SUPPLEMENT • SMALL CETACEANS

REVISTA DE Biología Tropical

https://doi.org/10.15517/rev.biol.trop..v71iS4.57287

Population size and demographic parameters of pantropical spotted dolphin (*Stenella attenuata graffmani*) (Cetartiodactyla: Delphinidae) in Golfo Dulce, Costa Rica

Lenin Oviedo Correa[1*]; https://orcid.org/0000-0001-8015-1367
David Herra-Miranda[1]; https://orcid.org/0000-0003-2056-5060
Juan Diego Pacheco-Polanco[1]; https://orcid.org/0000-0003-3592-0950

1. Laboratorio de Ecología de Mamíferos Marinos Tropicales, Centro de Investigación de Cetáceos-Costa Rica, Puntarenas, Costa Rica; leninovi1@gmail.com (*Correspondence); davidceic@gmail.com; dpachecop@gmail.com

Received 30-VIII-2022. Corrected 17-III-2023. Accepted 12-IV-2023.

ABSTRACT

Introduction: The coastal form of pantropical spotted dolphins (*Stenella attenuata graffmani*) is commonly found along the Pacific coast of Costa Rica. Within Golfo Dulce, a fiord-like-embayment bordering the Osa Peninsula, pantropical spotted dolphins are sympatric with inshore bottlenose dolphins (*Tursiops truncatus*) and these marine predators provide an important source of revenue for local communities through boat-based tours.

Objective: Here we estimated the population size and demographic parameters of the coastal pantropical spotted dolphins in Golfo Dulce.

Methods: The study area was surveyed using non-random boat surveys. Upon encounter, dolphins were individually photo-identified using natural marks in their dorsal fins to estimate population abundance and survival using three emigration scenarios.

Results: A total of 280 dolphins were photoidentified, 65 % of which were observed only once. A total of 30 models were produced, and only two were considered to be parsimonious. Both models explain seasonal apparent survival and its variation due to heterogeneity in capture-recapture probability, one under no emigration (ΔQAICc = 0.00) and the other under random emigration (ΔQAICc = 1.72). We deemed the latter to be a more realistic model as it better reflects our in-situ observations. Under this preferred model the population size of pantropical spotted dolphins in Golfo Dulce varied from 187.30 individuals (CI: 168.67 – 208.02, CV: 0.11) to 367.88 individuals (CI: 341.51 – 396.31, CV: 0.07), with no significant differences in abundance due to seasonality and very high apparent survival (S = 0.98, CI: 0.68 – 0.99, SE: 0.02).

Conclusions: The number of identified dolphins and the proportion of individuals seen only once suggest the fluid movement of the population in and out of the gulf. However, the population size and demographic estimates are characterized by several identified individuals regularly recaptured inside the gulf. This group of dolphins appears to favor the inner basin as a critical foraging habitat. Given the increase of anthropogenic impacts within Golfo Dulce, future management and conservation efforts will require the recognition of an ecologically discrete population unit of coastal pantropical spotted dolphins within the gulf.

Key words: Golfo Dulce; *Stenella attenuatta graffmani*; population size; survival; robust design; Costa Rica; photoidentification.

Revista de Biología Tropical, ISSN: 2215-2075 Vol. 71(S4): e57287, diciembre 2023 (Publicado Nov. 01, 2023)

RESUMEN

Tamaño poblacional y parámetros demográficos del delfín manchado pantropical (*Stenella attenuata graffmani*) (Cetartiodactyla: Delphinidae) en el Golfo Dulce, Costa Rica.

Introducción: La forma costera del delfín manchado pantropical (*Stenella attenuata graffmani*) se encuentra comúnmente a lo largo de la costa Pacífica de Costa Rica. En el Golfo Dulce, una bahía similar a un fiordo en la Península de Osa, los delfines manchados pantropicales son simpátricos con los delfines nariz de botella costeros (*Tursiops truncatus*) y estos depredadores marinos proporcionan una importante fuente de ingresos para las comunidades locales a través de actividades de avistamientos ecoturísticos.
Objetivo: Se estimó el tamaño de la población y los parámetros demográficos de los delfines manchados pantropicales costeros para el Golfo Dulce.
Métodos: El área de estudio se estudió mediante muestreos no aleatorios desde embarcaciones. Tras el encuentro, los delfines fueron foto-identificados individualmente usando marcas naturales en sus aletas dorsales, para estimar la abundancia y supervivencia de la población usando tres escenarios posibles de emigración.
Resultados: Un total de 280 delfines fueron foto-identificados, 65 % de los cuales fueron observados una sola vez. Se elaboraron un total de 30 modelos, y sólo dos se consideraron parsimoniosos. Ambos modelos explican la supervivencia estacional aparente y su variación debido a la heterogeneidad en la probabilidad de captura-recaptura, uno bajo emigración nula (ΔQAICc = 0.00) y el otro bajo emigración aleatoria (ΔQAICc = 1.72). Consideramos que este último es un modelo más realista, ya que refleja mejor nuestras observaciones in situ. Bajo este modelo seleccionado, el tamaño de la población de delfines manchados pantropicales en el Golfo Dulce varió de 187.30 individuos (CI: 168.67 – 208.02, CV: 0.11) a 367.88 individuos (CI: 341.51 – 396.31, CV: 0.07), sin diferencias significativas en la abundancia debido a la estacionalidad y una supervivencia aparente muy alta (S = 0.98, CI: 0.68 – 0.99, SE: 0.02).
Conclusiones: El número de delfines identificados y la proporción de individuos vistos una sola vez sugieren un movimiento fluido de la población dentro y fuera del golfo. Sin embargo, el tamaño de la población y las estimaciones demográficas se caracterizan por varios individuos identificados y re-capturados regularmente dentro del golfo. Este grupo de delfines parece favorecer la cuenca interior como hábitat crítico de alimentación. Dado el incremento de los impactos antropogénicos dentro del Golfo Dulce, los futuros esfuerzos de manejo y conservación requerirán el reconocimiento de una unidad poblacional ecológicamente discreta del delfín manchado pantropical costero dentro del golfo.

Palabras clave: Golfo Dulce; *Stenella attenuatta graffmani*; tamaño poblacional; sobrevivencia; diseño robusto; Costa Rica; fotoidentificación.

INTRODUCTION

The pantropical spotted dolphin, *Stenella attenuata* (Gray, 1846) is distributed throughout the Eastern Tropical Pacific (ETP) where two genetically and morphologically distinct populations or ecotypes are recognized, oceanic and coastal (Perrin 1975, Perrin 2001, Perrin 2018). The oceanic ecotype lives in pelagic waters where, along with spinner dolphins, *Stenella longirostris*(Gray, 1828), it tends to associate with yellowfin tuna, resulting in high mortality due to the tuna purse seine fishery (Ballance et al., 2021; Cramer et al., 2008; Scott et al., 2012). The coastal ecotype is distributed at < 200 km from the coast of Central America where it is exposed to various human activities including commercial whale watching (Montero-Cordero & Lobo 2010; Pacheco-Polanco 2016); water quality and coastal habitat modification (Pacheco-Polanco 2016); and marina development projects near critical coastal cetacean habitats (Herra-Miranda et al., 2016).

