Vol. 155: 87–102, 2023
https://doi.org/10.3354/dao03746

DISEASES OF AQUATIC ORGANISMS
Dis Aquat Org

Published August 31

Causes of death and pathogen prevalence in bottlenose dolphins *Tursiops truncatus* stranded in Alabama, USA, between 2015 and 2020, following the *Deepwater Horizon* oil spill

J. C. G. Bloodgood[1,2,5,*], A. C. Deming[3], K. M. Colegrove[4], M. L. Russell[1], C. Díaz Clark[1], R. H. Carmichael[1,2]

[1]Dauphin Island Sea Lab, 101 Bienville Blvd., Dauphin Island, Alabama 36528, USA
[2]Stoke's School of Marine and Environmental Sciences, University of South Alabama, 600 Clinic Dr., Mobile, Alabama 36688, USA
[3]Pacific Marine Mammal Center, 20612 Laguna Canyon Rd., Laguna Beach, California 92651, USA
[4]Zoological Pathology Program, University of Illinois College of Veterinary Medicine, 3300 Golf Rd., Brookfield, Illinois 60513, USA

[5]*Present address:* Cornell Wildlife Health Lab, Cornell University College of Veterinary Medicine, 240 Farrier Rd., Ithaca, New York 14853, USA

ABSTRACT: Between 2010 and 2014, an unusual mortality event (UME) involving bottlenose dolphins *Tursiops truncatus* occurred in the northern Gulf of Mexico, associated with the *Deepwater Horizon* oil spill (DWHOS). Cause of death (COD) patterns in bottlenose dolphins since then have not been analyzed, and baseline prevalence data for *Brucella ceti* and cetacean morbillivirus, 2 pathogens previously reported in this region, are lacking. We analyzed records from bottlenose dolphins stranded in Alabama from 2015 to 2020 with necropsy and histological findings to determine COD (n = 108). This period included another UME in 2019 associated with prolonged freshwater exposure. A subset of individuals that stranded during this period were selected for molecular testing for *Brucella* spp. and *Morbillivirus* spp. Causes of death for all age classes were grouped into 6 categories, including (1) human interaction, (2) infectious disease, (3) noninfectious disease (prolonged freshwater exposure and degenerative), (4) trauma, (5) multifactorial, and (6) unknown. Two additional categories unique to perinates included fetal distress and *in utero* pneumonia. Human interaction was the most common primary COD (19.4%) followed closely by infectious disease (17.6%) and noninfectious disease (freshwater exposure; 13.9%). *Brucella* was detected in 18.4% of the 98 animals tested, but morbillivirus was not detected in any of the 66 animals tested. *Brucella* was detected in some moderately to severely decomposed carcasses, indicating that it may be beneficial to test a broad condition range of stranded animals. This study provides valuable information on COD in bottlenose dolphins in Alabama following the DWHOS and is the first to examine baseline prevalence of 2 common pathogens in stranded animals from this region.

KEY WORDS: Mortality · Human interaction · Freshwater · Fetal distress · Cetacean · Gulf of Mexico

1. INTRODUCTION

Cetaceans are long-lived apex predators that share the coastal environment with humans and other animals, making them a sentinel species for ocean health (Bossart 2011). Bottlenose dolphins *Tursiops truncatus* are the most abundant marine mammal in the Gulf of Mexico (GoM) and are distributed throughout bays, sounds, and estuaries in this region (Mullin 1988). Understanding the causes of morbidity

*Corresponding author: bloodgood.jennifer@gmail.com

Publisher: Inter-Research · www.int-res.com

and mortality and the prevalence of infectious diseases in these animals may provide valuable information about the future success of their populations as well as the health of the ecosystem overall. Comprehensive mortality and disease investigations are typically conducted following large-scale mortalities, including mass strandings and unusual mortality events (UMEs; Bossart et al. 2007, Venn-Watson et al. 2015). While deaths associated with UMEs tend to be well studied, non-UME mortalities and prevalence of infectious agents in stranded animals are less frequently collated and published, even though these baseline data are important for informing stranding response and management decisions and identifying unusual events (IJsseldijk et al. 2020, Seguel et al. 2020, Russell et al. 2022).

Fifteen UMEs involving bottlenose dolphins have occurred in the GoM since 1990 (Litz et al. 2014; https://www.fisheries.noaa.gov/national/marine-life-distress/active-and-closed-unusual-mortality-events). The most recent of these, caused by extreme freshwater discharge leading to prolonged freshwater exposure, lasted from February to November 2019 and spanned the northern GoM (nGoM) coastline from Louisiana to Florida. A total of 337 dolphins stranded during this event, and a high prevalence exhibited skin lesions consistent with low salinity exposure (https://www.fisheries.noaa.gov/national/marine-life-distress/2019-bottlenose-dolphin-unusual-mortality-event-along-northern-gulf). The longest-lasting and most deadly UME in the GoM to date was associated with the *Deepwater Horizon* oil spill (DWHOS) and lasted from February 2010 until July 2014 (Litz et al. 2014). More than 1100 cetaceans died during the UME, and adrenal and lung disease reported in a number of animals was potentially related to oil exposure (Schwacke et al. 2014, Venn-Watson et al. 2015). In addition, in the years immediately following the oil spill, an increased number of perinatal bottlenose dolphins died, likely related to multifactorial stressors including oil exposure and late-term pregnancy failure of dams, increased susceptibility to *Brucella* infection, and environmental perturbations including extreme cold and freshwater discharge (Carmichael et al. 2012, Colegrove et al. 2016). The long-term effects of oil exposure on bottlenose dolphins in the nGoM are still being investigated (e.g. Smith et al. 2017, De Guise et al. 2021, Linnehan et al. 2021).

Infectious diseases have also been implicated in multiple GoM UMEs. Cetacean morbillivirus, a highly contagious paramyxovirus, has been suspected or confirmed in 3 GoM UMEs (1990, 1992, and 1994; Litz et al. 2014). In acutely fatal morbillivirus infection, death often results from bronchointerstitial pneumonia or central nervous system disease. More chronic cases can result in immunosuppression and predispose the animal to opportunistic infections and lead to chronic encephalitis (Van Bressem et al. 2014). Morbillivirus is suspected to be endemic in offshore GoM cetaceans, which may be reservoirs for susceptible naive coastal populations (Fauquier et al. 2017, Cloyed et al. 2021). *Brucella* is a bacterium with a wide host range and zoonotic potential that has been isolated from cetaceans across the world (Guzmán-Verri et al. 2012). In perinate dolphins, brucellosis typically presents as pneumonia acquired via *in utero* transmission, while in older animals it leads to reproductive tract infections and abortion, central nervous system disease, and osteomyelitis (Miller et al. 1999, Dagleish et al. 2008, Guzmán-Verri et al. 2012, Hernández-Mora et al. 2013). *Brucella* infections are a known cause of sporadic mortality in both nonperinatal and perinatal bottlenose dolphins in the GoM, though the prevalence of infection during non-UME periods and whether infection is endemic in this region are unknown (Venn-Watson et al. 2015, Colegrove et al. 2016). This lack of baseline information highlights the need for ongoing surveillance and subsequent data analyses.

Cause of death (COD) and infectious disease surveillance information and analyses are particularly lacking for cetaceans in the north-central GoM. Coastal Alabama marks an important suture zone that links the eastern and western portions of the nGoM region and results in a unique confluence of habitat attributes and environmental stressors that can affect cetacean mortality (Portnoy & Gold 2012, Vollmer & Rosel 2017, Russell et al. 2022). Bottlenose dolphins are the most common cetacean in Alabama waters and constitute nearly 90% of marine mammal strandings in the state (Russell et al. 2022). Photo identification and biopsy surveys are currently ongoing in this region to assess bottlenose dolphin population abundance and health. Known threats to this population include human and fisheries interactions (e.g. peracute underwater entrapment, entanglement, boat strike, harassment; Carmichael et al. 2022), infectious diseases (e.g. morbillivirus, brucellosis), prolonged freshwater exposure, biotoxins, and contaminants. Comprehensive baseline COD and infectious disease prevalence data for this state, however, have not been published. This study aims to summarize demographic patterns in COD and determine the prevalence of infectious diseases, *Brucella* and morbillivirus, for bottlenose dolphins stranded in

Alabama from 1 January 2015 to 31 December 2020, after the close of the DWHOS UME. This information will provide a valuable baseline to identify future UMEs and inform stranding response and management decisions such as fishing regulations and habitat restoration efforts.

