

# Relationships Between Common Bottlenose Dolphins (*Tursiops truncatus*) and Whalesuckers (*Remora australis*) at a Remote Archipelago in the Equatorial Atlantic Ocean

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## Abstract

The relationships between cetaceans and remoras are still poorly known, especially those involving the species commonly referred to as the whale-sucker (*Remora australis*), which attaches to cetaceans only. We report here on the association between resident common bottlenose dolphins (*Tursiops truncatus*) and whalesuckers at the remote São Pedro and São Paulo Archipelago (SPSPA) in the equatorial Atlantic Ocean. The study was conducted during four field expeditions between 2011 and 2013. A total of 13,720 photographs of the common bottlenose dolphins were taken from a small inflatable boat. From the analysed pictures, 141 were of dolphins with attached remoras, 70 of which were from 12 photo-identified dolphins (i.e., about 50% of the estimated population). The number of whalesuckers per dolphin, the size classes of these remoras, and their favoured attachment sites on the dolphins' bodies largely resemble the association of the same fish species with spinner dolphins (*Stenella longirostris*) at Fernando de Noronha Archipelago (FNA) in the Southwestern Atlantic Ocean. It is noteworthy that we found more similarities than differences in the relationships between the dolphins and the whalesuckers at both these oceanic islands, despite the dolphins belonging to different species, having marked differences in body size, and the great disparity in their numbers: about 25 individuals at SPSPA vs hundreds (sometimes up to 2,000) at FNA. The present study strengthens the view that this remora takes advantage of the association with small swift

cetaceans that congregate regularly in offshore areas and confirms the common bottlenose dolphin as a cetacean host for the whalesucker.

**Key Words:** remora, Echeneidae, cetacean, Delphinidae, marine association, Saint Paul's Rocks, Brazil

## Introduction

The association between marine mammals and remoras or diskfishes (Echeneidae) has been reported for at least 20 cetacean and two sirenian species (O'Toole, 2002; Williams et al., 2003; Fertl & Landry, 2018). This association usually has been regarded as a symbiotic relationship, although its precise nature (e.g., commensalism, phoresy, proto-cooperation) is still a matter of debate (Alling, 1985; O'Toole, 2002; Leung, 2014). In fact, many hypotheses about the advantages and detrimental effects for cetaceans resulting from this ecological relationship have been postulated (e.g., Alling, 1985; Norris et al., 1994; O'Toole, 2002; Leung, 2014). However, the disadvantages, including the energetic costs related to a hydrodynamic drag during swimming and manoeuvres to dislodge the remoras (Notarbartolo di Sciara & Watkins, 1980; Fertl & Landry, 2018), seem to outweigh the advantages for dolphins, in spite of the occasional cleaning of parasites and eating of sloughed or diseased skin by the remoras (Strasburg, 1959; Cressey & Lachner, 1970; Sazima et al., 2006; Silva-Jr. & Sazima, 2008). Nevertheless, a simulation study indicates that the

extra swimming effort required by a dolphin to overcome the parasitic drag force of an attached remora is relatively small, although its long-term effects or the combined effects of many remoras attached simultaneously to a single host should not be neglected (Beckert et al., 2016).

Even though about 50 cetacean species occur in Brazilian waters (Siciliano et al., 2008; Ott et al., 2013; Hrbek et al., 2014; Cypriano-Souza et al., 2017) and seven out of eight extant diskfishes have been reported in this vast area of the western South Atlantic (Vaske et al., 2005; Menezes, 2011), most studies related to cetacean hosts and remoras in this region are largely limited to brief reports. These include cases of humpback whales (*Megaptera novaeangliae*) with attached shark-suckers (*Echeneis naucrates*) in shallow waters (< 30 m depth) at Abrolhos Bank (Wedekin et al., 2004) in eastern Brazil, and the same remora species attached to a Guiana dolphin (*Sotalia guianensis*) in an inner estuary (about 23 km away from the river mouth) in southeastern Brazil (Santos & Sazima, 2008). However, much better documentation is available for the association between spinner dolphins (*Stenella longirostris*) and the remora commonly referred to as the whalesucker (*Remora australis*) in the shallow waters around the oceanic islands of Fernando de Noronha Archipelago (FNA) in the equatorial Atlantic Ocean (Silva-Jr. & Sazima, 2003, 2008; Silva-Jr. et al., 2005; see Figure 1 for the Brazilian locations mentioned above).

The whalesucker is well known for its strong host preference and attachment exclusively to cetaceans, including the blue whale (*Balaenoptera musculus*), fin whale (*Balaenoptera physalus*), sei whale (*Balaenoptera borealis*), and sperm whale (*Physeter macrocephalus*) (Notarbartolo di Sciara & Watkins, 1980; Fertl & Landry, 1999; Flammang et al., 2020). Among these large whales, the whalesucker seems to have a preference for blue whales (Rice & Caldwell, 1961); and in some localities where this whale aggregates (e.g., Sri Lanka), almost every blue whale sighted had at least one remora attached (Alling, 1985). The association of the whalesucker with cetaceans is also well documented for some delphinids, including, besides the spinner dolphin, the Atlantic spotted dolphin (*Stenella frontalis*) and the short-beaked common dolphin (*Delphinus delphis*) (Fertl & Landry, 1999; Becerril-García et al., 2019). There are also brief references for association between the whalesucker and common bottlenose dolphin (*Tursiops truncatus*) exclusively in offshore waters of the eastern North Pacific (published photo of *R. australis* by Pitman, 2003; see also Froese & Pauly, 2021) and in the Mediterranean Sea (Bas & Gönülal, 2017).

As both the common bottlenose dolphin and the whalesucker are widely distributed in tropical and

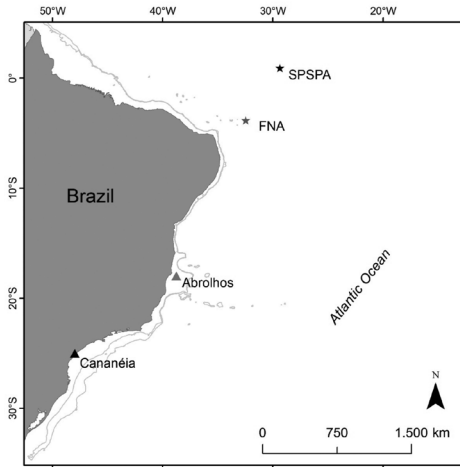
temperate oceans (Wells & Scott, 2009; Froese & Pauly, 2021), the association between them would be expected to occur frequently, which does not appear to be the case. Moreover, as this association is only briefly mentioned in the literature (e.g., Bas & Gönülal, 2017), several aspects of the ecological relationship between these two species are completely unknown. Herein, the interactions between resident common bottlenose dolphins and whalesuckers in the vicinity of the remote São Pedro and São Paulo Archipelago (SPSPA; Figure 1) in the equatorial waters off Brazil are described in detail. In addition, a comparison is made to examine what parallels would exist between this association at SPSPA and that reported for the spinner dolphins and whalesuckers at the FNA (Silva-Jr. & Sazima, 2008), the only locality in the Southwestern Atlantic where the cetacean-remora association has been comprehensively studied.

