



Gray Whale (*Eschrichtius robustus*) Health and Disease: Review and Future Directions

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The eastern North Pacific gray whale (Eschrichtius robustus) population is considered "recovered" since the days of commercial whaling, with a population of over 25,000 animals. However, gray whale habitat is changing rapidly due to urbanization of the migratory coastal corridor, increases in shipping, and climate change altering water conditions and prey distribution. Increased single strandings and intermittent large-scale mortality events have occurred over the past 20 years, raising questions about how gray whale health is affected by whale population size (density dependence), climate change, and coastal development. To understand the impacts of these factors on health and the role of health changes in whale population dynamics, increased understanding of the pathogenesis and epidemiology of diseases in gray whales is needed. To date, most information on gray whale health and disease is in single case reports, in sections of larger papers on whale ecology, or in technical memoranda and conference proceedings. Here we review existing data on gray whale health and disease to provide a synthesis of available information and a baseline for future studies, and suggest priorities for future study of gray whale health. The latter include nutritional studies to distinguish annual physiological fasting from starvation leading to mortality, identification of endemic and novel viruses through increased use of molecular techniques, quantifying parasitic infections to explore interactions among prey shifts and parasite infection and body condition, as well as enhancing necropsy efforts to identify stochastic causes of mortality such as vessel strikes, entanglements, and predation. Integration of health and disease studies on individual animals with population monitoring and models of whale/prey dynamics will require interdisciplinary approaches to understand the role of health changes in population dynamics of this coastal whale.

Keywords: health, disease, gray whale, stranding, mortality

INTRODUCTION

The recovery of the eastern North Pacific gray whale population since its decimation by commercial whaling has been heralded as a conservation success. Yet its northern feeding grounds are now experiencing unprecedented ecological change, and hundreds of dead gray whales stranded along the migratory corridor in 2019 (Raverty et al., 2020). High mortality of gray whales was also

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observed in 1999 and 2000 (Gulland et al., 2005), when the population concurrently decreased by almost 20% (Laake et al., 2012). Despite regular population surveys and post-mortem examination of individual whale carcasses, our understanding of gray whale health and how it is affected by whale population size (density dependence), climate change, and coastal development remains poor. Gray whales have been proposed as "sentinels" for Arctic Ocean health (Moore and Gulland, 2014), yet for us to interpret changes in health, baseline data are required. Surprisingly, there are only scant data, mostly single case reports, on lesions, diseases, marine biotoxins, and infectious diseases of gray whales, although the helminth fauna have long been described (Rice and Wolman, 1971; Dailey and Brownell, 1972). The detection and characterization of infectious agents, especially viruses, in marine mammals have increased considerably; however, establishment of a causal association between pathogens and clinical presentation or pathology for many agents has been difficult "due to inconsistencies in marine mammal morbidity/mortality investigative effort and the logistical and economic limitations for adequate pathologic investigations" (Bossart and Duignan, 2018). This is particularly true for gray whales, with limited studies available. Given the rapid changes in the North Pacific and Arctic ocean ecosystems, changes in gray whale health are likely. Here we review existing data on gray whale health and disease to provide a baseline, synthesize existing information, and suggest priorities for future study of gray whale health.

SOURCES OF HEALTH AND DISEASE DATA

Information on gray whale health and disease is available from four sources: whaling records, especially those from 1964 to 1969 for whales taken off the Richmond whaling station in central California (Rice and Wolman, 1971); the aboriginal whaling scheme (AWS) in Chukotka, Russia, and their ongoing harvest monitoring program¹; examination of stranded animals; and health assessment of live whales using both remote sampling (photography, biopsy, breath analysis) and hands on sampling of two temporarily captive whales.

