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Necrocoitus in Common Bottlenose Dolphins (*Tursiops truncatus*) near Sarasota, Florida

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Necrocoitus (historically referred to as Davian behavior) has been reported in a variety of vertebrate and invertebrate species (Dickerman, 1960; Moeliker, 2001; Izzo et al., 2012; Ashaharraza et al., 2020; Wang & Meyer-Rochow, 2020). Several marine mammal species have been observed engaging in necrocoitus, including the Florida manatee (*Trichechus manatus latirostris*), the southern sea otter (*Enhydra lutris nereis*), the Pacific pilot whale (*Globicephala scammonii*), and the common bottlenose dolphin (*Tursiops truncatus*), which represents the majority of cetaceans who have been observed engaging in postmortem attentive behavior (Brown, 1962; Harris et al., 2010; Bills et al., 2013; Bearzi et al., 2018; Methion & Díaz López, 2021). Most observations of postmortem attentive behavior in cetaceans involve epimeletic behavior from a live, adult female with a dead calf (Caldwell & Caldwell, 1966; Quintana-Rizzo & Wells, 2016; Bearzi et al., 2017, 2018). In addition to epimeletic behavior, accounts of bottlenose dolphins reacting to dead conspecifics include behavior consistent with mate-guarding, agonistic behavior, and arousal, but observed intromission is extremely rare and has not been photo documented (Brown, 1962; Dudzinski et al., 2003; Methion & Díaz López, 2021).

In Sarasota and Manatee Counties in west-central Florida, four separate events occurred over seven years in which two adult male bottlenose dolphins engaged in postmortem attentive behavior toward a female conspecific (Figure 1). The observed behaviors included escorting the carcass, aggressively swimming directly into or on top of the carcass, and vocalization. In at least one case, necrocoitus was observed, but postmortem examination findings indicate it likely occurred in the other three cases as well. All 12 of the dolphins involved were sexually mature; and in each respective case, the two adult males were pair-bonded (Wells et al., 1987; Owen et al., 2002).

The Stranding Investigations Program (SIP) at Mote Marine Laboratory (MML) in Sarasota, Florida, was formally established in 1985 and responds to reports of stranded (i.e., sick, injured, out-of-habitat, or dead) cetaceans in Sarasota and Manatee Counties. All confirmed strandings are documented according to protocols established by the National Oceanic and Atmospheric Administration's National Marine Fisheries Service (NOAA Fisheries). Most cetacean carcasses are necropsied and sampled for life history, pathology, toxicology, and other permitted research. SIP personnel work closely with the Chicago Zoological Society's Sarasota Dolphin Research Program (SDRP), whose staff members have been studying dolphins in and around Sarasota Bay since 1970. As the world's longest-running study of a wild dolphin population, the SDRP's efforts have identified a resident community of approximately 170 dolphins spanning as many as five concurrent generations in Sarasota Bay (Wells, 2020). The SDRP studies social structure, communication, and behavior, as well as ecology, biology, and individual and population health (Wells, 2020).

On 20 April 2016, at 1052 h, SIP personnel received a report of a dead dolphin floating belly-up in Anna Maria Sound, Florida (27.5052º, -82.7109º). Two subsequent reports were made about the same dolphin, and SIP recovered the carcass at 1320 h. The SDRP identified the female carcass as "ULYS" by her unique dorsal fin markings. ULYS had been seen 110 times and had calved at least four times during the period 28 August 1997 through 19 April 2016 (the day prior to recovery), with the most recent known calf born in 2013. Holmes Beach Police