2. MATERIALS AND METHODS

This study includes bottlenose dolphins found stranded dead in Alabama from 1 January 2015 to 31 December 2020. Like cetacean stranding response elsewhere along the US coast, stranding response in Alabama is conducted by a local stranding network, the Alabama Marine Mammal Stranding Network (ALMMSN), under a stranding agreement with the National Oceanic and Atmospheric Administration's National Marine Fisheries Service (NOAA Fisheries). Standardized marine mammal stranding data, including location, date, species, sex, and straight length, and other information such as evidence of human interaction that are important to determining COD were recorded and documented in the NOAA Fisheries' Marine Mammal Health and Stranding Response Program (MMHSRP) national database. Data for this study were obtained from the ALMMSN and included a combination of the basic data documented in the MMHSRP and data from subsequent necropsy and supporting histological and other ancillary testing reports (Table S1 in the Supplement at www.int-res.com/articles/suppl/d155p087_supp.pdf).

2.1. Determining COD

To determine COD, cases with both necropsy and histologic data were examined. Necropsies followed standardized protocols (Pugliares et al. 2007), and tissue sections from all major organs (e.g. skin, blubber, muscle, brain, spinal cord, trachea, thyroid, esophagus, heart, lung, liver, spleen, kidney, adrenal gland, pancreas, stomach chambers, small and large intestine, gonads, and representative lymph nodes) and lesions were fixed in 10% neutral buffered formalin for microscopic analysis. Formalin-fixed tissues were routinely processed and stained with hematoxylin and eosin. Histologic evaluation was performed by pathologists familiar with marine mammals in the region. For each case, gross necropsy and histopathology reports were independently reviewed by 3 veterinarians (J. C. G. Bloodgood, A. C. Deming, K. M. Colegrove), and a consensus COD was reached.

Causes of death based on gross and histologic findings were grouped into 6 primary categories for all age classes, including (1) human interaction (subdivided into peracute underwater entrapment, vessel strike, blunt and/or sharp trauma), (2) infectious disease (subdivided into *Brucella*, other bacterial, parasitic, fungal, mixed, and unknown), (3) noninfectious disease (subdivided into prolonged freshwater exposure and degenerative), (4) trauma, (5) multifactorial (when more than 1 diagnosis could have equally contributed to death), and (6) unknown (subdivided into those with poor and good body condition; Venn-Watson et al. 2015). For perinates, 2 additional categories were analyzed: fetal distress and *in utero* pneumonia (non-*Brucella* related). Human interaction cases were further classified as confirmed (known to have contributed to stranding), probable (very likely contributed to stranding), or suspect (possibly contributed to stranding), as previously described (Moore & Barco 2013). Multifactorial cases are discussed in each appropriate category and thus may be included in the total counts of more than 1 category.

2.2. Demographics of stranded animals

To determine whether there were any demographic patterns in COD, we analyzed the sex, age class, and decomposition code of each case. Sex was assigned based on visual assessment of the gonads. In cases where the genital region was scavenged and sex could not be determined visually, sex was recorded as undetermined. Age class was based on body length, sex, and gonadal development, including perinate (≤115 cm), calf (116–169 cm), subadult female (170–230 cm and sexually immature), subadult male (170–250 cm and sexually immature), adult female (>230 cm or sexually mature), and adult male (>250 cm or sexually mature) (Colegrove et al. 2016, Russell et al. 2022). All animals stranded deceased and were classified according to level of decomposition (Code 2 = fresh dead, Code 3 = moderately decomposed, Code 4 = severely decomposed; Pugliares et al. 2007).

2.3. Molecular testing for infectious diseases

To determine the prevalence of *Brucella* and morbillivirus, archived tissues from bottlenose dolphins stranded during the study period were selectively submitted for molecular testing based on sample availability, sample quality, and the suspicion of dis-

ease from necropsy or histopathological analyses. Samples were analyzed by quantitative PCR (qPCR) for *Brucella* spp. at the University of Illinois Zoo Pathology Program and by PCR for *Morbillivirus* spp. at the University of Georgia College of Veterinary Medicine, using previously developed protocols (Colegrove et al. 2016, Fauquier et al. 2017). Results of molecular testing were only considered in the COD analysis when the animal tested positive and had necropsy and/or histologic evidence of that disease.

3. RESULTS

3.1. COD analysis

A total of 234 bottlenose dolphins stranded in Alabama during the 6 yr study period. Of these, 190 were necropsied and 108 were also examined histologically. Cases that were not necropsied and/or not examined histologically either stranded alive, could not be recovered, or were too decomposed for analysis. The 108 cases with both necropsy and histological data were examined for COD analysis.

The sex distribution of animals included in the COD analysis was approximately equal (Table 1, Fig. A1 in the Appendix). The majority of cases were subadults and adults, followed by perinates and calves (Table 1, Fig. A2). Several animals that would have been classified as subadults based on their body length had necropsy and/or histologic findings that indicated they were sexually mature (e.g. active testes with spermatogenesis, ovaries with corpora albicantia, evidence of pregnancy). These animals were reclassified as adults for analyses (Table S1). All animals stranded deceased; most were in a moderate state of decomposition (Code 3), and the remaining cases were fresh dead (Code 2) (Table 1). Sixteen cases were classified as multifactorial; as such, these cases may be included in the total counts of more than 1 COD category, and they are clearly delineated (Table 1).

3.1.1. Human interaction

The most common primary COD was human interaction, which accounted for 21 of the 108 examined cases (19.4%; Table 1) and contributed to an additional 6 multifactorial cases (total human interaction involvement n = 27). Most cases were males (16, 59.3%) and subadults (11, 40.7%) followed by adults (8, 29.6%), calves (7, 25.9%), and perinates (1, 3.7%; Table 1). Most cases were classified as probable (17,

Table 1. Causes of death (COD) of 108 bottlenose dolphins *Tursiops truncatus* stranded in Alabama from 2015 to 2020 grouped by sex, age class, and decomposition code. Counts in the Multifactorial subcategories are included in the total counts of the primary COD categories described in Section 3. NA: not applicable

COD	Total	Sex			Age class				Decomposition code	
		Male	Female	Undetermined	Perinate	Calf	Subadult	Adult	2	3
Human interaction	21	14	7	0	1	6	10	4	8	13
Infectious disease	19	13	4	2	6	5	4	4	7	12
Noninfectious disease										
Freshwater	15	7	8	0	0	0	8	7	1	14
Degenerative	1	0	1	0	0	0	0	1	1	0
Trauma	1	0	1	0	0	0	0	1	0	1
Multifactorial	16	8	7	1	4	3	3	6	5	11
Human interaction	6	2	3	1	0	1	1	4	2	4
Infectious	9	6	3	0	3	3	2	1	3	6
Freshwater	2	2	0	0	0	1	0	1	0	2
Degenerative	2	0	2	0	0	0	0	2	1	1
Trauma	7	3	3	1	3	1	1	2	1	6
Fetal distress	3	3	0	0	3	NA	NA	NA	1	2
Unknown										
Good body condition	22	7	15	0	2	1	9	10	7	15
Poor body condition	4	3	1	0	0	0	3	1	2	2
In utero pneumonia (non-*Brucella*) and fetal distress	4	2	2	0	4	NA	NA	NA	1	3
Fetal distress	5	1	4	0	5	NA	NA	NA	1	4
Total	108	55	50	3	22	15	37	34	33	75

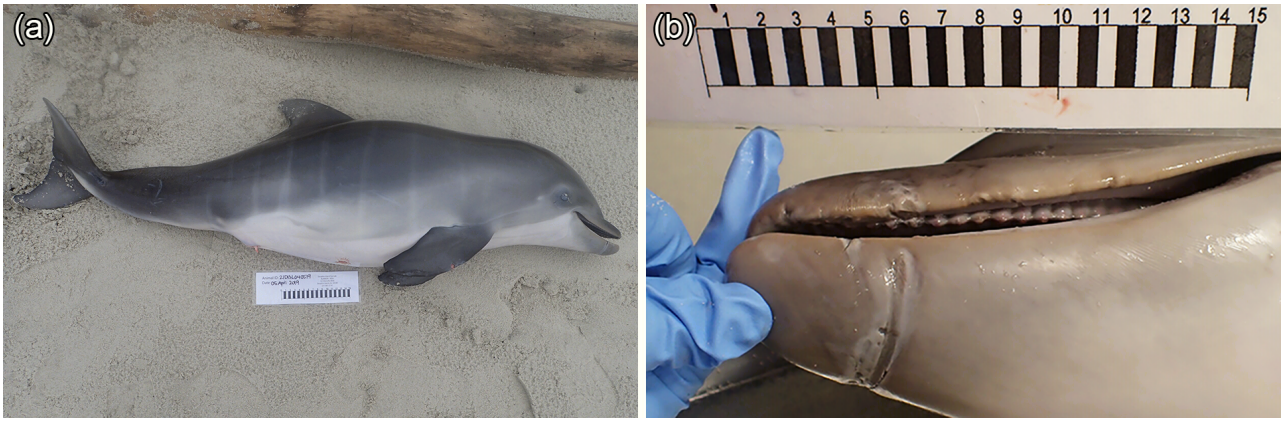

Fig. 1. (a) Case 21DISL040519, cause of death (COD) of a male calf bottlenose dolphin *Tursiops truncatus* categorized as human interaction (subcategory: peracute underwater entrapment) with (b) linear skin impressions on the rostrum consistent with entanglement in fishing gear

63.0%) followed by suspect (9, 33.3%) and confirmed (1, 3.7%) (Table S1). Human interaction was also suspected in 4 additional cases in which COD was classified as unknown.

