

Review



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Advances in research on the impacts of anti-submarine sonar on beaked whales

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Mass stranding events (MSEs) of beaked whales (BW) were extremely rare prior to the 1960s but increased markedly after the development of naval mid-frequency active sonar (MFAS). The temporal and spatial associations between atypical BW MSEs and naval exercises were first observed in the Canary Islands, Spain, in the mid-1980s. Further research on BWs stranded in association with naval exercises demonstrated pathological findings consistent with decompression sickness (DCS). A 2004 ban on MFASs around the Canary Islands successfully prevented additional BW MSEs in the region, but atypical MSEs have continued in other places of the world, especially in the Mediterranean Sea, with examined individuals showing DCS. A workshop held in Fuerteventura, Canary Islands, in September 2017 reviewed current knowledge on BW atypical MSEs associated with MFAS. Our review suggests that the effects of MFAS on BWs vary among individuals or populations, and predisposing factors may contribute to individual outcomes. Spatial management specific to BW habitat, such as the MFAS ban in the Canary Islands, has proven to be an effective mitigation tool and mitigation measures should be established in other areas taking into consideration known population-level information.

1. Introduction

Typical mass stranding events (MSEs) of cetaceans are defined as those in which two or more individuals strand alive at approximately the same place and time [1]. Various species of odontocetes have been reported in MSEs around the world, but underlying causes are often unknown. In contrast, causes of atypical MSEs (AMSEs) of beaked whales (BW), defined as two or

more whales found within a 6-day period up to 74 km apart [2,3], are most often associated with sound [4].

The temporal and spatial association of Cuvier's BW (*Ziphius cavirostris*) MSEs with naval exercises was first identified in the Canary Islands in the late 1980s [5]. The link between MSEs and mid-frequency active sonar was more definitively established during a similar stranding event in Greece in 1996 and another in the Bahamas in 2000 [6].

Naval mid-frequency active sonar (MFAS) was developed in the 1950s to detect submarines, using frequencies of 8 KHz or higher [3,7]. However, the BW AMSEs, mainly of Cuvier's BWs, did not occur until MFAS shifted to lower frequency ranges of 4.5–5.5 kHz [8]. Mass strandings of BWs were extremely rare worldwide before the 1960s (15 reported cases involving five species), and none were AMSE, but between 1960 and 2004, 121 BW MSEs were reported [3] and the number of species involved increased. The first reported Cuvier's BW AMSEs occurred in France (Corsica), followed by others in Italy, USA and the Bahamas during the 1960s [3]. At least 37 of these events were AMSEs that involved three or more individuals and were either strongly correlated in time and space with naval activities, or occurred in naval training areas where US Navy and/or NATO fleets were based or operated [3,7]. All 121 MSEs occurred in the Northern Hemisphere and 61 involved Cuvier's BW [3]. This led us to focus on Cuvier's BWs for much of our recent research.

Fourteen BWs stranded in the Canary Islands (Spain) in September 2002 during a NATO naval exercise using MFAS. Necropsies performed on 10 whales demonstrated disseminated microvascular haemorrhages associated with widespread gas and fat emboli within blood vessels and vital organs, consistent with decompression-like sickness [9,10]. Decompression sickness (DCS) is a syndrome defined by a set of symptoms that reverse upon recompression. It is described in scuba divers as being caused by the formation of intra- and extra-vascular gas bubbles, when the tension of dissolved atmospheric gases exceeds the local absolute pressure [11]. Similar pathology was found in Cuvier's BW from five AMSEs associated with MFAS in the Mediterranean region [12].

Although Scholander suggested in 1940 that marine mammals may experience gas emboli following repeated breath-hold dives [13], it had generally been assumed that marine mammals have evolved anatomical, physiological and behavioural adaptations that prevent and/or mitigate gas emboli [14]. Thus the AMSE-associated pathology generated scientific controversy and was intensely discussed at a multidisciplinary workshop on beaked whales and military sonar in Baltimore, USA, in 2004 [6]. Over the last 15 years, researchers from various disciplines have investigated questions raised after the first observations consistent with DCS in BWs. While the collective knowledge of BW biology has increased, many new questions have been raised as additional insights were gained.