Of the two ecotypes, the oceanic ecotype's population and demographic status are best known. Since the late 1970s, the U.S. government agency National Oceanographic Atmospheric Administration (NOAA) has generated management recommendations based on estimates of abundance, population size, survival, migration, and recruitment of oceanic pantropical spotted dolphins in the ETP (e.g., Gerrodette & Forcada 2005; Gerrodette et al., 2008; Wade et al., 2007). These efforts are the responsibility of NOAA, which is one of three U.S. federal agencies responsible for implementing the mandate of the Marine Mammal Protection Act. This mandate establishes that marine mammal populations that are endangered by the impact of human activities must be recovered, and to this end, periodic quantitative assessments of their population dynamics must be made (Marine Mammal Protection Act, 1972). However, such efforts have not been made for the coastal ecotype. Presently, there are few estimates of the population size of coastal spotted dolphins at the Central American region level (Gerrodette & Palacios, 1996; Palacios & Gerrodette 1996) or even by country, and they do not include demographic characterizations of the populations studied.

The coastal pantropical spotted dolphin (*S. attenuata graffmani*) is probably the most representative cetacean of the Pacific coast of Costa Rica. Several aspects regarding its ecology have been documented since the late 1990s, in particular, its presence and distribution (Acevedo & Buckhart, 1998; Cubero-Pardo, 1998; Cubero-Pardo, 2007a; Holst et al., 2017; Martinez-Fernandez et al., 2011, Martinez-Fernandez et al., 2014; May-Collado et al., 2005;; Oviedo, 2007, Oviedo, 2008; Oviedo et al., 2009, Oviedo et al, 2015), fine-scale relative abundance estimation (May Collado & Forcada, 2012), genetic identity (Escorza-Treviño et al., 2005; Leslie et al., 2019; Leslie & Morin, 2018), behavior (Cubero-Pardo, 2007b; May-Collado & Morales, 2005; Oviedo, 2007, Oviedo, 2008; Oviedo et al., 2018), interaction with fisheries (Palacios-Alfaro, 2006) and tourism activities (Montero-Cordero & Lobo, 2010). However, the size of the population in the Pacific of Costa Rican and their demography have not yet been assessed.

This study focuses on estimating the population size, and some demographic parameters (apparent survival, capture-recapture probability, and emigration) for the coastal pantropical spotted dolphins in Golfo Dulce. This gulf is a coastal marine habitat with tropical fiord characteristics, where the species has semi-pelagic habits and is sympatric with the inshore ecotype of the bottlenose dolphin (*Tursiops truncatus*). In Golfo Dulce, the spotted dolphins show habitat partitioning, facilitating the coexistence of both marine predators (Oviedo, 2018; Oviedo et al., 2018). Previous demographic assessments have shown that dolphins of coastal habits show seasonal variability in abundance, affecting demographic characteristics and possibly reproductive strategies in males and females (Bolaños-Jiménez et al., 2022). For these reasons, this study will consider the possible effects of dry (November-May, as reported in Oviedo et al., 2018) and rainy (June-October, as reported in Oviedo et al., 2018) seasons on the demography and population size of this delphinid in Golfo Dulce. There remains a need for a regional quantitative assessment of population dynamics and demographic information for this dolphin ecotype.

MATERIALS AND METHODS

Study Area: Golfo Dulce is a stratified estuary of tectonic origin, located in the South Pacific region of Costa Rica, centered at 8°33'N and 83°14'W (Svendsen et al., 2006). It has a 215 m deep internal basin with a 60 m sill that restricts ocean circulation (Morales-Ramírez et al., 2015; Svendsen et al., 2006); a length of 50 km; a width of 10-15 km; and a total area of approximately 750 km² (Von Wangelin & Wolff, 1996; Wolff et al.,1996). The climate is tropical and humid with a rainy season from June to early November, generating an average monthly rainfall of 100–700 mm. The main freshwater supply comes from the Coto Colorado, Tigre, Esquinas, and Rincón rivers, forming estuaries and mangrove zones in their areas of influence. They also affect the gulf's circulation pattern, resulting in a stratified current structure (Spongberg & Davis, 1998). Due to its physiographic and hydrological characteristics, Gulf Dulce can be divided into three sub-areas: 1) a deep inner basin with a maximum depth of about 215 m, an anoxic layer below 100 meters (Brenes & León, 1988) and restricted surface circulation; 2) a flat outer basin with an average depth of 70 m (Hebbeln et al., 1996), which begins 20 km from the mouth of the Gulf; and 3) a third area corresponding to the transitional-oceanic zone at the mouth of the Gulf (Oviedo et al., 2009, Oviedo et al., 2015), where this gulf communicates with the Pacific Ocean. In this external oceanic portion, depths close to 1 000 m are reached at a relative distance of 6 km (Fig. 1).

Field data collection: Pantropical spotted dolphin surveys were conducted from June 2011 to April 2014 in the three sub-areas described above. The surveys were conducted from a 7 m long boat with a 115 HP four-stroke outboard motor, zig-zagging from the point of origin (Bahía Rincón or Puerto Jiménez) to spatially cover as much of each sub-area as possible. The surveys were conducted between 7:00 am and 4:00 pm. During each survey, four observers were on board, one of which served as the main photographer, generally supported by another secondary photographer, they photographed as many dolphins as possible in each observed group using digital DSLR cameras (Canon 7D/70D) equipped with 400 mm telephoto lenses.

The definition of a group used in this study is that of Karczmarski et al. (2005): a spatial aggregation of animals engaged in similar (often the same) activities and interacting with each other on short enough time scales that there is little (or no) change in group membership. During each sighting, the boat approached within approximately 100 m of the group, and then the geographic position of the boat was recorded, as was its position relative to the group, the time of the encounter, group size, and composition, and the behavior records (initial and 10-minute) for the encounter. Specifically, group size was recorded, while group composition was classified according to the presence of adults, juveniles, and calves.

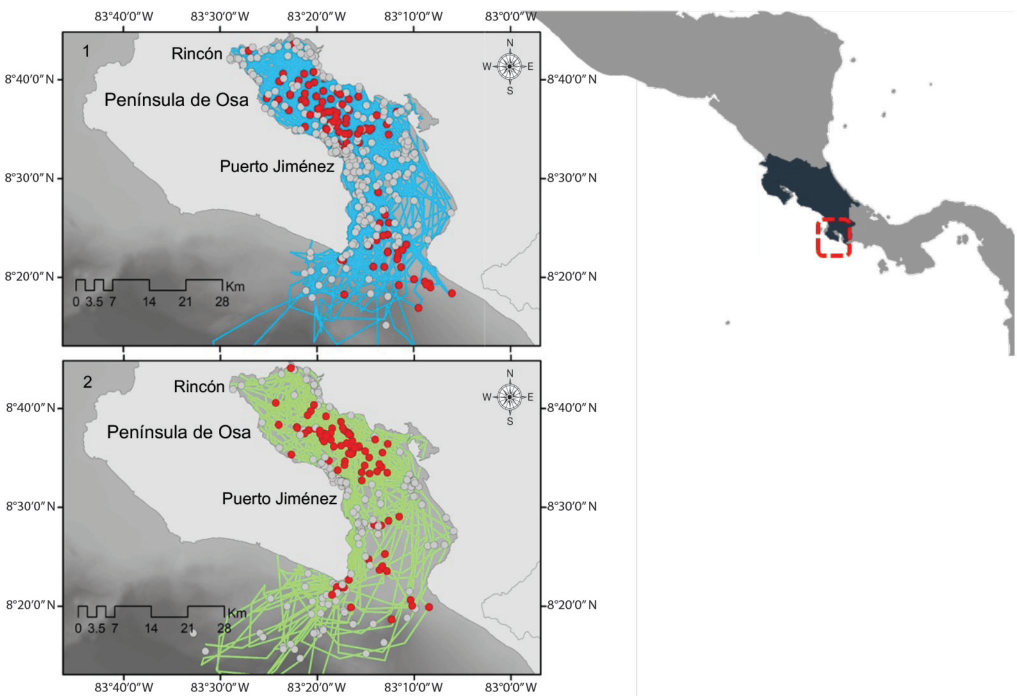

Fig. 1. The study area in Golfo Dulce: 1) Photoidentification sampling during the rainy seasons of 2011, 2012, and 2013. Blue lines correspond to the routes traveled during data collection. 2) Photoidentification sampling during the dry seasons of 2011–2012, 2012–2013, and 2013–2014. Green lines correspond to the routes traveled during data collection. Red circles: encounters and photographic sampling locations with the pantropical spotted dolphin (*S. a graffmani)*. Gray circles: encounters with other cetaceans.

