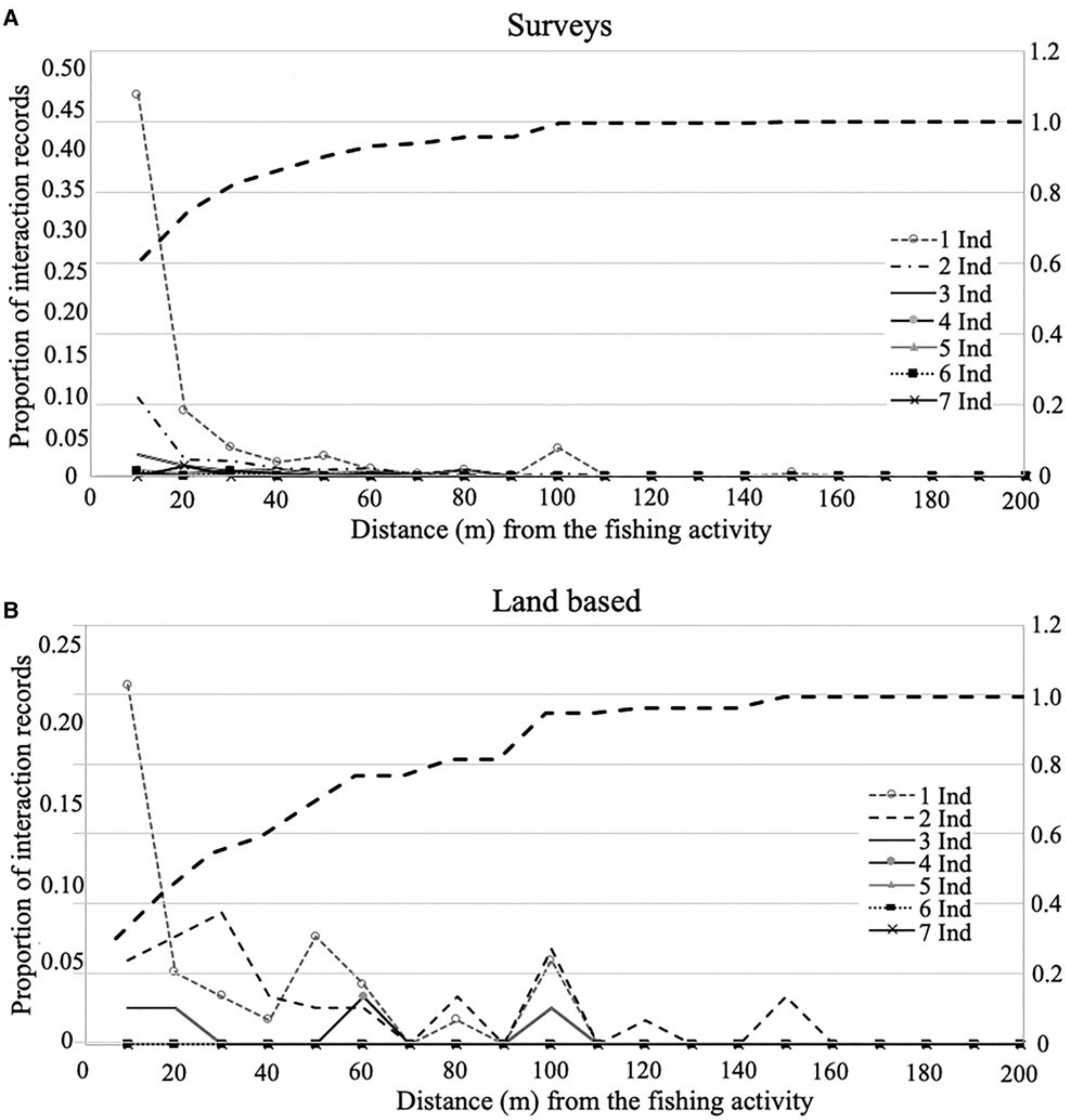

Fig. 4. Proportion of bottlenose dolphin records during interactions with fisheries (left scale) according to the number of individuals involved and the distance to the fishing gear (N = 28 sightings, 44% of the total). The grey dashed line at the top denotes the cumulative proportion for all records (right scale). (A) Distance of interaction in the surveys; (B) Distance of interaction in the land-based platform.