The near-shore behavior of gray whales results in occasional live strandings, a few of which have refloated with (Lahner et al., 2018) or without human assistance. Interestingly, the ability of stranded live gray whales to refloat themselves has been described by traditional ecological knowledge (TEK) and in the Russian literature (Tomlin, 1967). Corroborating evidence comes from historic Icelandic texts where the ability of gray whales to refloat after stranding is described "*it is very tenacious of life and can come on land to lie as seals like to rest the whole day. But in sand it never breaks up*" (Fraser, 1970). In Icelandic the gray whale is called *sandlier* (Icelandic *sandloegja*) reflecting this behavioral trait. TEK from Chukotkan native people also attest to the ability of gray whales to free themselves from stranding on sandbanks (Yablokov and Bogoslovskaya, 1984). Causes of live strandings

¹https://iwc.int/russian-federation

vary, with some animals having lesions or toxins (see below). Solar storms have recently been suggested as causal, but selective data were used for these analyses and the association is likely due to covarying factors (Granger et al., 2020). Remarkably two live stranded neonatal gray whales were successfully rehabilitated in San Diego and released at 1 year of age (Bruehler et al., 2001; Sumich et al., 2001). Blood parameters for single animals have been determined and can support diagnostic investigation in live stranded and euthanized gray whales (Gilmartin et al., 1974; Dailey et al., 2000; Reidarson et al., 2001). Samples for assessing health of free-swimming live whales have been obtained by collecting blow and dart-biopsying skin and blubber. Collected blow has been used to describe the microbiome in breath, and to identify metabolites (Acevedo-Whitehouse et al., 2010; Denisenko et al., 2012).

INFECTIOUS DISEASES

Viruses

Calicivirus

Calicivirus antibodies (San Miguel Sea Lion Virus; SMSVTypes 1, 2, and 3) were detected in five out of 16 (31%) California gray whales processed during 1968–1970 at the San Francisco whaling station (Akers et al., 1974). Vesivirus serotypes have been detected in other baleen whales including fin (*Balaenoptera physalus*), sei (*Balaenoptera borealis*), and bowhead whales (*Balaena mysticetus*) (for review, see Bossart and Duignan, 2018) typically associated with blistering skin disease, with variable lesion size (1–3 cm).

Enterovirus/Calicivirus

In 1968, an entero virus was isolated from the rectum of a gray whale (Smith and Skilling, 1979; Watkins et al., 1969 cited in Smith et al., 1987). Reexamination of the isolate using electron microscopy identified it 20 years later as a calicivirus (Gray VESV-A48) (Smith, 2000). The particular isolate Gray VESV-A48 causes fulminate vesicular disease in exposed pigs.

Equine Encephalitides (WEE, EEE, VEE)

A single case of neutrophilic encephalitis was reported in a juvenile gray whale during the 1999/2000 "Unusual Mortality Event" (UME) (Gulland et al., 2005). This animal live stranded and was euthanized. Serum titers to several alphaviruses including Western equine encephalitis (WEE), Eastern equine encephalitis (EEE), and Venezuelan equine encephalitis (VEE) were detected, with a serum neutralization titer of 1/100 for EEE. Virus isolation was negative from all tissues examined. Histopathology findings in this gray whale were similar to those documented for EEE and Japanese encephalitis virus (JEV) infection in seals (McBride et al., 2008; Jung et al., 2019). In comparison, two "control" blood samples (collected in the 1998 season from two gray whale neonates with no milk in their stomachs) had no detectable titers to these viruses. A third "control" blood sample from a gray whale which, based on presence of maternal immunoglobulins (Reidarson et al., 2001), had suckled prior to stranding and collection, showed a hemagglutination inhibition titer to WEE and EEE of 1/100 but none with serum neutralization. Positive titers from these whales were thought to represent a cross reactivity to a related but unknown virus (Gulland et al., 2005).

Titers against WEE, EEE, and VEE (without alpha virusassociated diseases) have been demonstrated in wild dolphins from Florida (2003-2007), thus transmission of arboviruses to coastal cetaceans likely occurs (Schaefer et al., 2009). Further support for this conclusion is provided by the detection of titers to West Nile Virus (WNV), another virus known to depend on biological transmission by mosquitoes (aka arbovirus), in captive killer whales in association with non-suppurative encephalitis (attributed to WNV) (St. Leger et al., 2011). Surface resting (passive floating) by coastal cetaceans probably increases the likelihood of mosquito bites as suggested by St. Leger et al. (2011). Neonates and calves given their thinner skin and greater propensity to stay quiescent at the surface may therefore be a cohort at greater risk. The plausibility of attributing the observed neutrophilic encephalitis of the gray whale to alpha virus infection remains speculative. However, gray whale MHC-I sequences show similarity to MHC-I in ungulates (Flores-Ramirez et al., 2000), and as alphavirus infection causes fulminant encephalitis in ruminants (Bauer et al., 2005; Schmitt et al., 2007), suggesting alpha virus infection in baleen whales is possible.