The majority of human interaction cases (25 of 27, 92.6%) were diagnosed as peracute underwater entrapment (i.e. bycatch or drowning in fisheries gear; Table S1). Diagnosis of peracute underwater entrapment was made when there was gross and histologic evidence of contact with fishing gear and/or struggle while entrapped (e.g. linear skin lesions, hemorrhage, fractures; Fig. 1, Case 21DISL040519) and hypoxia (e.g. pulmonary edema and congestion, fluid and/or froth in the airways; Moore & Barco 2013, Moore et al. 2013). Good nutritional condition, evidence of recent feeding (i.e. whole undigested prey in the stomach chambers), and a paucity of other histologic lesions supported this diagnosis in many cases.

The sharp trauma case (45DISL091716; Table S1) was a subadult male with amputated flukes. Histopathology revealed regionally marked myonecrosis and hemorrhage at the amputation site. Linear impressions on the rostrum and a forestomach full of partially digested fish and squid supported that this animal was entangled in fishing gear prior to mutilation.

The vessel strike case (33DISL052916; Table S1) was classified as confirmed human interaction and involved an adult male that stranded dead 1 d after being reported alive with lacerations consistent with propeller wounds. Upon recovery of the carcass, 10 parallel linear propeller lacerations were documented along the dorsum. On histopathology, this animal had evidence of sepsis and potential peritonitis prior to trauma, and thus the COD was classified as multifactorial (human interaction + other bacterial).

3.1.2. Infectious disease

Infectious disease was the second most common primary COD (19 of 108, 17.6%; Table 1). Including multifactorial cases (total n = 28), there were more males (19, 71.4%) than females (7, 25%), and there was similar representation from every size class (Table 1). Most infectious disease cases were parasitic (11 of 28, 39.3%), and all of these were cases of parasitic pneumonia (Table 2). Ten of these cases were lungworm infection (presumed or confirmed via histology as *Halocercus* sp.). The remaining case involved a 118 cm female (17DISL081315), and histologic examination of granulomas in the lung tissue revealed trematode ova.

Brucella infection was the second most common subcategory of infectious disease (6 of 28, 21.4%; Table 2). The 4 cases of brucellosis in perinates all had evidence of *in utero* pneumonia and fetal distress, and positive *Brucella* spp. qPCR results confirmed the COD as infectious disease. There were 2 cases of brucellosis among nonperinates. One was an

Table 2. Infectious causes of death (COD) of perinate and nonperinate bottlenose dolphins *Tursiops truncatus* stranded in Alabama from 2015 to 2020

COD	Perinate	Nonperinate
Brucella	4	2
Other bacterial	1	4
Parasitic	2	9
Fungal	0	1
Mixed	0	2
Unknown etiology	2	1

adult lactating female (36DISL092117) with moderate diffuse neutrophilic and histiocytic endometritis as well as evidence of recent placental attachment in the right uterine horn. Lung tissue was negative for *Brucella* spp. via qPCR; however, the cerebrospinal fluid (CSF) was positive (Table S2). The other brucellosis case was an adult male (35DISL060819) with marked lymphocytic meningitis. *Brucella* testing of lung and testis tissue via qPCR was negative; however, the spinal cord tissue was positive (Table S2).

Five other bacterial cases included 2 cases of *Erysipelothrix* spp. sepsis (10DISL022120 and 19DISL032020), 1 in a male calf and 1 in a male subadult. There was also 1 case of sepsis of unknown etiology (14DISL030919). The remaining 2 cases were multifactorial (1 bacterial pneumonia + trauma case described in Section 3.1.4 and 1 sepsis + vessel strike case described in Section 3.1.1).

The fungal case (32DISL053019) was a 248 cm sexually mature adult male that stranded dead in May 2019 with severe fungal pneumonia and tracheitis. Significant findings during gross necropsy included raised beige plaques on the mucosa of the trachea and multifocal beige abscesses throughout the parenchyma of both lung lobes (Fig. 2). Histopathology confirmed severe pyogranulomatous and necrotizing pneumonia and tracheitis with intralesional fungal hyphae. Fungal hyphae were morphologically consistent with *Aspergillus* spp., and PCR of lung tissue was negative for *Morbillivirus* spp.

The 2 mixed infectious disease cases included 1 bacterial + parasitic case in which COD was attributed to bacterial enteritis leading to peritonitis and 1 fungal + bacterial case in which COD was attributed to fungal and bacterial tracheitis and bronchitis with additional bacterial bronchopneumonia. Intralesional fungi were histologically most consistent with mucormycetes.

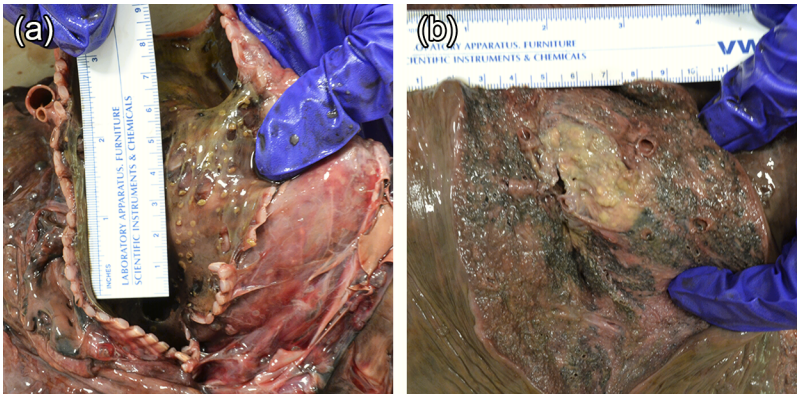

Fig. 2. Case 32DISL053019, COD of a male adult bottlenose dolphin *Tursiops truncatus* categorized as infectious disease (subcategory: fungal) with severe fungal pneumonia and tracheitis. Significant findings during gross necropsy included (a) raised beige plaques adhered to the mucosa of the trachea and (b) multifocal beige abscesses throughout the parenchyma of both lung lobes

3.1.3. Noninfectious disease (prolonged freshwater exposure and degenerative)

Prolonged freshwater exposure was the third most frequently diagnosed primary COD (15 of 108, 13.9%; Table 1). Including multifactorial cases (total n = 17), there were approximately equal numbers of males (9, 52.9%) and females (8, 47.1%), and most cases were subadults (8, 47.1%) and adults (8, 47.1%; Table 1). Cases were characterized grossly by pale thickened skin and multifocal to coalescing skin erosions (e.g. 02DISL020319, Fig. 3) with epiphytic growth (e.g. fungal, algal, and/or diatom). Histopathology of the skin from the peduncle of 02DISL020319 showed proliferative to pustular dermatitis with degeneration, edema, and superficial fungi (oomycetes), mixed bacteria, and ciliates consistent with exposure to low salinity water.

Degenerative disease was among the least common primary COD (1 of 108, 0.9%; Table 1). Including multifactorial cases (total n = 3), all 3 degenerative cases were adult females (Table 1). The primary case was an adult female with severe heart disease (11DISL022619). Grossly, the heart was enlarged, pale, and flaccid with a thin right ventricular wall, and the mitral valve had endocardiosis (Fig. 4). Histologically, the heart had severe multifocal interstitial and replacement fibrosis and moderate myocardial degeneration. The cause of the fibrosis could not be identified. The lung had moderate pulmonary edema and histiocytosis (heart failure cells) consistent with congestive heart failure. One of the multifactorial cases (33DISL053019) was an adult female with severe multifocal to coalescing pulmonary angiomatosis and interstitial fibrosis and moderate multifocal myocardial fibrosis consistent with chronic pulmonary and cardiac disease. This animal also had evidence of peracute underwater entrapment. The other case (01DISL010420) was a pregnant adult female with a cerebral infarction, moderate multifocal cerebellar hemorrhage, malacia, and cerebral edema and with acute to subacute aspiration pneumonia.

