Abundance, distribution and behaviour of common dolphins, *Delphinus* spp., off north-eastern Venezuela: implications for conservation and management

LENIN OVIEDO^{1,2}, MARÍA ALEJANDRA ESTEVES¹, ROMINA ACEVEDO², NOEMI SILVA², JAIME BOLAÑOS-JIMÉNEZ³, ANA MARÍA QUEVEDO⁴ AND MARC FERNÁNDEZ⁵

¹Proyecto Delphinus, Margarita Island, Venezuela, ²Proyecto Golfo de la Ballena—Biotrópica, Caracas, Venezuela, ³Sociedad Ecológica Venezolana Vida Marina (Sea Vida, AP 162, Cagua, Estado Aragua, Venezuela, ⁴Postgrado Ecología,

Instituto de Zoología tropical, UCV, ⁵CIRN/FCT and Departamento de Biologia, Universidade dos Açores (UAC), Portugal

The north-eastern coast of Venezuela hosts a high diversity of megafauna, particularly related with high productivity due to coastal upwelling. This area is mainly characterized by the existence of the primary fisheries in Venezuela, mostly supported by a great abundance of small pelagic species. This would explain why the area supports a wide range of marine top predators, including cetaceans. The current status of cetacean populations off north-eastern Venezuela is uncertain, mainly because research efforts have been very sparse. There are still many gaps of information in cetacean biology to establish a solid baseline that can be used for management decisions. Common dolphins (Delphinus spp.) are widely dispersed over the whole northeast basin, including waters off Araya and Paria Peninsula and around Margarita, Coche and Cubagua Islands. Areas of higher densities for Delphinus spp. coincide with the focal location of sardine fisheries and the most-active upwelling on the north-eastern coast. Therefore, a scheme of management should consider the areas of major productivity along the coast as potential critical habitat for the species. Further data collection is recommended, increasing aspects such as trophic ecology and the continuity of behavioural sampling, paired with systematic line transect estimation.

Keywords: common dolphin, Delphinus spp., critical habitat, upwelling, Cariaco Basin, north-eastern Venezuela

Submitted 11 April 2009; accepted 18 July 2009

INTRODUCTION

The north-east coast of Venezuela hosts a great diversity of megafauna, particularly related to increased productivity due to coastal upwelling. This area is characterized by the existence of large round sardinella schools (*Sardinella aurita*) among other species of importance for commercial fisheries (Guzman *et al.*, 1999; Cárdenas & Achury, 2000; Mendoza *et al.*, 2003). This would explain why the area supports a wide range of marine top predators, including cetaceans.

Acevedo (2007) detailed the distribution of 11 species of marine cetaceans, among them common dolphins (*Delphinus* spp.), and Guiana dolphins (*Sotalia guianensis*) as important species within shelf and coastal habitats all along the Venezuelan coast. Over 50% of the cetaceans (35 species) reported in the south Caribbean Sea occur in the study area (Acevedo, 2001; Oviedo & Silva, 2001, 2005; Romero *et al.*, 2001; Bermúdez-Villapol & Boher, 2003; Bolaños-Jiménez & Villarroel-Marín, 2005; Oviedo *et al.*, 2005). There only exists one marine protected area (MPA) in the north-east coast basin that provides their protection, even though it was not designed for cetacean conservation,

Corresponding author: L. Oviedo Email: leninovi1@gmail.com the Mochima National Park (Mochima NP), covering an important part of the coastline and waters off Anzoátegui and Sucre States (Rodriguez & Rojas-Suárez, 1999; Hoyt, 2005; Acevedo *et al.*, 2007). Cetacean conservation all along north-eastern Venezuela is, or will eventually be, compromised by anthropogenic activities such as oil and gas production facilities, fisheries interactions and commercial shipping traffic (Oviedo, 2005).

The current status of cetacean populations in the waters off north-eastern Venezuela is uncertain, at least from a quantitative point of view, mainly because research efforts are novel and sparse. Therefore, comparison with historical records or estimates is not possible. There still exist many gaps of information on cetacean biology and ecology that prevent the establishment of a solid baseline that could be used for management decisions. Acevedo (2007) identified the southern coast of Margarita Island and the northern coast of Araya Peninsula as key areas for the conservation of odontocete cetaceans, particularly for common and Guiana dolphins. The complex bathymetry and enhanced productivity due to upwelling processes promotes the occurrence of dolphin populations, as well as fisheries resources.

Within the region bounded by the 100 m isobath inside the Cariaco Basin, the upwelling seasonal plume usually covers a surface area that ranges between 0 and 1000 km² from August to October, and which then typically extends over an area

greater than 12,000 km² in March (Müller-Karger *et al.*, 2004). This would have a direct effect on the distribution of the main cetacean prey: round sardinella (*S. aurita*). Therefore species such as common dolphin should disperse over this greater area of complex topography, upwelling influence and sardines abundance.

The most recent study on the distribution of common dolphins in the western Atlantic indicated that common dolphins are not, in fact, a common species (Jefferson *et al.*, 2009). These authors described four putative stocks, including the western North Atlantic, the south Brazil Bight, the Brazil – Argentinean and the Venezuelan stocks. According to Jefferson *et al.* (2009), the Venezuelan stock 'is an isolated, coastal population of *D. capensis* that occurs over the continental shelf in central/northeastern Venezuela. Its abundance is unknown, but its status is of concern due to past and current threats'.

The taxonomic identity of the Venezuelan stock of common dolphins is currently unresolved (Jefferson et al., 2009). According to a morphometric study by Esteves & Oviedo (2007a) it was theorized that Venezuelan populations of common dolphins could constitute a potential distinct morphotype of Delphinus. In their review, Esteves & Oviedo (2007a) found that their results supported the Natoli et al. (2006) hypothesis that suggested an independent origin of the long-beaked form in different regions, where selection for this 'Venezuelan morphotype' would represent 'adaptation to local environments and may drive a potential speciation'. Consequently, we refer Delphinus spp. to the common dolphin form addressed in this report, under the premise that the taxonomic denomination will be elucidated in the near future. Research effort on taxonomy including evolutionary circumstances that might have triggered a geographical isolation is currently in progress.