The identification of the different age classes was based on Perrin (1975), Perrin (2001), and Perrin (2018), where the increase of spots on the body determines the maturity of the individuals. Accordingly, juveniles and calves with a length of 1/3 of the length of the mother have a coloration pattern composed of two shades of gray and a few ventral spots. In contrast, adults are more pigmented with white spots that merge dorsally.

The stable association of an adult with a small calf or medium size juvenile, though not always spotted in the infant position (Mann & Smut, 1998, Mann & Smut, 1999), was used as a cue to assign the female gender. On several occasions clear photographs of the genital slits supported sex identification. Highly acrobatic displays or bouts of social behavior such as copulation facilitated photographic evidence to differentiate male and female individuals. Behavior was described as feeding, resting, socializing, traveling, and milling, following the definitions of Marfurt et al., (2022) and Machado et al., (2019). Once the initial data collection was completed, the group-follow protocol for photoidentification was initiated.

Photoidentification: The traditional method of individual identification in dolphins uses photographs of the dorsal fin, which allows the modeling of presence/absence data by mark-recapture analysis (Bolaños-Jimenez et al. 2022; Brooks et al., 2017; Hupman et al., 2018; Parra et al., 2006; Wilson et al., 1999; Wursig & Jefferson, 1990; Zanardo et al. 2016). In one photography session, an individual may end up being photographed several times, depending on group size and behavior. After the photographs were collected, they were categorized based on their quality and distinctiveness and then used to build an identification catalog with images of each individual dolphin in Golfo Dulce. The selection process ensured that each sampling occasion was backed by a type-photo of every individual, if available. The type-photo was then associated with the presence record on a specific date and location. Photographic quality was scaled as 1-100, with a minimum use criterion of ≥ 70. A quality of more than 70 meant that the fin occupied no less than a quarter of the photo, was focused and defined, and was as perpendicular as possible to avoid distortion by angles (parallax) (Karczmarski et al., 2005). Distinctiveness refers to the presence of individual marks. Each high-quality photograph of the dorsal fin was assigned a distinctiveness (D) value between 0-4. Zero is when a dorsal fin is smooth, with no apparent markings, and four is a dorsal fin that is conspicuously distinctive, e.g., a malformed or partially mutilated fin. Individual dolphin identification in this study was based on the presence and distribution of marks (nicks and notches) on the dorsal fin profile. Other natural markings such as discolorations, scars, and spotting patterns were not ruled out but played a secondary role. Only dorsal fin photographs with quality ≥ 70 and distinctiveness from 1 to 4 were considered in this analysis. The construction of the catalog was carried out in the Discovery program (Galey & Karczmarski, 2012), which allows the processing and selection of the photographs based on the criteria described above. It also associated the sighting data with the identified dolphin and facilitated the construction of a matrix with the capture history of each individual (the basic input for the mark-recapture analysis).

Analysis of population size and demography: The capture-recapture matrices were used to estimate the population size and characterize the demography of pantropical spotted dolphins in Golfo Dulce, using a "robust design" model (Pollock et al., 1990). This model involves primary and secondary levels of sampling. The robust design integrated a series of short-time closed models at the secondary sampling level, where the effect of sampling time and individual heterogeneity on the probability of capture was controlled. The demographic closure models were connected by a frame model at the primary sampling level, which released the demographic closure, assuming a population where births, deaths, as well as the entry of immigrants and the exit of emigrants were considered temporally. This allowed us to infer dynamics associated with metapopulations (migratory movements in the absence of physical geographic barriers), following Kendall & Bjorkland (2001). For the secondary level, the sampling occasions were unified by month within the seasons, while the primary occasions were focused explicitly on the seasons (Rainy: June-October, Dry: November-May).

The above demographic aspects were met, pursuant with the validation of several basic assumptions of the mark-recapture analysis, under the robust design approach: (a) marks are not lost; although they can be modified, they are sufficiently distinctive to guarantee individual identification; b) samples are instantaneous at secondary levels; c) given a sampling occasion, all individuals in the population have the same probability of capture; d) survival of marked individuals does not vary from one capture occasion to the next at primary levels (seasons) of demographic openness; e) capture occasions at secondary levels (months) are with demographic closure within each primary level: and f) captures are independent among individuals without aggregation and overdispersion effect.

All models considered were analyzed using the Mark software interface in the "R" environment (R-Mark Laake et al., 2013). The following demographic parameters of pantropical spotted dolphins in Golfo Dulce were estimated:

- (Sj) apparent survival (does not refer to biological survival, but demographic survival by presence) at the first season j for j>1.
- (γ") probability of emigrating before season j, being present in j-1, for j>1
- (γ') probability of emigrating before season j, being absent in j-1, for j>2
- (pij) probability of the first capture in sample i of season j for i ≥ 1
- (cij) probability of recapture in sample i of season j for i > 1
- (Nj) the population size of marked individuals.

For this study, we set pij = cij, since photoidentification, being non-invasive and not promoting adverse reaction, did not directly affect the probability that a previously identified dolphin is recaptured (Parra et al., 2006). Three classes of temporal emigration models were evaluated: 1) Markovian emigration (γ' γ"), where the probability of a dolphin being present at Golfo Dulce would be conditional on presence or absence on the previous sampling occasion (Kendall & Nichols, 2002; Kendall et al., 1997); 2) random emigration (γ'= γ"), where the probability of a dolphin being present in the gulf is independent of presence or absence on the previous sampling occasion; and 3) no emigration (γ' = γ" = 0), where there is no movement out of the gulf.

Before the construction and evaluation of models by robust design, the fitting of the capture history matrix was corroborated, using a goodness-of-fit test in the Release GOF program. The lack of fit to temporality led to the estimation of a variance inflation factor (ĉ), which levelled the dispersion of the data. Thirty models were constructed and selected using the Akaike selection criterion (AICc). Considering the dispersion implied by the variance inflation factor (ĉ) the QAICc was used under the criterion that models with a difference expressed by Delta-QAICc greater than 10 lacked support (Burham & Anderson, 2004), and those less than two should not be discarded. To obtain the total population size, the number of marked individuals ($\hat{N}$) was related to the proportion of marked individuals in the sample ($\hat{\theta}$) (Wilson et al., 1999):

$$\hat{N}_{total} = \hat{N} / \hat{\theta}$$

The variance was estimated as follows:

$$Var(\hat{N}_{total}) = \hat{N}^2_{total} [Var(\hat{N}) / \hat{N}^2 + 1 - \hat{\theta}) / n\hat{\theta}^2]$$

Where n is the total number of individual dorsal fins for which was estimated. The coefficient of variation for the total population CV ($\hat{N}_{total}$) could be defined as the sum of the coefficients of variation of $\hat{N}$ and $\hat{\theta}$:

$$CV(\hat{N}_{total}) = \sqrt{((CV(\hat{N}))^2 + (CV(\hat{\theta}))^2}$$

The standard confidence interval could unrealistically set the lower bound to zero.