In September 2017 a workshop organized by the Institute of Animal Health of the University of Las Palmas de Gran Canaria was convened in Fuerteventura, Canary Islands, Spain to assess current knowledge on BWs and AMSEs. This workshop brought together 21 BW experts in different fields such as BW population assessments, behaviour, anatomy, physiology and pathology. This review summarizes the content discussed during the workshop, and focuses on questions posed regarding DCS and its role in recent AMSEs. Thus, we start by reviewing DCS findings in BWs, and then review

current knowledge of BW anatomy, physiology, diving behaviour and responses to sonar that may be relevant to AMSEs. We finish by reviewing the impact of AMSEs on beaked whales and mitigation measures to prevent AMSEs, and proposing future research directions.

2. What are the known diagnostic features of beaked whale strandings associated with naval exercises using mid-frequency active sonar?

To establish causes of death of stranded BWs, it had been recommended that detailed necropsies be performed on freshly dead individuals, regardless of potential association with MFAS, following standardized protocols [6,14]. This was achieved in Almería (Spain) in 2006 and 2011, and Corfu (Greece) in 2011 [15,16]. The pathological findings in these events were similar to those previously described in the Canary Islands in 2002 [9], but with the development of new methodologies and protocols, the bubble gas composition was analysed, demonstrating that the gas came from nitrogen (N_2) saturated tissues, as in DCS [16]. This was revealed from a single beaked whale that stranded in temporal and spatial association with a military exercise, suggesting that single strandings could also result from MFAS use.

To date, epidemiological and pathological data from AMSEs in the Canary Islands (2002/2004), Almería (2006/2011), and Greece (2011/2014) suggest the following diagnostic features for gas and fat embolic syndrome in BWs stranded in association with naval exercises [9,17]:

- (1) individual or multiple animals stranded within hours or a few days of an exercise in good body condition;
- (2) food remnants in the first gastric compartment ranging from undigested food to squid beaks;
- (3) abundant gas bubbles widely distributed in veins (subcutaneous, mesenteric, portal, coronary, subarachnoid veins, etc.) composed primarily of N_2 in fresh carcasses;
- (4) gross subarachnoid and/or acoustic fat haemorrhages;
- (5) microscopic multi-organ gas and fat emboli associated with bronchopulmonary shock;
- (6) diffuse, mild to moderate, acute, monophasic myonecrosis (hyaline degeneration) with 'disintegration' of the interstitial connective tissue and related structures, including fat depots, and their replacement by amorphous hyaline material (degraded material) in fresh and well preserved carcasses; and
- (7) multi-organ microscopic haemorrhages of varying severity in lipid-rich tissues such as the central nervous system, spinal cord, and the coronary and kidney fat when present.

All the fresh Cuvier's BWs that mass stranded in the Canary Islands (2002/2004), Almería (2006/2011), and Greece (2011/2014) had these seven diagnostic features. However, individual BWs that stranded alone on the Canary Islands between 2002 and 2015 ($n = 45$) beached with no correlation in space or time with MFAS. These individuals had one or more of the diagnostic features for gas and fat embolic syndrome in BWs stranded in association with MFAS exercises, but not all seven [9,17]. Death in these individuals was due to natural and human related causes, (ship collisions, foreign

body-associated pathology, and fisheries interactions) [18,19]. There was also a high prevalence of inflammation of the aorta and nematodes (*Crassicauda* sp.) in the kidneys of Cuvier's BWs that stranded individually [20], as well as those stranded in Almeria and Greece AMSEs (A. Fernández 2019, unpublished data).

3. Could many of the diagnostic features of beaked whales stranded in temporal and spatial association with naval exercises have been caused by the stranding event?

Pathological findings associated with stress-related capture-myopathy syndrome (CM), have been associated with the process of stranding [21]. In the AMSEs of BWs linked to sonar, 'disintegration' of the interstitial connective tissue and related structures was observed, in addition to the characteristic CM findings, which has only been described to date in BWs stranded in association with military exercises [17].

Fat embolism in humans has been associated with explosive DCS, together with dysbaric osteonecrosis, but has also been associated with bone fractures, and fat and soft tissue injury, diabetes, burns, pancreatitis [22,23]. Thus, a traumatic live beaching may cause or exacerbate fat embolism. However, the three animals found floating alive in the 2002 AMSE in the Canary Islands had fat emboli [9], as did four BWs that were found floating in a state of advanced decomposition in the 2004 Canary Islands event [24], the former animals demonstrating that fat emboli can occur prior to beaching.