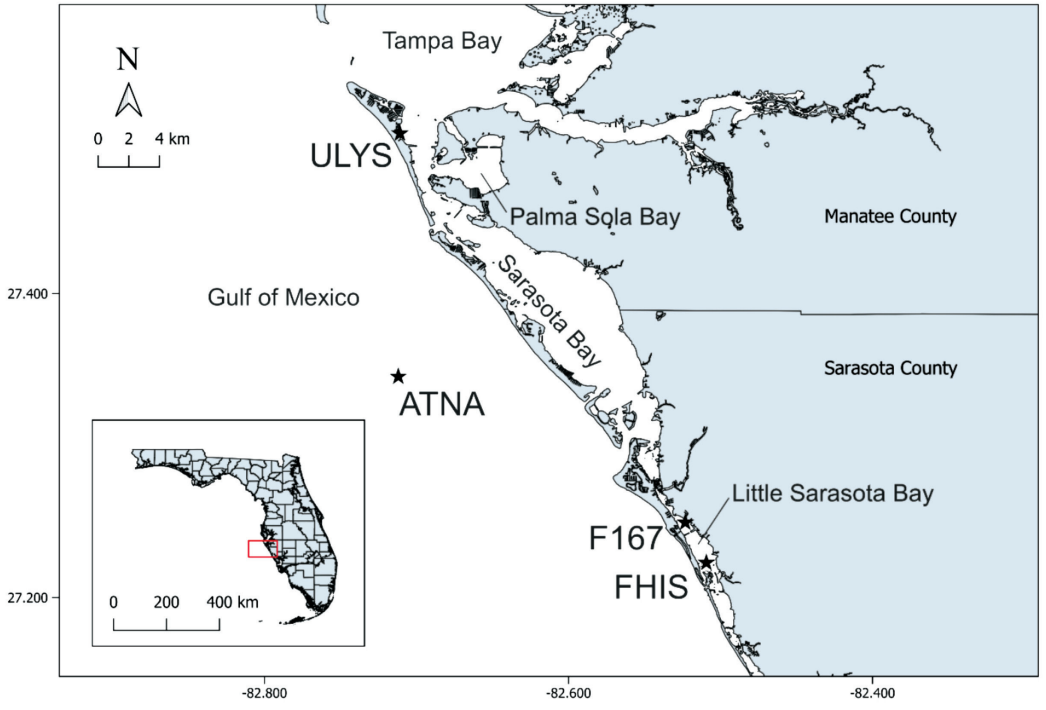

Figure 1. Locations of the four stranding events, denoted by the female bottlenose dolphins' (*Tursiops truncatus*) IDs: ULYS, ATNA, FHIS, and F167

Department (HBPD) officers secured the carcass prior to SIP's arrival by tying a line around the fluke insertion. After the dolphin was secured, the HBPD officers took photos and approximately 5 min of video over several smartphone recordings, capturing interactions between two live dolphins and the carcass (Figure 2). The live dolphins were identified by freeze brands that had been previously applied during health assessments (Scott et al., 1990) as pair-bonded males "F178" and "F188." F178 had been seen 400 times from 4 May 2006 (when the two were determined to be pair-bonded) through 21 April 2016, and F188 had been seen 404 times from 4 May 2006 through 21 April 2016. Sexes were known for both from health assessments. ULYS had never been seen with F178 or F188 prior to the recovery (see Figure S1 for a sighting history map; supplementary figures and video footage for this paper are available in the "Supplemental Material" section of the *Aquatic Mammals* website: https://www.aquaticmammalsjournal.org/index.php?option=com_content&view=article&id=10&Itemid=147). The recordings show the two male dolphins aggressively ramming and swimming over ULYS's carcass and briefly emitting vocalizations at the surface. These vocalizations were determined to be burst-pulse vocalizations (L. Sayigh, pers. comm., 9 March 2022; see Video Sequence S1), which have been associated with agonistic, aggressive, and sexual interactions, as well as successful cooperative tasks, in dolphins (Herzing, 1996; Blomqvist & Amundin, 2004; Eskelinen et al., 2016).

After recovering the carcass, SIP personnel conducted a full necropsy. Notable findings included fresh to healed conspecific rake marks, excessive splaying of the urogenital area (Figure 2), frank (fresh, bright red) blood in the thoracic cavity, broken epihyoid bone with associated tissue reaction, and an approximately 5-cm perimortem rupture in the uterus with green and decomposed tissue caudal to the rupture. Histopathology analysis concluded that trauma from conspecific aggression was a possible cause of death.