Therefore, we followed Burnham et al., (1987) using a log-normalized confidence interval, such that the lower limit is given by $\hat{N}_L = \hat{N}/r$, and the upper limit by $\hat{N}_U = \hat{N}\,r$.

For a 95% confidence interval, r would be given by:

$$r = \exp\{1.96\sqrt{\ln(1+(CV(\hat{N}_{total}))^2 + (CV(\hat{\theta}))^2)}$$

Where $(1+(CV(\hat{N}_{total}))^2$ is an approximation of $var(\ln \hat{N}_{total})$.

The variation of the total population size as a function of the seasons was explored using the non-parametric test Kruskal Wallis at a significance level (alpha) of 0.05.

RESULTS

There were 201 surveys for photographic capture of pantropical spotted dolphins in Golfo Dulce from 2011 to 2014, equating to 1 102 hours over 25 months and a travel effort of 18 730 km (Fig. 1). Details are shown in Table 1.

A total of 26 352 photographs were taken and analyzed, resulting in the identification of 280 individuals, 65 % of which were recorded only once. The rest of the dolphins cataloged showed an important level of recapture (98 individuals). The discovery curve, or the cumulative curve of entries into the catalog by sampling occasion, shows three trends (Fig. 2) that could explain the dynamics above: a non-asymptotic curve that incorporates all identifications, including those with individuals only captured once, and distinctiveness equal to one. Another curve becomes asymptotic only with distinctiveness greater than one, and finally, a nearly constant curve of individuals cataloged with very distinctive fins (D > 3).

For pantropical spotted dolphins the goodness-of-fit test showed significantly high dispersion ($\chi^2 = 22.81$, df = 8, p = 0.001). This is mainly due to the significant effects of the probability that capture-recapture is affected by individual heterogeneity, which is duly addressed by the robust design models. Due to the degree of dispersion, a variance inflation factor was estimated ($\hat{c} = 22.81/8 = 2.85$). Thirty models were generated from the capture history of individuals cataloged under the criteria of quality > 70 and distinctiveness ≥ 1.

The best-fitted models were those of apparent survival by sex group and the variation in the probability of capture due to heterogeneity during both seasons; among these, the best fit was that of no emigration (ΔQAICc = 0.00), followed by the random migration model (ΔQAICc = 1.72). Based on these two scenarios the population size differed in coefficient of variation (Table 2). For the no-emigration models, the coefficient of variation remained between 7 – 10 % (Table 3), and for the random-emigration models, the coefficient of variation was between 7 – 12 % (Table 4). If the spotted dolphin population in Golfo Dulce is considered under a pattern of no movement out of the study area, the population size of the

Table 1

Details of the search effort and the identification photographs included in the pantropical spotted dolphin catalog, including level of distinctiveness: D= 1, D≥ 2, D> 3.

Season	No. Months	No. Surveys	No. Hours	No. Cataloged IDs (New)		
				D = 1	D ≥ 2	D ≥ 3
Rainy 2011	3	28	143	17	22	24
Dry 2011_2012	5	18	94	74 (57)	59 (37)	25 (1)
Rainy 2012	4	44	263	89 (15)	65 (6)	25 (0)
Dry 2012_2013	4	29	155	111 (22)	71 (6)	25 (0)
Rainy 2013	5	56	291	134 (23)	72 (1)	25 (0)
Dry 2013_2014	4	26	156	182 (48)	73 (1)	25 (0)

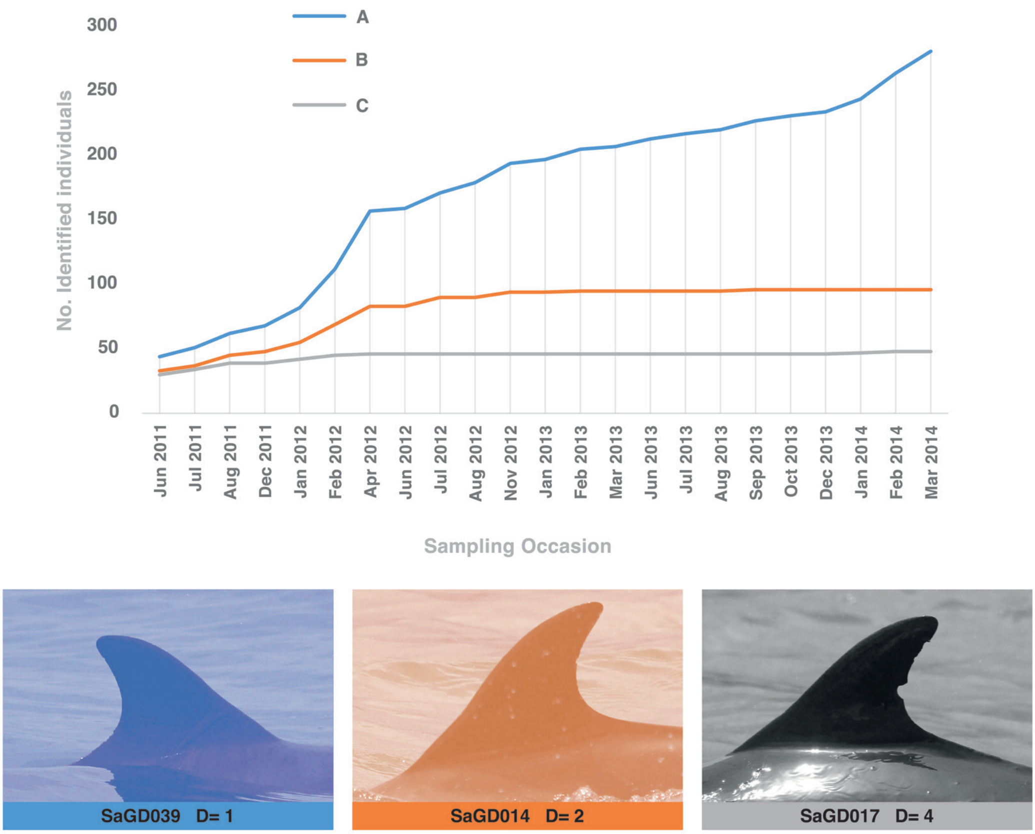

Fig. 2. Discovery curves for the coastal pantropical spotted dolphin in Golfo Dulce: A) The blue curve represents all cataloged individuals, including those recorded only once. B) The orange curve contains only the individuals with dorsal fins with D>1. C) The gray curve contains the individuals with dorsal fins classified under a distinctiveness level D>3. The bottom panel shows representative photographs of distinctiveness levels, from left: one (blue), two (orange), and 4 (gray).

Table 2

Selected best-fitted models generated from the capture history of pantropical spotted dolphins in Golfo Dulce under the Robust Design. S= apparent survival, P= capture probability, Het= heterogeneity, S♀ (CI) = apparent survival (confidence interval) for females, S♂ (CI)= apparent survival (confidence interval) for males, p-hat = capture probability, ψ ’ = ψ ” emigration probability. The notation ‘(.)’ implies that a given parameter was kept constant.