During the last years, the evaluation of the status of the genus *Delphinus* in the Atlantic Ocean has also been strongly recommended by the Scientific Committee of the International Whaling Commission (IWC, 2007, p. 306). In

this study, we evaluate the abundance, distribution, behaviour and habitat use of common dolphins on the basis of opportunistic and systematic surveys made independently by the authors between 1997 and 2008. Determination of critical habitat is the key to proposed designation of any special management status in any specific locations of the cetacean habitat (Lusseau & Higham, 2004; Hoyt, 2005). Hence, the ultimate goal of this paper is to determine what portions of the maritime habitats on the north-eastern coast of Venezuela represent key areas in the distribution and abundance of common dolphins. Based on the fact that spatial information is important for environmental management on an ecosystem basis (Watson & Pauly, 2001), we propose the identification of potential critical habitats.

MATERIALS AND METHODS

Study area

The study area has been subdivided at a major scale into four sections of the five subdivisions proposed by Acevedo *et al.* (2007) as important areas of conservation for mysticete cetaceans (Figure 1). Overall the four sections comprise approximately 35% (>5700 km²) of shelf habitat and 65%(>10,500 km²) of oceanic environment off the shelf break:

(1) The shelf edge on the north coast of Margarita Island and La Blanquilla Island (approximate area 6752 km²). This portion is a transition zone between the neritic and pelagic habitats; lesser upwelling centres are present on the northern coast of Margarita Island, including Macanao Peninsula. Although fishermen use the area, it has the lowest level of disturbance and change because of human activities. It is quite important to point out that this location is currently considered for oil industry exploration and exploitation activities in the near future (Oviedo, 2005; Martín *et al.*, 2006).

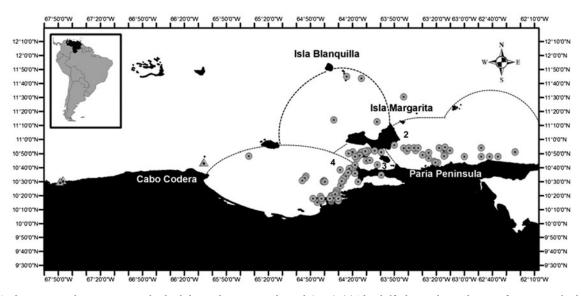


Fig. 1. Study area in north-eastern Venezuela, divided according to Acevedo *et al.* (2007): (1) The shelf edge on the north coast of Margarita Island and La Blanquilla Island; (2) Margarita Island's east coast and Margarita-Los Testigos submarine platform, including Central Paria Peninsula; (3) the north coast of Araya Peninsula, including Coche and Cubagua Islands; (4) the Cariaco Basin south-west of Margarita and Cumaná, including the Cariaco Gulf. Records of *Delphinus* spp., are represented by filled circles with concentric dot, records from the central coast around the area of influence of the Cabo Codera' upwelling, are denoted by a filled triangle with concentric dot, including those reported in Cobarrubia & Bolaños-Jiménez (2008).

- (2) Margarita Island's eastern coast and Margarita-Los Testigos submarine platform (approximate area 3898 km²). The continental shelf in this section of the study area is wide and relatively even, with both muddy and muddy-sandy bottoms. The latter features mostly constitute a key shallow neritic habitat, also influenced by the upwelling off Carupano's coast (Central Paria Peninsula). This zone has a traditional use of marine resources by humans; the coastal human population densities have been increasing in recent years, and also have significant land-based sources of pollution associated with port development and tourism (Oviedo, 2005).
- (3) The northern coast of Araya Peninsula, including Coche and Cubagua islands (approximate area 1812 km²). This region has a complex submarine topography due to the presence of Margarita, Coche and Cubagua Islands; an upwelling area is located off north Araya Peninsula, whose intensity is highly influenced by the seasonal variations associated with the annual cycles of trade winds. The most important human impacts are fisheries, chemical and acoustic pollution and commercial shipping traffic. For this study, common dolphin behaviour assessment was centred in this sub-area.
- (4) The Cariaco Basin, south-west of Margarita and Cumaná, including the Cariaco Gulf (approximate area 3889 km²). Although one portion of this area is protected under National Park status (Mochima NP), the human impact on the marine portion of the ecosystem is intense. The threats include fisheries, chemical and acoustic pollution, development of oil and gas production facilities, commercial shipping traffic (Oviedo, 2005) and unregulated dolphin watching activities (Jefferson *et al.*, 2009).

Dolphin sightings and data analysis

Opportunistic data collection on cetacean encounters (sightings) off north-eastern Venezuela has been carried out aboard several vessels since 1997 by the authors, resulting in an extensive database of published and non-published records that includes more than ten species including wintering humpback whales (Silva *et al.*, 2006; Acevedo *et al.*, 2007, 2008) along with *Balaenoptera edeni* (Oviedo & Silva, 2001, 2005; Acevedo *et al.*, 2007), *B. physalus* (Lira *et al.*, 1995; Acevedo *et al.*, 2007; Bolaños-Jiménez & Villarroel-Marín, 2008), *Physeter macrocephalus*, *Tursiops truncatus* (Oviedo *et al.*, 2005; Oviedo & Silva, 2005), *Stenella frontalis, Stenella attenuata* (Rangel, 2007; Rangel & Cobarrubia-Russo, 2008a), *Stenella coeruleoalba*, *Feresa attenuata*, *Grampus griseus*, *S. guianensis* (Esteves & Oviedo, 2007b; Oviedo & Esteves, 2008) and *Delphinus* spp.