Fig. 3. (a) Case 02DISL020319, COD of a subadult female bottlenose dolphin *Tursiops truncatus* categorized as noninfectious disease (subcategory: prolonged freshwater exposure) with severe skin lesions. Close-up images of the (b) right lateral peduncle and (c) dorsal flukes show multifocal to coalescing skin erosions with epiphytic growth

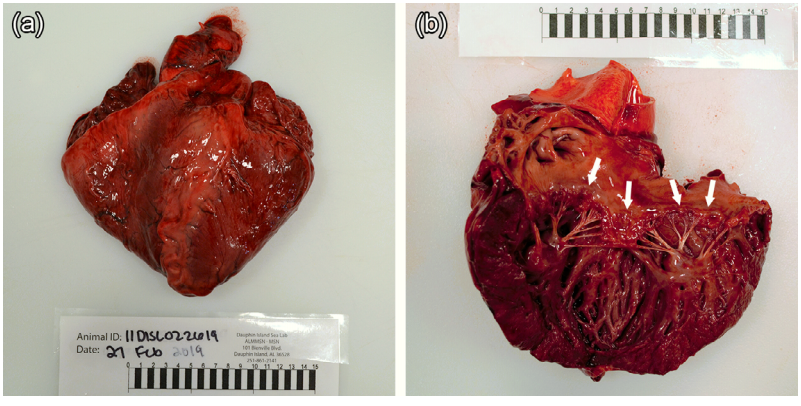

Fig. 4. Case 11DISL022619, COD of an adult female bottlenose dolphin *Tursiops truncatus* categorized as noninfectious disease (subcategory: degenerative) (heart disease). (a) The heart was large and pale, and (b) the mitral valve had firm small nodules (indicated by white arrows)

3.1.4. Trauma

Trauma was also among the least common primary COD (1 of 108, 0.9%; Table 1). Including multifactorial cases (total n = 8), there were approximately equal numbers of males (3 of 8, 37.5%) and females (4 of 8, 50.0%), and cases were distributed among all age classes (Table 1). The single case of trauma as the primary COD was an adult female (20DISL111015) with a 10.8 cm long and 1.3 cm deep melon laceration and compound fracture across both occipital condyles with associated hemorrhage. The multifactorial cases had evidence of trauma (i.e. bone fractures and/or soft tissue hemorrhage) as well as pneumonia (n = 4), evidence of peracute underwater entrapment (n = 1), fetal distress (n = 2), and/or cerebral edema and heart disease (n = 1). The multifactorial bacterial pneumonia + trauma case (07DISL031516) had histologic evidence of severe bacterial bronchopneumonia (most likely *Staphylococcus* or *Streptococcus* based on histomorphology). In addition, there was gross evidence of hemorrhage along the base of the skull as well as an acute intestinal perforation.

3.1.5. Perinates (fetal distress and *in utero* pneumonia [non-*Brucella* related])

Fetal distress was the most common primary COD in the perinate-only analysis (5 of 108, 4.6% of all dolphins; 5 of 22, 22.7% of perinates; Table 1). Including multifactorial cases (total n = 8), there were equal numbers of males and females (Table 1). The multifactorial cases included 1 case classified as parasitic, 1 as trauma (unknown origin), and 1 as parasitic + suppurative pneumonia + trauma (unknown origin with panniculitis). *In utero* pneumonia (non-*Brucella* related) and fetal distress together were also relatively common among perinates (4 of 108, 3.7% of all dolphins; 4 of 22, 18.2% of perinates; Table 1). There were equal numbers of males and females (Table 1).

3.1.6. Unknown

Cases in which COD remained unknown (26 of 108, 24.1%) were all moderately decomposed (Code 3). The majority of these cases were in good body condition (22 of 26, 84.6%). There were more females (16 of 26, 61.5%) than males (10 of 26, 38.5%), and the majority of cases were subadults (12 of 26, 46.2%) and adults (11 of 26, 42.3%; Table 1).

3.2. Molecular testing for infectious diseases

Among the individuals (including those not in the COD analysis) selected for molecular testing for *Brucella* spp. (n = 98 dolphins) and *Morbillivirus* spp. (n = 66 dolphins), *Brucella* spp. was detected in 18 (18.4%) animals, while *Morbillivirus* spp. was not detected in any animals tested (Table 3). Approximately equal numbers of males and females were positive for *Brucella*; however, there were some differences by age class, with perinates having the highest prevalence (30.3%) and subadults the lowest (9.1%). *Brucella* was detected in some moderately to severely decomposed carcasses (i.e. Codes 3 and 4; Table 3). The total number of tissue samples tested for *Brucella* spp. was 144 (78 lung, 20 testicle or uterus, 23 brain, 19 spinal cord, 1 prostate, 1 lymph node, 1 CSF, and 1 lung abscess; Table S2). For cases that tested positive for *Brucella* spp. and which had multiple tissue types submitted, not all tissues tested positive. The total number of tissue samples tested for *Morbillivirus* spp. was 116 (40 lung, 43 brain, 33 spinal cord; Table S2).

4. DISCUSSION

This study is the first to collate and summarize COD patterns and prevalence of infectious diseases in bottlenose dolphins stranded in Alabama since the closure of the DWHOS UME in 2014. While COD for populations of bottlenose dolphins in other areas has been reviewed (e.g. Bossart et al. 2003, 2013, McFee & Lipscomb 2009, Seguel et al. 2020), baseline data for populations in the nGoM are lacking. The age class and sex distributions of cases included in this study are consistent with a larger 41 yr dataset of strandings along the Alabama coast (Russell et al. 2022), suggesting these data are representative of historical stranding patterns in the area. In Section 4.1, we discuss each of the identified COD categories in the order of frequency and hypothesized importance to dolphins in Alabama waters.

Table 3. Quantitative PCR testing results for *Brucella* spp. and PCR testing results for *Morbillivirus* spp. in bottlenose dolphins *Tursiops truncatus* stranded in Alabama from 2015 to 2020

	Total	Sex			Size					Code		
		Male	Female	Undetermined	Perinate	Calf	Subadult	Adult	Unknown	2	3	4
Brucella												
Tested	98	46	46	6	33	15	22	26	2	23	69	6
Positive	18	8	7	3	10	2	2	3	1	1	15	2
Prevalence (%)	18.4	17.4	15.2	50.0	30.3	13.3	9.1	11.5	50.0	4.3	21.7	33.3
Morbillivirus												
Tested	66	32	30	4	16	12	17	20	1	23	40	3
Positive	0	0	0	0	0	0	0	0	0	0	0	0
Prevalence (%)	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0

4.1. COD analysis

4.1.1. Human interaction

Among human interactions, fisheries bycatch and boat collisions are known to be globally important causes of mortality in marine mammals (Moore et al. 2013). A recent study found that Alabama is a hotspot in the nGoM for cetacean strandings with signs of a wide range of human interactions and that these cases have increased in recent years (Carmichael et al. 2022). Both commercial and recreational shrimp and gillnet fisheries are legal in Alabama, providing opportunities for fisheries interactions in the region (https://www.outdooralabama.com/saltwater-fishing/saltwater-regulations-and-enforcement). As expected, these were the most documented COD in this study, contributing to death in 27 of 108 (25%) cases. Similarly, fishing gear interactions contributed to death in 27% of bottlenose dolphins stranded in Sarasota Bay on the Gulf coast of Florida from 1993 to 1996 (Wells et al. 1998). Fisheries interactions are also commonly documented in stranded cetaceans in other countries (e.g. Mannocci et al. 2012, Domiciano et al. 2016, Neimanis et al. 2022), but differences in fishing and reporting practices and detection or documentation among locations make stranding comparisons difficult. The numbers in the current study are much higher than those elsewhere along the Atlantic coast of the USA, including Massachusetts, where 10% (31 of 314) of marine mammals (8 cetaceans) that stranded from 2000 to 2006 died of human interaction, including harassment, entanglement, and vessel strikes (Bogomolni et al. 2010). Similarly, on Canada's Atlantic coast, nearly 10% (9 of 94) of harbor porpoises that stranded from 1988 to 2011 died from entanglement in fishing gear (Fenton et al. 2017). The disparity in the frequency of human interaction-related strandings in Alabama compared to the North Atlantic coast of the USA and Canada warrants further study. The vaquita *Phocoena sinus* is a cautionary example of how human and fisheries interactions can lead to significant population level declines and underscores the importance of conservation action before a population reaches critical lows (Sanjurjo-Rivera et al. 2021). Mitigation of high-risk fisheries practices and incentives for sustainable fishing may offer a tangible conservation approach for Alabama dolphin populations that have already been impacted by recent UMEs.