Models	Classification Criteria				Demographic Parameters			
	No. Parameters	QAICc	ΔQAICc	QAICc Weighted	S♀ (CI)	S♂(CI)	p-hat	ψ’=ψ”
S (. Sex) P(Het) No-Emigration	11	266.94	0.00	0.64	0.98 (CI: 0.81-0.99)	≈ 1 (CI: 0.99-1)	0.10	0.00
S (. Sex) P(Het) Random Emigration	12	268.67	1.72	0.27	0.98 (CI: 0.68-0.99)	≈ 1 (CI: 0.99-1)	0.12	0.16

Table 3
Population size of the pantropical spotted dolphin in Golfo Dulce under the no-emigration robust design model. ⊖ = proportion of individuals tagged per season, N-Marked= number of marked individuals, N-Total= Total population size, CI = Confidence Interval, CV Coefficient of Variation, ♀ = dolphins identified as females, ♂ = dolphins identified as male.

Seasons	Cluster	⊖	N-Marked	N-Total	CI	CV
Rainy 2011	♀		80.51	203.82	189.95-218.71	0.07
	♂	0.79	58.51	148.13	136.30-160.99	0.08
	Total			**351.95**	**326.24-379.70**	**0.07**
Dry 2011-2012	♀		81.38	235.88	220.95-251.82	0.07
	♂	0.69	64.38	181.61	173.35-200.88	0.07
	Total			**422.49**	**394.30-452.71**	**0.07**
Rainy 2012	♀		52.21	132.18	121.07-144.30	0.09
	♂	0.79	38.21	96.73	87.22-107.28	0.10
	Total			**228.91**	**208.29-251.59**	**0.09**
Dry 2012-2013	♀		47.48	137.62	126.30-149.96	0.09
	♂	0.71	55.16	99.94	90.30-110.62	0.10
	Total			**237.57**	**415.42-461.15**	**0.09**
Rainy 2013	♀		55.16	139.65	128.26-152.04	0.09
	♂	0.80	42.16	106.73	96.80-117.69	0.10
	Total			**246.38**	**225.06-269.73**	**0.09**
Dry 2013-2014	♀		42.42	122.96	112.27-134.66	0.09
	♂	0.68	32.42	93.97	**84.63-104.34**	**0.10**
	Total			**216.93**	196.90-239	0.09

species varies between 217 to 422 dolphins. For the random emigration model, the population size ranges from 187 to 368 individuals. However, these differences are not significant (Kruskal Wallis: χ^2 = 2.08, df = 1, p = 0.150), and similarly, there is no statistical difference in the population size of pantropical spotted dolphins in Golfo Dulce between seasons (Kruskal Wallis: χ^2 = 0.05, df = 1, p =0.827).

DISCUSSION

The demographic analysis of coastal pantropical spotted dolphins in Golfo Dulce through capture-recapture modeling resulted in the selection of two models, one where emigration was null and another one that suggested fluid dynamics of entries and exits to the population of pantropical spotted dolphins in Golfo Dulce, independent of the season evaluated. No matter the model, we found the population size of spotted dolphins in this gulf does not exceed 400 individuals. These results indicated that at least a portion of the population, equating to more than 90 individuals, remains for extended periods as demonstrated by a high level of recaptures and suggesting site fidelity throughout the year, particularly in the inner basin (Acevedo & Buckhart, 1998; Cubero-Pardo, 1998; Cubero-Pardo, 2007a; Oviedo, 2007; Oviedo et al., 2015, Oviedo et al., 2018). The study further indicates that the conditions associated with seasonality do not affect the population size and demographic patterns of spotted dolphins in Golfo Dulce. The discovery curves (Fig. 2) suggest that dolphins with low dorsal fin distinctiveness may not be readily recaptured. Hupman et al. (2018) found low

Table 4
Population size of the pantropical spotted dolphin in Golfo Dulce, under the robust design random emigration model. ⊖ = proportion of individuals tagged per season, N-Marked= number of marked individuals, N-Total= Total population size, CI = Confidence Interval, CV Coefficient of Variation, ♀ = dolphins identified as females, ♂ = dolphins identified as male.

Season	Cluster	⊖	N-Marked	N-Total	CI	CV
Rain 2011	♀		70.67	178.91	165.88-192.97	0.08
	♂	0.79	48.67	123.22	112.35-135.14	0.09
	Total			**302.13**	**278.23-328.10**	**0.08**
Dry 2011-2012	♀		71.96	208.58	194.51-223.67	0.07
	♂	0.69	54.96	159.30	147.00-172.64	0.08
	Total			**367.88**	**341.51-396.31**	**0.07**
Rain 2012	♀		45.8	115.95	105.43-127.40	0.09
	♂	0.79	31.8	80.51	71.78-90.29	0.12
	Total			**196.46**	**177.31-217.69**	**0.11**
Dry 2012-2013	♀		41.89	121.42	110.77-133.09	0.09
	♂	0.71	28.89	83.74	74.87-93.66	0.11
	Total			**205.16**	**185.64-226.75**	**0.10**
Rain 2013	♀		48.85	123.67	112.95-135.41	0.09
	♂	0.80	35.86	90.76	81.57-100.98	0.10
	Total			**214.43**	**194.52-236.40**	**0.09**
Dry 2013-2014	♀		37.31	108.14	98.11-119.20	0.10
	♂	0.68	27.31	79.16	70.55-88.81	0.12
	Total			**187.30**	**168.67-208.02**	**0.11**

dorsal fin distinctiveness in oceanic dolphins, such as *Delphinus* sp., to be associated with a low level of recaptures of identified individuals.

For the study population, apparent survival derived from the best-fitted models was relatively high. It only decreased slightly for females. When considering the no-immigration model, the survival of female pantropical spotted dolphins in Golfo Dulce would be above reported biological survival levels (Brooks et al., 2017; Taylor et al., 2007) and is supported by the low relative width of the confidence interval. However, it should be considered that the model based on non-immigration only describes a partial reality, focusing only on those individuals that develop long-term site fidelity. The model that considered random-type migration seemed closer to what was recorded in the capture histories of photo-identified individuals. Under this approach, the survival of females did not change in magnitude, but it did change in precision, as the width of the confidence interval was larger. Additionally, under this model, a comparatively low probability of emigration was established, which would support the dynamics of visiting individuals and resident individuals sharing the same seascape, as has been documented in coastal dolphin populations in Australia (Brooks et al., 2017), though with no apparent effect of seasonality.

The physiography of Golfo Dulce as a basin, or semi-enclosed internal sea, supported expectations of some demographic closure in the spotted dolphin population. Indeed, even during in situ sampling, several individuals evidenced a notable degree of recaptures, although there was no physical barrier to effectively prevent their departure from Golfo Dulce. In addition to the differences in individual behavior affecting the probability of capture (heterogeneity), there is nevertheless the possibility of fluid transience, which rules out the non-immigration that framed the best-fitted model (probability of capture as a function of individual heterogeneity, constant survival, and no emigration). Consequently, the model where the probability of capture was fitted as a function of individual heterogeneity with constant survival, under random emigration was considered the most parsimonious (Delta QAICc ≤ 2).

The seasonal survival estimate defined the true survival of pantropical spotted dolphins in Golfo Dulce, as well as the respective trend of random emigration, based on the high probability that the survival of an adult remains constant over relatively short periods when compared with its life span (≈ 45 years is the oldest age of a reproductive female) (Taylor et al., 2007). Notwithstanding a catastrophic event affecting pantropical spotted dolphin survival over the study period, emigration patterns are expected to be associated with individual heterogeneity and apparent survival estimates. The seasonal survival estimate is relatively high (0.99 +/- 0.01), but similar to that expected for other adult and sub-adult (non-calf) dolphins. For example, spinner dolphins (*S. longirostris*) from Hawaii have a survival of 0.97 +/- 0.05 (Tyne et al., 2014), and Mediterranean Sea common and striped dolphins, *Delphinus delphis, Linneaeus, 1758-Stenella coeruleoalba (Meyen, 1833)* of 0.94 +/- 0.05 (Santostasi et al., 2016).