Sighting records of long-beaked common dolphins from 1997-2006 (N = 146) were pooled together with observations from the Araya Peninsula area; these sighting records, however, have been collected from systematic surveys during 2007-2008 (N = 38). All records (N = 184) were analysed through descriptive statistics and integrated into a Geographical Information System (ArcGIS 9.2). Observations included information on date, seasonality (dry: December-April; rainy: May-November), time, group size, sea state (Beaufort scale), geographical coordinates, behaviour at initial encounter, and effort-corrected (days invested during searches) relative abundance and sighting indices (abundance per unit of effort (APUE) and sightings per unit of effort

(SPUE), respectively). Behaviour records were collected according to the standard definitions of behavioural states in Garcia & Dawson (2003), and through the recommended observational methods in Mann (1999, 2000).

Using the geo-statistical analysis tool of ArcGIS 9.2, densities were mapped using the effort corrected APUE and geographical coordinates as input parameters, interpolated in a 1.8×1.8 km grid, using a Gaussian kriging interpolation to generate thematic maps. The maps represent an empirical model of common dolphin distribution and the association with bathymetric features using effort corrected indices, following the recommendations on cetacean habitat modelling in Redfern et al. (2006). Group sizes were also plotted lognormalized and classified by means of the standard deviation. Sample stratification in classes of APUE, and distance to 100 m isobaths were determined through a cluster analysis (group average, square Euclidean). Confidence intervals were obtained through a non-parametric bootstrap (100,000 repetitions, 95% confidence). Statistical differences were established by the Kruskal-Wallis test, concurring with the non-parametric distribution of the sample (Zar, 1996).

RESULTS

Total field effort accounts for 153 days. From those, systematic surveys comprised 76 days of field surveys: 12 in coastal habitat plus 64 surveys distributed in shelf and transitional habitat. Overall, the encounter rate for common dolphin was over 50% of all sightings, followed by Atlantic spotted dolphins (*S. frontalis*, 15%) as the most common odontocete species observed.

Relative abundance of common dolphins (Table 1) is represented in five classes of APUE: very high, high, medium, low and very low. Differences between estimates were statistically significant (Kruskal–Wallis, χ^2 :41.46, df: 4, P < 0.05). Spatial distribution of common dolphin APUE (Figure 2) reflects a major abundance in the neritic habitat between the southern coast of Margarita Island–Central Paria Peninsula and north of Araya Peninsula, with important concentration of common dolphins along the Islands of the Mochima NP and within the eastern portion of the Cariaco Basin.

The density of common dolphin is shown in Figure 3. Approximately 63% (2094) of all the individuals recorded occurred within shelf waters. The distribution pattern in this important habitat of very high-density would concur with the distribution of APUE mentioned before, including the transitional habitat off the north-western coast off Araya Peninsula. High density would equally cover deep oceanic-like areas such as the Cariaco Basin. The lowest density would be localized at the shelf edge off the north Coast of Margarita Island. However, density would progressively increase in oceanic depths off the western coast of La Blanquilla Island.

Table 1. Relative abundance of common dolphins in the study area.

APUE class	Relative abundance	Confidence interval (CI 95%)
Very high	3.54	2.14-4.95
High	0.76	0.59-0.95
Medium	0.38	0.32- 0.46
Low	0.26	0.25-0.27
Very low	0.14	0.11-0.17

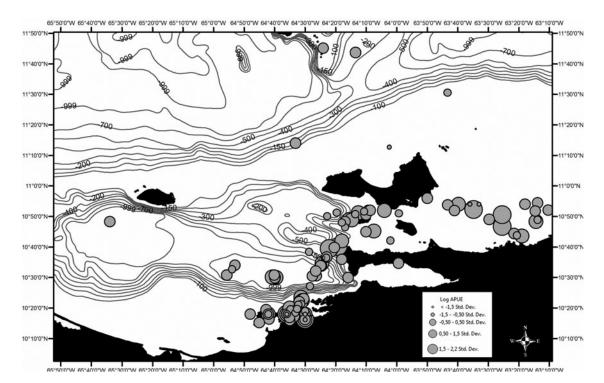


Fig. 2. Distribution of effort-corrected (APUE) during initial sightings of common dolphins in the study area. Classes were grouped by means of the standard deviation.

Seasonality in APUE spatial pattern was not statistically significant (Kruskal–Wallis, χ^2 :0.04, df: 1, P > 0.05).

From the most recent dataset (2007–2008) assessed for behaviour patterns, only three behavioural states were recorded during ethological sampling: foraging, travelling and socializing. Foraging bouts seemed to be directly proportional to distances closer to the shelf edge (100 m isobaths), with 50% of the recorded foraging bouts located at distances equal or less than 4 km (Figure 4). The opposite trend was observed with travelling groups of dolphins, the occurrence of travelling bouts seemed to be directly associated with an increased distance from the shelf edge. Both traits are supported statistically (Kruskal–Wallis, χ^2 :25.23, GL: 1, P < 0.05).

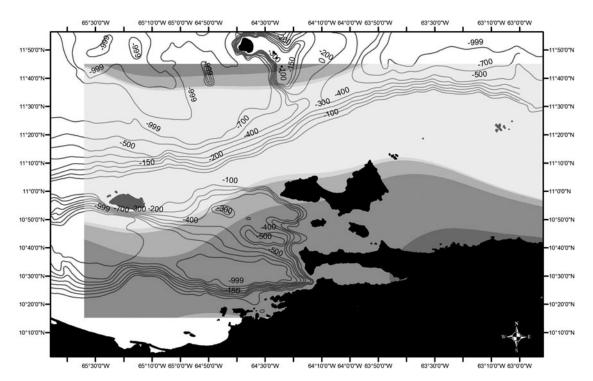


Fig. 3. Predicted density (generated from effort corrected APUE) of common dolphins off the north-east coast of Venezuela. Densities scale from the lowest values is shown in light grey to the highest values shown in dark grey.