As alphavirus activity has not been documented in California, with the exception of a single infection in a vaccinated foal during spring 2000 (Franklin et al., 2002), the gray whale most likely was exposed prior to reaching the California coast. Transmission via mosquitos is the likely exposure route, although direct and mechanical transmissions cannot be excluded (Kuno and Chang, 2005). The role of cyamids and epizoic barnacles, both abundantly present on gray whales, as vectors of viruses has not been explored but deserves attention (La Linn et al., 2001; Overstreet et al., 2009). As only one case was observed, one can only wonder whether this encounter between arboviruses (arthropod-borne virus) and gray whales occurs regularly or occurred by chance.

Parapoxvirus

A proliferative dermatitis with superficial ballooning degeneration and intracytoplasmic inclusions suggestive of parapoxvirus was observed in a stranded dead immature gray whale; however, tissue screening by polymerase chain reaction (PCR) with known parapoxvirus primers was negative (Raverty et al., 2006). Parapox viruses have been isolated and described from the bowhead whale and various toothed whale species (Bracht et al., 2006; Barnett et al., 2015).

Paramyxovirus

A few stranded gray whales have had lesions suggestive of paramyxovirus. In one whale, multisystemic vasculitis was observed (Raverty et al., 2006); in another (the above suspect EEE case), interstitial pneumonia with histiocytosis and formation of syncytia was described (Gulland, pers. comm.). Testing of tissues from both whales for morbillivirus using PCR was negative.

Bacteria, Fungi

A single case of extensive tissue necrosis (unknown etiology) involving the head and rostrum was reported in a landed gray whale from Chukotka (Tomlin, 1967). Localized tissue necrosis presenting as circular skin defects exposing the underlying blubber along the snout was present in another landed whale. A pyothorax with concurrent fibrinous pleuritis-pericarditis of unknown etiology was reported in a stranded yearling (Stroud and Roffe, 1979). Secondary bacterial infection has been observed with intestinal Bolbosoma sp. infestation. Secondary fungal infection (Mucor spp.) was present in a free-ranging gray whale mother/calf pair with freshwater associated skin lesions (Colegrove, 2018). Antibodies to Candida sp. were detected by enzyme-linked immunosorbent assay (ELISA) in serum of one of 21 healthy gray whales (Litkova et al., 2020). Limited screening for Brucella spp. by PCR in samples from multiple stranded juvenile gray whales that underwent post-mortem examination was negative (Raverty et al., 2006).

Protozoa

Sarcocystis spp. were detected in a stranded adult male gray whale in 1999, with no associated inflammation (Gulland, pers. comm.). Incidental sarcocystosis has been detected in other baleen whales including sei and bowhead whales (Akao, 1970; Stimmelmayr et al., 2021). Two of 21 gray whales hunted for subsistence during 2018-2019 were positive for Toxoplasma gondii by (ELISA) (Litkova et al., 2020). Given the coastal behavior of gray whales, exposure to T. gondii is not surprising. Terrestrial runoff leading to environmental contamination of near shore water and prey have been implicated as the major factors driving T. gondii infection in California sea otters (Conrad et al., 2005). T. gondii has been detected (light microscopy, PCR, immunohistochemistry, serology) in three other baleen whales, a fin whale (Mazzariol et al., 2012), a humpback whale (Megaptera novaeangliae) (Forman et al., 2009), and in a Bryde's Whale (Balaenoptera edeni) (Diaz-Delgado et al., 2020).

Helminths

Of the helminth parasites reported in gray whales (for review, see Kuramochi et al., 2017) only a few, Anisakis, Ogmogaster, Bolbosoma, and Lecithodesmus, have been associated with gastrointestinal lesions. Observed lesions include mild gastritis with heavy anisakid burden (single animal), colitis and proctitis associated with trematode infestation, and focal transmural abscessation in two cases (ileum; unspecified intestinal section) associated with Bolbosoma sp. infestation in three juvenile stranded gray whales (Rice and Wolman, 1971; Dailey et al., 2000; Gulland et al., 2005). Bacterial isolates from the transmural abscesses (remarkably extending along 75 m of the ileum) from one animal included Edwardsiella tarda, Escherichia coli and Clostridium perfringens (Dailey et al., 2000). Fluke infection (Lecithodesmus golitath) in two landed gray whales was associated with inflammation of the biliary duct system and characterized by "distorted, inflamed biliary epithelium and were rimmed with thick walls of dense scar tissue" (Rice and Wolman, 1971). Litkova et al. (2020) recently completed a multi-year survey for Trichinella spp.