On 25 November 2018, at 1208 h, SIP personnel received a report of a dead dolphin approximately 11 km offshore of Longboat Key in the Gulf of Mexico (27.3453°, -82.7120°). SIP recovered the carcass at 1305 h with the assistance of the Sarasota Police Department's (SPD) marine unit; the SDRP identified it by dorsal fin markings as "ATNA." During the recovery, two dolphins (identified by dorsal fin markings as pair-bonded males "TNBS" and "BELY") were observed in

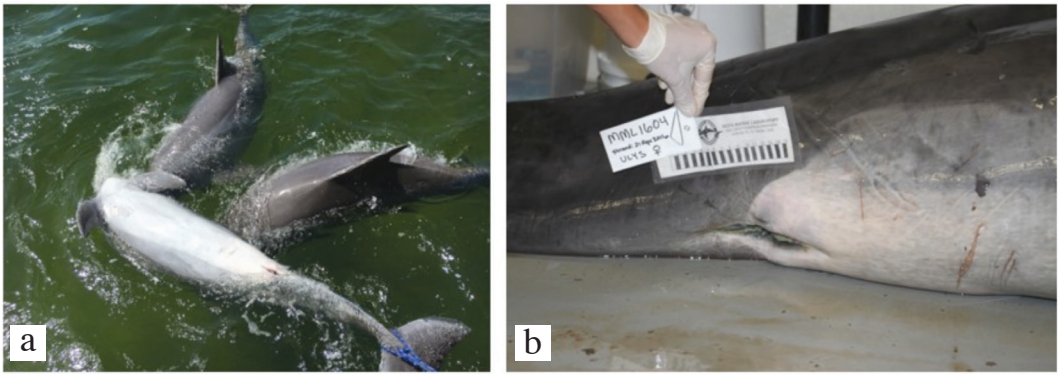

Figure 2. (a) Still from video footage showing F188 (left) and F178 (right) ramming into ULYS's carcass after it was secured with a dock line (Video footage courtesy of Holmes Beach Police Department); and (b) ULYS's urogenital slit, splayed and discolored (Photo courtesy of Mote Marine Laboratory).