Gas bubbles were also observed in floating BWs in the 2002 AMSE [9]. If beaching caused gas bubbles rather than decompression, gas bubbles should be observed in animals stranding alive unrelated to naval exercises. A study of freshly dead cetaceans did not find significant differences in the presence of gas bubbles in animals that beached alive compared with animals that were found floating offshore with absence of external signs indicative of prior stranding [25]. Stranding may exacerbate the presence of gas bubbles, but stranding itself has not been proven to cause large amounts of, or widely distributed, gas bubbles as in DCS cases. Thus, we do not know of any case of DCS that has been attributed to the stranding event alone.

4. Can gas bubbles be introduced during dissection? What is the composition of gas in bubbles?

Post-mortem studies in laboratory animals demonstrated that gas bubbles were not introduced into carcasses if an appropriate dissection protocol was followed [26]. Furthermore, *post-mortem* off-gassing was not relevant if the animal died after surfacing (decompression), and if large volumes of gas were found intravascularly in fresh animals dead after decompression, it was due to *in vivo* gas embolism.

Recent methodologies to sample, transport and analyse the constituents of intravascular gas bubbles have been developed [16] which distinguish gases produced by bacteria (e.g. clostridium) from gases produced during decompression [27,28].

5. Are there other indications of *in vivo* gas bubble formation in marine mammals or other diving animals? Are only beaked whales susceptible to decompression sickness?

Dysbaric osteonecrosis (DON) and liver cavities have been described in sperm whales (*Physeter macrocephalus*) and other cetacean species respectively [29,30]. DON is necrosis of bone caused by the blockage of blood vessels by a gas bubble, and is recognized in human divers [23]. Thus, DON is indirect evidence of *in vivo* gas bubble formation in marine mammals.

Ultrasound has been used to investigate intravascular gas bubbles in live marine mammals. Intravascular bubbles were not found in a trained common bottlenose dolphin (*Tursiops truncatus*) following repetitive shallow dives [31]. In contrast, gas bubbles were detected in kidneys and the hepatic portal vasculature of live-stranded short-beaked common and Atlantic white-sided dolphins (*Delphinus delphis* and *Lagenorhynchus acutus*), but not in live temporarily captured wild bottlenose dolphins [32]. Gas bubbles were observed in the brain of a single live California sea lion (*Zalophus californianus*), the cause of which was unknown [33].

Recently, pathological findings and gas composition analysis consistent with DCS were diagnosed in two Risso's dolphins (*Grampus griseus*), probably due to a stressful prey interaction [34] and individual predisposing factors similar to those described in human divers [35]. Clinical diagnosis of DCS has been demonstrated in live bycaught sea turtles showing symptoms that reversed upon recompression treatment [36].

6. How can decompression sickness occur in marine mammals?

Marine mammals were long considered protected from gas emboli and DCS symptoms. Some authors believed micro gas nuclei could not form in marine mammals given their anatomy and diving behaviour [37]. Additionally, alveolar collapse and perfusion matching would limit the amount of N₂ taken up by the tissues, thereby reducing the risk of DCS [13]. Alveolar collapse at shallow depth via specialized respiratory anatomy has been proposed as the main mechanism that limits uptake of N₂ in the tissues [13]. Cardiovascular changes associated with diving also alter gas exchange, and the blood and tissue N₂ tension will depend on alveolar collapse depth, cardiac output, blood flow to each tissue [38], compartment size and nitrogen solubility. A novel hypothesis proposes that pulmonary ventilation-perfusion mismatch would allow marine vertebrates to selectively exchange gases, thereby minimizing N₂ uptake while allowing O₂ and CO₂ exchange at depths above which the alveolae collapse [39].

Regardless of these adaptations, marine mammals may develop gas emboli under certain conditions [8,35]. Several mechanisms have been proposed to explain how sonar might lead to stranding and/or death of BWs including: (a) swimming away from the sound source into shallower waters and beaching, (b) a behavioural response disrupting their diving profile and resulting in nitrogen accumulation, bubble formation, and tissue damage, (c) physiological changes that

secondarily result in nitrogen accumulation, bubble formation and tissue damage, or (d) direct damage of tissue by sound exposure [6]. Given the current scientific information, gas embolism following behavioural and physiological responses to sound is considered the most plausible explanation [40].