The sharp trauma/mutilation case was consistent with other bycatch cases in which the flukes were severed to release the animal from a net (Camphuysen et al. 2008, Moore et al. 2013). Severed flukes have been documented at least 3 other times in Alabama (M. R. Munday et al. unpubl. data). In addition to interactions with fisheries gear, species in coastal waters are at increased risk of being struck by vessels, especially in urbanized areas with higher densities of boats (Schoeman et al. 2020). The vessel strike case described in this study that also included evidence of sepsis and potential peritonitis suggests the animal may have been sick or debilitated prior to the vessel strike, making it more vulnerable to being struck. Debilitated individuals with decreased body condition that die at sea are less buoyant and thus more likely to sink than wash ashore (Moore et al. 2020), making this case a valuable contribution to our understanding of human interaction.

Some human interaction cases may be related to behavioral responses of a specific demographic of animals. The majority of human interaction cases in this study involved males and subadults. Wells et al. (1998) also found that subadults were disproportionately represented in entanglement cases and suggested that curiosity and inexperience placed this age class at greater risk. Anecdotal evidence has also suggested that juvenile male bottlenose dolphins are overrepresented in cases of commercial fishing gear entanglement on the east coast of the USA (Moore et al. 2013). Identifying demographics that are overrepresented in human interaction cases in some regions may provide important information for management and mitigation.

The number of deaths from human interaction in this study is likely underestimated. Conclusive diagnosis of human interaction can be difficult because evidence may be obscured by other marks, damage from predation and scavenging, and decomposition (Moore & Barco 2013, Fenton et al. 2017). In addition, not all cases of human interaction leave evidence of contact with sources such as fishing gear, and some cases may be missed by untrained observers (Moore et al. 2013). In this study, human interaction was suspected in 4 additional cases that were classified as unknown COD. These difficulties underscore the importance of actively working to reduce the likelihood of human interactions and training first responders and necropsy staff in recognition and documentation of signs of human interaction. ALMMSN actively works with NOAA Fisheries and the Alabama Department of Conservation and Natural Resources to develop and distribute education and outreach materials that aim to reduce human and fisheries interactions with marine mammals. The large number of human interaction cases highlights the need for public education, management, and policy in this area.

4.1.2. Infectious disease

As found in other populations, dolphins in Alabama suffered from a variety of infectious diseases, primarily from parasites and microbial infections. Lungworm, which accounted for the majority of infectious disease cases in this study, is common in bottlenose dolphins in the GoM (Fauquier et al. 2009, Venn-Watson et al. 2015, Smith et al. 2017). During postmortem examinations of stranded dolphins in southwestern Florida, 77% of animals had evidence of chronic or active lungworm infection, although it was not the primary COD in any case (Fauquier et al. 2009). Lungworm was also the most common cause of pneumonia in bottlenose dolphins sampled in Louisiana, Mississippi, and Alabama during the DWHOS (Venn-Watson et al. 2015). Lungworm infection was only documented as a primary COD in perinate, calf, and subadult age classes in the current study. Fauquier et al. (2009) found infections in all age classes; however, active infections were more likely in younger animals, while adults were more likely to have chronic to resolving infections. The case of a young dolphin with trematode ova in the lung tissue is highly unusual. While transmission of lungworms from dolphin dams to offspring *in utero* has been documented, to our knowledge this has not been documented for trematodes in *Tursiops truncatus* (Fauquier et al. 2009). While the prevalence of parasitic infections in dolphins in Alabama was similar to that found in previous studies, the number of cases in which it contributed to death was higher than expected. This finding may indicate increased susceptibility of this population to diseases, and these cases should continue to be monitored.

Bacterial infections were primarily due to *Brucella* spp. and *Erysipelothrix* spp. The necropsy and histologic findings in the cases of brucellosis are consistent with what has been reported with sporadic *Brucella ceti* infections in bottlenose dolphins from the coastal USA (Venn-Watson et al. 2015, Curtiss et al. 2022). *Brucella* infection may cause abortion in marine mammals and is a top differential in dolphin perinates with *in utero* pneumonia and fetal distress (Miller et al. 1999, Colegrove et al. 2016). Histology of 3 of the 4 perinate cases showed diffuse pulmonary atelectasis, indicating that these individuals either died *in utero* and were aborted or died during the birthing process. *Erysipelothrix* is known to cause clinical disease in both aquarium-housed and free-ranging cetaceans (Díaz-Delgado et al. 2015, Van Bonn & Rogers 2020). The 2 cases of *Erysipelothrix* spp. sepsis in this study occurred in close proximity in space and time (February and March 2020; Nesbitt et al. 2022). One animal was biopsy darted as part of an ongoing project to assess the health of dolphins in Alabama, and histopathology revealed the biopsy site as the likely source of infection. Ancillary testing did not reveal any underlying disease in this individual that would have predisposed it to infection. In the other animal, a definitive point of entry for the bacteria was not identified. Sequencing of *Erysipelothrix* DNA isolated from infected tissues from both dolphins revealed it was most closely related to *E. rhusiopathiae* and *E. piscisicarius* isolated from pigs and may implicate pigs living around the riparian areas of Mobile Bay as a source of infection (Nesbitt et al. 2022). Because both *Brucella* and *Erysipelothrix* have zoonotic potential, the presence of these pathogens in stranded animals underscores the importance of proper personal protective equipment use by stranding responders.

Fungal infection demonstrated low morbidity and mortality in this study. The animal that died from a fungal infection in 2019 had been included in regional health assessments the previous fall (2018) to study the long-term effects of the DWHOS on bottlenose dolphins (Barratclough et al. 2019). Health assessment findings showed very mild lung disease via ultrasound examination, moderate dental disease, scars consistent with an old propeller wound, and a positive morbillivirus titer with negative *Morbillivirus* spp. PCR, suggestive of previous exposure but not active infection. Fungal pneumonia in bottlenose dolphins is often secondary to morbillivirus infection, and it is possible that this dolphin experienced chronic immunosuppression from previous morbillivirus infection. Lung tissue collected from this animal during necropsy, however, was also negative for *Morbillivirus* spp. via PCR; the carcass was moderately decomposed, making it possible that morbillivirus RNA was degraded and led to a false negative. While fungal infections were rare in this study, they have the potential to be significant contributors to dolphin health under the right environmental conditions, in immunocompromised individuals, or as a comorbidity and therefore should not be overlooked (e.g. Bossart et al. 2019).

4.1.3. Noninfectious disease (prolonged freshwater exposure and degenerative)

Freshwater exposure is a noninfectious disease threat of growing concern for dolphins along the nGoM coast due to documented freshwater incursion from both natural (e.g. Carmichael et al. 2012, Toms et al. 2021) and anthropogenic sources including pro-

posed coastal management activities (e.g. the Mid-Barataria Sediment Diversion Restoration Plan, https://www.gulfspillrestoration.noaa.gov). In this study, gross and histologic lesions seen in prolonged freshwater exposure cases were similar to those previously reported (Deming et al. 2020, Duignan et al. 2020, McClain et al. 2020, Toms et al. 2021). In 2019, a UME that killed more than 300 bottlenose dolphins from Louisiana to the Florida Panhandle resulted from low salinity exposure after extreme freshwater discharge into the nGoM (https://www.fisheries.noaa.gov/national/marine-life-distress/2019-bottlenose-dolphin-unusual-mortality-event-along-northern-gulf). Dolphins in Louisiana and Mississippi were the most affected during this time. Interestingly, the majority (10 of 17) of the dolphins with evidence of freshwater exposure in the current study stranded in 2020, after the closure of the UME. In spring 2020, Mobile Bay experienced the largest freshwater influx event since 1980 with daily average flows exceeding 12 000 m^3 s^{-1} (https://waterdata.usgs.gov/, combined data from Alabama River Site No. 02428400 and Tombigbee River Site No. 02469761), which likely contributed to the increase in freshwater strandings in 2020. Several cases of presumed freshwater exposure in this study were not submitted for histopathology due to advanced decomposition, and thus the number of these cases is likely underestimated. Further characterization of freshwater lesions and the relationship of freshwater-associated strandings to the duration and magnitude of low salinity exposure are needed.