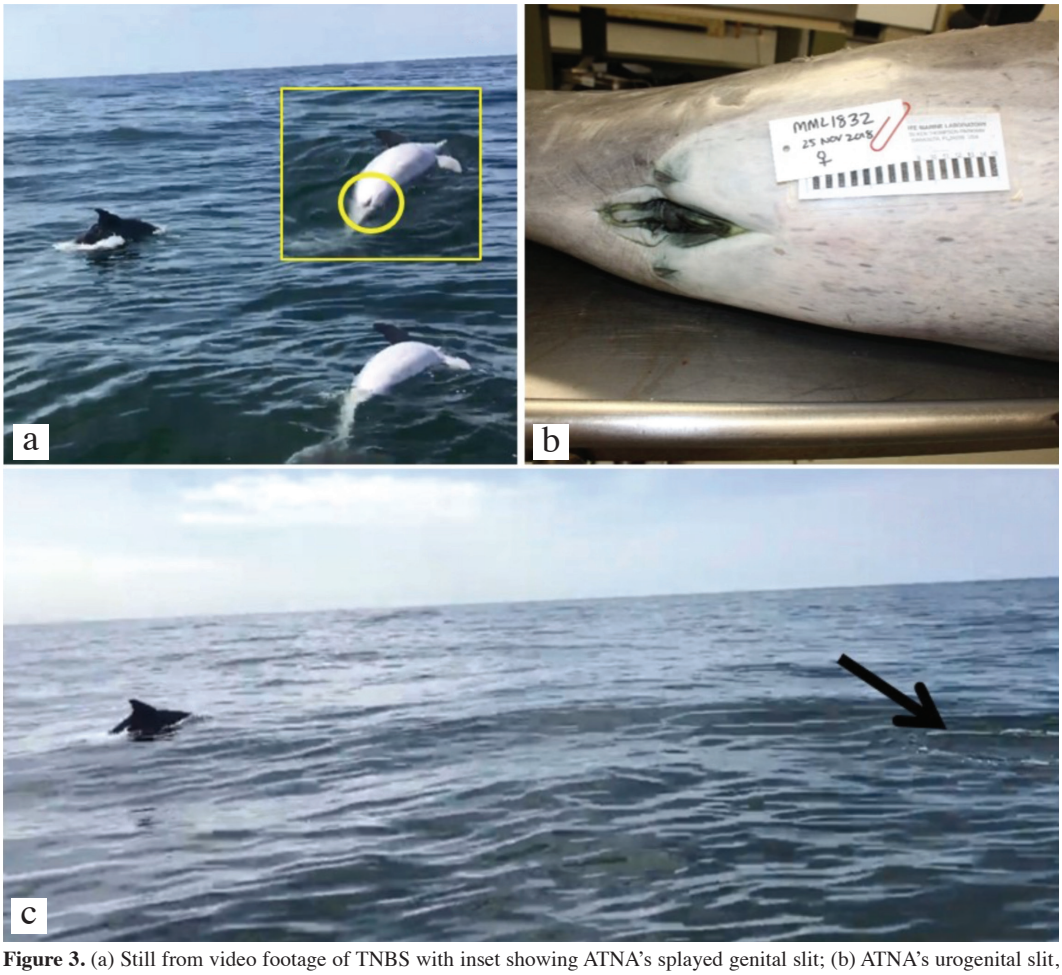

Figure 3. (a) Still from video footage of TNBS with inset showing ATNA's splayed genital slit; (b) ATNA's urogenital slit, splayed and discolored; and (c) BELY surfacing near ATNA's carcass as it is approached by SPD (arrow points to where TNBS surfaced in [a]). (Video footage and photo courtesy of Mote Marine Laboratory)

close proximity (~5 to 10 m) to the carcass, and the responding biologist recorded 19 s of video on her smartphone (Figure 3). Of note, the carcass exhibited a widely splayed genital slit (Figure 3). The SDRP had a limited sighting history of the three dolphins involved, none of whom were considered part of the year-round resident Sarasota Bay community (see Figure S2 for a sighting history map). ATNA had been seen 23 times from 12 October 1989 through 8 November 2018, TNBS 12 times during the period 12 December 1987 through 22 January 2015, and BELY eight times during the period 28 July 1998 through 22 January 2015. BELY was confirmed as male via remote biopsy, and it is presumed that TNBS is also a male given the high coefficient of association (COA) to BELY (Table 1). ATNA had never been seen with either male dolphin prior to the date of stranding. SIP personnel conducted a full necropsy, and while no cause of death was determined or inferred, there was marked distension and decomposition of the vagina as opposed to other soft tissue (Figure 3).

On the morning of 4 August 2020, SIP personnel received six reports of a dead dolphin with two live dolphins pushing the carcass near Intracoastal Waterway (ICW) channel marker 48B in Little Sarasota Bay (27.2228º, -82.5093º). SDRP personnel arrived on scene at 1024 h and observed nine live dolphins in the vicinity, including one dolphin interacting with the carcass. Behaviors during the interaction included ramming, swimming over the carcass, and intromission (Figure 4), sometimes involving the male lifting his fluke high into the air before quickly bringing it down to connect with the carcass. The dead female was identified by dorsal fin markings as "FHIS," and the two dolphins that were seen pushing her were identified as pair-bonded males "F276" and "F142" (sexed and freeze-branded during SDRP health assessments). F142 was identified as the dolphin interacting with FHIS when SDRP personnel first arrived. FHIS had been seen 41 times from 14 August 1991 through 15 July 2020, and she had calved five times during that period, with the most recent calf born in 2016 or 2017. F142 and F276 had been seen 295 times and 311 times, respectively, from 7 September 2010 through 4 August 2020. Consistent with the previous two cases, FHIS had not previously been observed with either male (see Figure S3 for a sighting history map). SIP personnel recovered the carcass at 1054 h with assistance from the Sarasota County Sheriff's Office marine unit and towed the carcass to land. F142 followed the boat for the ~4 km tow and milled in the area as the carcass was brought to land from the boat. Necropsy findings for FHIS included a widely splayed genital slit (Figure 4) with associated muscles and reproductive organs extremely friable; no cause of death could be determined.