evidenced; actually, the crew witnessed what was interpreted as creaking noises produced by the dolphin's teeth while releasing the netted prey. Conversely, within the non-operational distance (~31–150 m), dolphins spent their time moving and patrolling around the fishing spot. Our findings are consistent with Brotons *et al.* (2008) in the Balearic Islands during artisanal fishing; however, unlike their study, where the gear damage was focused only at the top, our nets were damaged in the upper half, which could be related to differences in the fishing techniques or in the distribution of the prey across the water column (Rechimont *et al.*, 2018). Our data also suggest that dolphins may change their behaviour, but also the frequency and intensity of their activities while using the space around the area where fisheries take place, thus bottlenose dolphins may reorganize their activities as an energy-efficient strategy around the fisheries (Powell & Wells, 2011).

It is noteworthy that frequencies for socio-sexual and play were low, but they showed significantly higher local rates during the operational interaction (Figure 4A and B, respectively). This may be explained considering that dolphins that are interacting with the fisheries are not categorized as residents, as shown by the occurrence records from the long-term photo-identification programme for this dolphin population since 2002 (Morteo, 2011; Morteo *et al.*, 2012, 2014, 2017, Garcia-Vital *et al.*, 2015). Thus intense social and playful contact between dolphins may be indicative of recognition among the individuals involved (Dudzinski, 1998).

Interaction distance vs *group size*

One of the most important attributes for the study of population ecology in dolphins is their social structure (Whitehead &

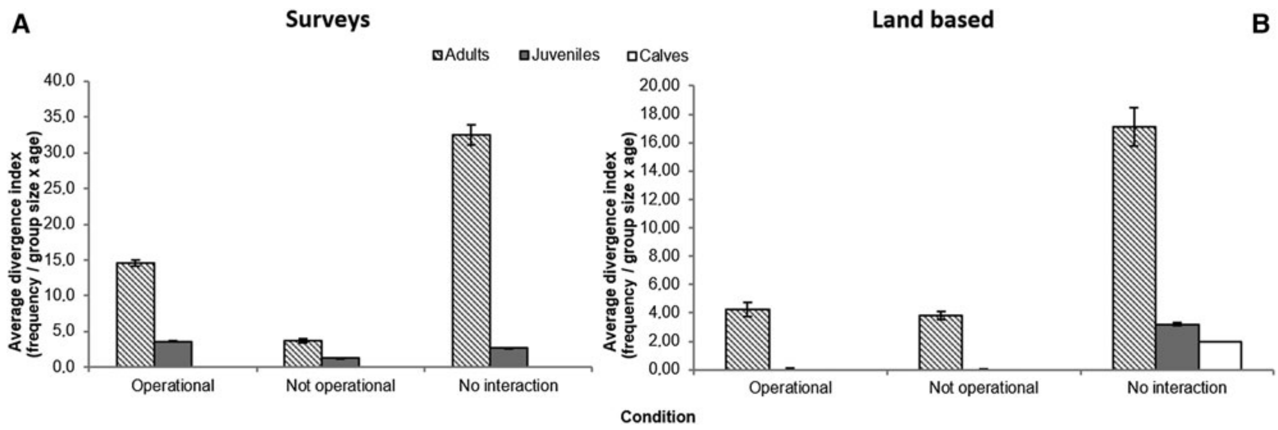

Fig. 5. Divergence index (i.e. frequencies of behavioural records by age class divided by the number of individuals in each sighting) for bottlenose dolphins according to the categories of their interaction with fisheries in the study area (N = 64 sightings) in the two platforms. (A) Divergence index in surveys platform; (B) Divergence index in land-based platform.

Dufault, 1999; Dinis *et al*., 2018); elements such as group size and individual identification are fundamental to understanding complex social relationships between these animals (Whitehead & Dufault, 1999). In this sense, bottlenose dolphin group formations are often determined by age, sex, hierarchical patterns and environmental cues (e.g. predators and food availability; Connor *et al*., 2001, Bouveroux & Mallefet, 2010). Group size in coastal bottlenose dolphins usually varies between 5 and 15 individuals (Morteo, 2011); however, smaller groups (<5 individuals) were found in the coastal waters of Alvarado. This seems typical for the studied population (Morteo, 2011), thus it has been hypothesized to constitute a strategy that reduces detectability by fishers while also decreasing the chances of negative outcomes for the dolphins (García-Vital *et al*., 2015); the latter as a response to the pressure by fishers that this dolphin population has suffered for decades, which was evidenced during this study, including violent retaliation to individuals that interacted with their gear (Del Castillo-Olvera, 2010; Morteo, 2011; Morteo *et al*., 2017; Rechimont *et al*., 2018). Conversely, in other study areas, where human-dolphin competition for fish is not as noticeable, dolphin group sizes observed around fishing activities are mostly related to the biomass of prey captured in the gear (Lauriano *et al*., 2004; Rocklin *et al*., 2009).