Pantropical spotted dolphin population size apparently fluctuated between seasons, but this pattern was not significant. The population size of pantropical spotted dolphins in Golfo Dulce is a relatively discrete number considering that groups larger than 1 000 individuals have been documented outside the gulf (Authors' unpublished data 2005-2022). Fluctuations in population size are expected to be primarily influenced by the availability of resources in Golfo Dulce, especially given the presence of another delphinid, the inshore bottlenose dolphin (*T. truncatus*), which, as another marine predator, exerts additional pressure on available prey resources (Cubero Pardo, 2007a; Oviedo, 2007; Oviedo et al., 2018).

Based on the above, potential prey availability in Golfo Dulce would be the primary determinant for the aggregation pattern, site fidelity, and movement of this species in the study area, as proposed by Gowans et al. (2007) for several dolphin species with an intermediate home range pattern. Those authors argue that variations in home range patterns reflect a gradient of resource availability from predictable to extremely variable. Golfo Dulce may be a relatively predictable resource locality for pantropical spotted dolphins in terms of prey availability, and considering the availability of females for breeding, and refuge from predation. Relatedly, a study by Marin-Alpizar (2011) found small pelagic fish of the family Hemiramphidae to be present in this gulf year-round. If this fish is an important source in the diet of spotted dolphins, it may support not only the resident dolphin population but also be available to transient dolphins. To expand our understanding of the habitat-use patterns of these dolphins, future studies should incorporate spatial and temporal variations of their prey into their models.

It is important to recognize that individual differences in behavior, as well as the possibility of each dolphin leaving the Golfo Dulce, influenced variation in survival and probability of capture. To minimize the associated bias during field sampling, efforts were made to provide an equal distribution of individual photographic capture probability within each spotted dolphin encounter. Still, the grouping pattern of the dolphins in this gulf, especially in group sizes of ≥ 100 individuals, may have affected photographic coverage. Additionally, the sample size could also have been affected by our strict selection and analysis protocol. Given the increased human impacts in the study area (Herra-Miranda et al., 2016; Pacheco et al., 2016), effective conservation and management of pantropical spotted dolphins and other coastal/inshore cetaceans within Golfo Dulce require the recognition of discrete populations as management units. Therefore, to facilitate the detection of population-level changes over time, it is important to effectively determine the demographic parameters, as estimated here.

Ethical statement: the authors declare that we all agree with this publication and made significant contributions; that there is no conflict of interest of any kind; and that we followed all pertinent ethical and legal procedures and requirements. All financial sources are fully and clearly stated in the acknowledgments section. A signed document has been filed in the journal archives.

Author contributions: LOC conceptualized the study. LOC, DHM, and JDPP designed boat surveys, carried out field data collection and data analysis, coordinated data management, and wrote this manuscript.

ACKNOWLEDGMENTS

This study was made possible by the valuable support of a major citizen science framework promoted by the following institutions: 1) International Student Volunteers (2011-2013); we appreciate the support of Wagner Quirós, 2) Earthwatch Institute (2013-2023) especially the following internal funding scheme: Arunas A & Pamela A Chesonis Family Foundation and Gaye Hill & Jeff Urbina (2013-2014) and Gaye Hill & Jeff Urbina (2015-2016). Special thanks to each volunteer that accompanied us on each field survey and observation. Special thanks to our CEIC colleagues: to "El Chontal" family Jorge Medina and Azucena Herra-Miranda for providing us with our base at Rincón de Osa. A special thanks to our captain "Taboga", Dr. David Aurioles, Dr. Hector M. Guzman, and Dr. Leszek Karczmarski for their valuable academic support. We appreciate the additional comments from our colleagues Dr. Brooke Bessesen and Msc. Phoebe Edge.

REFERENCES

Acevedo, A., & Burkhart, S. (1998). Seasonal distribution of bottlenose (*Tursiops truncatus)* and pan-tropical spotted (*Stenella attenuata*) dolphins (Cetacea: Delphinidae) in Golfo Dulce, Costa Rica. *Revista de Biología Tropical. 46*, 91–101.

Ballance, L. T., Gerrodette, T., Lennert-Cody, C. E., Pitman, R. L., & Squires, D. (2021). A History of the Tuna-Dolphin Problem: Successes, Failures, and Lessons Learned. *Frontiers in Marine Science*, 8, 754755. https://doi.org/10.3389/fmars.2021.754755

Bolaños-Jiménez, J., Morteo, E., Fruet, P. F., Delfín-Alfonso, C. A., Secchi, E. R., & Bello-Pineda, J. (2022). Seasonal population parameters reveal sex-related dynamics of common bottlenose dolphins in open waters of the southwestern Gulf of Mexico. *Marine Mammal Science*, *38,* 705–724.https://doi.org/10.1111/mms.12897

Brenes C. L., & León, S. (1988). Algunos aspectos físico-químicos del Golfo Dulce. *Ingeniería en Ciencia Química, 12*, 12–16.

Brooks, L., Palmer, C., Griffiths, A. D., & Pollock, K. H. (2017). Monitoring variation in Small Coastal dolphin populations: An example from Darwin, Northern Territory, Australia. *Frontiers in Marine Science, 4*, 1–16. https://doi.org/10.3389/fmars.2017.00094

Burnham, K. P., Anderson, D. R., White, G. C., Brownie, C., & Pollock, K. H. (1987). Design and analysis methods for fish survival experiments based on release–capture [Monographs 5]. American Fisheries Society.

Cramer, K. L., Perryman, W. L., & Gerrodette, T. (2008). Declines in reproductive output in two dolphin populations depleted by the yellowfin tuna purse-seine fishery. *Marine Ecology Progress Series*, *369*, 273–285. https://doi.org/10.3354/meps07606

Cubero-Pardo, P. (1998). Distribución y patrones de actividad del bufeo (*Tursiops truncatus*) y el delfín manchado (*Stenella attenuata*) en el Golfo Dulce [Tesis de Maestría no publicada]. Universidad de Costa Rica.

Cubero-Pardo, P. (2007a). Distribución y condiciones ambientales asociadas al comportamiento del delfín bufeo (*Tursiops truncatus*) y el delfín manchado (*Stenella attenuata*) (Cetacea: Delphinidae) en el Golfo Dulce, Costa Rica. *Revista de Biología Tropical 55*, 549–557.

Cubero Pardo, P. (2007b). Environmental factors governing the distribution of the bottlenose dolphin (*Tursiops truncatus*) and the spotted dolphin (*Stenella attenuata*) in Golfo Dulce, South Pacific, off Costa Rica. *Investigaciones Marinas, 35*, 15–23.

Escorza-Treviño, S., Archer, F. I., Rosales, M., Lang, A., & Dizon, A. E. (2005). Genetic differentiation and intraspecific structure of eastern tropical Pacific spotted dolphins, (*Stenella attenuata*), revealed by DNA analyses. *Conservation Genetics, 6*, 587–600.

Gowans, S., Würsig, B., & Karczmarski, L. (2007). The social structure and strategies of delphinids: Predictions based on an ecological framework. *Advance in Marine Biology, 53*, 195–293.

