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Influence of possible stressors on the respiration of three female Pacific Walruses (*Odobenus rosmarus divergens*), housed in managed care

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Alla mia famiglia...

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INTRODUCTION

1. THE PINNIPEDS

The pinnipeds are a widely distributed clade of carnivorous semiaquatic mammals that consists of 33 different species and 29 subspecies (Berta and Churchill, 2012). The pinnipeds range in size from 1 meter and 40-45 kg of the Baikal seal (*Pusa sibirica* - Gmelin, 1788), to approximately 5 meters and more than 3,000 kg of the southern elephant seal (*Mirounga leonina* - Linnaeus, 1758). The three families of this clade are represented by Otariidae (fur seals and sea lions), Phocidae (true seals) and Odobenidae (walruses, *Odobenus rosmarus* - Linnaeus, 1758). There are 19 species and 16 subspecies of phocid seals (Phocidae), 13 species of Otariidae and Odobenidae, which is a family restricted to the Arctic region and the adjacent seas, represented by only one species, the walrus. During their evolution, appendages such as limbs and feet have degenerated and gradually modified into fins and flippers that can propel the animals through the water with great force. Sex organs and mammary glands are retracted inside the body within slits or pockets beneath the skin. In the phocids and odobenids, the testes are inguinal, or inside the body. Otariids, however, have externally visible, scrotal testes. The otariid ear is tiny, and phocid seals have no external ears – only a hole visible on each side of the head. The otariid seal uses its long fore flippers, or pectoral fins, for balance and propulsion, while the phocid uses the rear flippers. The hair or fur has largely disappeared in walruses, while phocid and otariid seals have retained a fur coat that is visible (Riedman, 1990), and the sea lion males grow out a "mane" around the neck upon reaching adulthood. In the phocid the limbs are attached to the vertebral column while in otariid and walruses the articulation is still present, and it provides them with better mobility on land. True seals, like the Weddell (*Leptonychotes weddellii* - Lesson, 1826) and elephant seals, as well as walruses, generally perform longer and deeper diving sessions than the sea lions and otariid in general.

WALRUS BIOLOGY

Taxonomy and evolution

Repenning and Tedford in 1977 have traced the Odobenidae to a common origin with the Otariidae in the early Miocene some 20 million years ago from an aquatic ancestral group having close affinity to primitive ursine (bear-like) carnivores. The primitive, walrus-like

pinnipeds evidently flourished and became greatly diversified in late Miocene-early Pliocene times, but only one form has survived to the present — the living walrus (Figure 1), *Odobenus rosmarus* (Fay, 1982). Odobenid monophyly is strongly supported, although there is controversy about whether walruses are more closely related to otariid or phocid. Morphological studies support a sister relationship between walruses and earless seals whereas molecular data and recent genetic studies consistently position odobenids closer to Otariidae (Schröder et al., 2009, Berta and Churchill, 2012). Several fossils species have been recognized within the extant genus *Odobenus*, but most of these have been reallocated to the extinct genus of *Ontocetus*. Pleistocene fossils have been recovered from the Arctic, and from northern coastlines of the eastern Pacific and Atlantic (Berta and Churchill, 2012). The walrus has a disjunct circumpolar distribution. Two subspecies – the Atlantic walrus, *Odobenus rosmarus rosmarus* (Linnaeus, 1758) and the Pacific walrus, *Odobenus rosmarus divergens* (Illiger, 1815) – have long been recognized. A third subspecies, *Odobenus rosmarus laptevi*, confined to the Laptev Sea, was suggested by Chapskii in 1940. The status of this taxon is, however, questionable (Born et al., 1995).

Figure 1. Adult female walrus in Wrangel Island, Russia. Photo: Sergej Gorshkov (www.nationalgeographic.it).

Habitat and distribution

The Atlantic walrus ranges from the eastern and central Canadian Arctic eastward to the Kara Sea. Several, more or less, well defined subpopulations or stocks exist within this range (Born et al., 1995). There are at least six populations around the Northern Hemisphere that appear to be geographically isolated at present: in the Hudson Bay-Davis Strait region, eastern Greenland, Svalbard and Franz Josef Land, Kara Sea-Novaya Zemlya, Laptev Sea, and Bering and Chukchi seas (Figure 2). This last population is regarded as the Pacific walrus (Fay, 1982).

Figure 2. Bering-Chukchi region (Fay, 1982).

In 2011, Speckman and colleagues, estimated that the number of Pacific walruses was 129,000 with 95% confidence limit of 55,000-507,000 individuals, while the last assessment of 112,500 mature individuals of walrus (*Odobenus rosmarus*) was made on February 2016 and it is shown in the IUCN Red List as a vulnerable species (Figure 3). In the IUCN, it is also shown that the abundance of Atlantic walrus is likely more than 25,000 with some subpopulations increasing while the Pacific walrus total abundance is likely more than 200,000. In any case, for both subpopulations the trend is unknown. Past aerial surveys in the Alaskan region commonly observed walruses around St. Lawrence Island during spring, with very few animals observed to the east. It seems that walruses prefer large ice floes that were common in the interior ice pack. Many walruses migrate in conjunction with sea ice expansion and retreat, but a portion of the male walrus population remains in the Bering Sea and uses coastal haul-out sites during

the summer. They are observed primarily in the interior ice pack, which expands southward with the ice edge but is still available farther north. In this region, walruses were most commonly seen in the western benthic part, rarely seen within the northern region and they are also rarely, if ever, seen in light -coverage or cake-floes habitats (Simpkins et al., 2003). Walruses have a comparatively narrow ecological niche. Their populations probably depend on: 1) the availability of large areas of shallow water with suitable bottom substrate to support a productive bivalve community; 2) the presence of reliable open water over rich feeding areas, particularly in winter when access to many feeding areas is denied due to ice cover; 3) the presence of haul-out areas near feeding areas. Haul-out platforms are usually ice pans although terrestrial haul-out sites are used in the ice-free summer and autumn period (Born et al., 1995).

Figure 3. The IUCN Red List of Threatened Species (www.iucnredlist.org).