7. What parameters are involved in the beaked whales' management of N₂?

(a) Alveolar collapse depth

Depth estimates for alveolar collapse differ widely among studies, with recent research suggesting that collapse occurs much deeper than initially thought [41,42]. Variations in the apparent alveolar collapse depth are caused by differences in experimental methods and inter- and intra-specific variations in lung size, diving lung volume, and structure of the respiratory system [43]. The alveolar collapse depth is affected by the compliance of different parts of the respiratory system, and the diving lung volume; a lower volume results in shallower alveolar collapse depth [41,43]. Initial dive lung volume can be voluntarily adjusted based on expected dive depth and duration [44].

Unfortunately, there are no empirical data on alveolar collapse for any BW species. The compliance of the trachea of True's BW (*Mesoplodon mirus*) has been investigated and is more rigid than the trachea of other odontocete species [45]. Thus alveolar collapse might occur at shallower depths in BWs, reducing N₂ uptake during diving [45].

(b) Body compartments

The size of a body compartment affects the time taken to reach equilibrium after a change in pressure [46]. Body compartment sizes can be calculated from body composition analyses which describe body tissue types as a percentage of total body mass. True's, Blainville's (*M. densirostris*) and Sowerby's (*M. bidens*) BWs possess lower visceral mass (4.8%) and higher muscle mass (48.5%) compared with shallow divers (bottlenose dolphin and harbour porpoise, *Phocoena phocoena*: 14.7–15.8% viscera mass and 28.1–30.6% muscle mass), while integument (19.4%) and bone (9%) mass are similar [46]. Specific body compartment mass data for Cuvier's BW are absent for most compartments.

(i) Lung size

Recent studies have demonstrated that there are two groups of cetaceans differentiated by lung size: (1) short-duration, shallow divers (most dolphin and porpoise species), and (2) long-duration, deep divers (Physeteridae, Ziphiidae and Kogiidae) [43]. Relative lung mass to total body mass of True's, Blainville's and Sowerby's BWs is 1.4% compared with 3.4% for the bottlenose dolphin [46]. Diving respiratory volume of a sperm whale is 28 ml kg⁻¹ compared with 40 ml kg⁻¹ of the bottlenose dolphin [47].

(ii) Blood volume

Marine mammals can have as much as 3 times the blood volume, 1.5 times haemoglobin concentration and 10 times the myoglobin concentration of a human. Empirical measurements of blood volumes in cetaceans are complicated and there is only one measurement in a deep-diving species: the sperm whale [48]. Estimated total blood volume for dolphins

and porpoises ranges from 7–14% of total body mass [49] compared with 12–20% of total body mass in deep divers: Total blood volume for True's, Blainville's and Sowerby's BWs is 14.8%, for short-finned pilot whale (*Globicephala macrorhynchus*) 12%, and for sperm whale 20.1% [48,50], while human blood volume is 7–8% of body weight [51].

(iii) Muscle mass

Locomotor muscle mass in True's, Blainville's and Sowerby's BWs is around 50% of total body mass compared with 28–30% in shallower diving species [46]. Recent studies in deep-diving cetaceans suggest that they share muscle features such as large muscle fibres, high myoglobin content, low mitochondrial volume densities, intramyocyte lipid droplets and higher percentage of intramuscular adipose tissue [50,52]. Cuvier's BW present one of the largest fibre sizes for any marine mammal to date [52]. Mesoplodonts have one of the highest myoglobin concentration values reported for any mammal [46], and their muscle is composed primarily of fast, glycolytic fibres [50].

(c) Gas solubility

N₂ solubility in most marine mammal tissues has not been determined, but advances have been made in understanding the lipid composition of, and N₂ solubility in, blubber, acoustic fat and melon [53]. The blubber of most shallow-diving species is mainly composed of triacylglycerides with few or no wax esters (0–10%), while the blubber of deep divers contains wax esters in higher proportions, ranging from 62% in kogiids to over 99% in BWs. Wax esters have a higher N₂ solubility [54]. In addition, the acoustic fats contain a mixture of waxes and triacylglycerols with short and branched chain fatty acids; in most species (including BWs) this composition leads to significantly higher nitrogen solubility in the acoustic tissues compared to the blubber [53].