DISCUSSION

Distribution and abundance

The spatial pattern of the abundance estimates provides good insight into the wide distribution of common dolphin off the north-eastern coast of Venezuela. The species inhabits all major marine habitats, from shelf waters to transitional areas, and even oceanic habitats such the Cariaco Basin (Rangel et al., 2005; Acevedo, 2007). Information drawn from the APUE estimates indicates an uneven distribution of common dolphin abundance. The latter is an indication of a differential pattern of habitat use. Although levels of occurrence differ quantitatively and spatially, the trend of dominance and representativeness of the species over the region's cetacean diversity prevails. Common dolphin importance as the main component of the cetacean fauna off the north-east coast of the country has been previously documented, even at proportions over 50% of the total cetaceans sighted (Naveira, 1996; Acevedo, 2001, 2007; Quevedo, 2004; Bolaños-Jiménez et al., 2006, 2007; Molero-Lizarraga, 2005; Orlando, 2005; Rangel, 2007; Rangel & Cobarrubia-Russo, 2008b).

Common dolphins might be a key predator for the main fishery resource of the north-east coast basin: sardines. At this point of the research progress, we can only suggest the relevance of *S. aurita* in the diet of common dolphins, firstly according with observations of foraging events, plus anecdotal accounts of stomach content of stranded dolphins, and secondly through the only quantitative diet assessment done on two stranded specimens by Naveira (1996). Foraging habits are determinant in the distribution of the species in the rich environment of the study area.

The predicted density pattern within shelf habitat would reflect the close spatial relation between predator and preys; particularly round sardinella, and specifically on the sectors (Nos 2, 4 and 6) referred by Freon *et al.* (1997) as key fishing grounds. The latter also coincides with the location of the most-important coastal upwelling area, off the coast of Central Paria Peninsula and Araya Peninsula, similar to the documented occurrence of *D. delphis* as an indicator species of upwelling modified waters in the eastern tropical Pacific (Ballance *et al.*, 2006, Fernández *et al.*, 2007, Fernández & Oviedo, 2009). Since density distribution would locally emulate that of its potential prey (Forcada, 2002), and consequently overlap with areas of coastal upwelling, the latter trend comprises discrete areas limited by boundaries, which defines a system diverging by physical and biological features.

The increasing trend of predicted density in oceanic waters, such as the deep waters of the Cariaco Basin and beyond the shelf break west of La Blanquilla Island, could also be interpreted in terms of prey distribution, particularly on the occurrence of mesopelagic prey species such as myctophids. There is a strong possibility that myctophids might play a relevant role as prey items, probably more in the case of common dolphins occurring in oceanic-like environments, such as the Cariaco Trench, however, the latter requires further systematic study, since it is based in anecdotally gathered observations. The elements considered above could imply the possible migration to diversified foraging grounds, similar to the local migratory movement considered by Stockin (2008) with common dolphins in New Zealand waters.

Records close to Farallón Centinela (Crescini, personal communication; Figure 1), and even those from the central Venezuelan coast (Cobarrubia & Bolaños-Jiménez, 2008) would be associated with the upwelling off Cabo Codera, which itself has a particular temporal and intensity pattern, when compared to the coastal upwelling in north-eastern Venezuela (Lorenzoni, 2000). Nevertheless, it is the

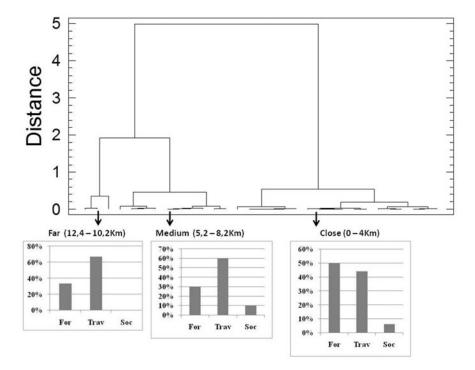


Fig. 4. Cluster analysis of frequency of behaviour bouts of Delphinus spp. by distance to the 100 m isobaths: foraging (For); travelling (Trav); socializing (Soc).

westernmost boundary of the Cariaco Basin, where the narrow Centinela Channel connects the basin to the Caribbean Sea (see figure 1 in Müller-Karger et al., 2004). The influence of Cabo Codera's upwelling might turn into a gradient of productivity influencing the central coast. This might explain the recent documented records of common dolphin of Cobarrubia & Bolaños-Jiménez (2008), and even the potentially extralimital record of Ramírez-Carroz & González-Fernandez (2004), off the Venezuela Gulf (possibly associated with lesser coastal upwelling off the west coast, such as the one in Paraguaná Peninsula). Density and level of occurrence of common dolphin in these areas would not be as concentrated as in north-eastern Venezuela, where the most intense coastal upwelling is localized. Consequently, the definition of an isolated Venezuelan stock, as suggested by Jefferson et al. (2009) would be supported and bounded, by a gradient of coastal upwelling influence concentrated in the Cariaco Basin.

Seasonality could have a non-significant influence in the spatial distribution of common dolphin on the north-eastern coast of Venezuela, where the species seems to be present year-round (Naveira, 1996, Acevedo, 2007). Additionally, the effect of the Orinoco River influx during rainy season, could potentially balance the difference in productivity between dry (upwelling) and the rainy seasons (see figure 1 in Müller-Karger *et al.* 2004), supporting the presence year-round of predators such as common dolphin due to prey availability.