## Methods

The study was conducted at the SPSPA, also known as Saint Paul's Rocks, a small oceanic archipelago (covering an area around 16,000 m<sup>2</sup>) that rises from the 4,000-m deep ocean floor (Feitoza et al., 2003) in the equatorial Atlantic Ocean (00° 56' N, 29° 22' W; Figure 1). The archipelago is located 1,010 km from the Brazilian mainland and was recognized as a distinct marine ecoregion due to its distance from the coast and its unique biodiversity (Spalding et al., 2007). The closest oceanic islands to the study site are the Fernando de Noronha Archipelago (FNA), located approximately 625 km southwest of the SPSPA (Figure 1), which belongs to a vast volcanic edifice that rests on the ocean floor at a depth of around 4,000 m (Lopes & Ulbrich, 2015).

The surrounding waters of the SPSPA are inhabited by a resident population of common bottlenose dolphins estimated to include approximately 25 individuals (Milmann et al., 2017). The association between these dolphins and the whalesucker was recorded during four field expeditions designed to characterize common bottlenose dolphin population dynamics and ecology in the region from May 2011 to February 2013 (Milmann et al., 2017).

During each field expedition, boat surveys circumnavigated the archipelago (< 2 nmi from the islands), and all common bottlenose dolphins sighted were counted and photographed for individual recognition purposes, based on their natural marks (Würsig & Würsig, 1977; Milmann et al., 2017). The photographs were taken above the water surface and mostly at a perpendicular angle to the dolphins' bodies (Figure 2), using digital cameras (Canon 75-300-mm zoom lenses) with autofocus.



**Figure 1.** Locations of the archipelagos of São Pedro and São Paulo (SPSPA) and Fernando de Noronha (FNA), where whalesuckers (*Remora australis*; indicated by stars) have been recorded in association with common bottlenose dolphins (*Tursiops truncatus*) and spinner dolphins (*Stenella longirostris*), respectively. The locations of the Abrolhos Bank and the estuary of Cananéia, where the sharksucker (*Echeneis naucrates*; indicated by triangles) was recorded attached, respectively, to humpback whales (*Megaptera novaeangliae*) and to a Guiana dolphin (*Sotalia guianensis*) in Brazilian waters are also indicated. The map also shows the 100 and 200 m isobaths.

All dolphin photographs containing at least one visible remora were selected, and only a subset was chosen for dolphins that could be positively identified by natural marks. This procedure was adopted to avoid data replication of remora presence (i.e., pseudoreplication) and to give an idea of the extent of this association at a population level. For this purpose, we used a pre-existent photo-identification catalogue of 19 known common bottlenose dolphins of the SPSPA (Milmann et al., 2017). The same catalogue was used to estimate the percentage of dolphins with attached remoras in the total dolphin population, estimated to be 25 individuals (Milmann et al., 2017). Only dolphins with distinct natural marks (categories D1 and D2 of Milmann et al., 2017) were considered (i.e., 19 out of the 25 photo-identified dolphins during the study period). Since multiple photographs were taken of the same individual in each encounter, an *image sequence* was defined as a set of photographs of a photo-identified individual separated from a second set of the same individual by an interval of at least 2 min. To avoid data dependence and sample bias, the presence/absence of remoras on a particular dolphin was considered only for the first time it was recorded on a given day (i.e., first image sequence). Thus, even if a dolphin was photographed at different times during a day, only the first record was considered, regardless of any change related to the presence/



**Figure 2.** Partial view of the SPSPA, with three common bottlenose dolphins in the foreground. A large whalesucker is attached near the blowhole of the third dolphin. (Photo credit: Lucas Milmann, GEMARS)

absence of remoras or to the dolphin's body sector where the remoras were attached (see below).

To assess a possible preference for a particular place for attachment by the remoras, the dolphin's body was divided into 12 sectors (see Figure 3), according to Scott et al. (2005). Despite these sectors not being the same size and that some bias could occur when comparing them (e.g., sectors with larger areas may be more likely to contain remoras), they are easily recognized by morphological features (e.g., base of the dorsal fin) and provide a good proxy for the distribution of the remoras on a dolphin's body. As the photographs were taken above the water surface and, thus, the totality of the dolphin's body surface was unavailable, the frequency of remoras in each sector (summed for both the left and right dolphin sides) was weighted considering the times it was photographed. For example, if sector #7 (i.e., middle flank; see Figure 3) of 10 photo-identified dolphins was photographed on the same day and remoras were observed in two of them, the proportion of remora presence in sector #7 for all dolphins would be equal to 0.2. Alternatively, this same value would be found if sector #7 of the same dolphin was photographed in 10 distinct days and remoras were observed in two of them.

The total length (TL) of the remoras attached to the common bottlenose dolphins at the SPSPA was estimated against the mean dorsal fin base length (see Rowe & Dawson, 2009) recorded for common bottlenose dolphins stranded on the coast of Rio Grande do Sul, southern Brazil (from 29° 19' S to 31° 21' S; GEMARS, unpub. data). The TL of the stranded dolphins was 248 to 339 cm ( $\bar{x}$  = 289 cm, SD = 34 cm,  $n$  = 6), and the mean dorsal fin base length was estimated as 43 cm (SD = 4.2 cm;  $n$  = 6). According to estimated size, the remoras attached to the common bottlenose dolphins were classified into three size categories according to Silva-Jr. & Sazima (2008): class 1 – up to 10 cm TL (i.e., about ¼ of the base of the dolphin's dorsal fin); class 2 – between 11 and 35 cm TL; and class 3 – larger than 35 cm TL.

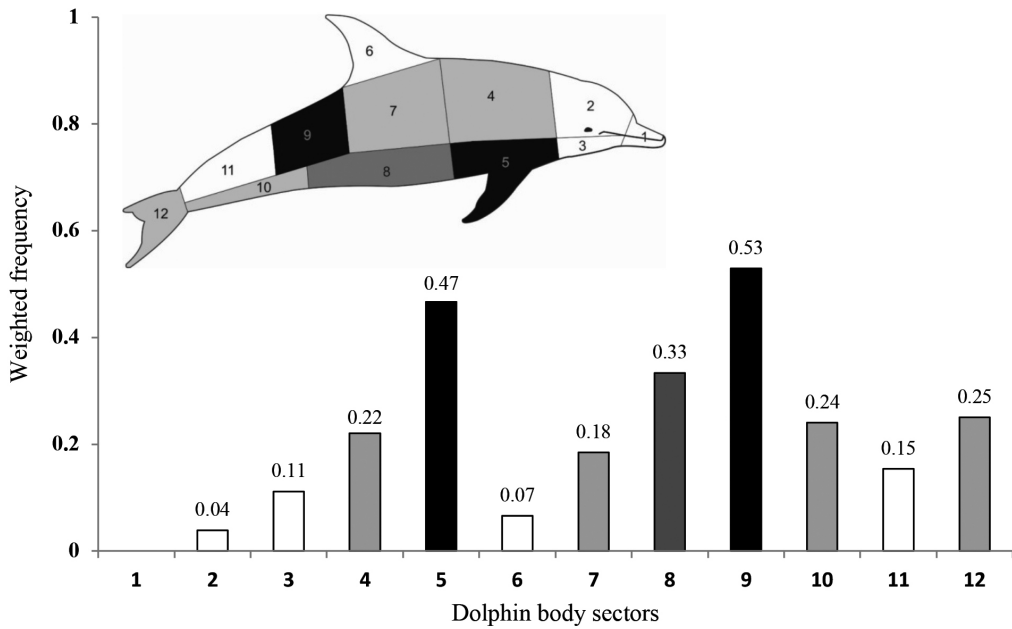
Potential problems associated with accurately identifying echeneid fishes attached to cetaceans from photographic records have been debated by some authors who emphasize the importance of examining in-hand specimens and caution about misidentifications (Fertl & Landry, 2018). However, although examination of collected specimens is desirable (Williams et al., 2003; Becerril-García et al., 2019), this is not possible in most instances related to cetaceans, and the use of high-quality images has proven to be a reliable method for the taxonomic identification of remora species attached to many different hosts (e.g., Sazima, 2006; Flammang et al., 2020). In