(d) Heart rate, cardiac output and compartment perfusion

A decreased heart rate in marine mammals during diving is a hallmark of the dive response, initially studied in captive pinnipeds [13]. This decrease, together with peripheral vasoconstriction, was suggested to regulate oxygen consumption by tissues and to limit N₂ diffusion and distribution. However, changes in cardiac output may also cause increased DCS risk, and the overall effect is difficult to predict [55].

The recent development of heart rate data-loggers has enabled the study of heart rate in cetaceans diving voluntarily. Studies on short-duration and shallow-diving cetacean species swimming voluntarily showed a similar heart rate profile in response to diving [31,56,57], but also indicate that the dive response is less abrupt and more variable in voluntary divers. Porpoises can modulate bradycardia based on the planned dive duration, showing cognitive control of heart rate [58] and the exercise response (increased heart rate and vasodilation) can override the dive response, especially at high activity levels [56,59].

Stroke volume in bottlenose dolphins appears to change during exercise [60] and to decrease during static surface apnoea (A. Fahlman *et al.* 2019, unpublished observation). There are few studies on blood flow distribution during diving because of the technical difficulty and invasiveness of

current methods. Studies in restrained pinnipeds suggest a marked reduction in blood flow to all organs except the brain [61,62], although studies in trained and free diving seals suggest that muscle perfusion might be higher than previously thought from studies on forcibly submerged animals [63,64].

8. What is the normal diving behaviour of beaked whales?

Information on diving behaviour is available for Cuvier's, Blainville's and Baird's (*Berardius bairdii*) BWs, and northern bottlenose whales (*Hyperoodon ampullatus*). BWs dive deeper and longer than other cetaceans, often diving to more than 1000 m multiple times per day. In general, there is a tri-modal dive pattern composed of inter-respiration (i.e. ventilation) dives, long-duration and deep-foraging dives (typically greater than 400 m and 30 min), and shorter and shallower (intermediate) non-foraging dives that separate foraging dives, though there is considerable variation [65–68]. For deep foraging and intermediate dives, ascent rates are typically slower than descent rates [69]. The function of the intermediate dives is not fully understood, but may be related to some combination of digestion, processing of lactic acid, gas exchange and predator avoidance [38,70,71]. Recent studies suggest there is variability both within and between individuals and populations, indicating that foraging success may also play a role [67]. Deep-foraging dives occur during day and night at similar rates and to similar depths [71,72], suggesting that BWs target mostly prey that do not migrate vertically.

Where data on prey exist, Cuvier's BWs primarily forage on deep-water squid and fish in the lower mesopelagic and benthopelagic zones [73]. However, diet and foraging strategies probably vary significantly among species and regions. Despite long, deep dives, it has been estimated that BWs can dive within their aerobic dive limit, given their large oxygen stores and low metabolic rate [50]. However, BW could exceed their aerobic dive limit regularly during long, foraging, deep dives, and thus use intermediate dives to recover and process lactic acid [66].

9. What information is there on beaked whales' reaction to simulated sonar?

Short-term tags have been used to assess the response of BWs to simulated sonar or predator signals, with similar results found across species, though sample sizes are limited. Avoidance and/or termination of foraging efforts in four species have been documented, with some responses starting at very low received sound levels [68,74–76]. However, in the case of Cuvier's BWs in southern California, whales that had probably been regularly exposed to MFAS did not respond to more distant operational Navy MFAS at similar received levels [76], suggesting the context of the simulated source may be important.

10. What information is there on beaked whales' reaction to naval exercises where mid-frequency active sonar was used?

To assess the behavioural response of BWs to operational Navy MFAS on a Navy training range in southern California, 16 dive

reporting satellite tags were attached to Cuvier's BWs [77]. Animals were exposed to two different types of MFAS signal: mid-source level helicopter deployed sonar (217 dB re 1 μ Pa @ 1 m), and the ship-based sonar (235 dB re 1 μ Pa @ 1 m) implicated in most stranding events to date [78]. Although there was variation in response, tagged whales generally increased their time between foraging dives in the presence of sonar, with foraging disruption increasing in duration as the distance to sonar decreased. Unexpectedly, tagged whales responded to ship and helicopter sonar at roughly the same distances, which, given the significantly different source levels, suggests that range to source, source type and/or context may play a large role in response to sonar, at least within a population that is regularly exposed [77].