Behaviour and habitat use

The behaviour data processed here corresponded with initial behavioural states (at first encounter with the group of dolphins) during systematic surveys, and the descriptive statistics presented are only an expression of frequencies rather than proportions. Nevertheless, there is an evident overall dominance of travelling groups over foraging and socializing. Travel dominancy in the behaviour records of common dolphin has been previously documented (Quevedo, 2004; Molero-Lizarraga, 2005; Orlando, 2005; Rangel, 2007; Molero-Lizarraga *et al.*, 2008; Rangel & Cobarrubia-Russo, 2008b).

A clear preliminary spatial pattern can be drawn from the clumping of the foraging bouts on localized areas at the shelf edge. That pattern is supported by half of the episodes of prey capture and consumption at close-range distance from the limiting isobaths of 100 m, which apparently is a boundary in terms of habitat used; the occurrence of socializing bouts could be interpreted as a subordinate activity, apparently associated with foraging. However, in order to elucidate any spatial pattern in social activities, further data are needed. Acevedo (2007) reported that the slope index range (a percentage value describing the complexity of submarine relief in terms of slope) for common dolphin off the north-eastern coast is between 0 and 71% (almost flat bottom to deeply prominent slope); this relationship between foraging and slope is a common trait in cetaceans, due to advantages that complex slope areas provide in prey capture (Hui, 1979; 1985; Baumgarther, 1997; Wilson et al., 1997; Davis et al., 1998; Cañadas et al., 2002; Ingram & Rogan, 2002). The key fact in this case, is that the latter, along with the increase in travelling with distance from the 100 m isobaths, could suggest frequent migration towards a localized foraging area. More data are needed on activity patterns and, above all, on dietary (prey) preferences, in order to support the local migration hypothesis. In forthcoming sections of this contribution, limitations are identified and acknowledged.

Behaviour at first encounter presented in this paper coincides with several accounts generated by ferry-boats observations. Nonetheless, ethological records drawn from platform of opportunity (especially from ferry-boats), would be considered representative just as an observation of a behaviour bout at first encounter. Lagged behaviour events or progression of a behavioural state would not be properly recorded, due to the continuity of movement of the observation platform; consequently, this means impairment in keeping an observation record of the group, and even termination of sighting. Additionally, there are induced behaviour events related to the effect of the observation platform on the group encountered, such as bow-riding. This could be mistakenly interpreted as a travelling bout, due to the movement of the dolphins along with the ferry-boat. Interplay between travelling and foraging bouts is expected, but a solid behavioural (activity) budget is needed to obtain the proper insights.

Management and conservation

An issue of concern is the declining trend of the round sardinella stock that resulted in o catch in 2005, according with the landing statistics of the Venezuelan Fishery Administration Agency (INSOPESCA). The effect of common dolphins in a possible trophic cascade scenario was suggested before (Oviedo, 2005). The actual sardine fishery situation seemed to accelerate the need for understanding the predator-prey interrelationship between *S. aurita* and common dolphins.

Focal upwelling localized within shelf habitat, particularly in central Paria Peninsula and adjacent waters would represent areas with a key value to promote a healthy population growth and survival of the Venezuelan stock of common dolphin, as a result, they can be identified as potential critical habitat (Hoyt, 2005). A trend of regionalization is reflected in the distribution and abundance of common dolphins off the north-east coast of Venezuela. According to Pauly & Zeller (2003), the latter will serve as a baseline to assess ecosystem health and evaluate management scenarios.

Based on the considerations above, if the relevance of S. aurita in the diet of common dolphin is confirmed by research in progress, common dolphin will serve not only as an indicator-species for upwelling-modified waters, but also as an effective means to monitor sardine stock and ecosystem stability, specifically if the primary productivity required (a similar index to the ecological footprint) to sustain the stock of dolphins is monitored, and contrasted with the one required to sustain the sardine fishery (Oviedo & Achury, 2009). Added to the latter, the fact that critical habitats for the species, as proposed in this report, are the key centres of primary productivity, and sardine abundance, this would represent an important argument to be weighted in the proposal of candidate areas for MPA status, due to the relevance of these locations for the complex trophodynamics of the maritime environment off north-eastern Venezuela. Prey depletion has been an influential factor for cetacean population decrease (particularly common dolphins) in locations within the eastern Mediterranean basin. A degradation of the food web has been documented in the Mediterranean, where the current situation of exploitation of marine resources could

lead to additional species loss (Coll *et al.*, 2008). According to Bearzi *et al.* (2008) the common dolphin population decreased from 150 animals in 1996 to 15 in 2007. This situation described previously would be greatly prevented in waters off north-eastern Venezuela if a management scheme not only considered strict fishery regulations, but *in situ* protection of prey-predator abundance sites, an MPA will benefit both the predator species (human and dolphins) and the main prey resource; sardines.

Limitations

We acknowledge the potential effects of the heterogeneity of sampling protocols and distribution of field efforts, even though there is a solid representation of search efforts in every of the four sections assessed, the uneven investment in search efforts might produce biased results.

Behavioural and acoustic assessment of common dolphin in the study area, is still in progress, quantification of behavioural bouts presented in this contribution, should be only considered as frequencies of initial behavioural states, and not the proportion of time invested in particular behavioural activities produced by means of an unbiased ethological sampling method such as scan sampling.

ACKNOWLEDGEMENTS

Lenin Oviedo's data gathering was supported by funds from the Whale and Dolphin Conservation Society (WDCS), the Rufford Project Small Grant for Nature Conservation, and Cetacean Society International (CSI). Logistic support to Jaime Bolaños-Jiménez was provided by Marino Diaz and the boat crew of 'Aventura Marina' in Puerto la Cruz. Oceanographic data were provided by the Cariaco Project of Estación de Investigaciones Marinas de Margarita (EDIMAR-FLASA) and the University of South Florida (USF); many thanks to Professors Irene Astor and Ramón Varela. Fisheries statistics were provided by INSOPESCA-Gobierno Bolivariano de Venezuela (www.insopesca.gob.ve). We thank PDVSA-the Venezuelan Oil Company-for authorizing the use of data collected aboard the oceanographic cruises for the Plataforma Deltana Project (LBAPD). We are also grateful to the Captain and the crew of the RV 'Hermano Ginés' and Fundación la Salle de Ciencias Naturales (FLASA). We appreciate the valuable insights and suggestions of William F. Perrin, Dagmar Fertl, Thomas Jefferson and two anonymous referees.