the specific case of the SPSPA waters, although four other remora species have been recorded in the region (*Remora albescens*, *Remora brachyptera*, *Remora osteochir*, and *Remora remora*; Vaske et al., 2005), based on the unmistakable morphological features visible on the photographs, the remoras attached to these common bottlenose dolphins were confidently identified as *R. australis*. Its main diagnostic features are its robust body and the length of the sucking disc (Follett & Dempster, 1960; O'Toole, 2002; Sazima, 2006; Flammang et al., 2020). *R. australis* has the largest disc among the eight extant species of remoras (O'Toole, 2002), comprising more than 40% of the standard length (see proportions in Figure 4). In only two remora species (*R. australis* and the marlinsucker [*R. osteochir*]), the posterior end of the sucking disc extends well beyond the end of the pectoral fins (Clemens & Wilby, 1961; Strasburg, 1964; Collette, 2016), a morphological feature also visible in the individual in Figure 4. However, *R. osteochir* is more slender than *R. australis* in dorsal and ventral views (Tuncer et al., 2012; Becerril-García et al., 2019). Additionally, *R. australis* and *R. osteochir* have distinct and strong host preferences (Cressey & Lachner, 1970). *R. osteochir* has a primary relationship with billfishes (Pampillón, 1996; Battaglia et al., 2016), with no records on cetaceans (Fertl & Landry, 2018). On the other hand, *R. australis* attaches exclusively to cetaceans (Rice & Caldwell, 1961; O'Toole, 2002; Silva-Jr. & Sazima, 2008; Fertl & Landry, 2018). The highly diagnostic morphological features of *R. australis* enabled the correction of a published mistaken identification of the remora species on a spinner dolphin at FNA (Fertl & Landry, 1999; Sazima, 2006).

## Results

A total of 13,720 photographs of common bottlenose dolphins was obtained in 16 d on four field expeditions, including 141 image sequences showing whalesuckers attached to the dolphins. From these, 70 image sequences were obtained from 12 photo-identified individuals, representing 63.2% of the 19 recognized archipelago's resident individuals and about 50% of the estimated population (Milmann et al., 2017). The maximum number of photo-identified dolphins and image sequences of remora–dolphin interactions was obtained in May 2011, but in each field expedition we recorded at least three photo-identified dolphins associated with whalesuckers (Table 1).

Most of the photo-identified dolphins recorded in association with remoras (7 out of 12; 58.3%) had only one visible whalesucker attached, but



**Figure 3.** Weighted frequency of attachment places (sectors 1 to 12) of whalesuckers ( $n = 70$ ) on common bottlenose dolphins in offshore waters of the SPSPA from 2011 to 2013. White = up to 0.15; light gray = 0.16 to 0.30; dark gray = 0.31 to 0.45; and black = 0.46 to 0.60. Numbered body sectors modified from Scott et al. (2005).



**Figure 4.** A breaching common bottlenose dolphin with a large whalesucker attached to its right flank in offshore waters of the SPSPA. Solid arrows mark the end of the pectoral fin, and the dashed arrow marks the posterior end of the sucking disc of the whalesucker. (Photo credit: Lucas Milmann, GEMARS)

**Table 1.** Dates and survey effort for the study of the association between common bottlenose dolphins (*Tursiops truncatus*) and whalesuckers (*Remora australis*) during each field expedition to São Pedro and São Paulo Archipelago (SPSPA) from 2011 to 2013.  $\bar{X}$  = mean; SD = standard deviation.

Study period	Photographic effort (days)	No. of photographs taken	No. of photo-identified dolphins with attached remoras	No. of image sequences of photo-identified dolphins (see text)	No. of image sequences per photo-identified dolphin ( $\bar{X} \pm SD$ )
May 2011	10	5,184	9	55	6.11 $\pm$ 6.95
August 2012	3	2,189	3	8	2.67 $\pm$ 1.53
October 2012	1	3,281	3	3	1.00 $\pm$ 0.00
February 2013	2	3,066	3	4	1.33 $\pm$ 0.58
Total	16	13,720	12*	70	5.83 $\pm$ 6.22

\*Some of the photo-identified dolphins were recorded in more than one expedition.

**Table 2.** Summary data of photo-identified common bottlenose dolphins associated with whalesuckers at the SPSPA from 2011 to 2013. ID = identification; VDSs = visible dolphins' body sectors; and SARs = dolphins' body sectors with attached remoras.

Dolphin ID	No. of image sequences (see text)	$\Sigma$ VDSs	$\Sigma$ SARs	Maximum no. of remoras	Proportion SARs/VDSs
#1	12	90	15	2	0.17
#3	23	115	41	10	0.36
#6	4	19	4	1	0.21
#8	4	19	4	1	0.21
#10	1	4	1	1	0.25
#12	4	19	4	1	0.21
#13	3	20	3	1	0.15
#14	3	15	3	1	0.20
#16	5	46	6	2	0.13
#17	2	20	3	2	0.15
#18	8	59	11	5	0.19
#21	1	10	1	1	0.10

on one individual, we observed 10 whalesuckers, mostly of the smallest size category (class 1; Table 2). Although the number of photographs was not homogeneous between each field expedition, the photo-identified dolphins showed a relatively similar ratio (around 0.20) of visible body sectors with attached remoras (Table 2), both in each field expedition as well as throughout the study period ( $\bar{x} = 0.19$ ,  $SD = 0.08$ ,  $n = 17$ ; Table 3).

The dolphins had whalesuckers attached with the highest frequencies to the anterior peduncle (sector #9 = 0.53) and to the region close to the pectoral fins (sector #5 = 0.47) (Table 4), even though these sectors did not have the largest