in gray whales hunted for subsistence along the Chukotka coast where infection is observed in <2% Pacific walrus (*Odobenus rosmarus divergens*). No *Trichinella* larvae were detected in 53 gray whales, and no serum antibodies to *Trichinella* spp. were detected by ELISA in 21 gray whales. Investigations for trichinosis in toothed and baleen whales are rare (Rausch et al., 1956; Smith, 1976) but given the zoonotic potential and food safety concerns, screening of gray whales hunted for subsistence is relevant.

Whale Lice and Barnacles

Gray whales are commonly infected with whale lice (Cvamis ceti, Cyamis kessleri, Cyamis boopis) and epizoic barnacle colonies (Cryptolepas rhachianecti) (Hurley and Mohr, 1957; Rice and Wolman, 1971). Barnacle infections of young of the year occur in nursery lagoons and become fully established during the northward migration. Cyamid infection is thought to be direct (from animal to animal) and ample opportunities for cyamid transfer occur during suckling and close contact. The level of cyamid infection varies among individuals but this has not been systematically assessed. For example, all gray whales landed in Chukotka were reported to carry cyamids, without a clear pattern. Some animals carried cyamids in layers several cm deep (Berzin and Vlasova, 1982). Landed whales examined at Point Barrow, and California during the 1960s all carried cyamids (Leung, 1976). The abundance of cyamids on gray whales that have been to brackish waters is markedly reduced. Survival of whale lice off the host can be several days, thus providing a crude but useful proxy to narrow the window of time of death of whales (Leung, 1976). Cyamids show body site specificity on the host (Cyamis scammoni belly; jaw line; C. ceti, creases of the lips, flippers, and flukes; C. kessleri umbilicus, genital opening, and anal aperture of the host). Whether gray whales actively engage in ectoparasite removal is unclear, but breaching, and rubbing behavior against rocks has been interpreted that way. It is also suggested that gray whales' visitation of freshwater lagoon systems may reduce ectoparasite load (Yablokov and Bogoslovskaya, 1984). Reports from Russia indicating that gray whales allow seagulls to peck at their backs while passively floating nearshore have been interpreted as cooperative behavior. Rare observations of parasitic behavior of gulls feeding on live stranded neonate gray whales were made in the nursery lagoons (Eberhardt and Norris, 1964). Parasitic behavior of gulls on southern right whale calves (Eubalaena australis) has emerged as a significant health problem in Argentinian waters (Fiorito et al., 2016; McAloose et al., 2016).

TOXINS AND CONTAMINANTS

Biotoxins

Domoic acid (DA) was detected in a juvenile whale that stranded alive and was euthanized during the 1999/2000 UME, suggesting DA toxicosis may have contributed to stranding (Gulland et al., 2005). DA was detected in the serum, urine, and feces of this whale by receptor binding assay and was confirmed in the urine and feces by HPLC-MS/MS with levels of 1.6 and 0.528 μ g/ml, respectively. On histology ulcerative glossitis and

neuronal changes of the frontal cortex and hippocampus were observed. DA associated mortalities occurred in California sea lions (*Zalophus californianus*) during that period (Gulland et al., 2002). In the ongoing 2019–2020 gray whale UME very low levels of biotoxins (DA/STX) were detected in limited samples from six animals (Raverty et al., 2020). The limited data available suggest gray whales are exposed to marine biotoxins, the occurrence of which are increasing throughout the gray whale's range (Lefebvre et al., 2016). Thus, future research should focus on investigating the effects of biotoxin exposure on health, reproduction, and survival of gray whales.

Oil

Gray whale mortalities were observed after the 1969 Santa Barbara and 1989 Exon Valdez oil spills (Moore and Clarke, 2002). Behavioral observations of gray whales encountering slicks did not reveal avoidance and whales were observed lying in or swimming through oil slicks during both spills (Evans, 1982; Harvey and Dahlheim, 1994). Stranded gray whales examined after the Exon Valdez oil spill had oil in their baleen but not in their digestive systems. The observed post spill mortalities (25 in Alaska, six in Santa Barbara) were not attributed to the respective spills. Given our greater understanding of the impact of oil on cetaceans after research on the effects of the Deepwater Horizon spill (i.e., acute and chronic effects) in particular inhalation toxicity of compounds at the air water interface (for review, see Takeshita et al., 2017), the above conclusions need to be revisited.