REFERENCES

- Acevedo R. (2001) Distribución y caracterización de hábitat de cetáceos marinos en Venezuela. BSc thesis. Universidad Central de Venezuela, Caracas, Venezuela.
- Acevedo R. (2007) Potential geographical distribution of seven species of marine cetaceans reported in Venezuela, Southeast Caribbean. Acta Zoológica Sinica 53, 853–864.
- Acevedo R., Oviedo L. and Silva N. (2007) Identification of key areas for the conservation of misticete cetaceans in the waters near Margarita Island, Venezuela. *Memorias de la Sociedad de Ciencias Naturales La Salle* 167, 73–88.

- Acevedo R., Oviedo L., Silva N. and Bermúdez L. (2008) A note on the spatial and temporal distribution of humpback whales (*Megaptera novaeangliae*) off Venezuela, Southeastern Caribbean. Journal of Cetacean Research and Management 10, 73–79.
- Ballance T.L., Pittman R.L. and Fiedler P.C. (2006) Oceanographic influence of seabirds and cetaceans of the Eastern Tropical Pacific: a review. *Progress in Oceanography* 69, 360–390.
- Baumgarther M.F. (1997) The distribution of Risso' dolphin (Grampus griseus) with respect to the physiography of the northern gulf of Mexico. Marine Mammal Science 13, 614–638.
- Bearzi G., Agazzi S., Goncalvo J., Costa M., Bonizzoni S., Politi E., Piroddi C. and Reeves R. (2008) Overfishing and the disappearance of short beak common dolphin from western Greece. *Endangered Species Research* 5, 1–12.
- **Bermudéz Villapol L. and Boher S.** (2003) Update list of Venezuelan cetaceans. *Boletin de la Sociedad Venezolana de Ciencias Naturales* 46, 113–118.
- Bolaños-Jiménez J. and Villarroel-Marín A. (2005) Scientific knowledge as the basis for the sustainability of dolphin watching in the Mochima National Park, North-Eastern Venezuela. XVI Marine Mammals Biennial Conference. San Diego, California. 12–16 December 2006.
- Bolaños-Jiménez J., Bermúdez-Villapol L., Sayegh A. and Solé G. (2006) Current status of small cetaceans in Venezuela. IWC/ SC/58/ SM9.
- Bolaños-Jiménez J., Villarroel-Marín A.J., Parsons E.C.M. and Rose N. (2007) Origin and development of whale watching in the state of Aragua, Venezuela: laying the groundwork for sustainability. In Lück M., Gräupl A., Auyong J., Miller M.L. and Orams M.B. (eds) Proceedings of the 5th International Coastal and Marine Tourism Congress. School of Hospitality & Tourism and New Zealand Tourism Research Institute, AUT University, Auckland. New Zealand, pp. 16-27.
- Bolaños-Jiménez J. and Villarroel-Marín J. (2008) Rorcual común Balaenoptera physalus Linnaeus 1758. In Rodríguez J.P. and Rojas-Suárez F. (eds) Libro Rojo de la Fauna Venezolana. Caracas, Venezuela: Provita and Shell Venezuela S.A., p. 110.
- Cañadas A.R., Sagarminga R. and Garcia-Tiscar S. (2002) Cetacean distribution related with depth and slope in the Mediterranean waters off southern Spain. Deep-Sea Research I 49, 2053–2073.
- Cardenas J. and Achury A. (2000) Acústica pesquera de los recursos marinos de Venezuela: evaluación y seguimiento espacio temporal del stock de sardinas (Sardinella aurita Valennciennes 1847). Memorias de la Sociedad de Ciencias Naturales La Salle 154, 39–54.
- **Coll M., Lotze H.K. and Romanuk T.N.** (2008) Structural degradation in Mediterranean Sea food webs: testing ecological hypotheses using stochastic and mass-balance modelling. *Ecosystems* 11, 939–960.
- **Cobarrubia-Russo S. and Bolaños J.** (2008) Western range extension (from northeastern and central Venezuela) of the long-beaked common dolphin (Delphinus capensis). IWC/60/SC/SM9.
- Davis R.W., Fargion G.S., May N., Leming T.D., Baumgartner M., Evans W.E., Hansen L.J. and Mullin K. (1998) Physical habitat of cetaceans along the continental slope in the north-central and western Gulf of Mexico. *Marine Mammal Science* 14, 490–507.
- **Esteves M.A. and Oviedo L.** (2007a) A potential morphotype of common dolphin (*Delphinus* spp.) on the northeast coast of Venezuela. *Aquatic Mammals* 33, 229–234.
- Esteves M.A. and Oviedo L. (2007b) El redescubrimiento del delfín estuarino 'tonino' (Sotalia guianensis) al norte de la Península de Paria. Paper presented at the VII Congreso Venezolano de Ecología, Ciudad Guayana, Venezuela. 5 November-9 November 2007.