Large-scale passive acoustic recording arrays have also been used to study changes in vocal patterns of BWs around navy ranges. A cessation of clicking was documented in the presence of sonar, indicating a reduction in foraging effort and/or spatial displacement of whales [79,80].

11. Does the diving profile of beaked whales favour N₂ accumulation?

Theoretical models can be used to predict N₂ levels after a dive. However, the reliability of these models depends on the accuracy of the parameters used in their development, and many of these parameters are unknown or poorly understood for BWs so data from other marine mammal species and humans are used. Thus, results from such models should be interpreted cautiously, but are useful to determine which variables in a complex system are most likely to alter the risk of gas embolization. The models predict high-end dive N₂ levels in BWs that would cause a high prevalence of DCS in terrestrial mammals [38,81]. However, none of the models have indicated that behavioural changes significantly increase the risk. Changes in behaviour in combination with variations in physiology are required to alter the risk [82].

12. Does the behavioural response pose an increased risk of suffering from decompression sickness?

Behavioural responses to MFAS vary among and within individuals [77], and with sound source and by regions (areas with more or less sonar use) [70,74,77]. Theoretical models agree that increasing the number of shallow avoidance dives (shallower than the depth of theoretical alveolar collapse) would increase DCS risk [70,81], while the interruption of a single foraging dive does not, if it is assumed that regular dives do not cause N₂ super-saturation and are free of large bubbles [70]. However, some reported responses include BWs diving deeper and/or longer during sonar exposure, in addition to increased time in the upper 50 m of the water column [74,77].

A behavioural response to navy sonar, as described by DeRuiter *et al.* [76], in which the BW increased its fluke stroke frequency, probably results in an increase in metabolic rate, reducing the aerobic dive limit. Additionally, increased musculoskeletal activity has long been suggested to facilitate DCS by means of bubble formation through cavitation, decreasing

hydrostatic pressure while increasing super-saturation in the muscle [83]. Moreover, CO₂ produced in the muscle while stroking might contribute to bubble formation and growth [84].

13. If under normal circumstances marine mammals do not suffer from decompression sickness, what triggers decompression sickness in atypical mass stranding events?

DCS in marine animals is rarely reported, and in the very different circumstances where it has been documented, one key condition was present: stress. Animals may respond to stressful situations by exhibiting the 'flight or fight response' with increased heart [85] and metabolic rates, often accompanied by fast movement away from the perceived stressor, or the 'freeze response' with decreased heart and metabolic rates [86]. There might be differences in how individuals and species react to similar stimuli, according to differences in physiology and experience [87].

The physiological changes experienced by BWs during MFAS exposure remain unknown and merit further investigation. However, the behavioural response described by DeRuiter *et al.* [76] and the live strandings of BWs associated with MFAS suggest that these animals are most likely to have experienced a 'flight or fight' response to escape the sonar. The flight response may override the dive response, as the exercise response can [56,59]. We suggest that if these changes are severe, they could drive the animals with individual risk factors to a non-reversible condition, leading to death. Since the physiological responses and health risk factors probably vary among individuals, this variability, and potential differences in exposure level, might explain why not all individuals in a local population strand or perish at the same time and location, as in typical mass strandings.

14. What is the impact on populations?

While the number of BW MSEs known or thought to have resulted from exposure to MFAS is relatively small, it is important to note that there have been repeated AMSEs in very localized areas [3,7,12], and cryptic mortality probably also occurs [88]. Anthropogenic mortalities may have a significant negative effect on BW populations for several reasons, including high site fidelity for some populations [89–91], low reproductive rates [92] and/or disruption of social structure. The social behaviour of BWs is poorly known and appears to be different from other odontocetes [93].

Resident populations of BWs might have suffered declines in areas where recurring sonar deployment occurs: off Japan, Hawaii, southern California, Puerto Rico, the Bahamas, the Canary Islands, Greece and Italy. However, there is no way to assess population trends because no pre-sonar BWs population data exist for these regions. Off AUTEK, in the Bahamas, where Blainville's BWs are regularly exposed to MFAS, they appear to have lower reproductive rates than a nearby population off Abaco [91,94]. BWs repeatedly exposed to MFAS may suffer other adverse consequences such as lower survival rates although this has not been documented. If exposure to sonar does generally increase the time between

foraging dives, this effect alone may result in at least a short-term decrease in fitness [77].