Morphological characteristics

At birth and for at least one month thereafter, male and female walrus calves are about equal in length. During the first two months, the calves increase in length by about 10 to 15 cm per month, and the males tend to grow slightly faster than the females. In the females, full development in length is reached at about 10 years, in the males, the adult length is not attained until about 15 years (Fay, 1982). Adult males can reach a length of more than 320 cm, while females normally reach a length of about 270 cm and both can reach an age, in the wild, up to 30-35 years. The tusks of the males can reach one meter and weigh up to 5.4 kg (Berta et al., 2015). These tusks are present in both sexes, but are shorter in females, and are used, among other, for hauling out (Kastelein and Gerrits, 1990). Pacific walruses are about four to seven percent longer than their Atlantic counterparts. In both populations, the males tend to be 15 to

20% longer than the females. The calves at birth and for most of the first month after birth weigh between 45 to 75 kg, and by the end of their second month, they have increased in weight by only about 30%. Females appear to reach an average weight of about 830 kg at an age of 12 to 14 years; males reach their maximum weight sometime thereafter the sixteenth year, with an average of 1,200 kg. In general, adult males tend to be about 45% heavier than adult females. The skin of walruses is extraordinarily thick; at birth is uniformly leaden gray to gray-brown, and has a thin coat of fine hair, about five millimetres long, of similar colour; by the end of the third week, the flippers are nearly black and the pelage, about seven to 10 mm long, is rusty brown to tawny. At this stage in development, the skin is pigmented similar to the haired seals (*Phocidae*) of the Bering-Chukchi region and more intensely than in fur seals and sea lions (*Otariidae*). With advancing age, the skin of the walrus becomes progressively paler, as does the pelage. The thickness of the skin is greatest on the neck and shoulders, greater on the dorsal than on the ventral surfaces, and greater in males than in females. The skin is thinnest on some parts of the face and attains its greatest thickness on the neck and shoulders of adult males, where it is supplemented by rounded bosses or "lumps" about one centimeter thicker than the surrounding skin. The bosses are generally absent in males whose length is less than 300 cm, and they are usually well developed on males whose zoological length is 340 cm or greater. Like other pinnipeds, the walrus has a thick layer of cutaneous fat, the blubber or hypodermis. This layer varies in thickness over different parts of the animal; it is thickest on the torso and thinnest on the head and appendages. The pelage of adult walruses is coarser and less dense than that of the calves. On the bosses of the neck and shoulders of adult males, the hair is very sparse or absent, exposing the surface of the skin to view. The walrus, moreover, may be the only pinniped that bears three different pelages and undergoes two true moults within one year of fetal to early postnatal life. In those animals, the annual moult is triggered as much by thermal as by photoperiodic stimuli (Fay, 1982). Most of the cranial muscles are found to be related to the movements of the vibrissae pads, which is of ecological importance for communication and food identification, excavation, manipulation, and processing (Kastelein et al., 1991). In this species the mystacial vibrissae are well developed and they range in number from about 400 to nearly 700 per walrus and are situated in 13 to 18 rows on the anterior surface of the rostral. The mean number per side is slightly greater in males. The dense population of those vibrissae in the walrus identifies the broad snout as an organ of extreme tactual importance. They are extremely mobile, and each vibrissae can be moved up, down and laterally, and can be rotated through at least 100° of arc, such that the tips can be turned upward and inward, toward the centre of the snout, as well as downward and outward (Fay, 1982). The walrus eye is small in

comparison to that of other pinnipeds and the extrinsic eye muscles are well-developed. The strong palpebral muscles can open the eyelids and probably protrude the eye by thickening during contraction. The protrusion and mobility of the eyes enlarges the monocular visual field. Supraorbital processes are not found in the walrus but, for protection, the eyes can be retracted deep into the orbital cavity. Based on behavioural observations, anatomical findings and histological investigation of the retina, visual acuity in walruses is judged to be less than in the other investigated pinnipeds and seems specialized for short range use underwater (Kastelein et al., 1993). Walrus ears have special features which are not found in the ears of most terrestrial carnivores. They lack of the pinnae, the long, tubular outer ear of which the lateral side is covered with fat and skin, the ability to open and close the external meatal orifice by auricular muscles, the lining of ear wax, the large middle ear cavity by vascularized tissue, the elastic fibres, collagen tissue and cartilaginous rods in the wall of the Eustachian tube, and the dense bones surrounding the base of the outer ear and the entire middle and inner ears (Kastelein et al., 1996). The nose has anatomical turbinates which are used for warming inspired air to prevent heat and water loss like in all mammals (Hillenius, 1992). It is represented by anteriorly placed and forwardly diverted nostrils, that can be hermetically closed while underwater by the contraction of the surrounding muscles.

Diet

In the wild, walrus pups depend on their mother's milk for at least 15 months. However, little is known about the suckling period because wild walruses live in remote areas and only a few pups have been reared by their mothers under human care. In fact, most of them have been hand-reared. In addition, the milk transfer and early growth patterns in wild walruses are not well known (Kastelein et al., 2003). Walruses are gregarious and forage in large groups throughout their range and feeding bouts may last up to 36 hours. Walruses usually feed in depths less than 100 m on prey that range in size and classification from tiny crustaceans to adult seals. Walruses feed by oral suction and typically ingest only the soft tissues of their prey (Fay 1982, Sheffield et al. 2001, Sheffield and Grebmeier, 2009). Walruses mainly eat sessile benthic prey. Usually only the siphons and feet of bivalve molluscs are found in walrus stomachs, and it is thought that walruses use oral suction to separate the molluscs from their shells. The walrus has good control of its tongue muscles and both pressure and duration of suction. Many adults have been observed feeding on bivalve molluscs in a sandy substrate