Incidentally, F276 and F142 were found dead over the following 2 days. A cause of death was not determined for either of these dolphins, and testing on all three carcasses ruled out morbillivirus, influenza, coronavirus, and brevetoxicosis.

On the afternoon of 20 May 2022, SIP personnel received a report of a dead dolphin floating north of ICW channel marker 57 in Little Sarasota Bay (27.2492°, -82.5231°). With assistance from an SPD officer and a boat, SIP personnel recovered the carcass, identified by dorsal fin markings as "F167," at 1520 h. F167 had been seen 256 times since 11 May 2000 and had birthed six known calves, including a yearling calf that was seen in the vicinity of F167's carcass. Two adult dolphins were observed interacting with the carcass in a similar fashion as the previous incidents (Figure 5), ramming the carcass, swimming over it, and emitting burst-pulse vocalizations (L. Sayigh, pers. comm., 20 June 2022; see Video Sequence S2). These dolphins were identified as male "F182" (sexed and freeze-branded during SDRP health assessments) and "C834" (identified by dorsal fin markings), presumed to be a male based on the high COA with F182. F182 had been seen 702 times from 2 February 1989 through 18 May 2022, and C834 had been seen 617 times from 19 June 1992 through 4 May 2022. F167 had occasionally been seen with the two males in the past (see Figure S4 for a sighting history map), but

Table 1. Lifetime half-weight coefficients of association (COA) between bottlenose dolphins (*Tursiops truncatus*) involved in Davian behavior events

Dolphins	F178-F188	TNBS-BELY	F276-F142	F182-C834	C834-F142	C834-F276	F182-F276	F182-F142	F167-F182	F167-C834
Half-weight COA	0.619	0.700	0.662	0.294	0.157	0.128	0.087	0.086	0.013	0.021

Note: Dolphin pairings with COAs lower than 0.05 are not listed, with the exception of pairings including F167, the only female dolphin to have been seen alive with any of the males. Pair-bonded males (highlighted) show the highest association. COAs were calculated from the first sighting of each dolphin through 1 January 2022 (29 August 2022 for the dolphins involved in the most recent case).

Figure 4. F142 prior to (a) and during (b) intromission with FHIS's carcass—the first known photograph of intromission between a live male bottlenose dolphin and a dead female conspecific; and (c) FHIS's urogenital slit, widely splayed and discolored. ([a] & [b] Photos courtesy of Sarasota Dolphin Research Program; and [c] Photo courtesy of Mote Marine Laboratory)

the COAs between F167 and the two males were not significant (Table 1). The three live dolphins followed the carcass as it was towed to land. F167 was heavily raked, and necropsy findings included perimortem trauma to the genital region (Figure 5) and areas of edema and consolidated hemorrhage in the left mammary.

Intromission was confirmed in the case of FHIS, and the similar conditions of the four females' urogenital slits leads to the belief that intromission occurred in the other three instances. F142 exhibited aggressive behavior toward FHIS as did F178 and F188 toward ULYS and F182 and C834 toward F167; TNBS and BELY are suspected to have done so toward ATNA prior to SIP's arrival on scene. While other highly intelligent mammals with complex social systems, such as chimpanzees (*Pan troglodytes*) and rhesus macaques (*Macaca mulatta*), have been observed beating dead conspecifics, they also live in societies organized by rank in which violence may be more common than in dolphin species (Wrangham & Wilson, 2004; Bulh et al., 2012; Wells, 2013). Sarasota Bay common bottlenose dolphins typically do not exhibit the aggressive behavior that is especially associated with sexual frustration (Herzing, 1996; Methion & Díaz López, 2021) or reproductive behavior that is common for