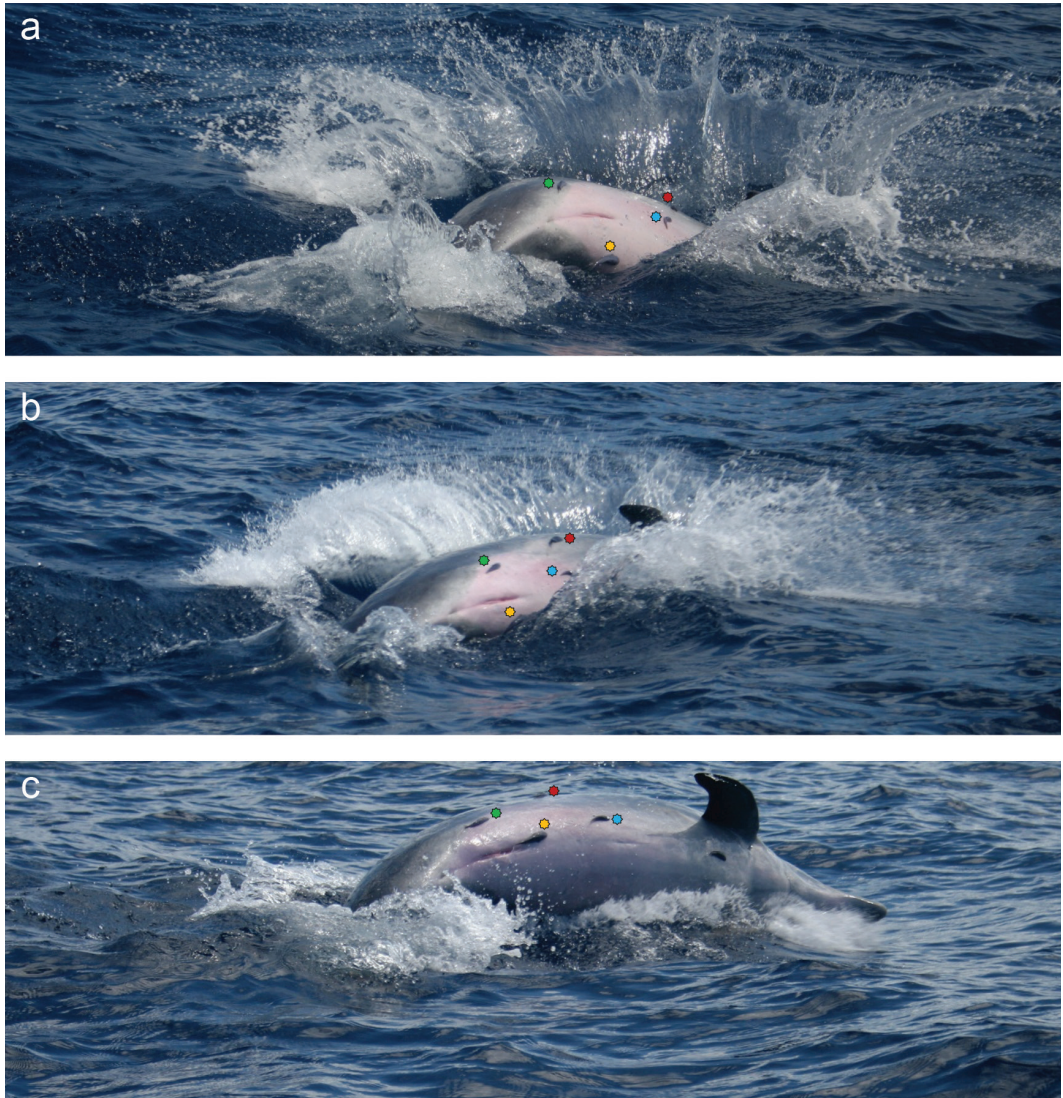
available areas (see Figure 3). Most remoras ( $n = 75$ ; 70.1% of the total) were smaller than 10 cm TL (class 1). Remoras of classes 2 and 3 accounted for 18.7 and 11.2% of the sample, respectively (Table 4). Although sampling effort was not equal across the seasons, it is worth mentioning that the highest frequency of remoras smaller than 10 cm TL was observed in May (94.7%). This size class showed a much lower frequency in August (5.3%) and was not recorded in October and February. The size of the whalesuckers also presented differences in relation to the dolphin's body sectors. Remoras smaller than 10 cm TL occurred with relatively

**Table 3.** Proportion of dolphin body sectors with attached whalesuckers per number of visible body sectors on photo-identified common bottlenose dolphins at the SPSPA from 2011 to 2013. ID = identification; VDSs = visible dolphins' body sectors; and SARs = dolphins' body sectors with attached remoras.

Dolphin ID	2011			2012			2013		
	$\Sigma$ VDSs	$\Sigma$ SARs	Proportion SARs/VDSs	$\Sigma$ VDSs	$\Sigma$ SARs	Proportion SARs/VDSs	$\Sigma$ VDSs	$\Sigma$ SARs	Proportion SARs/VDSs
#1	76	14	0.18	14	1	0.07	--	--	--
#3	115	41	0.36	--	--	--	--	--	--
#6	19	4	0.21	--	--	--	--	--	--
#8	19	4	0.21	--	--	--	--	--	--
#10	4	1	0.25	--	--	--	--	--	--
#12	15	3	0.20	--	--	--	--	--	--
#13	11	2	0.18	--	--	--	9	1	0.11
#14	--	--	--	12	2	0.17	3	1	0.33
#16	20	2	0.10	26	4	0.15	--	--	--
#17	--	--	--	--	--	--	20	3	0.15
#18	21	6	0.29	38	5	0.13	--	--	--
#21	--	--	--	10	1	0.10	--	--	--
Total	300	77	0.26	100	13	0.13	32	5	0.16

**Table 4.** Weighted distribution of different whalesucker size classes attached to visible body sectors of photo-identified common bottlenose dolphins at the SPSPA from 2011 to 2013. DBS = dolphin body sectors (see Figure 3); VDSs = visible dolphins' body sectors; and SARs = dolphins' body sectors with attached remoras.

DBS code	$\Sigma$ VDSs	$\Sigma$ SARs	Proportion SAR/VDS	Remora size classes			Total no. of remoras
				< 10 cm	11 to 35 cm	> 35 cm	
1	22	0	0.00	0	0	0	0
2	26	1	0.04	1	0	0	1
3	9	1	0.11	1	0	0	1
4	50	11	0.22	12	0	0	12
5	15	7	0.47	7	1	0	8
6	76	5	0.07	3	2	0	5
7	65	12	0.18	9	2	1	12
8	24	8	0.33	8	4	1	13
9	68	36	0.53	27	8	5	40
10	25	6	0.24	0	1	5	6
11	52	8	0.15	6	2	0	8
12	4	1	0.25	1	0	0	1
Total	--	--	--	75	20	12	107



**Figure 5.** Sequence of three side slappings of a common bottlenose dolphin at the SPSPA in May 2011 shows the relocation of two small whalesuckers attached to the dolphin's belly. Note that one remora (yellow star) appears close to the genital slit at the end of the manoeuvres (c). Additionally, one of the two smaller individuals (red star) that were close to each other at the beginning of the sequence (a & b) relocated afterwards, probably attaching to a more lateral position on the dolphin's body (c). (Photo credit: Paulo H. Ott, GEMARS)

high frequencies on both the dolphin's anterior (e.g., sectors #4 and 5 in Figure 3) and posterior (e.g., sectors #9 and 11 in Figure 3) body regions, whereas remoras larger than 35 cm TL were recorded only on the posterior area of a dolphin's body (from sectors #7 to 10 in Figure 3; also see Table 4).

Although the presence/absence of remoras in different body zones of a particular dolphin was

considered only for the first time it was recorded on a given day (i.e., first image sequence), the analysis of a series of photographs of the dolphin recorded with the largest number of whalesuckers (10) taken during a sequence of three side slapping behaviours (*sensu* Saayman et al., 1973) revealed the relocation of two individuals attached to the dolphin's belly after the aerial manoeuvres that were displayed in less than a minute (Figure 5).



## Discussion

This is the first study that provides information on the association rate between the common bottlenose dolphin and remoras conducted at a population level. Although the recapture probabilities of the dolphins (i.e., probability to photograph an individual) may differ among population members (Morteo et al., 2012), and some individual variation may exist in the probability of attachment by remoras, the analysis of photo-identified dolphins assures that the data are not based on a single individual and provides an idea of the extent of this ecological association in a given population. In this sense, these 12 photo-identified common bottlenose dolphins associated with whalesuckers in the waters of SPSPA correspond to 63.2% of the 19 recognized individuals from an estimated total population of 25 dolphins (Milmann et al., 2017). The high number of dolphins associated with whalesuckers and the occurrence of these remoras over the whole study period clearly indicates that this ecological relationship is well established in the area.