leaving the empty shells on the bottom. The suction force of the walrus, required to separate the body or body parts from the shells, probably depends on the degree of retraction and closure of the clam. It is probable that beyond a certain state of retraction, the walrus is unable to extract the edible parts. This foraging technique is highly efficient as adult walruses in the ocean eat about 50 kg of food per day. This would be about 3000 adult sand gapers *Mya arenaria* (Linnaeus, 1758) with an average soft body weight of 17 g (Kastelein et al., 1994). Early diet studies were largely based on the numbers and volume of prey items in stomachs. Due to the large amount of bivalve parts found in these stomachs it was thought that walruses were highly selective for bivalves. Non-bivalve prey species were considered of minor importance and assumed to be eaten accidentally when bivalves were scarce or nutrient-poor. Later diet studies used larger sample sizes over a larger geographic area than the earlier studies and the samples contained many new non-bivalve prey items. Bivalves, gastropods and polychaete worms were the most frequent prey items in both Bering and Chukchi seas. Male and female walruses consumed essentially the same prey when in the same location, however, current climatic changes may affect walrus's access to diverse, productive shallow water feeding areas. Moreover, benthic faunal composition and biomass vary regionally due to heterogeneous food availability, depth, substrate types, predation and physical disturbances such as ice gouging. The ability of walruses to feed on a wide variety of soft-bodied prey types gives the population the flexibility to adapt to potential changes in benthic community structure. In addition, an increase in the occurrence of some taxa in walrus diets, such as sea stars, brittle stars, and sea urchins that are found throughout the Bering and Cukchi seas may indicate a food-limited population and be a cause of concern. These taxa are likely poor food for walruses because much effort is required to separate soft tissue from the substantial skeletal parts (Sheffield and Grebmeier, 2009); further information concerning the interpretation of walrus stomach contents are given by Sheffield et al. (2001). Fish are generally not present in walrus stomachs and frequency of octopus is negligible. While seal eating walruses have been described, they do not represent the norm of the population. Based on nitrogen isotope ratios obtained from samples in a study conducted by Dehn (2007), it was shown that it was not likely that these walruses had consumed other pinnipeds in the recent past. On the other hand, Lowry and Fay (1984) Rausch et al. (2007) and more recently, Seymour et al. (2014), supports the hypothesis that predation on seals by walruses has been increasing over the last 40 years, due to the environmental changes, that can alter the abundance, distribution, size, digestibility and energetic content of prey (Barboza et al., 2009). Anyway, walruses are specialists and rely almost exclusively on benthic prey and the benthic food chain. Interesting studies about the

walrus feeding excavation and disturbance on the Bering Sea benthos were conducted by Oliver et al. (1985) and Nelson et al. (1987). It was thought that walruses only consume the foot and the siphons of the clams. For this reason, if walruses do consume all clam soft parts, then their impact on clam stocks was probably overestimated (Sheffield et al., 2001).

Reproduction

Reproductive patterns of 79 female and fetal growth of Atlantic walruses were well described by Garlich-Miller and Stewart (1999). The reproductive tracts of 152 female and 174 male Atlantic walruses were analysed by Born (2001, 2003). The breeding behaviour of Atlantic walruses were studied and described by Sjare and Stirling (1996) while Pacific walrus reproductive behaviours were previously described by Fay (1982). Like all pinnipeds, walruses are polygynous, in the sense that males will mate with more than one female. Walruses give birth to a single calf at intervals of two or more years. Spotte (1982) analysed the incidence of twins in pinnipeds but it seems that there is exist no study that has reported this in this species. The average sexual maturity in females is reached between six and eight years of age and around 11 years for males. Mating normally occurs in winter, but implantation of the fertilized egg in the uterus does not occur until June-July of the same year, a phenomenon known as "delayed implantation" or "diapause". Consequently, walruses are among the slowest reproducing of all marine mammals (Krupnik and Ray, 2007). However, females show fertility from late summer to may.

Social structure

Walruses are extremely social animals, and when on land or ice they are normally found in tight groups (Figure 4) ranging in size from a few individuals up to thousands. They travel in groups as well and the adult males normally migrate in summer, while separating from the females and calves, to haul-out on ice blocks or land when possible. This strong sexual segregation ends with the migration back to the females, that usually starts in late fall, for the mating season. The herd structure and activity budgets of summering males was described by Miller (1976). The walrus ethology and the social role of tusks in males were also described by Miller (1975) and Fay (1982), while the complex structure of sounds and structural variations of the songs were

studied by Sjare et al. (2003). Further information about the walrus communications are given by Miller (1985) and vocal learning in pinnipeds is described by Reichmuth and Casey (2014). More detailed information about the behaviour and social structure of those animals are given by Fay (1982, 1985).

Figure 4. 10 August 1993, 43 walruses were hauled out on Brooman Point. Eight others, including females with newborn calves, were in the water. Photo: E W Born (Born et al., 1995)

Relationship with humans

One of the most remarkable creatures in the Artic is the walrus, whose very existence and natural history were cloaked in mysticism and anthropomorphism until the 19th century. For thousands of years, this mammal was regarded by Eskimos and other native people of the North as having supernatural powers and human attributes (Fay, 1982). People spoke of walruses in tales and myths, honoured them in ceremonies and prayers, and called children and geographical places by names used to described them. Thus, indigenous knowledge of walruses, springs from millennia of use. Indigenous people have been exploiting Beringian marine ecosystem for at least 6000 years; walrus hunting became the staple of local economies as early as 2000 years ago. Prior to the economic era, walrus hunting supplied 60-80% of all subsistence food consumed in many communities in the Bering Strait region (Krupnik and Ray, 2007).

When European man arrived on the scene in the 18th century, he brought with him both the means and the incentive to take quantities far in excess of the requirements for mere survival. The over exploitation that resulted from introducing new technological and social innovations was such that walruses were extirpated from some areas in the Bering Sea by the end of the 18th century and severely depleted overall before the last two decades of the 19th century (Fay, 1982). Whaling ship logbooks and statistical models indicate that about 200,000 walruses were killed from 1867 to 1883, with 35,700 killed in 1876 alone (Bockstoce and Botkin, 1982). Apparently, the retrieved harvest of some 10,000 to 20,000 walruses per year at the time were far greater than the population could sustain. Up until about half a century ago most of the taking of walruses by Alaskan Eskimos in the 20th century was done from homemade boats (*umiak*), which consisted of a wooden frame about 10 m long, one meter deep, and 1.5 to two meters wide, over which a covering split walrus hides or whole bearded seal hides was stretched (Figure 5).

Figure 5. Six Eskimos standing beside native skinboat (*umiak*) on sled, Point Borrow, Alaska, 1935. Unknown or not provided author (from the web).