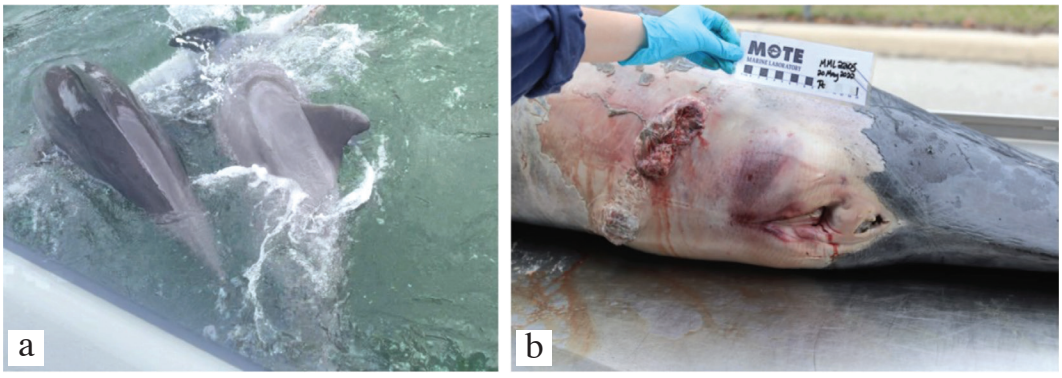

Figure 5. (a) C834 (left) and F182 (right) swimming over F167's carcass while it was being towed to shore; and (b) F167's urogenital slit, discolored and splayed. (Video footage and photo courtesy of Mote Marine Laboratory)

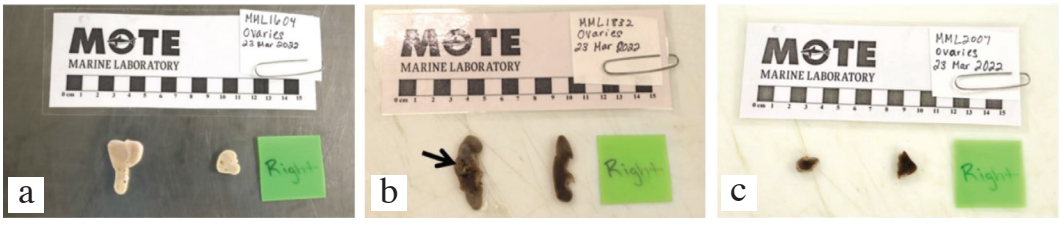

Figure 6. Cross-sections of ovaries from (a) ULYS, (b) ATNA, and (c) FHIS. None of the ovaries contained estrogen-producing follicles, though all animals had at least one ovary that contained *corpora albicantia*, and ATNA's left ovary contained a regressing *corpus luteum* ([b], arrow). (Photos courtesy of Mote Marine Laboratory)

bottlenose dolphins of multiple species in other parts of the world (Bloom, 1991; Connor et al., 1992; Samuels & Spradlin, 1995; Mann et al., 1996; Smolker & Connor, 1996; Moors, 1997; Wells, 2013; Cords & Mann, 2014; Robinson, 2014). Though Sarasota Bay dolphins practice a polygamous, promiscuous mating system and are sexually dimorphic with larger males (Wells et al., 1987; Tolley et al., 1995), the male dolphins have not been documented using aggressive tactics to successfully copulate with females, in contrast to the aggressive mating behaviors exhibited by Indo-Pacific bottlenose dolphins (*Tursiops aduncus*) in areas such as Shark Bay, Australia (Connor et al., 2005; Wells, 2013).

Necrocoitus has been documented in a wide array of species, though it is not common in any one species. Most observed instances of necrocoitus span reptiles, amphibians, and birds (e.g., How & Bull, 1998; Costa et al., 2010; Izzo et al., 2012; Tomita & Iwami, 2016; Swift & Marzluff, 2018; Ashaharraza et al., 2020). Dolphins are highly intelligent mammals with complex social systems (Marino, 2004; Connor, 2007; Wells, 2013) and are, therefore, unlikely to have the same motivating factors behind instances of necrocoitus as other taxa. For example, male anurans (*Rhinella proboscidea*) copulate with female corpses to fertilize and express viable oocytes (Izzo et al., 2012), which can be ruled out as a benefit of this behavior for mammals and other viviparous species. It has been questioned whether animals have a concept of death (Monsó & Osuna-Mascaró, 2021), but there is evidence that dolphins experience grief toward dead conspecifics (Bearzi et al., 2017). It can therefore be assumed that the male dolphins were aware that the females were dead in each case and were not trying to mate in earnest. While many species across taxa have exhibited necrocoitus in response to conspecific carcasses in mating posture (Dickerman, 1960; Russell, et al., 2012; Tomita & Iwami, 2016; Wang & Meyer-Rochow, 2020), the belly-up position of the female carcasses discussed here would not have led the males to believe they were alive and sexually receptive.