A similar relationship was reported between spinner dolphins and whalesuckers at FNA where a high remora–host association rate (1 to 1.8 whalesuckers per spinner dolphin) was recorded over a year (Silva-Jr. & Sazima, 2008). It is noteworthy that in both of these localities, each dolphin species congregates regularly, and the individuals have a high degree of site fidelity (Silva-Jr. et al., 2005; Milmann et al., 2017). The number of remoras usually attached to each common bottlenose dolphin in the SPSPA also resembled that reported for spinner dolphins (one to three fishes per dolphin) at FNA (Silva-Jr. & Sazima, 2008). This resemblance is remarkable as the dolphins belong to different species, have marked differences in body size, and there is a great disparity in their population numbers at these two oceanic islands in the Western Atlantic: about 25 common bottlenose dolphins at SPSPA and hundreds (sometimes up to 2,000) of spinner dolphins at FNA (De Carli et al., 2018). A high incidence (about 0.44) of an unidentified remora species attached to spinner dolphins was also reported at the Kealake'akua Bay located on the island of Hawai'i, Central North Pacific Ocean, where dolphins congregate in groups of up to about 400 individuals (Norris et al., 1994). Dolphins' aggregations and site fidelity potentially increase the opportunities for encounters and reproduction of the remoras (Silva-Jr. & Sazima, 2003, 2008). The reproductive advantage of echeineid fishes when attached to hosts that commonly aggregate has already been pointed out by Strasburg (1964).

Besides the possible advantages for reproductive purposes (Strasburg, 1964; Silva-Jr. & Sazima, 2003, 2008), further known or suspected

benefits to whalesuckers associated with dolphins include feeding on waste, ectoparasites, sloughed skin, and diseased tissue, besides ram-feeding on plankton and enhanced gill ventilation (Strasburg, 1957, 1959; Radford & Klawe, 1965; Fertl & Landry, 1999; Sazima et al., 2003; Silva-Jr. et al., 2005, 2007; Silva-Jr. & Sazima, 2008). Another advantage for remoras attached to cetaceans would be protection from predators (Alling, 1985; Silva-Jr. & Sazima, 2008). Nevertheless, at least two predators of remoras attached to very large hosts with slow or predictable movements are reported to date. One is the rough-toothed dolphin (*Steno bredanensis*) preying on *E. naucrates* attached to humpback whales (Wedekin et al., 2004). The other is the double-crested cormorant (*Nannopterum auritus*) preying on common remora (*R. remora*) juveniles attached to a whale shark (*Rhincodon typus*) (Sazima, 2018). Thus, at least small whalesuckers would be more protected on swift-swimming cetaceans (e.g., spinner dolphins, common bottlenose dolphins) than they would be on a large host with relatively more predictable behaviours.

Regardless of some methodological differences between the present study and the spinner dolphin study at FNA (e.g., topside vs underwater observations; Silva-Jr. & Sazima, 2008), both showed that remoras are found attached mainly to some specific dolphin body parts. In the underwater study at FNA, most spinner dolphins had whalesuckers attached to the belly or flanks (Silva-Jr. & Sazima, 2008). In the topside study at SPSPA, the ventral area of common bottlenose dolphins was poorly sampled, but whalesuckers were found on the belly as well, and with high frequency on the dolphins' flanks. Moreover, in both studies, larger remoras (class 3) were found exclusively on the ventral surface or flanks, mainly in the posterior part of a dolphin's body (see also Silva-Jr. & Sazima, 2003). These favoured attachment sites are probably related to regions with reduced drag forces (e.g., Silva-Jr. & Sazima, 2008; Fertl & Landry, 2018; see also Flammang et al., 2020, for a study on blue whales), minimum deformation of the host tissue during locomotion that could break the remora's suction seal (Beckert et al., 2016), and lesser interference with the habitual behaviours and sensitive areas of dolphins (Silva-Jr. & Sazima, 2008). It is worth mentioning that a study about the relationship between the parasitic sea lamprey (*Petromyzon marinus*) and the common bottlenose dolphin at the Central Adriatic Sea (Miočić-Stošić et al., 2020) also indicates preferred attachment sites, with a high incidence on dolphin flanks. In addition, the sea lampreys seem to cause a behaviour reaction in dolphins such as leaping and fast swimming (Miočić-Stošić et al., 2020).

As mentioned earlier, changes in dolphin behaviour likely to dislodge remoras from their body have also been reported (Notarbartolo di Sciarra & Watkins, 1980; Fertl & Landry, 2018). Whereas aerial behaviours displayed by spinner dolphins seem to be primarily related to social communication rather than remora removal (Norris et al., 1994; Utley, 2014), the force of aerial spinning and water impact is considered sufficient to dislodge an attached remora from a spinner dolphin (Fish et al., 2006; Weihs et al., 2007). In fact, Silva-Jr. & Sazima (2008) recorded relocations of the whalesuckers on a host's body after the spinning and water splash of spinner dolphins in FNA, although not a single whalesucker was recorded to be completely displaced by a spinning dolphin in numerous observations (Silva-Jr. & Sazima, 2008), a view shared by Norris et al. (1994). Nevertheless, it should be noted that the total mass of an adult common bottlenose dolphin can be two- to threefold greater than that of a spinner dolphin (e.g., Perrin et al., 2005; Hart et al., 2013), and the force and resultant impact on the water generated by an aerial manoeuvre of a common bottlenose dolphin is likely greater.

In the present study, the relocation of two small whalesuckers attached to the common bottlenose dolphin's belly was recorded after a series of aerial manoeuvres by the dolphin. However, most relocations seem to be a voluntary action by the remoras and not necessarily caused by dolphin aerial behaviours as observed for whalesuckers associated with spinner dolphins at FNA (Silva-Jr. & Sazima, 2008; I. Sazima, pers. obs., June & October 2001). Nevertheless, Norris et al. (1994) also reported a high incidence of remoras attached to common bottlenose dolphins displaying aerial behaviour in Florida, although the authors questioned its relationship with the remora–host association. It is worth mentioning that a repetitive aerial behaviour has been reported for an adult common bottlenose dolphin with an attached remora in the Gulf of Mexico (Shane, 1978). Frequent aerial behaviours were also observed in common bottlenose dolphins from SPSPA during the study period, but their direct relationship to the presence of remoras could not be fully confirmed.

Regardless of many similarities in the relationship between dolphins and whalesuckers at SPSPA and FNA (i.e., overall rate of remora–host association, number of remoras per dolphin, preferred attachment sites), a higher frequency (20.85%;  $n = 211$ ) of large remoras (class 3) is reported for this association at FNA (Silva-Jr. & Sazima, 2008) in comparison with the common bottlenose dolphins at SPSPA (11.21%;  $n = 107$ ). Moreover, the 10 small, probably recently recruited whalesuckers attached to a single dolphin recorded at

SPSPA seems an unusual occurrence, with no similar record on spinner dolphins at FNA (Silva-Jr. & Sazima, 2008). Still, there are a few other instances of a high number of recently recruited remoras not assigned to a species attached to a mother–calf pair of killer whales (*Orcinus orca*) in the Gulf of California, Mexico (Guerrero-Ruiz & Urbán R., 2000), and to an adult blue whale in waters off California in the eastern North Pacific (Flammang et al., 2020).

Common bottlenose dolphins with unidentified remora species have been reported occasionally (e.g., Townsend, 1916; Norris et al., 1994; Fertl et al., 2002; Noke, 2004; Yoshida et al., 2010; Jaiteh et al., 2013). Moreover, there is a single record of *R. remora* attached to a common bottlenose dolphin in the Caribbean Sea (Rodríguez-Ferrer et al., 2017). However, a careful examination of the photograph published by these latter authors revealed another case of misidentification, comparable to that reported by Sazima (2006). In the report by Rodríguez-Ferrer et al. (2017), the remora attached to the dolphin is clearly *E. naucrates*. Among other features, a robust body and nearly uniform colour in *R. remora* contrasting with the elongated body and presence of lateral stripes in *E. naucrates* differentiate these two species (see these details in Williams et al., 2003; Sazima & Grossman, 2006; Collette, 2016).