In recent years, these boats were powered by an outboard engine, as in some Alaskan localities along most of the Siberian coast, where wooden boats of various kinds are equipped in the same way (Fay, 1982). The walrus population is an economic resource of considerable importance to many coastal inhabitants of the region, in both Alaska and Chukotka, hence a sustainable harvest is desirable. The declines occurred when large numbers were killed for commercial purposes firstly by annual removal by man, and secondly, there are those killed but lost due to

sinking during the hunting. Some are killed outright; others are wounded, most of which eventually die from their wounds. Thirdly, the annual removal is the dependent calves and yearlings that die when their mothers are killed. Many calves are harvested in Alaska, and some are taken along the Russian coast as well (Fay et al., 1997). Walrus meat is excellent for food for sled dogs as well as people for several reasons: The hide is strong and durable; the blubber produces good-quality oil for burning; and the ivory has always been popular for constructing tools and weapons and, more recently, for carving. The commercial exploitation of walruses for their oil, tusk ivory and hides proceeded on an enormous scale, with no check whatsoever to ensure sustainability. As a result, by the mid-20th century the aggregate population of walrus has been reduced in nearly all areas and its range has shrunk substantially (Born et al., 1995). However, nowadays this kind of hunting is more selective; the kinds of animal taken, in terms of sex and age, vary with the season, location, availability, and local preferences, and, of course, with the current regulations and quotas. The scientific information is highly dynamic and is advancing rapidly. In contrast, the body of data typical for indigenous knowledge is based on long-term personal observations and elders' memories, and thus changes very slow. Although the body of scientific information on the walrus increased from the late 1800s to the mid-1900s, the dynamics of hunter's knowledge has been totally different. If one were to ask hunters of the 1800s about walruses, the observational side of their knowledge would probably be similar to that in recent years. Actually, the knowledge of subsistence hunters is, perhaps, changing faster than the knowledge of the scientist. The generation of elders that once held traditional worldviews and belief is mostly gone. Alaskan subsistence hunters have been working closely with wildlife biologists for over half-century and they are now quite familiar with the biologist's views and studies (Krupnik and Ray, 2007). To conclude, walruses can be negatively affected by various human activities apart from hunting, such as the disturbance from different sources of noise, the pollution like the oil spills and the interactions with fisheries and changes in walrus food resources (Born et al., 1995).

2. PHYSIOLOGY AND ADAPTATIONS

ENERGY SUPPLY AND METABOLISM

Mammals adapted to aquatic life

In his work, Lavigne et al. (1986) says that the perception that pinnipeds and cetaceans have metabolic rates that are higher than those of terrestrial mammals of similar size has been widely accepted for decades. The basal metabolic rate of mammals is described by the Kleiber's power equation $Y=aM^b$ (Kleiber, 1975). Regarding that, many marine mammals appear to have metabolic rates about two times the value predicted by Kleiber (Lavigne et al. 1982). Elevated metabolic rates in seals and whales have also been linked with consumption of high protein diet, large livers in whales, relatively large thyroid glands in porpoises, and increased output of thyroid hormone (Lavigne et al, 1986). Williams et al. (2001) discovered that the morphology of the gastrointestinal tract reflects the metabolic demands of the animal and individual requirements for processing, distributing and absorbing nutrients. She found out that the basal metabolic rates of Weddell seals and dolphins resting on water surface are higher than the predicted levels for similarly sized domestic terrestrial mammals resting in air, confirming that there are different things that could affect the metabolism. Even more, when we talk about the field metabolic rate, regarding diet specialization and foraging mode, carnivorous mammals scale differently (significantly higher slope in the equation of power) than non-carnivore mammals (Nagy, 2005). Small intestinal lengths for carnivorous marine mammals depend on body size and are comparatively longer than those of terrestrial carnivores. Those large intestinal tracts of marine mammals are presumably required for sustain the energetic demands of an aquatic lifestyle and predation, in fact, there is considerable selective pressure for energetic efficiency during underwater hunting by marine mammals. A study of how those rates in marine animals can be evaluated in relation to deep gradient and temperature was conducted by Seibel and Drazen (2007) but they were principally not focused on marine mammals. In any case, there are differences in opinions regarding basal and field metabolic rates, some of which consider the marine mammals ones as the same of terrestrial ones.

Metabolism in relation to body size

In his review, Speakman (2005), described the relationship between body size, energy metabolism and lifespan. In this work he showed that bigger animals live longer, and they also expend more energy and due to this, the relationship of resting metabolic rate (RMR) to body mass lies somewhere between 0.66 and 0.8. Moreover, independent of the body size effect, he assumed that animals living in colder habitats tend, on average, to have greater lifetime expenditures energy per gram of body tissue. The result is that body mass and ambient temperature, when combined, explain the 45% of the variability in the lifetime energy expenditure per gram of the mammals.

Walrus metabolic demand

An animal's energetic costs are dependent on the amount of time it allocates to various behavioural activities. For Arctic pinnipeds, the time allocated to active and resting behaviours could change with future reductions in sea ice cover and longer periods of open water. Large numbers of walruses foraging near land haul-outs could deplete nearshore prey, and thus lead walruses to either move to other land haul-out sites or spend more time searching for prey. Greater searching efforts by foraging walruses would likely lead to greater individual daily energetic demands. A mammal's metabolizable energy is either stored (somatic and reproductive growth) or respired. Respired energy is used for basal metabolism, digestion, thermoregulation, and activity. Therefore, energy used for foraging activities (swimming and feeding) is not available for growth and endogenous energy reserves (blubber lipid). The amount of time an animal allocates to various activities affects its energetic costs. For example, a walrus that spends 93% of its time in water expends 18% more energy than a walrus that spends 70% of its time in water (Jay et al., 2017). The only direct measurement of field metabolic rate in this species were conducted by Acquarone et al. (2006) while the main studies present in literature were conducted in captivity. The main problem is that specific data, such as total food consumption per day, fluctuations in food intake during the year, and changes in intake due to age, sex or individual differences, are difficult to obtain in wild, thus, food records of captive mammals usually provide the only available information (Kastelein et al., 2000). Even more, compared to free-ranging walruses in the Arctic, walruses in aquaria are likely to have relatively low base (basal and activity) energetic demands because in aquaria, at least in temperate regions, thermoregulatory demands are lower. Also, because the captive walruses do