Persistent Organic Pollutants, Mercury

Reported blubber contaminant levels and heavy metals in blubber and epidermis in gray whales are lower than levels in odontocetes from the North Pacific, presumably due to their feeding on benthic invertebrates rather than prey from higher trophic levels (reviewed in Varanasi et al., 1993; Krahn et al., 2001; Tilbury et al., 2002; Ruelas-Inzunza et al., 2003; Dehn et al., 2006; Dudarev et al., 2019a,b,c,d; Lian et al., 2020; Litkova et al., 2020). Differences in reported blubber concentrations of organochlorines between stranded and hunted gray whales have been attributed to changes in blubber lipid composition post-mortem (Chukmasov et al., 2019). The health effects of the measured contaminant levels in gray whales are unknown, but upregulation of genes involved in detoxification has been described in liver tissue from stranded gray whales (Moskalev et al., 2017).

Chlorophenate

In 1985 unusual mortality of several gray whales occurred after a toxic spill involving chlorophenate (45,000 L) in the Serpentine River near White Rock, BC (Coloday, 1986). Nine animals washed up in the Georgia Strait and Puget sound area. The gray whale mortality coincided with a large freshwater fish kill, mostly of salmonid fish. Mortality among marine species (sculpins; flounders) occurred to a lesser extent. Chlorophenate at levels ranging from 1.5 (muscle tissue) to 300 ppb (liver) was detected in various samples (feces, digestive tract, liver) from two whales. One whale had bilateral serosanguineous pleural effusion (6000 cc) and acute massive hemorrhagic liver necrosis suggestive of a toxic insult (Gornall and Fouty, 1990). As no histopathology and further diagnostics besides toxicology were done in this whale, other causes, i.e., viral, bacterial, for observed liver lesions cannot be excluded.

Plastics and Marine Litter

Marine debris is a global issue (IWC 2019 Marine Debris workshop) and not surprisingly plastics, wood, and miscellaneous human garbage have been detected in the stomachs of stranded gray whales as bottom feeding gray whales frequently ingest sand, gravel, and cobbles (i.e., Kasuya and Rice, 1970; Cascadia Research Collective²). Rare cases of impalement injuries of the head by metal and wood debris in free-ranging and dead gray whales have been reported (Calambokidis and Huggins, 2008). The latter unusual injuries are probably also related to their neritic foraging. Interestingly, Kasuya and Rice (1970) provided limited but solid evidence that more head and skin injuries from hard bottom contact during feeding, greater baleen wear (shorter) and reduced barnacle burden appear to be right-side biased (right mouth-ness).

TRAUMA

Predation

Orca predation is the primary cause of death in stranded immature gray whales along the northern portion of the Alaskan migratory corridor (Willoughby et al., 2020). Off central California, Rice and Wolman (1971) reported parallel scars from the teeth of killer whales on 57 (18%) of the 316 gray whales taken during scientific whaling operations. During the 2019 UME, 19 animals had evidence of mortality due to killer whale attack, and an additional eight whales with fresh rake marks were observed (12% of whales examined had evidence of killer whale bites) (Raverty et al., 2020). In this UME, many animals were too decomposed for full necropsy examination, so this may be an under-estimate of the number of cases of orca predation.

Entanglement

Fisheries interaction (net and line entanglement) is well documented as a cause of death in yearling calves along the California migratory corridor (Swartz and Jones, 1983; Heyning and Lewis, 1990; Barlow et al., 1994). The types of fisheries involved in calf entanglement events include salmon drift gillnet, salmon seine, longline, and trap fisheries. Additional records detail rare individual entanglement and drowning in a herring net pen, as well as an individual entangled in a herring set gillnet. Entanglement (dead or live) of immature and mature animals in commercial and artisanal fishing gear continues to be common on the US West coast and Sakhalin islands (Baird et al., 2002; Scordino and Mate, 2011; Scordino et al., 2014; Lowry et al., 2018; NOAA Fisheries, 2019). Additional single entanglement cases have been reported from Japan, China, and Korea (for review, see Kuramochi et al., 2017). Rare marine debris entanglements (e.g., in a metal frame) have been reported in the media³. Tail amputations as a sequela to entanglement (fisheries interaction) have been reported in the 1960s (Gilmore, 1961) and more frequently since the 2000s (Urbán et al., 2004⁴). Sightings of whales with missing flukes have been restricted to the southern range (i.e., California, Oregon, Mexico) with no cases in the Alaska stranding dataset and 2009–2019 aerial survey data (Willoughby et al., 2020).