Considering that taxonomic accuracy of echeneid fishes determined from remote observations could be problematic in some cases (Fertl & Landry, 2018), high-quality voucher photographs, such as those used in this study, are decisive for identifying remoras attached to freely swimming dolphins or whales (Flammang et al., 2020). Regarding the common bottlenose dolphin as a remora host, *E. naucrates* is the only species whose identification is based on collected specimens. The first record was based on a fish collected from a live-stranded dolphin in Galveston, Texas, in the Gulf of Mexico (Fertl & Landry, 1999). Two additional records involved stranded common bottlenose dolphins found dead along the Atlantic Coast of Florida (Fertl et al., 2002; Noke, 2004). The association between *T. truncatus* and *R. australis* was previously suspected to occur based on photographs of free-swimming dolphins in offshore waters of the Gulf of Mexico in the western North Atlantic, although it was not fully proven due to uncertainties about the visible diagnostic features of the remoras (Shane, 1978; Fertl et al., 2002). This association was then reported, based on photographs, in offshore waters of the eastern North Pacific, approximately 600 km off Mexico's west coast (Pitman, 2003; Froese & Pauly, 2021) and in Turkish waters in the Mediterranean Sea (Bas & Gönülal, 2017).

In conclusion, the present study substantiates the common bottlenose dolphin as a host for the whalesucker and confirms this ecological relationship in the western Atlantic Ocean. The study also strengthens the view that whalesuckers may take advantage of the association with small, swift offshore cetaceans that congregate regularly in specific areas (Norris et al., 1994; Silva-Jr. & Sazima, 2008), regardless of its association with large whales (e.g., Alling, 1985; Flammang et al., 2020). The benefits of this association for the whalesuckers may include reproduction opportunities, diverse food types provided by dolphins directly and indirectly, and potential protection from some predators. However, further ecological and behavioural studies in offshore areas are still needed to fully understand this relationship.

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### Literature Cited

- Alling, A. (1985). Remoras and blue whales: A commensal or mutual interaction? *Whalewatcher (Journal of the American Cetacean Society)*, 19(1), 16-19.
- Bas, A. A., & Gönülal, O. (2017). First case of whalesucker, *Remora australis*, in association with delphinids in Antalya Bay, Turkey. *Mediterranean Marine Science*, 18(3), 410.
- Battaglia, P., Potoschi, A., Valastro, M., Andaloro, F., & Romeo, T. (2016). Age, growth, biological and ecological aspects of *Remora osteochir* (Echeneidae) in the Mediterranean Sea. *Journal of the Marine Biological Association of the United Kingdom*, 96(3), 639-645. <https://doi.org/10.1017/S0025315415000867>
- Becerril-García, E. E., Rosales-Nanduca, H., Paniagua-Mendoza, A., Robles-Hernández, R., & Elorriaga-Verplancken, F. R. (2019). Records of whalesuckers *Remora australis* on short-beaked common dolphins *Delphinus delphis* in the Gulf of California, Mexico. *Aquatic Mammals*, 45(3), 299-302. <https://doi.org/10.1578/AM.45.3.2019.299>
- Beckert, M., Flammang, B. E., Anderson, E. J., & Nadler, J. H. (2016). Theoretical and computational fluid dynamics of an attached remora (*Echeneis naucrates*). *Zoology*, 119(5), 430-438. <https://doi.org/10.1016/j.zool.2016.06.004>
- Clemens, W. A., & Wilby, G. V. (1961). *Fishes of the Pacific coast of Canada* (Bulletin No. 68, 2nd ed.). Fisheries Research Board of Canada.
- Collette, B. B. (2016). Echeneidae. In K. E. Carpenter & N. De Angelis (Eds.), *The living marine resources of the Eastern Central Atlantic: Bony fishes part 2 (Perciformes to Tetradontiformes) and sea turtles* (FAO Species Identification Guide for Fishery Purposes, Vol. 4, pp. 2441-2443). Food and Agriculture Organization.
- Cressey, R. F., & Lachner, E. A. (1970). The parasitic copepod diet and life history of diskfishes (Echeneidae). *Copeia*, 1970(2), 310-318. <https://doi.org/10.2307/1441652>
- Cypriano-Souza, A. L., de Meirelles, A. C. O., Carvalho, V. L., & Bonatto, S. L. (2017). Rare or cryptic? The first report of an Omura's whale (*Balaenoptera omurai*) in the South Atlantic Ocean. *Marine Mammal Science*, 33(1), 80-95. <https://doi.org/10.1111/mms.12348>
- De Carli, R. C., Silva, F. J., & Silva-Jr., J. M. (2018). Daily patterns in aerial activity by spinner dolphins in Fernando de Noronha. *Journal of the Marine Biological Association of the United Kingdom*, 98(5), 1151-1157. <https://doi.org/10.1017/S0025315417000327>
- Feitoza, B. M., Rocha, L. A., Luiz-Júnior, O. J., Floeter, S. R., & Gasparini, J. L. (2003). Reef fishes of St. Paul's rocks: New records and notes on biology and zoogeography. *Aqua: Journal of Ichthyology and Aquatic Biology*, 7, 61-82.
- Fertl, D., & Landry, A. M., Jr. (1999). Sharksucker (*Echeneis naucrates*) on a bottlenose dolphin (*Tursiops truncatus*) and a review of other cetacean-remora associations. *Marine Mammal Science*, 15(3), 859-863. <https://doi.org/10.1111/j.1748-7692.1999.tb00849.x>