not need to forage for their food or avoid predators, their activity demands are undoubtedly lower (Noren et al., 2012). In his work, Fisher et al. (1992) confirmed that the approximate maintenance gross energy requirements for a 1200 kg nonpregnant, nonlactating adult walrus in captivity were 31,350 kcal day^{-1}. In accord, the amount of energy required to maintain healthy walruses, thought to weigh 250- 1200 kg, is known to range from 22,500 to 70,300 kcal day^{-1} (Fay, 1982, Kastelein et al., 2000). With his bioenergetics model, Noren et al., (2012, 2014) estimated that the caloric demand of nonreproductive females 0–12 years old (65−810 kg) ranged from 16,359 to 68,960 kcal d^{-1} for years with readily available sea ice assuming the animals spending 83% of their time in water, and that a caloric requirements which ranges from 26,900 kcal d^{-1} to 93,370 kcal d^{-1} is needed for simultaneously lactating and pregnant walruses. Daily consumption requirements are higher for pregnancy than lactation, reflecting energetic demands of increasing body size and lipid deposition during this stage. In fact, some of the energetic demand of lactation in walruses is undoubtedly met by utilizing endogenous energy reserves (blubber) accumulated during pregnancy. Moreover, youngest animals must consume nine to ten percent of their body mass on a daily basis, while older animals need to consume only seven to eight percent of their body mass to satisfy their caloric demand (Noren et al., 2014). Indeed, immature animals require more energy per unit of body mass each day than do adults (Kleiber 1975). Estimating the daily energy requirements of marine mammals is difficult. Metabolic rates are influenced by activity level, age (and hence growth), body size, moult (for pinnipeds), reproductive status, and environmental conditions. Directed research on walruses to determine how caloric intake and energy stores (body mass) are linked to meet energy requirements, are always recommended (Noren et al., 2012). Sadly, greater reductions in sea ice cover and longer periods of open water are expected in coming decades, which could increase energetic demands on walruses during summer and autumn. Estimates of the cost of altered behaviours from habitat change will be key to forecasting the status of walruses in a warming Arctic (Jay et al., 2017).

The walrus digestion

In their study, Sheffield et al., (2001) explained that the time of passage of food through the digestive system of a captive walrus is about ten hours — more rapid than in most other carnivores. Presumably, not more than half of that passage time is involved in gastric digestion. Sheffield et al. (2001) made a full laboratory digestion of a different cluster of walrus preys:

polychaetes; echiurids; sipunculid worms; clam; snails and crabs. They demonstrated that these prey items did not remain equally identifiable during digestion. Polychaetes and sipunculids were the least persistent prey, and they were both unidentifiable after two to three hours of digestion. Echiurids part were unidentifiable at hour five and none of the worms was persistent at the sixth hour of digestion trials. Over 50% of the clams maintained their diagnostic tissues (foot and/or siphon) through hour six while the viscera did not survive hour two. Snails and crustaceans were the most persistent prey. Anyway, it is known that no significant differences in the caloric values of those kind of walrus prey were found (Wacasey and Atkinson, 1987). Since the caloric value of clams and other prey are similar, no apparent energy loss occurs in consuming non-clam prey. Non-clam prey which are easily ingested and rapidly digested would be energetically valuable to walruses. Thus, the optimal walrus foraging strategy might be to consume any potential prey item, including non-clam taxa, encountered while rooting along the seafloor during a feeding bout (Sheffield et al., 2001). An interesting study on the fluctuations of food consumption and body weight related to sex, age, lactation, pregnancy and seasonal changes through the year were conducted by Kastelein et al. (2000). Fisher et al. (1992) conducted a study on four captive walruses to determine their digestive efficiency. All of them where fed on a diet of herring and clams for a total of six combinations for each animal. His results showed that the digestive efficiency of male walruses may be lower than that on females while the coefficients of protein in the animals fed with both herring and clams seems to be similar to the values reported for other carnivores. The apparent lipid digestibility in animals on the herring diet was significantly greater than in those on the clam diet. As aforementioned, we are facing an important climate change which, in addition to changing the composition of habitats, could affect a possible change in the prey composition and diet of these animals. Thus, analyzing the digestive efficiency is a fundamental step for the conservation and preservation of this species.

BREATHING

The mammalian respiratory system

The lungs are the primary organs of the respiratory system in mammals and are located within the thoracic cavity of the chest. The respiratory tract begins with the trachea that is divides into two branches, the bronchi. The bronchi further divide into the bronchioles. The gas exchange with the blood, in 'normal' lungs, takes place in the alveoli, that are the terminal part of the alveolar ducts originating from the respiratory bronchioles. The quantity of oxygen inspired and exchanged with the blood needs to be sufficient to support the aerobic metabolic demands of the animal. As previously said, the metabolic needs are related to activity efforts, for example, if a well-trained man runs, the mitochondria of his muscles can consume over five litres of O_2 every minute. To maintain oxidative metabolism at such level a continuous flow of O_2 has to be maintained: From the pool in environmental air O_2 is carried into the lung by inspiration, is transferred to the blood's erythrocytes, moved into the tissues by circulation, and finally reaches the cells and their mitochondria by diffusion. Conversely, the CO_2 produced needs to be removed by a similar mechanism in the reverse direction. In order to maintain steady state condition in any situation, the flow of O_2 at each level of the respiratory system must equal the O_2 flow into the mitochondrial sink. Hence, each of the steps could potentially limit the overall O_2 flow thus the O_2 available for aerobic metabolism in the muscle cells. Moreover, the size of the pulmonary gas exchange apparatus is normally large enough to afford the conductance required to allow an O_2 flow rate matched to the muscles' needs during maximal work. For this reason, the structural design of the respiratory system should thus be matched to the functional requirements. Anyway, animals are known to be designed economically, so to speak, and that, at each step in the respiratory system, the flow of oxygen at maximum volume is limited by structures involved, in fact, animals do not build or maintain structures that exceed what is needed (Taylor and Weibel, 1981).