- Fernández M. and Oviedo L. (2009) Distribution and abundance of Delphinus delphis off the southern Pacific Coast of Costa Rica. IWC/ 61/SC/SM9
- Fernández M., Oviedo L., Echeverría D. and Goodman S. (2007) Co-occurrence of cetaceans indicator species in up-welling modified waters and tropical warm waters off Osa Peninsula, Costa Rica, Paper presented at the XVIII Biennial Conference on the Biology of Marine Mammals, Cape Town, South Africa. 29 November-3 December 2007.
- Forcada J. (2002) Distribution. In Perrin W.F., Würsig B. and Thewissen J.G.M. (eds) *Encyclopedia of marine mammals*. San Diego: Academic Press, pp. 327–333.
- Freón P., El Khattabi M., Mendoza J. and Guzmán R. (1997) Unexpected reproductive strategy of *Sardinella aurita* off the coast of Venezuela. *Marine Biology* 128, 363–372.
- García C. and Dawson S. (2003) Distribution of pantropical spotted dolphins in Pacific coastal waters of Panama. *Latin American Journal of Aquatic Mammals* 2, 29–38.
- **Guzmán R., Gómez G., Penott M. and Vizcaíno G.** (1999) Estructura de tallas y aspectos reproductivos de la sardina, *Sardinella aurita* en el nororiente de Venezuela. *Zootecnia Tropical* 17, 149–162.
- **Hoyt E.** (2005) Marine Protected Areas for whales, dolphins and porpoises: a world handbook for cetacean habitat conservation. London: Earthscan, 512 pp.
- Hui C.A. (1979) Undersea topography and distribution of dolphins of the genus *Delphinus* in the southern-California Bight. *Journal of Mammalogy* 60, 521–527.
- Hui C.A. (1985) Undersea topography and the comparative distribution of two pelagic cetaceans. *Fishery Bulletin* 83, 472-475.
- Ingram S. and Rogan E. (2002) Identifying critical areas and habitat preferences of bottlenose dolphins *Tursiops truncatus*. *Marine Ecology Progress Series* 244, 247–255.
- IWC (International Whaling Commission) (2007) Report of the Sub-Committee on Small Cetaceans. Journal of Cetacean Research and Management 9 (Supplement), 297-325.
- Jefferson T.A., Fertl D., Bolaños-Jiménez J. and Zerbini A.N. (2009) Distribution of common dolphins (*Delphinus* spp.) in the western Atlantic Ocean: a critical re-examination. *Marine Biology* 156:1109– 1124.
- Lira C., Bolaños-Jiménez J. and Mondolfi E. (1995) On two stranding of fin whale (*Balaenoptera physalus*) and its presence in Venezuelan waters. Paper presented at the XI Biennial Conference on the Biology of Marine Mammals, Orlando, Florida. 18–21 December 1995.
- Lorenzoni L. (2000) Detección de surgencias en costas Venezolanas mediante sensores remotos. BSc thesis de Licenciatura. Universidad Simón Bolivar, Caracas, Venezuela.
- Lusseau D. and Higham J.E.S. (2004) Managing the impacts of dolphinbased tourism through the definition of critical habitats: the case of Doubtful Sound, New Zealand. *Tourism Management* 25, 657–667.
- Mann J. (1999) Behavioral sampling methods for cetacean: a review and critique. *Marine Mammal Science* 15, 102–122.
- Mann J. (2000) Unraveling the dynamics of social life: long-term studies and observational methods. In Mann J., Connor R.C., Tyack P.L. and Whitehead H. (eds) *Cetacean societies*. London: University of Chicago Press, pp. 45–64.
- Martín A., Malavé L., Sánchez D., Aparicio R., Arocha F., Bone D., Bolaños J.A., Bolaños-Jimenez J., Castañeda J., Cardenas J.J., Carbonini A.K., Díaz Y., Guada H.J., Klein E., Lazo R., Lemus A., Lentino M., Lira C., Lodeiros C., Lopez R., Marin B., Martinez G., Marque B., Marquez A., Molinet R., Morales F., Posada J.,

Prieto A., Riera A., Rodriguez C.T., Ramirez A., Senior W., Solana P., Severeyn H., Spiniello P., Valera E., Yanes C. and Zoppi E. (2006) Línea base ambiental plataforma Deltana. Un enfoque multidisciplinario para el desarrollo costa afuera de gas en Venezuela. Paper presented at VII Congreso de Ciencias del Mar. MarCuba. La Habana, Cuba. Diciembre 2006.