There is little evidence to support altruistic acts in the cases presented here, contrary to reports of dolphins aiding ill or distressed live conspecifics or attempting resuscitation (Park et al., 2013; Kuczaj et al., 2015). In addition to the finding that F178 and F188 may have killed ULYS, none of the female dolphins occupied the same home ranges as the respective male pairs, nor did they have significant prior associations (Table 1). While the

dolphins in and around Sarasota Bay tend to have relatively discrete home ranges, they do not tend to defend specific territories (Wells & Scott, 1990; Samuels & Spradlin, 1995; Wells, 2013), so the presence of unfamiliar females is unlikely to have incited aggressive behavior in contrast to reports in southern sea otters (Staedler & Riedman, 1993; Harris et al., 2010). Given the minimal overlap of home ranges and small COAs between the male pairs and the females, grief is also not a viable explanation for the observed behavior. In cases where grief behavior has been documented in cetaceans, the grieving animals were known to have prolonged relationships of evolutionary significance (e.g., mother–calf) with the dead animals (Archer, 2001; Bearzi et al., 2017).

Since the male dolphins in the cases presented here were presumably aware the females were dead, it is unlikely that they were reacting to perimortem pheromone expression, which has been posited as an explanation for necrocoitus in several taxa (Costa et al., 2010; Siqueira et al., 2015; Ashaharraza et al., 2020; Colombo & Mori, 2020), including Florida manatees, who occasionally pursue females to the point of exertional myopathy and death (Bills et al., 2013; Walsh & de Wit, 2015; Reynolds et al., 2018). This was investigated through ovary examination. The ovaries of all four females were preserved in 10% buffered formalin and examined grossly; and those of ULYS, ATNA, and FHIS were examined histologically (Figure 6). Three of the four encounters documented here occurred during breeding season (Owen et al., 2002), but none of the ovaries had follicles of sufficient size to produce estrogen (Robeck et al., 2005). Given that the females were not producing estrogen at the time of death, the theory that the males were responding to hormonal stimulation can be ruled out (T. Robeck, pers. comm., 6 April 2022).

Regardless of season, sexual behavior is part of dolphins' normal social repertoire (Wells et al., 1987; Mann et al., 1996; Furuichi et al., 2014). Sexual arousal and aggression have been correlated with displays of dominance in cetaceans (Pack et al., 1998; Connor et al., 2005; Furuichi et al., 2014; Bearzi et al., 2017; Methion & Díaz López, 2021; Volker & Herzing, 2021). The male pairs may have been exhibiting dominance over the females if they were alive at first contact and continued the behavior after the females died.

The four pairs of males had few to no previous sightings together (Table 1), so this is not believed to be a learned behavior. Play can be ruled out as a possible explanation for these events as the observed behaviors of the pair-bonded adult males toward the female carcasses are inconsistent with reports of cetacean social or object play (Ross & Wilson, 1996; Paulos et al., 2010; Greene et al., 2011).

In more than 50 years' worth of data collected by the SDRP and 35 years' worth of data collected by SIP, only these four observations have been made of necrocoitus in the Sarasota Bay area. This is clearly the exception and not the rule regarding bottlenose dolphin behavior toward dead conspecifics and constitutes an unusual opportunity to investigate extremely rare behavior. Additionally, the similarities among the four females' genital slit characteristics upon postmortem examination may provide evidence against which future cases can be compared to determine if a similar behavior occurred.

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