Breathing system in marine mammals and lung adaptations

In marine mammals, in general, the airways are reinforced with an unusual amount of cartilage which extends in some species to the openings to the alveolar sacs. As the animal descends, the gas in the much weaker alveoli is forced into the non-absorptive airways. Comparing to fresh-water aquatic mammals and terrestrial mammals one of the most remarkable divergencies is, in

fact, the structure of the small airways. In general, the lung volume in marine mammals tends to be slightly larger than that of terrestrial mammals (Kooyman, 1973) However, in terms of maximal lung volumes, except deep-diving cetaceans and the sea otters, diving animals seem to be in range with terrestrial ones (Kooyman, 1973; Fahlman et al., 2011; Piscitelli et al., 2013; Fahlman et al., 2017). There also is a great variability in the diving lung volume within and between species or different dives of same individuals. While most seals exhale before diving, sea lions and cetaceans dive on inhalation taking full advantage of their lung store (Kooyman, 1973; Kooyman, 1989; Fahlman et al., 2017). Moreover, it has been demonstrated that deep-diving species with smaller lungs had a higher myoglobin concentration whereas species that are assumed to be shallow divers, like the walrus, had larger lungs. Larger lungs help to increase the quantity of available O_2 during short shallow dives, while higher muscle myoglobin concentration with lower lungs volume prevent the increase of the amount of N_2 during deep dives (Piscitelli et al., 2010; Fahlman et al., 2017). Marine mammals are also known to have an efficient ventilatory strategy, because they can exchange almost the entire lung volume in a single breath, minimizing dead space ventilation (Fahlman et al., 2017). Moreover, when compared with terrestrial mammals with similar size, the breathing frequency is generally significantly lower, and the tidal volume is higher in resting cetaceans and pinnipeds when in water or breathing at the surface, and for pinnipeds on land. In addition, the terrestrial breathing in mammals involves a brief expiratory pause whereas the aquatic breathing in marine mammals involves an inspiratory pause that can lasts from seconds to minutes (Scholander, 1940; Kooyman et al., 1971; Kooyman, 1973; Fahlman et al., 2017). In cetaceans and pinnipeds, it also appears that the expiratory phase represents the peak of maximal respiratory flow and it is not limited by the conducting airways and lung volume as in terrestrial mammals (Fahlman et al., 2017). To conclude, we know that diving animals are subjected to continue chest compressions due to the different pressure gradient through the water column, and that the consequence is an alteration of the properties of the lung (Fahlman et al., 2014). For that reason, a certain degree of plasticity in the anatomical and physiological structure of the lungs and related mechanical properties and pulmonary size, may depend on the life history of the animals (Fahlman et al., 2017).

Breathing system in pinnipeds

Seals (*Phocidae*) have the least-modified airway structure, where a non-cartilaginous segment of bronchiole is present and merges into respiratory bronchiole and finally into the alveolar duct. The cartilage-free portion have a large amount of smooth muscle, while the cartilage normally extends far out into the respiratory tree. In the walrus and sea otter there are some parts of the terminal airways that, like in seals, are without cartilage, while in other portions the airways with cartilage empty directly into alveolar sacs. Sea lions have the most divergent airway structures. There are only cartilaginous supported airways, which empty into alveolar sacs, moreover, respiratory bronchioles and alveolar ducts have been lost (Figure 6).
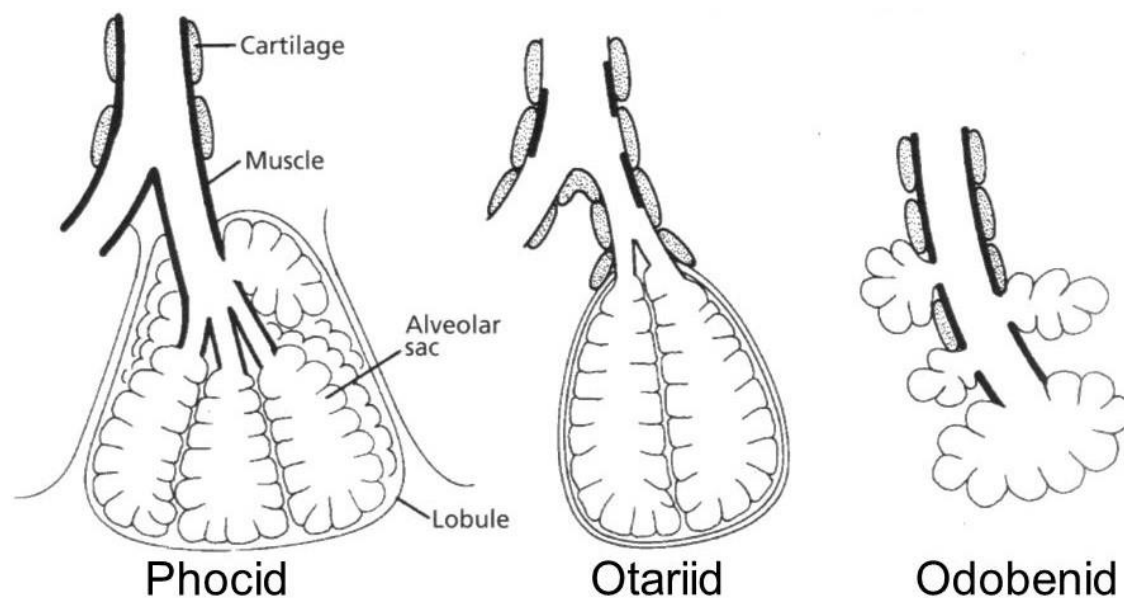

Figure 6. Diagram of the structure of alveoli and associated cartilage and muscle in pinnipeds (Berta et al., 2006).

In seals, the trachea does compress during diving and submucosal vascular structures in the conducting airways have been reported in some cetaceans and phocids. This plexus consists of large veins and arterioles, which may engorge and fill the tracheal lumen with blood, reducing the internal volume of the airway, preventing intraluminal negative pressures and minimizing deformity of the tracheal wall (Fahlman et al., 2017). Anyway, in pinnipeds, the chest does not resist compression and is highly compliant (Leith, 1976; Fahlman et al. 2014, Fahlman et al., 2017), in fact, one of the mechanical and structural properties of lungs in pinnipeds is that the chest can be compressed to the limit of collapse without the risk of lung squeeze (Scholander, 1940), because the functional residual capacity (FRC) and residual volumes (RV) are equal. FRC and RV are, respectively, the amounts of air that remain in the lung following a passive

and maximal exhalation. The high compliance of the chest in seals and sea lions is, indeed, a great example of how those species prevent lung squeeze (Fahlman et al., 2017).