There were few other noninfectious diseases, and these were primarily degenerative in nature. The prevalence of myocardial fibrosis in dolphins in the nGoM after the DWHOS was higher than that in reference dolphins (Linnehan et al. 2021). Based on tooth wear and the presence of neuronal lipofuscinosis and age-related vascular changes histologically, the dolphin with primary heart disease in this study (11DISL022619) was likely old enough to have lived through the oil spill; however, without further evaluation of the individual's age and exposure to polycyclic aromatic hydrocarbons, this connection is speculative. *Brucella* infection has also been associated with heart lesions in cetaceans (Guzmán-Verri et al. 2012, Curtiss et al. 2022); however, uterus, cerebellum, and lung tissues were all negative via qPCR in this animal. The multifactorial case with evidence of peracute underwater entrapment had one of the most severe cases of pulmonary angiomatosis in dolphins from the GoM (K. M. Colegrove pers. obs.). The underlying pathogenesis could not be determined, although infectious agents and environmental factors were considered. In the pregnant female case, the fetal tissues were fresh, supporting that fetal death likely occurred around the same time as death of the dam. Cerebellar lesions in the dam were suggestive of a vascular accident and may have occurred secondary to age-related vascular changes including arteriosclerosis noted in other areas of the brain. An estimation of age was not available for this case. Pregnancy-related alterations in circulation and blood pressure also could have contributed to the development of vascular lesions, especially with underlying age-related vascular disease. The acute to subacute aspiration pneumonia suggests that multiple bouts of aspiration had occurred. Aspiration pneumonia is a relatively common finding in cetaceans that strand live or are struggling in the surf or shallow waters prior to death, which may have been the case for this animal. These degenerative cases highlight that while degenerative diseases are not commonly reported as a primary COD in cetaceans, they may play an important role as a comorbidity.

4.1.4. Trauma

Trauma in cetaceans can be due to a variety of factors from human-caused to interspecific and intraspecific interactions (e.g. Díaz-Delgado et al. 2015). The melon laceration and compound fractures of the skull in the case of trauma as the primary COD in this study were suspected to have been caused by a vessel strike, although the exact source of trauma could not be determined. The multifactorial trauma cases in this study were also of unknown origin; however, several were suspected to be related to fisheries interaction or intraspecific aggression as evidenced by bone fractures and/or soft tissue hemorrhage. Bottlenose dolphin calf-directed intraspecific aggression has been documented in the nGoM, including an individual from this study (07DISL031516; Ronje et al. 2020). Speculatively, bacterial pneumonia may have weakened this calf and made it more susceptible to subsequent trauma either from the dam or another conspecific. It is important to differentiate anthropogenic and natural causes of trauma when possible to better document and understand these interactions.

4.1.5. *In utero* pneumonia (non-*Brucella* related) and fetal distress

The cause of non-*Brucella* related *in utero* pneumonia and fetal distress in cases in the current study

could not be determined. *In utero* pneumonia may arise from *in utero* infection of the placenta, amniotic fluid, or hematogenous spread, and fetal distress may be caused by factors such as infection, fetal hypoxia, and dystocia (Colegrove et al. 2016). In a case-reference study, perinatal bottlenose dolphins that stranded inside compared to outside the DWHOS UME footprint were more likely to have died *in utero* or very soon after birth (88 vs. 15%), have fetal distress (87 vs. 27%), and have pneumonia not associated with lungworm infection (65 vs. 19%; Colegrove et al. 2016). The prevalence of *in utero* pneumonia and fetal distress (18.2% of perinates) and fetal distress alone (22.7% of perinates) in the current study more closely resembles that of populations not affected by the DWHOS and may indicate a return to more baseline levels.

4.1.6. Unknown

It is not always possible to determine COD. The number of cases classified as unknown in the current study is within the range of other studies of similar scale. COD could not be determined in 7.3% of cetaceans stranded in the Canary Islands and 51% of harbor porpoises stranded in Canada (Arbelo et al. 2013, Fenton et al. 2017). Autolysis is a major hindrance to COD determination. All unknown cases in the current study were moderately decomposed (Code 3). Nevertheless, at least 4 unknown cases were speculated to have died as a result of fisheries interaction. Evidence of human and fisheries interaction may be obfuscated with decomposition and contribute to underreporting in this category, particularly among Code 3 or more decomposed carcasses (Moore & Barco 2013). The majority of cases classified as unknown in the current study were in good body condition, indicating that they likely did not die of chronic disease. This finding is consistent with a previous study of bottlenose dolphins in the nGoM (Venn-Watson et al. 2015). Hence, even examination of autolyzed carcasses, when done with care, may provide some inferences about COD.

4.2. Molecular testing for infectious diseases

Prevalence of *Brucella* and morbillivirus among all samples tested, whether included in the COD analysis or not, provided data on the baseline levels of infection in this population. For *Brucella* spp., the number of positive animals found in this study (18.4%) may indicate some level of endemicity and ultimately decrease reproductive success and subsequently affect population dynamics, especially given the population is still in a recovery phase following recent UMEs (Guzmán-Verri et al. 2012). The prevalence in perinates in this study (29.4%) was lower than that in Mississippi and Alabama from 2010 to 2013 during the DWHOS UME (61%; Colegrove et al. 2016). The prevalence in subadults and adults (7.4 and 12.5%, respectively) was similar to the 5 to 6% prevalence that was found in stranded dolphins in Louisiana, Mississippi, and Alabama from 2010 to 2012 during the DWHOS UME (Venn-Watson et al. 2015). Of note, *Brucella* was detected in some moderately to severely decomposed carcasses (i.e. Codes 3 and 4), indicating that estimates of population prevalence may be improved by testing a broad condition range of stranded animals.

For cases that were positive for *Brucella* spp. via qPCR, not all tissues submitted were positive. Lung tissue was most likely to test positive in perinates, consistent with the typical presentation of pneumonia acquired via *in utero* transmission (Colegrove et al. 2016). In contrast, for the 2 cases of brucellosis in adults in this study, lung tissue was negative, while other tissues (i.e. CSF, spinal cord) were positive. In older cetaceans, it is known that brucellosis often leads to reproductive tract infections, central nervous system disease, and osteomyelitis (Miller et al. 1999, Dagleish et al. 2008, Guzmán-Verri et al. 2012, Hernández-Mora et al. 2013). These findings suggest that different tissues may need to be tested to best detect *Brucella* in different age classes of dolphins, with lung tissue potentially best to test in perinates and reproductive (i.e. uterus, testicle) and nervous (i.e. spinal cord, brain, CSF) tissues best to test in older age classes.

Although morbillivirus was not detected via PCR in any animals during the current study period, this finding does not indicate a lack of susceptibility to the disease. Prevalence of morbillivirus in stranded bottlenose dolphins in the nGoM during the DWHOS UME using PCR ranged from 9 to 15% (Venn-Watson et al. 2015, Fauquier et al. 2017). In addition, morbillivirus has been suspected in several UMEs on the Gulf coast and was confirmed in a UME in Texas, Louisiana, and Alabama that killed >200 bottlenose dolphins in 1993 and 1994 (Lipscomb et al. 1996, Litz et al. 2014). A recent study using serological methods showed that bottlenose dolphins in interior estuarine habitats may have lower morbillivirus titers and thus could be at higher risk of morbillivirus infection (Cloyed et al. 2021). Future work should pair the PCR

results from this study with antibody studies to better understand susceptibility of the dolphins in this region to a morbillivirus outbreak.

5. CONCLUSION

This study is the first to summarize COD patterns in bottlenose dolphins stranded in Alabama waters, an important and understudied dolphin habitat in the nGoM, after the close of the DWHOS UME. As in other coastal areas globally, human interaction was the most frequently observed primary COD and may be not only pervasive but also on the rise in this region (e.g. Mannocci et al. 2012, Domiciano et al. 2016, Carmichael et al. 2022, Neimanis et al. 2022). We highlight the importance of public education, management, and policy as a means to mitigate the effects of human interactions on dolphins in this region. The relatively high number of prolonged freshwater exposure cases is also an important consideration as an ongoing endemic stressor as well as a growing threat (e.g. Carmichael et al. 2012, Toms et al. 2021, Thomas et al. 2022). Hydrodynamic and associated salinity changes are anticipated to continue to occur in this region due to climate change and management efforts (e.g. Dykstra & Dzwonkowski 2021, Thomas et al. 2022, https://www.gulfspillrestoration.noaa.gov/). This study is also the first to establish baseline prevalence of 2 infectious diseases in this region that are known to affect dolphin populations globally and thus demand further location-specific surveillance. *Brucella* and morbillivirus may pose ongoing and future threats, respectively, to local dolphin populations that may decrease reproductive success and have larger implications for population recovery and conservation. The nGoM bottlenose dolphin population experienced significant mortalities and decreased reproductive success following the DWHOS, and region-specific data on COD and prevalence of infectious diseases may help identify hurdles to recovery. This study demonstrates the importance of stranding response and necropsy in identifying region-specific baseline health of, and threats to, marine mammal populations.