Although differences in group sizes were not significant in our study, it is noteworthy that most individual dolphins and pairs occurred within the first 30 m (see Figure 2), which seems to argue in favour of the 'lower detectability' hypothesis. We feel inclined towards this explanation, given the long-term exposition to antagonistic responses by fishers, and the decrease in behaviours that imply greater body exposure as dolphins approach the fishing spots. Admittedly, it is a common assumption that dolphins may be attracted to gear settings since fish are congregated and/or weak when entangled, and therefore are easier to catch (Lauriano *et al*., 2004; Rocklin *et al*., 2009; Powell & Wells, 2011); in that sense, the participation of multiple dolphins would be unnecessary. Other studies have classified the interaction radius between dolphins and fishing activities within a much broader range (e.g. 400 m by Lauriano *et al*., 2004, and 200 m by Morteo *et al*., 2012), such that these may have referred mostly to non-operational interactions, and thus preventing feasible comparisons.

Interactions may depend on sex and age class

The coastal waters of Alvarado are highly productive such that artisanal fishing is frequent and intense (Morteo *et al*., 2012; Rechimont *et al*., 2018); also, over 125 distinct dolphins are present every day, and many of them are resident (Morteo *et al*., 2017). Therefore, in light of the antagonistic nature of their interactions, the behavioural changes reported here, in addition to the reported trends in temporal and spatial distributions for the bottlenose dolphins (Morteo, 2011; Morteo *et al*., 2014; La Fauci, 2017), there is an apparent 'tolerance' or at least a certain degree of 'habituation' to artisanal fisheries in the study area. This has been documented in other bottlenose dolphin populations, with different human activities, and with other dolphin species as well (i.e. *Delphinus delphis*) (Neumann & Orams, 2005; Waples *et al*., 2013).

For instance, the overall annual distribution of bottlenose dolphins and artisanal fishing in the area show reciprocal evasion, thus a high proportion of their encounters are deemed fortuitous (Morteo *et al*., 2012). Moreover, dolphins display different core distribution areas according to sex (Medellín-Ortiz, 2012) and age (La Fauci, 2017), showing sexual segregation (Morteo *et al*., 2014), where nursing groups tend to be further away from the areas with greater human activities. However, intentional interactions, measured as higher than expected interaction rates with fisheries, have actually been documented for some individuals within the study area by means of dorsal fin photo-identification, which were first assumed to be males (Morteo *et al*., 2012), and then confirmed through direct and indirect sexing methods (Morteo *et al*., 2014).

Bottlenose dolphins group into fluid and dynamic associations by sex and age classes (Nowacek & Wells, 2001; Owen *et al*., 2002; Bouveroux & Mallefet, 2010; Dinis *et al*., 2018). The social structure of the females in the study area resembles 'bands' of multiple individuals, including offspring and juveniles; whereas males form smaller and more durable unions similar to the so-called 'first order alliances' (see Morteo *et al*., 2014 after Connor *et al*., 2001). Although the sex of individuals that participated in interactions with fisheries recorded during this research was initially unknown, comparisons of their dorsal fins to the photo-id catalogue of bottlenose dolphins in the area found no matches with any of the 84 known females, and that at least five of the 15 known males were involved in these encounters (Morteo, unpublished data). Consequently, given the strong social affiliation and low number of affiliates in male alliances, it is highly likely that a large part of these sightings involved only males.