Walrus respiration

There are few studies in literature that aim to measure and study the respiratory rates and patterns in walruses (Stirling and Sjare, 1988; Bertelsen et al., 2006; Lyamin et al., 2012) and little is known about physiological parameters of free-raging walruses (Bertelsen et al., 2006). Most of the data that we have, comes from studies conducted in parks and zoo and many estimated values on the breathing patterns were taken before immobilization or anesthesia (Stirling and Sjare, 1988; Born and Knutsen 1990*a*) and they might have been disturbed or stressed by the manipulation (Bertelsen et al., 2006). In 2006, Bertelsen and colleagues have measured the resting respiratory rates in ten male walruses in Northeast Greenland, while the animals were hauled-out for at least one hour. They obtained values which ranged from 2.7 to 3.7 breaths per minute, with a mean of 3.3 ± 0,3. Most of the values presented in this study corresponded well with Stirling and Sjare's (1988) and Born and Knustsen's (1990*a*).

General diving adaptations

The description of diving behaviours, respiratory characteristics and adaptations of air-breathing vertebrates and marine mammals is the topic of many reviews and studies both past and recent (Scholander, 1940; Lenfant et al., 1970; Kooyman et al., 1971; Kooyman, 1973; Zapol et al., 1979; Kooyman et al., 1980; Schreer and Kovacs, 1997; Piscitelli et al., 2010; Piscitelli et al., 2013; Fahlman et al., 2014; Fahlman et al., 2015*b*; Fahlman et al., 2017). Is known that diving mammals exhibit an exceptional tolerance to sustained hypoxia compared with mammals which do not dive habitually. However, the ability to endure submersion asphyxia varies among aquatic mammals. The physiological factors responsible for the degree of hypoxic endurance can be summarized as: Metabolic adjustments in relation to the aerobic and anaerobic heat production; oxygen storage factors and respiratory properties of blood; oxygen economy factors which tend to conserve available oxygen stores (Lenfant et al., 1970). The first important thing to know in describing what happens to the animal organism when diving is that, following the dive, and in relation to its duration, there is an increase in the lactic acid circulating in the blood and a consequent drop in pH. As the concentration of this substance

decreases exponentially when the animal starts to ventilate at the surface, the pH rises. The moment in which the diving animal switches the aerobic metabolism to the anaerobic one and starts to produce lactic acid, is known as the aerobic dive limit (ADL) (Kooyman, 1973; Kooyman et al., 1980). The advantage of an aerobic diving schedule is that no anaerobic metabolites are accumulated, and there is little acid-base disruption. If so, only the oxygen store needs to be replenished, a process which can be rapidly accomplished. For example, while hunting, it is useful for a seal to spend as much time as possible underwater and when a single 45-minute dive requires about 70 minutes of surface time for blood to return to normal-lactate concentration (39% time spent diving), a succession of six 15-minute dives only requires four recovery minutes for each (79% time spent diving). Thus, close interval and short dives are twice effective as long, single dives (Kooyman et al., 1980). In fact, as previously said, long diving sessions led to a greater production in lactic acid. As the quantity of this substance increase, the recovery-time needed by the animal to absorb it, will be prolonged. Regarding the oxygen storage factors and the properties of blood, we know that it is possible, during the dive, central respiratory control is more responsive to blood oxygen tension than to carbon dioxide or pH (Kooyman et al, 1971). Anyway, we know that the maximum oxygen store differs among species of marine mammals, in relation to the diving habits (Lenfant et al., 1970) and that considering total body oxygen stores, cetaceans have available considerably less oxygen per unit mass than either penguins or phocids (Schreer and Kovacs, 1997). Following the theories of Lenfant et al. (1970), the respiratory properties of blood show no significant adaptive features in O_2 haemoglobin affinity or Bohr shift in the marine mammal species present in his studies, but that a distinctly higher buffering capacity distinguishes blood of marine mammals from terrestrial non-diving species. He also discovered that generally, in marine mammals, adult haemoglobin concentrations are high only in phocid seals. For example, phocid seals have higher concentrations of haemoglobin for a given blood volume and more myoglobin per unit of muscle than otariids, which allows them to store more oxygen and hence dive deeper and longer (Schreer and Kovacs, 1997). Moreover, a notable difference exists between new born and young or adult sea lions in that the new born have about a 30% higher haemoglobin content, difference that is present in the Weddell seal as well (Lenfant et al., 1969a). Focusing on the myoglobin maturation, it has been demonstrated that generally in odontocetes is correlated with the calf nursing interval, suggesting that the rate for muscle maturation evolves to match the maternal dependency period (Noren et al., 2014), while the pattern across pinnipeds demonstrates a delineation between phocids and otariids. Phocids typically show more rapid development of myoglobin contents compared to otariids and this may be attributed to early

entry into water and short maternal dependency periods. Walruses demonstrate one of the most rapid developmental trajectories of myoglobin among pinnipeds and is similar to the development patterns observed for phocids (Noren et al., 2015). Moreover, it appears that phocid diving capacity is significantly correlated with mass, while that of otariids is not. Additionally, observations of phocids generally indicate that they dive deeper and longer in relation to body mass than otariids do. They also seem to have lower metabolic rates while diving, in part because of slower swim speeds, which decreases their rate of oxygen consumption. On the basis of body size, both odontocete and mysticetes are surpassed by the relative smaller phocids in average diving capacity, if fact, plots of duration and depth versus mass shows that mysticetes always fell below the overall regression lines. This means that if phocids were as large as mysticetes or even odontocete, they would dive deeper and longer (Schreer and Kovacs, 1997). To conclude, we know that animals normally show diving behaviours that rarely exceed the ADL. For example, on his field study near Svalbard, Wiig et al., (1993), described the diving patterns of a walrus with a time-dive recorder and he estimated, for a 1500 kg male walrus, an aerobic dive limit of about 10.5 minutes and only about five percent of all the walrus dives he recorded exceeded the estimated ADL, and never for more than two minutes. More recently Noren et al., (2015), with their calculations, demonstrated that a mature 830 kg female and a 1200 kg male walrus can dive aerobically for up to 13.3 and 14.8 minutes respectively, achieving a maximum possible depth of 319 and 355 m, respectively. They also measured that calves (first two years postpartum) only dive aerobically for 4.7 minutes. In his study, Kooyman and colleagues (1971), demonstrated that in the Weddell seal dives up to 15 minutes do not completely exhaust muscle aerobic stores and that beyond that value the dive is primarily anaerobic as far as the major muscle mass is concerned and the accumulation of metabolites results in maximal post-dive recovery stimulus and prolonged recovery times. He also recorded dives that lasted for more than 80 minutes and he demonstrated that those animals would dive longer after a 100% oxygen ventilation.