15. What can be done to monitor and mitigate the effects of mid-frequency active sonar?

The European Parliament urged its member states 'to adopt a moratorium on the deployment of high-intensity active naval sonars until a global assessment of their cumulative environmental impact on marine mammals, fish and other marine life has been completed' [95]. However, this was a non-binding resolution, and the Spanish government was the only member to adopt this recommendation, and only around the Canary Islands from 2004. Since the moratorium started, no AMSEs have occurred in the Canaries, providing strong evidence of the efficacy of this mitigation measure [96]. Meanwhile, AMSEs coincident with MFAS use have continued in areas identified as prime habitat for Cuvier's BWs [12].

Given that MFAS is used by many nations, it is important to find ways to mitigate its impact. If the likelihood or degree of an individual's response to MFAS depends, in part, on its prior exposure history, one option to mitigate acute effects of MFAS exposure on BWs would be to restrict use to areas where training and testing are already regularly (e.g. multiple times a year) undertaken with no associated AMSEs, and prohibiting use in areas where AMSEs have previously occurred, or BW populations are known or suspected to occur, and where MFAS is rarely or never used. Areas where MFAS is regularly deployed should be considered a high priority for long-term monitoring to study possible sub-lethal impacts of acoustic disturbance. Results should be compared with data from sonar-free populations.

16. Future research directions

Although knowledge about BW biology and AMSEs has increased dramatically since the workshop in 2004 [6], we suggest additional research is needed in the following areas:

- *Anatomy*: Alveolar collapse depth, vascular anatomy studies on blood circulation and tissue perfusion [97] for any BW species, body compartment measurements for Cuvier's BW.
- *Physiology*: New technology to measure blood chemistry, heart rate, stroke volume, cardiac output and blood flow in diving cetaceans. Determine how pressure affects gas exchange and N₂ solubility in marine mammal tissues, and BW metabolic rate.
- *Pathology*: Distribution of gas bubbles in diving marine mammals, aetiology and pathogenesis of fat emboli, individual health factors predisposing to DCS, whether repetitive sonar exposure causes cumulative effects and other anthropogenic cumulative impacts.
- *Ecology*: BW social structure, population dynamics and life-history parameters (e.g. adult length, body condition, age at first reproduction, calving intervals, calf survivorship) by continuation of the few long-term population studies on BWs.
- *Behaviour*: New or continuing studies on populations of BWs that have not been exposed to MFAS to better understand aspects of their normal behaviour, and longer

durations of behavioural data to better define the range of normal behaviour.

- *Technology development*: Many of the above research directions require new technology to monitor free-ranging whales.

17. Conclusion

Atypical BW MSEs continue to occur in some areas (i.e. Mediterranean Sea) but not at other sites where naval training has been frequent or is banned (e.g. Bahamas and Canary Islands, respectively). BW AMSEs mainly involve Cuvier's BW with a few individual mesoplodonts. This might suggest that the effects of MFAS on BWs are strongest on Cuvier's BW, but other factors including individual experience probably play a role. We hypothesize that BWs that are not routinely exposed to MFAS display stronger behavioural and physiological responses to sonar. The effects of repeated exposures and deaths on BW populations remain unknown due to the lack of data on abundance trends, life history, social structure and behaviour. Nonetheless, the removal of dozens of individuals from local populations that tend to be small is likely to be detrimental, and any effects of DCS have clear impacts on the welfare of the individual BW. From this review, we suggest that the effects of sonar on BWs vary individually, and maybe among species, although there are clear commonalities. In some individuals, the response to sonar may disrupt nitrogen

regulation leading to gas and fat embolic syndrome. Additionally, as noted in human divers, individual health risk factors can contribute to the onset and outcome of DCS. We recommend: (1) a moratorium on MFAS in those regions where atypical MSEs continue (e.g. regions of the Mediterranean Sea), (2) continued research in areas with MFAS to determine if sub-lethal impacts on individuals result in population-level impacts, (3) comparative studies on populations of BWs in the absence of MFAS, (4) determination of life-history parameters, (5) studies in anatomy, physiology, and pathophysiology to better understand the development of decompression-like sickness in whales, and (6) continued development of technologies to measure physiological responses of free-swimming BW. Continued interdisciplinary studies and exchanges, as occurred in this workshop, will facilitate better understanding of this complex problem.

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