- Mendoza J., Booth S. and Zeller D. (2003) Venezuela marine fisheries catches in space and time: 1950–1999. *Fisheries Centre Research Reports* 11, 171–180.
- Molero-Lizarraga A. (2005) Distribución y abundancia relativa de cetáceos en la ruta marítima Isla de Margarita—Cumaná. BSc thesis. Universidad del Zulia, Maracaibo, Venezuela.
- Molero-Lizarraga A., Hernández J. and Bermúdez L. (2008) Patrones de comportamiento del delfín común de hocico largo (Delphinus capensis, Gray 1828) en la ruta maritima Isla de Margarita—Cumana, Cuenca Oriental de Venezuela, 2003–2004. Paper presented at XIII Reunión de Trabajo de Especialistas de Mamíferos Marinos de América del Sur, 7mo Congreso SOLAMAC, Montevideo, Uruguay, 13–17 Octubre 2008.
- Müller-Karger F., Varela R., Thunell R., Astor Y., Zhang H., Luerssen R. and Hu C. (2004) Processes of coastal upwelling and carbon flux in the Cariaco Basin. *Deep-Sea Research Part II* 51, 927–943.
- Natoli A., Cañadas A., Peddemors V.M., Aguilar A., Vaquero C., Fernandez-Piqueras P. and Hoelzel A.R. (2006) Phylogeography and alpha taxonomy of the common dolphin (*Delphinus* sp.). *Journal of Evolutionary Biology* 19, 943–954.
- Naveira J.L. (1996) El orden cetacea en la región nor-oriental de Venezuela. MSc thesis. Universidad de Oriente, Cumana, Venezuela.
- **Orlando M.** (2005) Uso de hábitat por la especie de delfín común de hocico largo *Delphinus capensis* (Gray, 1828) (Cetacea: Delphinidae) en la ruta marítima Punta de Piedras-Puerto la Cruz. Undergraduate thesis. Instituto Universitario de Tecnología del Mar, Fundación La Salle, Isla de Margarita, Venezuela.
- **Oviedo L.** (2005) Cetaceans as seascape species on the northeast coast of Venezuela: a preliminary assessment based in the Seascape Species Approach. Paper presented at XVI Marine Mammals Biennial Conference. San Diego, California. 12–16 December 2006.
- **Oviedo L. and Silva N.** (2001) Utilización del Archipiélago de los Frailes por Tursiops truncatus (Montagu, 1821) (Cetacea: Delphinidae), incluyendo la costa este de la Isla de Margarita. Undergraduate thesis. Instituto Universitario de Tecnología del Mar, Fundación La Salle, Isla de Margarita, Venezuela.
- **Oviedo L. and Silva N.** (2005) Sighting frequency and relative abundance of bottlenose dolphins (*Tursiops truncatus*) along the northeast coast of Margarita Island and Los Frailes archipelago, Venezuela. *Revista de Biología Tropical* 53, 595–600.
- Oviedo L., Silva N., Bermúdez L. and Odell D.K. (2005) Distribution of bottlenose dolphins (*Tursiops truncatus*) on the east coast of Isla Margarita and the Los Frailes Archipelago, Venezuela. Aquatic Mammals 31, 442-446.
- **Oviedo L. and Esteves A.** (2008) Evaluación preliminar sobre el uso de hábitat de *Sotalia guianensis* en la Península de Paria (Bahía Guaraguao–Bahía Guaca), Venezuela. Paper presented at XIII Reunión de Trabajo de Especialistas de Mamíferos Marinos de América del Sur, 7mo Congreso SOLAMAC, Montevideo, Uruguay, 13–17 Octubre 2008.
- **Oviedo L. and Achury A.** (2009) Cetaceans' trophic impact on the Spanish sardine fishery off the northeastern coast of Venezuela. Paper presented at *Ecopath Twenty-five Years Conference*, *Vancouver, Canada, 30 August-1 September 2009.*

- Pauly D. and Zeller D. (2003) The global fishery crisis as a rationale for improving the FAO's database of fisheries statistic. Part 1. Fisheries Center Research Report, Volume 11, 85 pp.
- **Quevedo M.A.** (2004) Distribución, abundancia relativa y comportamiento en superficie de cetáceos en la ruta Punta de Piedras-Puerto La Cruz. BSc thesis. Universidad Central de Venezuela, Caracas, Venezuela.
- Ramírez-Carroz S. and González-Fernández M. (2004) Primer registro del delfín común (Delphinus capensis: Gray, 1828) en el Golfo de Venezuela. Boletín del Centro de Investigaciones Biológicas 38, 140-149.
- Rangel M. (2007) Distribución e índices relativos de frecuencia y abundancia de cetáceos en la ruta Cumaná–Punta de Piedra (Junio 2006–Junio 2007). Paper presented at the VII Congreso Venezolano de Ecología, Ciudad Guayana, Venezuela. 5 November–9 November 2007.
- Rangel M. and Cobarrubia-Russo S. (2008a) Inventario de cetáceos en el transecto Punta de Piedra–Cumaná. Paper presented at XIII Reunión de Trabajo de Especialistas de Mamíferos Marinos de América del Sur, 7mo Congreso SOLAMAC, Montevideo, Uruguay, 13–17 Octubre 2008.
- Rangel M. and Cobarrubia-Russo S. (2008b) Patrones de comportamiento de Delphinus capensis en la ruta Cumaná-Punta de Piedra. Paper presented at XIII Reunión de Trabajo de Especialistas de Mamíferos Marinos de América del Sur, 7mo Congreso SOLAMAC, Montevideo, Uruguay, 13-17 Octubre 2008.
- Rangel M., Esteves M. and Oviedo L. (2005) Long beaked common dolphin (Delphinus spp.): the dominant cetacean species associated with the complex topography in the Cariaco Trench. Abstract XVI Marine Mammals Biennial Conference, San Diego, California.

- Redfern J.V., Ferguson M.C., Becker E.A., Hyrenbach K.D., Good C., Barlow J., Kaschner K., Baumgartner M.F., Forney K.A., Balance L.T., Fauchald P., Halpin P., Hamazaki T., Pershing A.J., Qian S.S., Read A., Reilly S.B., Torres L. and Werner F. (2006) Techniques for cetacean-habitat modeling. *Marine Ecology Progress* Series 310, 271-295.
- Rodríguez J.P. and Rojas-Suárez F. (1999) El Libro Rojo de la Fauna Venezolana. Segunda Edición. Caracas, Venezuela: PROVITA.
- Romero A., Agudo A., Green S. and Notarbartolo Di Sciara G. (2001) Cetaceans of Venezuela: their distribution and conservation status. NOAA Technical Report NMFS (151): 60.
- Stockin K. (2008) The New Zealand common dolphin (Delphinus sp.) identity, ecology and conservation. PhD thesis. Massey University, Auckland, New Zealand.
- Watson R. and Pauly D. (2001) Systematic distortions in world fisheries catch trends. *Nature* 414, 534–536.
- Wilson B., Thompson P.M. and Hammond P.S. (1997) Habitat use by bottlenose dolphins: seasonal distribution and stratified movement patterns in the Moray Firth, Scotland. *Journal of Applied Ecology* 34, 1365–1374.

and

Zar J.H. (1996) *Biostatistical analysis*. London: Prentice-Hall International (UK) Ltd.

Correspondence should be addressed to:

L. Oviedo Proyecto Delphinus Margarita Island, Venezuela email: leninovi1@gmail.com