Conclusion

The adaptation of strategies for food acquisition (Sargeant & Mann, 2009), where adult male dolphins moving alone or in small groups are more frequently associated with fishing gear depredation (Adimey *et al*., 2014; Morteo *et al*., 2014; Labadie *et al*., 2018; Rechimont *et al*., 2018) has been linked to their curious and predatory behaviour, as well as their easy habituation to the varying conditions in their habitat (Adimey *et al*., 2014; Morteo *et al*., 2014, 2017; La Fauci, 2017). Many of these interactions have been attributed to adult males and point to the development of a sex-biased strategy to take advantage of captured fish (Morteo *et al*., 2012, 2017; Garcia-Vital *et al*., 2015; Rechimont *et al*., 2018). Furthermore, female individuals within the population are more resident and thus experienced (Morteo *et al*., 2014), and especially nursing or lactating individuals are known to avoid fishing areas (La Fauci, 2017), since these present a higher risk of injury (Srinivasan *et al*., 2017), due to fishers' antagonistic responses to the encounters with bottlenose dolphins (Morteo *et al*., 2012; Rechimont *et al*., 2018). Therefore, the risks involved in this activity would also potentially represent a sex-biased pressure for this population (Morales-Rincon, 2016; Morteo *et al*., 2017). Behavioural variations in the dolphins' repertoire are likely a strategy to reduce the risk of injuries or death when interacting with human activities; thus these dolphins seem to have habituated or at least tolerate fishing activities within the study area.

Acknowledgements. The authors are thankful to M.E. Rechimont, K. Chávez, M. Quiroga, E. Bolaños, J. Bolaños, M. Tenorio, E. Tiburcio and J. Tiburcio for their support in the field during data collection. We also appreciate the insights of I. Martínez-Serrano and. P. Dias at Universidad Veracruzana for their contributions during the writing of the thesis from which this paper derived. We thank the authorities of the Mexican Federal Secretariat of Communications and Transport (SCT) and the Mexican Navy (SEMAR) for the permission to use the facilities of the sea lighthouse at Monte Simón to collect data.

Financial support. This work was part of the MSc thesis of the lead author who benefited from a National Council of Science and Technology Grant (CONACyT grant No. 635385, 2014). This work was part of the project 'Trophic ecology of bottlenose dolphins (*Tursiops truncatus*) and artisanal fisheries interactions in coastal waters off Veracruz state' funded by the CONACyT project number 221750. All boat-based behavioural observations were non-invasive and were also carried out without intervention during the normal fishing operations of the local artisanal fleet, thus no official permit for fieldwork was required.

References

Adimey N, Hudak C, Powell J, Bassos-Hull K, Foley A, Farmer N, White L and Minch K (2014) Fishery gear interactions from stranded bottlenose dolphins, Florida manatees and sea turtles in Florida, U.S.A. *Marine Pollution Bulletin* **81**, 103–115.

Altmann J (1974) Observational study of behavior: sampling methods. *Behaviour* **49**, 227–267.

Amador-Alcalá S, Naranjo E and Jiménez-Ferret G (2013) Wildlife predation on livestock and poultry: implications for predator conservation in the rainforest of south-east Mexico. *Oryx* **47**, 243–250.

Bearzi G (2002) Interactions between cetaceans and fisheries in the Mediterranean Sea. In Di Sciara N (ed.), *Cetaceans of the Mediterranean and Black Seas: State of Knowledge and Conservation Strategies*. Les Terrasses de Fontvieille, Monaco: ACCOBAMS, pp. 78–97.

Bjordal A (2002) The use of technical measures in responsible fisheries: regulation of fishing gear. *FAO Fisheries Technical Paper* No. 434. Rome: FAO, pp. 21–48.

Bouveroux T and Mallefet J (2010) Social structure of bottlenose dolphins, *Tursiops truncatus*, in Panama City, Florida. *Journal of the Marine Biological Association of the United Kingdom* **90**, 1685–1692.

Brotons J, Grau A and Rendell L (2008) Estimating the impact of interactions between bottlenose dolphins and artisanal fisheries around the Balearic Islands. *Marine Mammal Science* **24**, 112–127.

Chávez-Martínez K (2017) *Interaction between the bottlenose dolphin (*Tursiops truncatus*) and the artisanal fishing of Alvarado, Veracruz depending on the capture, nutritional quality and isotopic composition of the fish community* (Master's thesis). Scientific Research Center and Higher Education of Ensenada, Baja California, MX.

Chilvers B and Corkeron P (2001) Trawling and bottlenose dolphins' social structure. *Proceedings Biological Sciences/The Royal Society* **268**, 1901–1905.

Connor R, Heithaus M and Barre L (2001) Complex social structure, alliance stability and mating access in a bottlenose dolphin 'super-alliance'. *Proceedings Biological Sciences/The Royal Society* **268**, 263–267.