- Fertl, D., & Landry, A. M., Jr. (2018). Remoras. In B. Würsig, J. G. M. Thewissen, & K. M. Kovacs (Eds.), *Encyclopedia of marine mammals* (3rd ed., pp. 793-794). Academic Press. <https://doi.org/10.1016/B978-0-12-804327-1.00016-9>
- Fertl, D., Landry, A. M., Jr., & Barros, N. B. (2002). Shark sucker (*Echeneis naucrates*) on a bottlenose dolphin (*Tursiops truncatus*) from Sarasota Bay, Florida, with comments on remora-cetacean associations in the Gulf of Mexico. *Gulf of Mexico Science*, 20(2), 151-152. <https://doi.org/10.18785/goms.2002.07>
- Fish, F. E., Nicastro, A. J., & Weihs, D. (2006). Dynamics of the aerial maneuvers of spinner dolphins. *Journal of Experimental Biology*, 209(4), 590-598. <https://doi.org/10.1242/jeb.02034>
- Flammang, B. E., Marras, S., Anderson, E. J., Lehmkuhl, O., Mukherjee, A., Cade, D. E., Beckert, M., Nadler, J. H., Houzeaux, G., Vázquez, M., Amplo, H. E., Calambokidis, J., Friedlaender, A. S., & Goldbogen, J. A. (2020). Remoras pick where they stick on blue whales. *Journal of Experimental Biology*, 223(Pt 20), jeb226654. <https://doi.org/10.1242/jeb.226654>
- Follett, W. I., & Dempster, L. J. (1960). First records of the echeneid fish *Remilegia australis* (Bennett) from California, with meristic data. *Proceedings of the California Academy of Sciences*, 31(7), 169-184.
- Froese, R., & Pauly, D. (Eds.). (2021). *Remora australis* (Bennett, 1840). *FishBase*. [www.fishbase.org](http://www.fishbase.org)
- Guerrero-Ruiz, M., & Urbán R., J. (2000). First report of remoras on two killer whales (*Orcinus orca*) in the Gulf of California, Mexico. *Aquatic Mammals*, 26(2), 148-150.
- Hart, L. B., Wells, R. S., & Schwacke, L. H. (2013). Reference ranges for body condition in wild bottlenose dolphins *Tursiops truncatus*. *Aquatic Biology*, 18, 63-68. <https://doi.org/10.3354/ab00491>
- Hrbek, T., da Silva, V. M. F., Dutra, N., Gravena, W., Martin, A. R., & Farias, I. P. (2014). A new species of river dolphin from Brazil or: how little do we know our biodiversity. *PLOS ONE*, 9(1), e83623. <https://doi.org/10.1371/journal.pone.0083623>
- Jaiteh, V. F., Allen, S. J., Meeuwij, J. J., & Loneragan, N. R. (2013). Subsurface behavior of bottlenose dolphins (*Tursiops truncatus*) interacting with fish trawl nets in northwestern Australia: Implications for bycatch mitigation. *Marine Mammal Science*, 29, E266-E281. <https://doi.org/10.1111/j.1748-7692.2012.00620.x>
- Leung, T. L. F. (2014). Fish as parasites: An insight into evolutionary convergence in adaptations for parasitism. *Journal of Zoology*, 294(1), 1-12. <https://doi.org/10.1111/jzo.12148>
- Lopes, R. P., & Ulbrich, M. N. C. (2015). Geochemistry of the alkaline volcanic-subvolcanic rocks of the Fernando de Noronha Archipelago, southern Atlantic Ocean. *Brazilian Journal of Geology*, 45(2), 307-333. <https://doi.org/10.1590/23174889201500020009>
- Menezes, N. A. (2011). Checklist dos peixes marinhos do Estado de São Paulo, Brasil [Checklist of marine fishes from São Paulo State, Brazil]. *Biota Neotropica*, 11(1a). <https://www.biotaneotropica.org.br/v11n1a/en/abstract?article+bn0031101a2011>; <https://doi.org/10.1590/S1676-06032011000500003>
- Milman, L. C., Danilewicz, D., Baumgarten, J., & Ott, P. H. (2017). Temporal-spatial distribution of an island-based offshore population of common bottlenose dolphins (*Tursiops truncatus*) in the equatorial Atlantic. *Marine Mammal Science*, 33(2), 496-519. <https://doi.org/10.1111/mms.12380>
- Miočić-Stošić, J., Pleslić, G., & Holcer, D. (2020). Sea lamprey (*Petromyzon marinus*) attachment to the common bottlenose dolphin (*Tursiops truncatus*). *Aquatic Mammals*, 46(2), 152-166. <https://doi.org/10.1578/AM.46.2.2020.152>
- Morteo, E., Rocha-Olivares, A., & Morteo, R. (2012). Sensitivity analysis of residency and site fidelity estimations to variations in sampling effort and individual catchability. *Revista Mexicana de Biodiversidad*, 83(2), 487-495. <https://doi.org/10.22201/ib.20078706e.2012.2.972>
- Noke, W. D. (2004). The association of echeneids with bottlenose dolphins (*Tursiops truncatus*) in the Indian River Lagoon, Florida, USA. *Aquatic Mammals*, 30(2), 296-298. <https://doi.org/10.1578/AM.30.2.2004.296>
- Norris, K. S., Würsig, B., & Wells, R. S. (1994). Aerial behavior. In K. S. Norris, B. Würsig, R. S. Wells, & M. Würsig (Eds.), *The Hawaiian spinner dolphin* (pp. 103-121). University of California Press. <https://doi.org/10.1525/9780520913547>
- Notarbartolo di Sciarra, G., & Watkins, W. A. (1980). A remora, *Remilegia australis*, attached to an Atlantic spinner dolphin, *Stenella longirostris*. *Bulletin of the Southern California Academy of Sciences*, 79(3), 119-121.
- O'Toole, B. (2002). Phylogeny of the species of the superfamily Echenoidea (Perciformes: Carangoidei: Echeneidae, Rachycentridae, and Coryphaenidae), with an interpretation of echeneid hitchhiking behavior. *Canadian Journal of Zoology*, 80(4), 596-623. <https://doi.org/10.1139/z02-031>
- Ott, P. H., Tavares, M., Secchi, E. R., & Di Tullio, J. C. (2013). Cetacea. In M. M. Weber, C. Roman, & N. C. Cáceres (Eds.), *Mamíferos do Rio Grande do Sul* [Mammals of Rio Grande do Sul] (pp. 457-550). Editora da UFSM.
- Pampillón, J. A. C. (1996). Rémoras (Pisces: Echeneidae) del golfo de Guinea: Especificidad por sus hospedadores y estudio de algunos parámetros biológicos [Remora (Pisces: Echeneidae) from the gulf of Guinea: Host specificity and some biological parameters]. *Boletín Instituto Español de Oceanografía*, 12(1), 31-42.
- Perrin, W. F., Dolar, M. L. L., Chan, C. M., & Chivers, S. J. (2005). Length-weight relationships in the spinner dolphin (*Stenella longirostris*). *Marine Mammal Science*, 21(4), 765-778. <https://doi.org/10.1111/j.1748-7692.2005.tb01264.x>
- Pitman, R. (2003). *Remora australis*. *FishBase*. [www.fishbase.org](http://www.fishbase.org)