Acknowledgements. We thank the current and previous ALMMSN staff, interns, and many volunteers who assisted with stranding response for these cases, with particular thanks to Maureen Goretti and Tori McMahon. We also thank Drs. Martha Delaney, Mike Kinsel, and Dave Rotstein for their diagnostic work on some of these cases and Dr. Matthew Bloodgood for assistance with photo editing. Stranding response was conducted under the stranding agreement between Dauphin Island Sea Lab and NOAA Fisheries. Response was funded by NOAA Fisheries and *Deepwater Horizon* natural resource damage settlement funds provided by the Alabama Trustee Implementation Group with funding support and participation of the Alabama Department of Conservation and Natural Resources.

LITERATURE CITED

Arbelo M, Espinosa de Los Monteros A, Herráez P, Andrada M and others (2013) Pathology and causes of death of stranded cetaceans in the Canary Islands (1999–2005). Dis Aquat Org 103:87–99

Barratclough A, Wells RS, Schwacke LH, Rowles TK and others (2019) Health assessments of common bottlenose dolphins (*Tursiops truncatus*): past, present, and potential conservation applications. Front Vet Sci 6:444

Bogomolni AL, Pugliares KR, Sharp SM, Patchett K and others (2010) Mortality trends of stranded marine mammals on Cape Cod and southeastern Massachusetts, USA, 2000 to 2006. Dis Aquat Org 88:143–155

Bossart GD (2011) Marine mammals as sentinel species for oceans and human health. Vet Pathol 48:676–690

Bossart GD, Meisner R, Varela R, Mazzoil M and others (2003) Pathologic findings in stranded Atlantic bottlenose dolphins (*Tursiops truncatus*) from the Indian River Lagoon, Florida. Fla Sci 66:226–238

Bossart GD, Hansen L, Goldstein JD, Kilpatrick D and others (2007) Pathological findings in a rare mass stranding of melon-headed whales (*Peponocephala electra*) in Florida. Aquat Mamm 33:235–240

Bossart GD, Hurley W, Biedenbach G, Denny M and others (2013) Pathologic findings in stranded cetaceans from northeastern Florida. Fla Sci 76:36–50

Bossart GD, Romano TA, Peden-Adams MM, Schaefer AM, Rice CD, Fair PA, Reif JS (2019) Comparative innate and adaptive immune responses in Atlantic bottlenose dolphins (*Tursiops truncatus*) with viral, bacterial, and fungal infections. Front Immunol 10:1125

Camphuysen K, Smeenk C, Addink MJ, Jansen OE (2008) Cetaceans stranded in the Netherlands from 1998 to 2007. Lutra 51:87–122

Carmichael RH, Graham WM, Aven A, Worthy G, Howden S (2012) Were multiple stressors a 'perfect storm' for northern Gulf of Mexico bottlenose dolphins (*Tursiops truncatus*) in 2011? PLOS ONE 7:e41155

Carmichael RH, Hodanbosi MR, Russell ML, Wingers NL (2022) Human influence on bottlenose dolphin (*Tursiops truncatus*) strandings in the northern Gulf of Mexico. Front Environ Sci 10:951329

Cloyed CS, Balmer BC, Schwacke LH, Takeshita R and others (2021) Linking morbillivirus exposure to individual habitat use of common bottlenose dolphins (*Tursiops truncatus*) between geographically different sites. J Anim Ecol 90:1191–1204

Colegrove KM, Venn-Watson S, Litz J, Kinsel MJ and others (2016) Fetal distress and *in utero* pneumonia in perinatal dolphins during the Northern Gulf of Mexico unusual mortality event. Dis Aquat Org 119:1–16

Curtiss JB, Colegrove KM, Dianis A, Kinsel MJ and others (2022) *Brucella ceti* sequence type 23, 26, and 27 infections in North American cetaceans. Dis Aquat Org 148: 57–72

Dagleish MP, Barley J, Finlayson J, Reid RJ, Foster G (2008) *Brucella ceti* associated pathology in the testicle of a harbour porpoise (*Phocoena phocoena*). J Comp Pathol 139: 54–59

De Guise S, Levin M, Jasperse L, Herrman J, Wells RS, Rowles T, Schwacke L (2021) Long-term immunological alterations in bottlenose dolphin a decade after the *Deepwater Horizon* oil spill in the northern Gulf of Mexico: potential for multigenerational effects. Environ Toxicol Chem 40:1308–1321

Deming AC, Wingers NL, Moore DP, Rotstein D and others (2020) Health impacts and recovery from prolonged freshwater exposure in a common bottlenose dolphin (*Tursiops truncatus*). Front Vet Sci 7:235

Díaz-Delgado J, Arbelo M, Sierra E, Vela A and others (2015) Fatal *Erysipelothrix rhusiopathiae* septicemia in two Atlantic dolphins (*Stenella frontalis* and *Tursiops truncatus*). Dis Aquat Org 116:75–81

Domiciano IG, Domit C, Broadhurst MK, Koch MS, Bracarense APFRL (2016) Assessing disease and mortality among small cetaceans stranded at a World Heritage site in southern Brazil. PLOS ONE 11:e0149295

Duignan PJ, Stephens NS, Robb K (2020) Fresh water skin disease in dolphins: a case definition based on pathology and environmental factors in Australia. Sci Rep 10:21979

Dykstra SL, Dzwonkowski B (2021) The role of intensifying precipitation on coastal river flooding and compound river–storm surge events, Northeast Gulf of Mexico. Water Resour Res 57:e2020WR029363

Fauquier DA, Kinsel MJ, Dailey MD, Sutton GE, Stolen MK, Wells RS, Gulland FMD (2009) Prevalence and pathology of lungworm infection in bottlenose dolphins *Tursiops truncatus* from southwest Florida. Dis Aquat Org 88:85–90

Fauquier DA, Litz J, Sanchez S, Colegrove K and others (2017) Evaluation of morbillivirus exposure in cetaceans from the northern Gulf of Mexico 2010–2014. Endang Species Res 33:211–220

Fenton H, Daoust PY, Forzán MJ, Vanderstichel RV and others (2017) Causes of mortality of harbor porpoises *Phocoena phocoena* along the Atlantic and Pacific coasts of Canada. Dis Aquat Org 122:171–183

Guzmán-Verri C, González-Barrientos R, Hernández-Mora G, Morales JA, Baquero-Calvo E, Chaves-Olarte E, Moreno E (2012) *Brucella ceti* and brucellosis in cetaceans. Front Cell Infect Microbiol 2:3

Hernández-Mora G, Palacios-Alfaro J, González-Barrientos R (2013) Wildlife reservoirs of brucellosis: *Brucella* in aquatic environments. Rev Sci Tech 32:89–103

IJsseldijk I, ten Doeschate LL, Brownlow MTI, Davison A and others (2020) Spatiotemporal mortality and demographic trends in a small cetacean: strandings to inform conservation management. Biol Conserv 249:108733

Linnehan BK, Gomez FM, Huston SM, Hsu A and others (2021) Cardiac assessments of bottlenose dolphins (*Tursiops truncatus*) in the northern Gulf of Mexico following exposure to *Deepwater Horizon* oil. PLOS ONE 16: e0261112

Lipscomb TP, Kennedy S, Moffett D, Krafft A and others (1996) Morbilliviral epizootic in bottlenose dolphins of the Gulf of Mexico. J Vet Diagn Invest 8:283–290

Litz JA, Baran MA, Bowen-Stevens SR, Carmichael RH and others (2014) Review of historical unusual mortality events (UMEs) in the Gulf of Mexico (1990–2009): providing context for the multi-year northern Gulf of Mexico cetacean UME declared in 2010. Dis Aquat Org 112: 161–175

Mannocci L, Dabin W, Augeraud-Véron E, Dupuy JF, Barbraud C, Ridoux V (2012) Assessing the impact of bycatch on dolphin populations: the case of the common dolphin in the eastern North Atlantic. PLOS ONE 7: e32615

McClain AM, Daniels R, Gomez FM, Ridgway SH, Takeshita R, Jensen ED, Smith CR (2020) Physiological effects of low salinity exposure on bottlenose dolphins (*Tursiops truncatus*). J Zool Bot Gard 1:61–75

McFee WE, Lipscomb TP (2009) Major pathologic findings and probable causes of mortality in bottlenose dolphins stranded in South Carolina from 1993 to 2006. J Wildl Dis 45:575–593

Miller WG, Adams LG, Ficht TA, Cheville NF and others (1999) *Brucella*-induced abortions and infection in bottlenose dolphins (*Tursiops truncatus*). J Zoo Wildl Med 30:100–110

Moore KT, Barco SG (2013) Handbook for recognizing, evaluating, and documenting human interaction in stranded cetaceans and pinnipeds. NOAA Tech Memo NMFS-SWFSC 510