Vessel Strike

Vessel strike causing death due to extensive trauma (fractured skulls, vertebrae and ribs, subcutaneous hemorrhages) has been documented along the Pacific coast and in southeast Alaska, especially in the proximity of ports, such as Los Angeles, San Francisco Bay, and Seattle (Norman et al., 2000; Douglas et al., 2008; Scordino and Mate, 2011; Neilson et al., 2012; Scordino et al., 2014; Raverty et al., 2020). Although strikes are frequently fatal, an example of a live gray whale with multiple parallel scars on the lateral head caused by sharp trauma from propeller blades has been reported (Furuta, 1984). The frequency of vessel strikes to gray whales resulting in mortality during the 2019 UME has been reviewed by Raverty et al. (2020) and was most commonly reported in areas near busy ports.

Entrapment

Gray whales have been observed in spring and summer leads among moving ice off Barrow and towards Wrangel Island, Russia (Tomlin, 1967). Limited gray whale hunting has historically occurred in Wainwright and Utqiagvik (formerly Barrow) Alaska during summer and fall months (Marquette and Braham, 1982). A single case of ice entrapment involving three animals, a calf and two adults, was reported of Barrow during October 1988 (Caroll et al., 1989). The whales were spotted at Point Barrow in the Beaufort Sea pack ice by an Inupiaq hunter. Recent acoustic studies indicating gray whales calls near Barrow, Alaska, throughout the winter of 2003-04, suggests over wintering seems to occur (Stafford et al., 2007). It is unclear if the "overwintering" was involuntary and reflected ice entrapment. With ongoing northward range expansion into the eastern Beaufort Sea (Rugh and Fraker, 1981; in September 2019, 15 adult whales with calves observed off Tuktoyaktuk Peninsula, Canada⁵) coupled with increasing unpredictability of the timing of ice formation, the risk of ice entrapment of gray whales could increase. Gray whales do not have the ability to break sea ice like the bowhead whale and skin laceration with substantial bleeding was observed in entrapped gray whales coming into contact with sea ice (Craig George, pers. comm.).

MALNUTRITION

Malnutrition leading to emaciation was the presumptive cause of death for the 1999/2000 UME (Le Boeuf et al., 2000) and

²http://www.cascadiaresearch.org/projects/stranding-response/examinationgray-whale-west-seattle-reveals-unusual-stomach-contents-no

³https://www.klcc.org/post/where-whale-stuck-metal-frame-west-coast ⁴https://www.nationalgeographic.com/news/2018/05/whales-animalsentanglement-fishing/

⁵https://www.fisheries.noaa.gov/science-blog/2019-aerial-surveys-arctic-marinemammals-post-5

may be contributing to mortality in the current 2019/2020 UME (see Raverty et al., 2020). The ecological processes leading to starvation are unclear however. Interannual variation in the sites and duration of the foraging season due to sea ice dynamics is thought to play a role in body condition changes and calving rates (Moore et al., 2001; Perryman and Lynn, 2002; Perryman et al., 2002; Gailey et al., 2020). Disturbance has also been proposed to contribute to poor body condition (Gailey et al., 2016; Villegas-Amtmann et al., 2017). Calf mortality may be high in some years, with estimates from breeding lagoons between 2.8 and 5.4%, and further mortality occurring along the migration route from Mexico to California (White and Griese, 1978; Swartz and Jones, 1983; Sumich and Harvey, 1986; Sánchez Pacheco, 1998). The role of maternal nutritional status in calf mortality is unclear. Interestingly adoption of orphaned suckling calves by lactating females has been reported (Tomlin, 1967).