Cox T, Read A, Swanner D, Urian K and Waples D (2003) Behavioral responses of bottlenose dolphins, *Tursiops truncatus*, to gillnets and acoustic alarms. *Biological Conservation* **115**, 203–212.

Del Castillo-Olvera V (2010) *Population ecology of bottlenose dolphin (*Tursiops truncatus*), on the coast of Alvarado, Veracruz, México* (Bachelor's thesis). Autonomous University of Puebla, MX.

Dinis A, Alves F, Nicolau C, Ribeiro C, Kaufmann M, Cañadas A and Freitas L (2018) Social structure of a population of bottlenose dolphins (*Tursiops truncatus*) in the oceanic archipelago of Madeira, Portugal. *Journal of the Marine Biological Association of the United Kingdom*, **98**, 1141–1149.

Dudzinski K (1998) Contact behavior and signal exchange in Atlantic spotted dolphins (*Stenella frontalis*). *Aquatic Mammals* **24**, 129–142.

Dudzinski K, Gregg J, Melillo-Sweeting K, Seay B, Levengood A and Kuczaj S (2012) Tactile contact exchanges between dolphins: self-rubbing *vs* inter-individual contact in three species from three geographies. *International Journal of Comparative Psychology* **25**, 21–43.

Faeth S, Warren P, Shochat E and Marussich W (2005) Trophic dynamics in urban communities. *BioScience* **55**, 399–407.

Fisher R, Corbet A and Williams C (1943) The relation between the number of species and the number of individuals in a random sample of an animal population. *Journal of Animal Ecology* **12**, 42–58.

García-Vital M (2012) *Relationship of association patterns and the activities of bottlenose dolphin* Tursiops truncatus *in the coastal waters of Alvarado, Veracruz* (Master's thesis). Veracruzana University, Veracruz, MX.

García-Vital M, Morteo E, Martínez-Serrano I, Delgado-Estrella A and Bazúa-Durán C (2015) Inter-individual association levels correlate to behavioral diversity in coastal bottlenose dolphins (*Tursiops truncatus*) from the Southwestern Gulf of Mexico. *Therya* **6**, 337–350.

Goldstein I (2013) Technical Guidelines and Strategies for the Management of Conflicts due to Interference between Fauna and Agricultural Activities in the Countries of the Andes Community (CAN). Technical Report. Programa Regional de Biodiversidad en las Regiones Andino Amazonicas. Formin: Ministry of Foreign Affairs Finland. 30 pp.

Hill S, Burrows M and Hughes R (2003) The efficiency of adaptive search tactics for different prey distribution patterns: a simulation model based on the behaviour of juvenile plaice. *Journal of Fish Biology* **63**, 117–130.

Hurlbert SH (1984) Pseudoreplication and the design of ecological field experiments. *Ecological Monographs* **54**, 187–211.

Jaiteh V, Allen S, Meeuwig J and Loneragan N (2013) Subsurface behavior of bottlenose dolphins (*Tursiops truncatus*) interacting with fish trawl nets in northwestern Australia: implications for bycatch mitigation. *Marine Mammal Science* **29**, 266–281.

Jiménez M and Castro L (2007) Artisanal fishing in the Veracruz Reef System National Park, México. In Granados A, Arenas L and Vargas J (eds), *Scientific Research in the Veracruz Reef System*. Campeche: Autonomous University of Campeche, pp. 221–240.

Jiménez N and Domínguez C (2007) *Presence and spatial location of cetaceans in the Tayrona National Natural Park – Colombia* (Bachelor's thesis). Jorge Tadeo Lozano University, Bogotá, CO.

Jiménez M, Granados A and Ortiz L (2007) Analysis of scientific information in the Veracruz Reef System. In Granados A, Arenas L and Vargas J (eds), *Scientific Research in the Veracruz Reef System*. Campeche: Autonomous University of Campeche, pp. 1–15.

La Fauci D (2017) *Spatial segregation by age class in the bottlenose dolphin* Tursiops truncatus *(Montagü, 1821) of the central coast of Veracruz* (MSc thesis). Instituto de Investigaciones Biológicas, Universidad Veracruzana, Veracruz, MX.