Moore MJ, van der Hoop J, Barco SG, Costidis AM and others (2013) Criteria and case definitions for serious injury and death of pinnipeds and cetaceans caused by anthropogenic trauma. Dis Aquat Org 103:229–264

Moore MJ, Mitchell GH, Rowles TK, Early G (2020) Dead cetacean? Beach, bloat, float, sink. Front Mar Sci 7:333

Mullin KD (1988) Comparative seasonal abundance and ecology of bottlenose dolphins (*Tursiops truncatus*) in three habitats of the north-central Gulf of Mexico. PhD dissertation, Mississippi State University, Starkville, MS

Neimanis A, Stavenow J, Ågren EO, Wikström-Lassa E, Roos AM (2022) Causes of death and pathological findings in stranded harbour porpoises (*Phocoena phocoena*) from Swedish waters. Animals (Basel) 12:369

Nesbitt K, Bloodgood J, Mullis MM, Deming AC, Colegrove K, Kiel Reese B (2022) Draft genome sequences of *Erysipelothrix* sp. strains isolated from stranded septic bottlenose dolphins in Alabama, USA. Microbiol Resour Announc 11:e0027322

Portnoy DS, Gold JR (2012) Evidence of multiple vicariance in a marine suture-zone in the Gulf of Mexico. J Biogeogr 39:1499–1507

Pugliares KR, Bogomolni A, Touhey KM, Herzig SM, Harry CT, Moore MJ (2007) Marine mammal necropsy: an introductory guide for stranding responders and field biologists. Woods Hole Oceanographic Institution Technical Report WHOI-2007-06

Ronje E, Piwetz S, Whitehead H, Mullin KD (2020) Intraspecific aggression towards common bottlenose dolphin calves, northern Gulf of Mexico. Gulf Caribb Res 31:SC6–SC12

Russell ML, Bloodgood JCG, Carmichael RH (2022) Spatial, temporal and demographic patterns of cetacean strandings in the northcentral Gulf of Mexico. J Cetacean Res Manag 23:171–182

Sanjurjo-Rivera E, Mesnick SL, Ávila-Forcada S, Poindexter O and others (2021) An economic perspective on policies to save the vaquita: conservation actions, wildlife trafficking, and the structure of incentives. Front Mar Sci 8: 644022

Schoeman RP, Patterson-Abrolat C, Plön S (2020) A global review of vessel collisions with marine animals. Front Mar Sci 7:292

Schwacke LH, Smith CR, Townsend FI, Wells RS and others (2014) Health of common bottlenose dolphins (*Tursiops truncatus*) in Barataria Bay, Louisiana, following the *Deepwater Horizon* oil spill. Environ Sci Technol 48:93–103

Seguel M, George RC, Maboni G, Sanchez S and others (2020) Pathologic findings and causes of death in bottlenose dolphins *Tursiops truncatus* stranded along the Georgia coast, USA (2007–2013). Dis Aquat Org 141: 25–38

Smith CR, Rowles TK, Hart LB, Townsend FI and others (2017) Slow recovery of Barataria Bay dolphin health following the *Deepwater Horizon* oil spill (2013–2014), with evidence of persistent lung disease and impaired stress response. Endang Species Res 33:127–142

Thomas L, Marques TA, Booth CG, Takeshita R, Schwacke L (2022) Model predicts catastrophic decline of common bottlenose dolphin (*Tursiops truncatus*) population under proposed land restoration project in Barataria Bay, Louisiana, USA. Mar Mam Sci 38:1654–1664

Toms CN, Stone T, Och T (2021) Skin lesion and mortality rate estimates for common bottlenose dolphin (*Tursiops truncatus*) in the Florida Panhandle following a historic flood. PLOS ONE 16:e0257526

Van Bonn W, Rogers MA (2020) Incidence rate of *Erysipelothrix rhusiopathae* clinical disease in cetaceans is reduced following water treatment changes in a closed artificial seawater system. J Zoo Aquar Res 8:218–220

Van Bressem MF, Duignan P, Banyard A, Barbieri M and others (2014) Cetacean morbillivirus: current knowledge and future directions. Viruses 6:5145–5181

Venn-Watson S, Colegrove KM, Litz J, Kinsel M and others (2015) Adrenal gland and lung lesions in Gulf of Mexico common bottlenose dolphins (*Tursiops truncatus*) found dead following the *Deepwater Horizon* oil spill. PLOS ONE 10:e0126538

Vollmer NL, Rosel PE (2017) Fine-scale population structure of common bottlenose dolphins (*Tursiops truncatus*) in offshore and coastal waters of the US Gulf of Mexico. Mar Biol 164:160

Wells RS, Hofmann S, Moors T (1998) Entanglement and mortality of bottlenose dolphins (*Tursiops truncatus*) in recreational fishing gear in Florida. Fish Bull 96:647–650

Appendix.

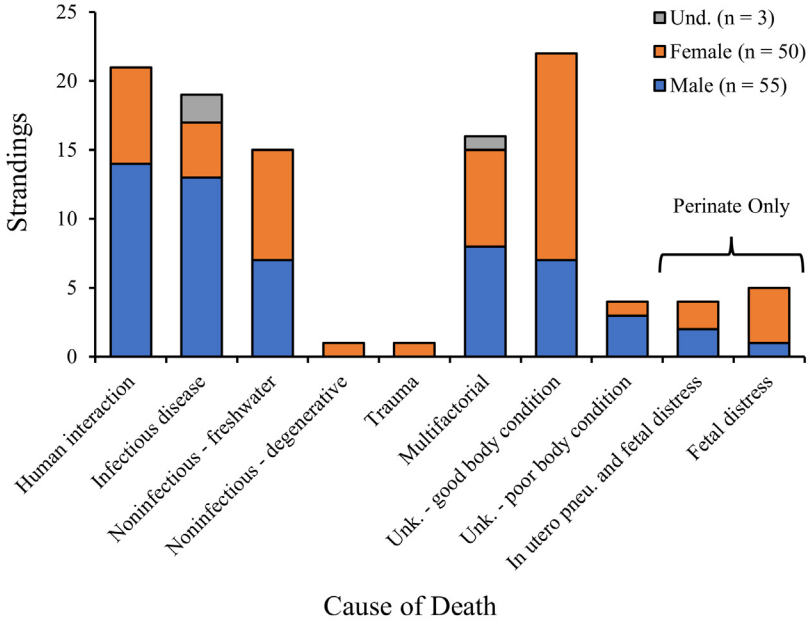

Fig. A1. Causes of death of 108 bottlenose dolphins *Tursiops truncatus* stranded in Alabama from 2015 to 2020, grouped by sex. Unk.: unknown; Und.: undetermined

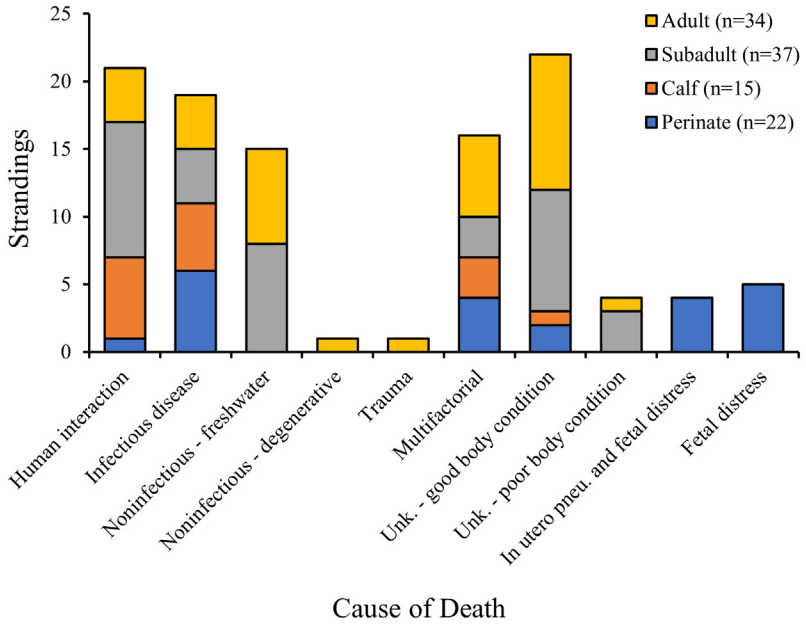

Fig. A2. Causes of death of 108 bottlenose dolphins *Tursiops truncatus* stranded in Alabama from 2015 to 2020, grouped by age class. Unk.: unknown

Editorial responsibility: Stephen Raverty, Abbotsford, British Columbia, Canada
Reviewed by: M. Seguel and 2 anonymous referees

Submitted: March 20, 2023
Accepted: June 23, 2023
Proofs received from author(s): August 21, 2023