Gailey, G. & Karczmarski, L. (2012) DISCOVERY: A photo-Identification data management system for individually recognizable animals. The Swire Institute of Marine Science, University of Hong Kong https://www.biosch.hku.hk/ecology/staffhp/lk/Discovery/

Gerrodette, T., & Forcada, J. (2005). Non-recovery of two spotted and spinner dolphin populations in the eastern tropical Pacific Ocean. *Marine Ecology Progress Series*, *291*, 1–21.

Gerrodette, T., Watters, G., Perryman, W. & Ballance, L., (2008). Estimates of 2006 dolphin abundance in the eastern tropical Pacific, with revised estimates for 1986-2003[NOAA-TM-NMFS-SWFSC-422]. National Oceanic and Atmospheric Administration. https://repository.library.noaa.gov/view/noaa/3639/noaa_3639_DS1.pdf

Gerrodette, T., & Palacios, D. M. (1996). Estimates of cetacean abundance in EEZ waters of the eastern tropical Pacific [Administrative Report LJ-96-10]. National Marine Fisheries Service, Southwest Fisheries Science Center.,

Gowans, S., Würsig, B., & Karczmarski, L. (2007). The social structure and strategies of delphinids: predictions based on an ecological framework. *Advances in Marine Biology*, *53*, 195–294. https://doi.org/10.1016/S0065-2881(07)53003-8

Hebbeln, D., Beese, D., & Cortés, J. (1996). Morphology and sediment structures in Golfo Dulce, Costa Rica. *Revista de Biología Tropical, 44*, 1–10.

Herra-Miranda, D., Pacheco-Polanco, J. D., Oviedo, L., & Iñíguez, M. (2016). Análisis espacial de los hábitats críticos del delfín nariz de botella (*Tursiops truncatus*) y la ballena jorobada (*Megaptera novaeangliae*) en el Golfo Dulce, Costa Rica: Consideraciones acerca de un proyecto de construcción de marina. *Revista de Ciencias Marinas y Costeras, 8*, 9–27. http://www.redalyc.org/articulo.oa?id=633766724001

Holst, M., Smultea, M. A., Koski, W. R., Sayegh, A. J., Pavan, G., Beland, J., & Goldstein, H. H. (2017). Cetacean sightings and acoustic detections during a seismic survey off Nicaragua and Costa Rica, November-December 2004. *Revista de Biología Tropical, 65*, 599–611.

Hupman, K., Stockin, K. A., Pollock, K., Pawley, M. D. M., Dwyer, S. L., Lea, C., & Tezanos-Pinto, G. (2018). Challenges of implementing Mark-recapture studies on poorly marked gregarious delphinids. *PLoS ONE, 13*, e0198167. https://doi.org/10.1371/journal.pone.0198167

Karczmarski, L., Wursig, B., Gailey G., Larson, K. L., & Vanderlip, C. (2005). Spinner dolphins in a remote Hawaiian atoll: social grouping and population structure. *Behavioral Ecology, 16*, 675–685. https://doi.org/10.1093/beheco/ari028

Kendall, W. L., & Bjorkland, R. (2001). Using open robust design models to estimate temporary emigration from capture-recapture data. *Biometrics, 57*, 1113–1122. https://doi.org/10.1111/j.0006-341X.2001.01113.x

Kendall, W. L., & Nichols, J. D. (2002). Estimating state-transition probabilities for unobservable states using capture-recapture/resighting data. *Ecology, 83*, 3276–3284. https://doi.org/10.2307/3072078

Kendall, W. L., Nichols, J. D., & Hines, J. E. (1997). Estimating temporary emigration using capture-recapture data with Pollock's robust design. *Ecology, 78*, 563–578.

Leslie, M. S., Archer, F. I., & Morin, P. A. (2019). Mitogenomic differentiation in spinner (*Stenella longirostris*) and pantropical spotted dolphins (*Stenella attenuata*) from the eastern tropical Pacific Ocean. *Marine Mammals Science, 35*, 522–551. https://doi.org/10.1111/mms.12545

Leslie, M. S., & Morin, P. A. (2018). Structure and phylogeography of two tropical predators, spinner (*Stenella longirostris*) and pantropical spotted (*Stenella attenuata*) dolphins, from SNP data. *Royal Society Open Science, 5*, 171615. http://dx.doi.org/10.1098/rsos.171615

Machado, A. M. S., Cantor, M., Costa, A. P., Righetti, B. P., Bezamat, C., Valle-Pereira, J. V., Simoes-Lopez, P.C., Castilho, P. V. & Daura-Jorge, F. G. (2019). Homophily around specialized foraging underlies dolphin social preferences. *Biology letters, 15,* 20180909. https://doi.org/10.1098/rsbl.2018.0909

Mann, J., & Smuts, B. B. (1998). Natal attraction: allomaternal care and mother–infant separations in wild bottlenose dolphins. *Animal Behaviour*, *55*(5), 1097–1113.

Mann, J., & Smuts, B. B. (1999). Behavioral development in wild bottlenose dolphin newborns (*Tursiops* sp.). *Animal Behaviour*, *136*, 529–566.

Marfurt, S. M., Allen, S. J., Bizzozzero, M. R., Willems, E. P., King, S. L., Connor, R. C., Kopps, A.M., Wild, S., Gerber, L., Wittwer, S. & Krützen, M. (2022). Association patterns and community structure among female bottlenose dolphins: environmental, genetic and cultural factors. *Mammalian Biology*, *102*, 1373–1387. https://doi.org/10.1007/s42991-022-00259-x

Marin-Alpizar, B. (2011). Evaluación biológica y pesquera de la población de aguja pajarito o ballyhoo (Hemiramphus saltator) en el Golfo Dulce, Pacífico Sur de Costa Rica [Informe Técnico No. 3]. Instituto Costarricense de Pesca y Acuicultura.

Martínez-Fernández, D., Montero, A., & May-Collado, L. (2011). Cetáceos de las Aguas Costeras del Pacífico

Norte y Sur de Costa Rica. *Revista de Biología Tropical, 59*, 283–290.

Martínez-Fernández, D., Montero-Cordero, A., & Palacios-Alfaro, J. D. (2014). Áreas de congregación de cetáceos en el Pacífico norte de Costa Rica: propuestas para su manejo. *Revista de Biología Tropical, 62*, 99–108.

May-Collado, L.J., & Morales, A.R. (2005). Presencia y patrones de comportamiento del delfin manchado costero, (*Stenella attenuata graffmani*) (Cetacea: Delphinidae) en el Golfo de Papagayo, Costa Rica. *Revista de Biología Tropical 53*, 265 – 276.

May-Collado, L. J., & Forcada, J. (2012) Small-scale estimation of relative abundance for the coastal spotted dolphins (*Stenella attenuata*) in Costa Rica: the effect of habitat and seasonality. *Revista de Biología Tropical, 60*, 133–142.

May-Collado, L., Gerrodette T., Calambokidis J., Rasmussen K., & Sereg, I. (2005) Patterns of cetacean sighting distribution in the Pacific Exclusive Economic Zone of Costa Rica, based on data collected from 1979-2001. *Revista de Biología Tropical 53*, 249–263.

Montero-Cordero, A., & Lobo, J. (2010). Effect of tourist vessels on the behaviour of the pantropical spotted dolphin, (*Stenella attenuata*), in Drake Bay and Caño Island, Costa Rica. *Journal of Cetacean Research and Management, 11*, 285–291. https://doi.org/10.47536/jcrm.v11i3.608

Morales-Ramírez, A., Acuña-Gonzáles, J., Lizano, O., Alfaro, E., & Gómez, E. (2015). Rasgos oceanográficos en el Golfo Dulce, Pacífico de Costa Rica: una revisión para la toma de decisiones en conservación marina. *Revista de Biología Tropical, 63*, 131–160.