Labadie G, Tixier P, Barbraud C, Fay R, Gasco N, Duhamel G and Guinet C (2018) First demographic insights on historically harvested and poorly known male sperm whale populations off the Crozet and Kerguelen Islands (Southern Ocean). *Marine Mammal Science*, **34**, 595–615

Lauriano G, Fortuna C, Moltedo G and Notarbartolo di Sciara G (2004) Interactions between common bottlenose dolphins (*Tursiops truncatus*) and the artisanal fishery in Asinara Island National Park (Sardinia): assessment of catch damage and economic loss. *Journal of Cetacean Research and Management*, **6**, 165–173.

Lee P and Graham M (2006) African elephants and human–elephant interactions: implications for conservation. *International Zoo Yearbook* **40**, 9–19.

López-Portillo J, Martínez ML, Hespe P, Hernández JR, Méndez AP, Vásquez-Reyes V, Gámez-Aguilar LR, Jiménez-Orocio O and Gachuz-Delgado SI (2011) *Atlas of the Coasts of Veracruz Mangroves and Coastal Dunes*. Xalapa, Veracruz: Secretaría de Educación-Gobierno del Estado de Veracruz, Universidad Veracruzana, 248 pp.

López-Rull I (2013) Behaviour measurement methods. In Martínez-Gómez M, Lucio R and Rodríguez-Antolín J (eds), *Behavioral Biology: Contributions From Physiology*. Tlaxcala: Autonomous University of Tlaxcala, pp. 47–60.

Medel R, Aizen M and Zamora R (2009) *Ecology and Evolution of Plant–Animal Interaction*. Santiago of Chile: Editorial Universitaria.

Medellín-Ortiz B (2012) *Sex-specific differences in the core areas of dolphin* Tursiops truncatus *in front of the lagoon system of Alvarado. Gulf of Mexico* (Master's thesis). Veracruzana University, Veracruz, MX.

Miller L, Solangi M and Kuczaj S (2010) Seasonal and diurnal patterns of behavior exhibited by Atlantic bottlenose dolphins (*Tursiops truncatus*) in the Mississippi sound. *Ethology* **116**, 1127–1137.

Morales-Rincon N (2016) *Behaviour of bottlenose dolphin Comportamiento de tursiones (*Tursiops truncatus*) in interaction with artisanal fisheries on the central coast of Veracruz, México* (Master's thesis). Veracruzana University, Xalapa, MX.

Morteo E (2011) *Social ecology of dolphins* (Tursiops truncatus*) in the coastal waters of Alvarado, Veracruz, México* (Doctoral thesis). Universidad Veracruzana, Veracruz, Mexico.

Morteo E and Hernández-Candelario I (2007) Preliminary results about the relationships between dolphins *Tursiops truncatus*, boats and fishing gear in the Veracruz Reef System. In Granados A, Arenas L and Vargas J (eds), *Scientific Investigations in the Veracruz Reef System*. Campeche: Autonomous University of Campeche, pp. 241–256.

Morteo E, Rocha-Olivares A, Arceo-Briseño P and Abarca-Arenas LG (2012) Spatial analyses of bottlenose dolphin–fisheries interactions reveal human avoidance off a productive lagoon in the western Gulf of Mexico. *Journal of the Marine Biological Association of the United Kingdom* **92**, 1893–1900.

Morteo E, Rocha-Olivares A and Abarca-Arenas L (2014) Sexual segregation of coastal bottlenose dolphins (*Tursiops truncatus*) in the Southwestern Gulf of Mexico. *Aquatic Mammals* **40**, 375–385.

Morteo E, Rocha-Olivares A and Abarca-Arenas LG (2017) Abundance, residency and potential hazards for coastal bottlenose dolphins (*Tursiops truncatus*) off a productive lagoon in the Gulf of Mexico. *Aquatic Mammals* **43**, 308–319.

Murillo J and Díaz J (1995) *Cognitive Architecture in Cats: an Ethological and Quantitative Approach*. Mexico, DF: National Autonomous University of Mexico.

Nadeau A (2013) *Operational interaction between the common sea lion* Otaria flavescens (Shaw, 1800) *and artisanal purse seine fishing off the coast of Caldivia, XIV River region* (Bachelor's thesis). Austral University of Chile, Valdivia, CL.

Neumann R and Orams B (2005) Behaviour and ecology of common dolphins (*Delphinus delphis*) and the impact of tourism in Mercury Bay, North Island, New Zealand. *Science for Conservation* **254**, 1–40.