- Radford, K. W., & Klawe, W. L. (1965). Biological observations on the whalesucker, *Remilegia australis* Echeneiformes: Echeneidae. *Transactions of the San Diego Society of Natural History*, 14, 67-72.
- Rice, D. W., & Caldwell, D. K. (1961). Observations on the habits of the whalesucker (*Remilegia australis*). *Norsk Hvalfangst-Tidende*, 5, 181-189.
- Rodríguez-Ferrer, G., Appeldoorn, R. S., & Schizas, N. V. (2017). Abundance of the common bottlenose dolphin, *Tursiops truncatus* (Montagu, 1821) (Mammalia: Artiodactyla: Delphinidae) off the south and west coasts of Puerto Rico. *Life: The Excitement of Biology*, 4(4), 242-271. [https://doi.org/10.9784/LEB4\(4\)RodríguezFerrer.01](https://doi.org/10.9784/LEB4(4)RodríguezFerrer.01)
- Rowe, L. E., & Dawson, S. M. (2009). Determining the sex of bottlenose dolphins from Doubtful Sound using dorsal fin photographs. *Marine Mammal Science*, 25(1), 19-34. <https://doi.org/10.1111/j.1748-7692.2008.00235.x>
- Saayman, G. S., Tayler, C. K., & Bower, D. (1973). Diurnal activity cycles in captive and free-ranging Indian bottlenose dolphins (*Tursiops aduncus* Ehrenburg). *Behaviour*, 44(3-4), 212-233. <https://doi.org/10.1163/156853973X00409>
- Santos, M. C. O., & Sazima, I. (2008). The sharksucker (*Echeneis naucrates*) attached to a tucuxi dolphin (*Sotalia guianensis*) in estuarine waters in south-eastern Brazil. *Marine Biodiversity Records*, 1(e7). <https://doi.org/10.1017/S1755267205000746>
- Sazima, I. (2006). Species records, mistaken identifications, and their further use: The case of the diskfish *Echeneis naucrates* on a spinner dolphin. *Neotropical Ichthyology*, 4(4), 457-460. <https://doi.org/10.1590/S1679-62252006000400010>
- Sazima, I. (2018). Tenacious underwater fishers: Double-crested cormorants, *Nannopterum auritus* (Suliformes: Phalacrocoracidae) dislodge and prey on suckerfish attached to a whale shark in Mexico. *Atualidades Ornitológicas*, 201, 21-23.
- Sazima, I., & Grossman, A. (2006). Turtle riders: Remoras on marine turtles in Southwest Atlantic. *Neotropical Ichthyology*, 4(1), 123-126. <https://doi.org/10.1590/S1679-62252006000100014>
- Sazima, I., Sazima, C., & Silva-Jr., J. M. (2003). The cetacean offal connection: Feces and vomits of spinner dolphins as a food source for reef fishes. *Bulletin of Marine Science*, 72(1), 151-160.
- Sazima, I., Sazima, C., & Silva-Jr., J. M. (2006). Fishes associated with spinner dolphins at Fernando de Noronha Archipelago, tropical Western Atlantic: An update and overview. *Neotropical Ichthyology*, 4(4), 451-455. <https://doi.org/10.1590/S1679-62252006000400009>
- Scott, E. M., Mann, J., Watson-Capps, J. J., Sargeant, B. L., & Connor, R. C. (2005). Aggression in bottlenose dolphins: Evidence for sexual coercion, male-male competition, and female tolerance through analysis of tooth-rake marks and behaviour. *Behaviour*, 142(1), 21-44. <https://doi.org/10.1163/1568539053627712>
- Shane, S. (1978). Suckerfish attached to a bottlenose dolphin in Texas. *Journal of Mammalogy*, 59(2), 439-440. <https://doi.org/10.2307/1379936>
- Siciliano, S., Emin-Lima, N. R., Costa, A. F., Rodrigues, A. L. F., Magalhães, F. A., Tosi, C. H., Garri, R. G., Silva, C. R., & Silva, J. S., Jr. (2008). Revisão do conhecimento sobre os mamíferos aquáticos da costa norte do Brasil [Review on the knowledge about aquatic mammals of the north coast of Brazil]. *Arquivos do Museu Nacional, Rio de Janeiro*, 66(2), 381-401.
- Silva-Jr., J. M., & Sazima, I. (2003). Whalesucker and a spinner dolphin bonded for weeks: Does host fidelity pay off? *Biota Neotropica*, 3(2), 1-5. <https://doi.org/10.1590/S1676-06032003000200012>
- Silva-Jr., J. M., & Sazima, I. (2008). Whalesuckers on spinner dolphins: An underwater view. *Marine Biodiversity Records*, 1(e22). <https://doi.org/10.1017/S1755267206002016>
- Silva-Jr., J. M., Silva, F. J. L., & Sazima, I. (2005). Rest, nurture, sex, release, and play: Diurnal underwater behaviour of the spinner dolphin at Fernando de Noronha Archipelago, SW Atlantic. *Aqua: Journal of Ichthyology and Aquatic Biology*, 9(4), 161-176.
- Silva-Jr., J. M., Silva, F. J. L., Sazima, C., & Sazima, I. (2007). Trophic relationships of the spinner dolphin at Fernando de Noronha Archipelago, SW Atlantic. *Scientia Marina*, 71(3), 505-511. <https://doi.org/10.3989/scimar.2007.71n3505>
- Spalding, M. D., Fox, H. E., Allen, G. R., Davidson, N., Ferdeña, Z. A., Finlayson, M., Halpern, B. S., Jorge, M. A., Lombana, A. L., Lourie, S. A., Martin, K. D., McManus, E., Molnar, J., Recchia, C. A., & Robertson, J. (2007). Marine ecoregions of the world: A bioregionalization of coastal and shelf areas. *BioScience*, 57(7), 573-583. <https://doi.org/10.1641/B570707>
- Strasburg, D. W. (1957). Notes on the respiration of small *Remora remora*. *Copeia*, 1957(1), 58-60. <https://doi.org/10.2307/1440529>
- Strasburg, D. W. (1959). Notes on the diet and correlating structures of some central Pacific echeneid fishes. *Copeia*, 1959(3), 244-248. <https://doi.org/10.2307/1440398>
- Strasburg, D. W. (1964). Further notes on the identification and biology of echeneid fishes. *Pacific Science*, 18(1), 51-57.
- Townsend, C. H. (1916). Porpoises at sea. *Zoological Society Bulletin*, 19, 1427-1428.
- Tuncer, S., Orlov, A. M., & Ozen, O. (2012). First record of marlin sucker, *Remora osteochir* (Cuvier, 1829), from the northeastern Aegean Sea, Turkey. *Journal of Ichthyology*, 52, 400-408. <https://doi.org/10.1134/S0032945212040145>
- Uteley, L. (2014). *Using aerial behavior to predict remora presence in Hawai'i island associated spinner dolphins* (*Stenella longirostris longirostris*) (Master's thesis). Duke University, Durham, NC. [dukespace.lib.duke.edu](https://dukespace.lib.duke.edu)
- Vaske, T., Jr., Lessa, R. P., Nóbrega, M., Montealegre-Quijano, S., Marcante Santana, F., & Bezerra, J. L., Jr. (2005). A checklist of fishes from Saint Peter and Saint Paul Archipelago, Brazil. *Journal of Applied Ichthyology*, 21, 75-79. <https://doi.org/10.1111/j.1439-0426.2004.00600.x>

- Wedekin, L. L., Freitas, A., Engel, M. H., & Sazima, I. (2004). Rough-toothed dolphins (*Steno bredanensis*) catch diskfishes while interacting with humpback whales (*Megaptera novaeangliae*) off Abrolhos Bank breeding ground, Southwest Atlantic. *Aquatic Mammals*, 30(2), 327-329. <https://doi.org/10.1578/AM.30.2.2004.327>
- Weihls, D., Fish, F. E., & Nicastro, A. J. (2007). Mechanics of remora removal by dolphin spinning. *Marine Mammal Science*, 23(3), 707-714. <https://doi.org/10.1111/j.1748-7692.2007.00131.x>
- Wells, R. S., & Scott, M. D. (2009). Common bottlenose dolphin: *Tursiops truncatus*. In W. F. Perrin, B. Würsig, & J. G. M. Thewissen (Eds.), *Encyclopedia of marine mammals* (2nd ed., pp. 249-255). Academic Press.
- Williams, E. H., Jr., Mignucci-Giannoni, A. A., Bunkley-Williams, L., Bonde, R. K., Self-Sullivan, C., Preen, A., & Cockcroft, V. G. (2003). Echeneid-sirenian associations, with information on sharksucker diet. *Journal of Fish Biology*, 63, 1176-1183. <https://doi.org/10.1046/j.1095-8649.2003.00236.x>
- Würsig, B., & Würsig, M. (1977). The photographic determination of group size, composition, and stability of coastal porpoises (*Tursiops truncatus*). *Science*, 198(4318), 755-756. <https://doi.org/10.1126/science.198.4318.755>
- Yoshida, H., Compton, J., Punnett, S., Lovell, T., Draper, K., Franklin, G., Norris, N., Phillip, P., Wilkins, R., & Kato, H. (2010). Cetacean sightings in the eastern Caribbean and adjacent waters, spring 2004. *Aquatic Mammals*, 36(2), 154-161. <https://doi.org/10.1578/AM.36.2.2010.154>