As whales are at the late stages of fasting during the northward migration, distinguishing animals in thin condition due to fasting (from which summer recovery occurs) from emaciated whales dying from starvation is challenging in decomposing carcasses. Photography of bony prominences and shape are useful in live animals, but post-mortem changes and positions when beached alter these assessments in dead animals. Loss of internal fat stores, including fat below the blubber layer, discoloration of blubber, and pericardial fluid presumed to be associated with hypoproteinemia, have been observed in emaciated whales (Gulland et al., 2005). Splenic and hepatic hemosiderosis presumed a consequence of emaciation has also been observed in stranded, dead, northward bound gray whales (Dailey et al., 2000; Raverty et al., 2006, 2020), although rare hepatic hemosiderosis (<0.5%) has been observed in healthy bowhead whales hunted for subsistence (Stimmelmayr et al., 2020). Variable systemic edema suggestive of hypoproteinemia was present in a number of stranded gray whales that presented with tissue hemosiderosis (Raverty et al., 2006).

MISCELLANEOUS

Miscellaneous incidental findings in gray whales stranded in Alaska have included aging related yellowing of the ocular lens and juvenile cataract, and an unusual case of blunt trauma to the "stink sac," the post-anal cyst (Stimmelmayr, 2020; Stimmelmayr et al., 2020). Developmental anomalies are rare with no reports found in the historic US-Russia whaling literature (Tomlin, 1967; Rice and Wolman, 1971), but one report of an extra digit in a calf (Cooper and Dawson, 2009) and a conjoined twin (TBL 14.1'; thoracophagus) (Tamburin et al., 2017) stranded in Mexico. Twinning is exceedingly rare with only one report of twins reported in a landed female gray whale in San Diego (Tomlin, 1967).

Skin Lesions

Skin blistering similar to lesions attributed to ultra violet damage in other baleen whales (Martinez-Levasseur et al., 2011; St. Leger et al., 2018) has been observed in a stranded live gray whale (Cascadia Cetacean Research⁶ skin blistering). Skin lesions associated with protracted freshwater exposure have been documented in a gray whale that went up the Klamath River, in Oregon (and gray whales have been reported in other rivers, the Zhupanova River, Russia 1912; Kuskokwim River, Alaska 2017). Histopathological findings included epidermal hyperplasia with regions of epidermal degeneration, edema and necrosis, ulcerations, and colonization with algae, diatoms, and fungi (Colegrove, 2018). In living gray whales, satellite tag implantation has been associated with swellings and skin depression (Norman et al., 2018). Post deployment swelling occurred in 74% of reencountered gray whales. Scaring response to entanglement, ectoparasites, tagging wounds is thought to be more pronounced in gray whales than other baleen whales.

Stinky Whales

A phenomenon referred to as the "stinky gray whale phenomenon" reported from Russia is characterized by a "medicinal smell" to the blow and/or meat/blubber. It is primarily a public health issue (food security and food safety) as affected whales are not considered desirable to eat, with no apparent ill effects (i.e., pathological findings; body condition decline) noted in affected gray whales. "Stinky whales" were first observed in the 1960s (Ilyashenko, 2007; Rowles and Ilyashenko, 2007; Litovka and Blokhin, 2009; Blokhin and Litovka, 2011) with increasing numbers noted since 1998. Consumption of meat and blubber from stinky whales has been associated with transient clinical symptoms of "numb mouth, stomach upset and skin rashes" in people, with no reported long-term medical consequences. Dogs reject (will not eat) meat/blubber from stinky whales. In recent years, similar odors have been reported by Russian hunters and communities from the muscle of ringed seals, bearded seals, walruses, fish (cod), and the eggs of murres. Despite analysis of volatile compounds in samples from Russian whales, the etiology of this phenomenon (i.e., toxins (legacy pesticides, POPs, poly-aromatic hydrocarbons; heavy metals), marine biotoxins, nutritional (i.e., dietary shifts, fatty acid profiles), microbes (i.e., microbiome), remains undetermined (for review, see Rowles and Ilyashenko, 2007; Denisenko et al., 2012; Litkova et al., 2020).