Nowacek S and Wells R (2001) Short-term effects of boat traffic on bottlenose dolphins, *Tursiops truncatus*, in Sarasota Bay, Florida. *Marine Mammals Science* **17**, 673–688.

Owen E, Wells R and Hofmann S (2002) Ranging and association patterns of paired and unpaired adult male Atlantic bottlenose dolphins, *Tursiops truncatus*, in Sarasota, Florida, provide no evidence for alternative male strategies. *Canadian Journal of Zoology – Revue Canadienne De Zoologie* **80**, 2072–2089.

Peña-Mondragón J and Castillo A (2013) Predation of cattle by jaguar and other carnivores in northeastern Mexico. *Therya* **4**, 431–446.

Petryna A and Bavera G (2002) Ethology. Animal Production Courses, National University of Rio Cuarto.

Powell J and Wells R (2011) Recreational fishing depredation and associated behaviors involving common bottlenose dolphins (*Tursiops truncatus*) in Sarasota Bay, Florida. *Marine Mammal Science* **27**, 111–129.

Read AJ, Kraus SD, Bisak KD and Palka D (1993) Harbor porpoises and gill nets in the Gulf of Maine. *Conservation Biology* **7**, 189–193.

Rechimont ME, Lara-Domínguez AL, Morteo E, Martínez-Serrano I and Equihua M (2018) Depredation by coastal bottlenose dolphins (*Tursiops truncatus*) in the southwestern Gulf of Mexico in relation to fishing techniques. *Aquatic Mammals* **44**, 458–470.

Reeves R, Read A and Notarbartolo di Sciara G (2001) *Report of the Workshop on Interactions between Dolphins and Fisheries in the Mediterranean: Evaluation of Mitigation Alternatives*.

Rocklin D, Santoni M-C, Culioli J-M, Tomasini J-A, Pelletier D and Mouillot D (2009) Changes in the catch composition of artisanal fisheries attributable to dolphin depredation in a Mediterranean marine reserve. *Journal of Marine Science*, 699–707.

Sargeant B and Mann J (2009) Developmental evidence for foraging traditions in wild bottlenose dolphins. *Animal Behaviour* **78**, 715–721.

Shane S (1990) Behavior and ecology of the bottlenose dolphin at Sanible Island, Florida. In Leatherwood S and Reeves RR (eds), *The Bottlenose Dolphin*. New York, NY: Academic Press, pp. 541–558.

Shane S, Wells R and Wursig B (1986) Ecology, behavior and social organization of the bottlenose dolphin: a review. *Marine Mammal Science* **2**, 34–63.

Simultea M and Lomac-MacNair K (2016) Assessing 'observer effects' from a research aircraft on behavior of three delphinidae species (*Grampus griseus*, *Delphinus dephis* and *Orcinus orca*). *Wildlife Biology in Practice* **12**, 75–90.

Srinivasan M, Swannack T, Grant W, Rajan J and Würsig B (2017) To feed or not to feed? Bioenergetic impacts of fear-driven behaviors in lactating dolphin. *Ecology and Evolution* **8**, 1384–1398.

Tinbergen N (1963) On aims and methods of ethology. *Zeitschrift für Tierpsychologie* **20**, 410–433

Villamizar N (2001) *Preliminary aspects on the ethology of the seahorse* Hippocampus reidi *(Ginsig, 1933) under conditions of captivity at the Marine World Aquarium UJTL Santa Marta* (Bachelor thesis). University of Bogotá Jorge Tadeo Lozano, Bogotá, Colombia.

Waples D, Thorne L, Hodge L, Burke E, Urian K and Read A (2013) A field test of acoustic deterrent devices used to reduce interactions between bottlenose dolphins and a coastal gillnet fishery. *Biological Conservation* **157**, 163–171.

Whitehead H and Dufault S (1999) Techniques for analysing vertebrate social structure using identified individuals: review and recommendations. *Advances in the Study of Behavior* **28**, 33–74.

Würsig B, Cipriano F and Würsig M (1998) Dolphin movements patterns: information from radio and theodolite tracking studies. In Pryor K and Norris K (eds), *Dolphin Societies: Discoveries and Puzzles*. Berkeley, CA: University of California Press, pp. 79–111.

Yin S (1999) *Movement patterns, behaviors, and whistle sounds of dolphin groups off Kaikoura, New Zealand* (Master's thesis). Brown University, EU.