Oviedo, L. (2007). Dolphin sympatric ecology in a tropical fjord: habitat partitioning by bathymetry and topography as a strategy to coexist. *Journal of Marine Biological Association of the United Kingdom 87*, 1–9. https://doi.org/10.1017/S0025315407056366

Oviedo, L. (2008). Análisis del uso de hábitat del delfín manchado pantropical (*Stenella attenuata*) (Cetacea: Delphinidae) en el Golfo Dulce, Costa Rica[master's. thesis, Universidad Nacional (UNA)], Repositorio Académico Institucional https://repositorio.una.ac.cr/handle/11056/25774

Oviedo, L. (2018). Patrones y procesos de selección de hábitat en delfines simpátricos en Golfo Dulce, Costa Rica [Unpublished doctoral dissertation]. Instituto Politécnico Nacional, México. https://delfin.cicimar.ipn.mx/Biblioteca/Busqueda/Tesis/952?Origen=coleccion_tesis.

Oviedo, L., Pacheco-Polanco, J. D., & Herra-Miranda, D. (2009). Evaluación de los riesgos de afectación por el establecimiento de granjas atuneras en relación con la distribución espacial de cetáceos en el Golfo Dulce, Costa Rica. *Revista Ciencias Marinas y Costeras, 1*, 159 – 174. https://doi.org/10.15359/revmar.1.9

Oviedo, L., Herra-Miranda, D., Pacheco-Polanco, J. D., Figgener, C., Márquez-Artavia, A., Quiros-Pereira, W., & Iñiguez, M. (2015). Diversidad de cetáceos en el paisaje marino costeros de Golfo Dulce, Península de Osa, Costa Rica. *Revista de Biología Tropical*, *63*, 395–406.

Oviedo, L., Fernández, M., Herra-Miranda, D., Pacheco-Polanco, J. D., Hernández-Camacho, C. J., & Aurioles-Gamboa, D. (2018). Habitat partitioning mediates the coexistence of sympatric dolphins in a tropical fjord-like embayment. *Journal of Mammalogy, 99*, 554–564. https://doi.org/10.1093/jmammal/gyy021

Pacheco-Polanco, J. D. (2016). Uso de la población residente de delfines nariz de botella (*Tursiops truncatus*) ecotipo costero como bioindicador ambiental en Golfo Dulce, Costa Rica: implicaciones para una gestión integrada del recurso[Unpublished master's. thesis]. Universidad de Costa Rica.

Palacios-Alfaro, J. D. (2006). Presencia y comportamiento de dos especies de delfines en el Pacífico central de Costa Rica[Thesis of Licenciatura, Universidad Nacional de Costa Rica (UNA)]. Repositorio Académico Institucional. https://repositorio.una.ac.cr/handle/11056/24135

Palacios, D. M. & T. Gerrodette. (1996). Potential impact of artisanal gillnet fisheries on small cetaceans populations in the Eastern Tropical Pacific [Administrative Report JL-96-11]. National Marine Fisheries Service, Southwest Fisheries Science Center.

Parra, G. J., Corkeron, P. J., & Marsh, H. (2006). Population sizes, site fidelity and residence patterns of Australian snubfin and Indo-Pacific humpback dolphins: Implications for conservation. *Biological Conservation, 129*, 167–180. https://doi.org/10.1016/j.biocon.2005.10.031

Perrin, W. F. (1975). Variation of spotted and spinner porpoise (genus *Stenella*) in the eastern Pacific and Hawaii. *Bulletin of the Scripps Institution of Oceanography 21*, 1–206.

Perrin, W. F. (2001). *Stenella attenuata*. *Mammilan Species*, *633*, 1–8.

Perrin, W. F. (2018). Pantropical spotted dolphin. In B. Wursig, , J. G. M. Thewissen, & K. M. Kovacs (Eds.). *Encyclopedia of Marine Mammals (3rd ed.* pp. 676–678). Academic Press.

Pollock, K. H., Nichols, J. D., Brownie, C., & Hines, J. E. (1990). Statistical inferences for capture-recapture experiments. *Wildlife Monographs, 107*, 1–97

Santostasi, N. L., Bonizzoni, S., Bearzi, G., Eddy, L., & Gimenez, O. (2016). A robust design capture-recapture analysis of abundance, survival and temporary emigraton of three odontocete species in the Gulf of Corinth, Greece. *PLoS ONE, 11*, e0166650. https://doi.org/10.1371/journal.pone.0166650

Scott, M. D., Chivers, S. J., Olson, R. J., Fiedler, P. C., & Holland, K. (2012). Pelagic predator associations: tuna and dolphins in the eastern tropical Pacific Ocean. *Marine Ecology Progress Series, 485*, 283–302. https://doi.org/10.3354/meps09740

Spongberg, A., & Davis, P. (1998). Organochlorinated pesticide contaminants in Golfo Dulce, Costa Rica. *Revista Biología Tropical, 46*, 111–124.

Svendsen, H., Rosland, R., Myking, S., Vargas, J. A., Lizano, O. G., & Alfaro, E. C. (2006). A physical oceanographic study of Golfo Dulce, Costa Rica. *Revista de Biología Tropical, 54*, 147–170.

Taylor, B. L., Chivers, S. J., Larese, J., & Perrin, W. F. (2007). Generation Length and Percent Mature Estimates for IUCN Assessments of Cetaceans [Administrative Report LJ-07-01]. Southwest Fisheries Science Center..

Tyne, J. A., Pollock, K. H., Johnston, D. W., & Bejder, L. (2014) Abundance and Survival Rates of the Hawai'i Island Associated Spinner Dolphin (*Stenella longirostris*) Stock. *PLoS ONE, 9*, e86132. https://doi.org/10.1371/journal.pone.0086132

Von Wangelin, M., & Wolff, M. (1996). Comparative biomass spectra and species composition of the zooplankton communities in Golfo Dulce and Golfo de Nicoya, Pacific coast of Costa Rica. *Revista de Biología Tropical*, *44*, 135–155.

Wade, P. R., Watters, G. M., Gerrodette, T., & Reilly, S. B. (2007). Depletion of spotted and spinner dolphins in the eastern tropical Pacific: modeling hypotheses for their lack of recovery. *Marine Ecology Progress Series*, *343*, 1–14.https://doi.org/10.3354/meps07069

Wilson, B., Hammond, P. S., & Thompson, P. M. (1999). Estimating size and assessing trends in a coastal bottlenose dolphin population. *Ecological Applications, 9*, 288–300. https://doi.org/10.2307/2641186

Wolff, M., Hartmann, H. J., & Koch, V. (1996). A pilot trophic model for Golfo Dulce, a fjord-like tropical embayment, Costa Rica. *Revista de Biologia Tropical*, *44*, 215–231.

Wursig, B., & Jefferson, T. A. (1990). Methods of photo-identification for small cetaceans. *Reports of the International Whaling Commission (Special Issue) 12*, 43–55.

Zanardo, N., Parra, G. J., & L. M. Möller. (2016). Site fidelity, residency, and abundance of bottlenose dolphins (*Tursiops sp*.) in Adelaide's coastal waters, South Australia. *Marine Mammal Science, 32*, 1381–1401. https://doi.org/10.1111/mms.12335