FUNDAMENTAL ISSUES, RESEARCH GAPS, AND FUTURE DIRECTIONS

As most data available to date on diseases of gray whales are from gross examinations of stranded animals that are frequently decomposed, tissues may often be of limited value for histology and pathogen isolation. Thus, our understanding of the epidemiology and pathogenicity of viruses, bacteria, and parasites in these whales remains limited to a few case reports. As some of the pathogens identified can have varying impacts on the host depending upon intensity of infection and host resistance (in turn influenced by nutritional status), to resolve

⁶https://www.sanjuanjournal.com/news/whale-necropsy/

the role of pathogens in gray whale morbidity and mortality, and hence population dynamics, future efforts should focus on enhancing our understanding of the host/pathogen interaction and pathogen epidemiology. This will require prioritizing fresh carcasses for immediate examination; using techniques to characterize and quantify infections that are not compromised by post-mortem change (examining and sampling live animals with photography, biopsy, and drones); quantifying helminth burdens in dead animal digestive tracts and exploring relationships between parasite burden, pathology and prey type; and improved infectious disease screening using PCR and -omics. Continued basic health investigations and pathogen screening of healthy gray whales hunted for subsistence in Chukotka, Russia will be important to provide context for pathological findings in stranded animals.

The second challenge to our understanding of gray whale health is distinguishing excessive starvation that causes mortality from the changing nutritional status during the annual migration. To address this knowledge gap, future efforts must characterize the annual nutritional cycle and its relationship to reproduction. This will require standardizing assessment of nutritional status in live and dead whales, including evaluation of quantity and quality of lipid stores, and integrating assessment of individual dead whales with large scale interannual assessment of live whale body condition. In addition, effects of changes in prey availability and host density on whale body condition can be explored by comparing the condition of western and eastern gray whale populations across years (Weller et al., 2002; Bradford et al., 2012).

A third challenge to understanding the role of disease and health changes in gray whale population dynamics is the limited development of health assessment tools that can evaluate underlying health of an animal in addition to identifying proximate traumatic causes of death (vessel strikes, entanglements, killer whale attacks). Novel methods of health assessment through use of blow samples, baleen plates, and fecal analyses for endocrine and stable isotope research will be important in future studies of gray whale morbidity and mortality (Hunt et al., 2013; Cumeras et al., 2014). Increasing exposure to harmful algal blooms throughout the gray whale's range (as is occurring in other baleen whale's ranges) is an emerging threat that can reduce reproduction and cause mortality (Goldstein et al., 2009; Doucette et al., 2012). Future research on developing methods to evaluate exposure and effects will be increasingly important. Hunt et al. (2017) demonstrated that baleen plates, although short in gray whales (\sim up to 48 cm) are useful for the analysis of various hormones. A single baleen plate records about 1.3-1.4 years in the life of a gray whale. Litkova et al. (2020) recently analyzed baleen plates for cortisol and reproductive hormones (progesterone and testosterone) in gray whales hunted for subsistence along the Chukotka coast. Hayden et al. (2017)

explored the use of blubber for measuring steroidal hormone levels which will be very useful for free-ranging gray whale studies.

The gray whale's habitat is changing dramatically with climate change, leading to speculation on how these changes impact this iconic species (Moore and Gulland, 2014). Mortality events along the coastal migration receive considerable attention as carcasses are easily observed by the public. Yet despite the relative accessibility of this whale species compared to other more pelagic oceanic species, our knowledge of its health and disease, and resilience to pathogens and prey changes, remain limited. The recent characterization of the gray whale transcriptome is exciting as it sets the stage for pursuing further omics research on gray whale health (DeWoody et al., 2017; Moskalev et al., 2017). Furthermore, the gray whale MHC I is characterized by polymorphism indicating continued positive selection, suggesting adaptability to changes in pathogen pressure (Flores-Ramirez et al., 2000). The gray whale thus offers us an ideal model whale species to explore the effects of prey changes on nutritional status, toxin and pathogen exposure, and susceptibility to trauma through changes in habitat. To take advantage of this model, we will need to enhance efforts to understand its health and disease by continued inter-disciplinary collaboration and development of new research approaches.

ETHICS STATEMENT

All information reported here was compiled from previously published reports. No animals were handled or sampled for this review. All whales reported on were examined legally under laws of the countries where animals were found (Mexico, United States, Canada, Russia), and international conventions (International Whaling Commission, Convention for Trade in Endangered Species).

AUTHOR CONTRIBUTIONS

Both authors jointly reviewed the literature and wrote the manuscript.

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Conflict of Interest: The authors declare that the research was conducted in the absence of any commercial or financial relationships that could be construed as a potential conflict of interest.

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