General cardiac adaptations while diving

There have been many studies on diving physiology of air-breathing animals in the first half of 20th century, but the experimental protocol for many of them has been to forcibly dive restrained and static animals. Some of the responses that may occur under these restrained dive conditions are upon immersion like marked bradycardia with reduction in cardiac output, widespread

redistribution of blood flow in which circulation to many regions of the body decreases profoundly while blood flow to the brain is maintained at or above pre-dive levels and a drop in body temperature as the result of a decline in metabolic rate (Kooyman et al., 1980). Anyway, the decrease in mean cardiac outputs is a well-recognized physiological modification that happens while diving and it has been measured in many studies (Murdaugh et al., 1966; Kooyman and Campbell, 1972; Sinnet et al., 1978; Zapol et al., 1979) and the action of arteriovenous anastomoses in the skin and many other organs, that drive the blood flow to the primary vital organs like brain and heart and thus prevent heat dissipation, has been demonstrated as well (Molyneux and Bryden, 1975; Zapol et al., 1979). All the mentioned studies are related to pinnipeds — both restrained and freely diving — and they all sow an average decrease of heart rate of about 85% while diving, an analogous cardio-vascular adaptation mechanism is likely to be present in cetaceans too.

3. THE STRESS

Through the ages, a lot of researchers worked on theories concerning stress, in which they tried to give many different definitions that aimed to fit on what exactly stress is. In this section, this author assumes, following modern theories, that stress is a simple state in which the homeostasis is lost (Reeder and Kramer, 2005) or the experience of having intrinsic or extrinsic demands that exceed an individual's resources for responding those demands (Morgan and Tromborg, 2007). The event that causes the disruption in equilibrium, or that force that challenges homeostasis, that may be physical, psychological or both, is defined as "stressor" (Selye, 1976; Reeder and Kramer, 2005; Morgan and Tromborg, 2007). Physiological stressors may include those internal or external to the animal, such as anoxia and hypoglycaemia, heat or cold, exercise or injury and many others. Psychological stressors may include stimuli or forces that affect emotions like eliciting fear, anger, anxiety, depression or frustration (Reeder and Kramer, 2005). In either case, stressors result in a cascade of physiological events, and behavioural reactions, designed to prepare the body for homeostatic challenge, requiring the animal a higher expenditure of energy (Reeder and Kramer, 2005; Morgan and Tromborg, 2007). The stress response is mediated by an integrated network of neuroanatomical structures and peripheral organs that produce the behavioural and physiological changes used to re-establishing equilibrium (Reeder and Kramer, 2005). Regarding those neuroanatomical structures, Porges (1995) created a model which emphasized the role of the brainstem in regulating behavioural and physiological reactivity to stress. This model is based on neurophysiological structures common to all mammals, like the nucleus ambiguous, which coordinate the sucking, swallowing, breathing and regulate shift in heart rate and vocalization frequencies in response to stressful events. The two most important physiological responses to stress are the stimulation of the sympathetic nervous system (SNS) and the hypothalamic-pituitary-adrenal (HPA) axis, which result in altered physiological processes (Reeder and Kramer, 2005). To better understand the complex mechanism of the responses we can also divide the stressors in two principal branches in which they are associated with different reactions: short-term or acute stressor; long-term or chronic stressors. Acute, or short-term stressors are typically associated with behavioural responses of orientation, alarm, increased vigilance (Morgan and Tromborg, 2007), escape or avoidance, altered cognition and attention span, increased awareness, altered sensory threshold, stress-induced analgesia, suppression of feeding behaviour (Reeder and Kramer, 2005). On the other hand, physiological components of this response profile include

tachycardia, increased respiration rate, increased glucose metabolism, and an increase in various isomers of glucocorticoids (GCCs), which shift metabolism toward energy mobilization and away from energy conservation (Romero, 2004; Morgan and Tromborg, 2007). In comparison, chronic, long-term stress results in prolonged elevation of GCC levels (Romero, 2004) that in effect become self-sustaining, as prolonged high levels of circulating GCCs damage areas of the brain responsible for terminating stress response (Morgan and Tromborg, 2007). Physiologically, chronic stress may be indicated by suppressed reproductive cycling or reduced growth hormone with inhibited growth rate (Chrousos, 1997) reduced body weight and others. The main behavioural responses are also related with altered reproductive conduct, abnormal behaviour like increased aggression (Bartolomucci et al., 2004) or increased behavioural inhibition with a reduction in complexity (Rutheford et al., 2004; Vyas and Chattaii, 2004; Carlstead and Brown, 2005) and many more that can be found in literature (Morgan and Tromborg, 2007). To conclude, it is useful to know that this particular cascade of events, which starts when a stressor is perceived as such by the brain, can vary over time within an individual. That is, what initiates a stress response in one animal may not do so in another, and also may depend on factors such as the life-history stage, developmental history and reproductive conditions (Reeder and Kramer, 2005).

Stress sources in captivity and reactions

Approximately 26 billion animals spanning more or less ten thousand species are kept under managed care. The locations vary and include farms, zoos, conservation breeding centres, household and laboratories. Animals held under managed care are known to be healthier, longer-lived and sometimes more fecund than wild ones, because they receive food and water, veterinary care and protection from predation and conflict. It is not always true, however, that all captive wild animals do not flourish in this way, with some surviving breeding less than might be expected, and there is much evidence of compromised welfare that suggests that physiological or psychological needs, or both, are not being met. As previously summarized, they can include avoidance of potential threat, associated acute stress responses like the release of catecholamine and corticosteroid and their functional consequences as increased heart and respiration rates, while long-term responses such as adrenal enlargement, compromised growth, reproductive suppression, immunosuppression and stereotypic behaviour are often present (Mason, 2010). In their work, Morgan and Tromborg (2007) accurately described a wide variety of stress sources that can be found in managed care animals and regarding this, I will briefly

summarize the ones of interest for this section. First of all, they explain that greatest stressors for captive mammals are those over which the animals have no control and form, which they cannot escape. Perhaps unexpectedly, one of sources stress for animals may be the artificial environment or enrichment that normally aim to offer greater opportunity of exploration and withdrawal from observation enhancing the complexity of the animal surrounding. It is clear that many environmental enrichment techniques and strategies have improved the captivity conditions, but we must pay heed to the fact that we are often unaware of sensory elements of the captive environment that animals may find stressful (Figure 7).
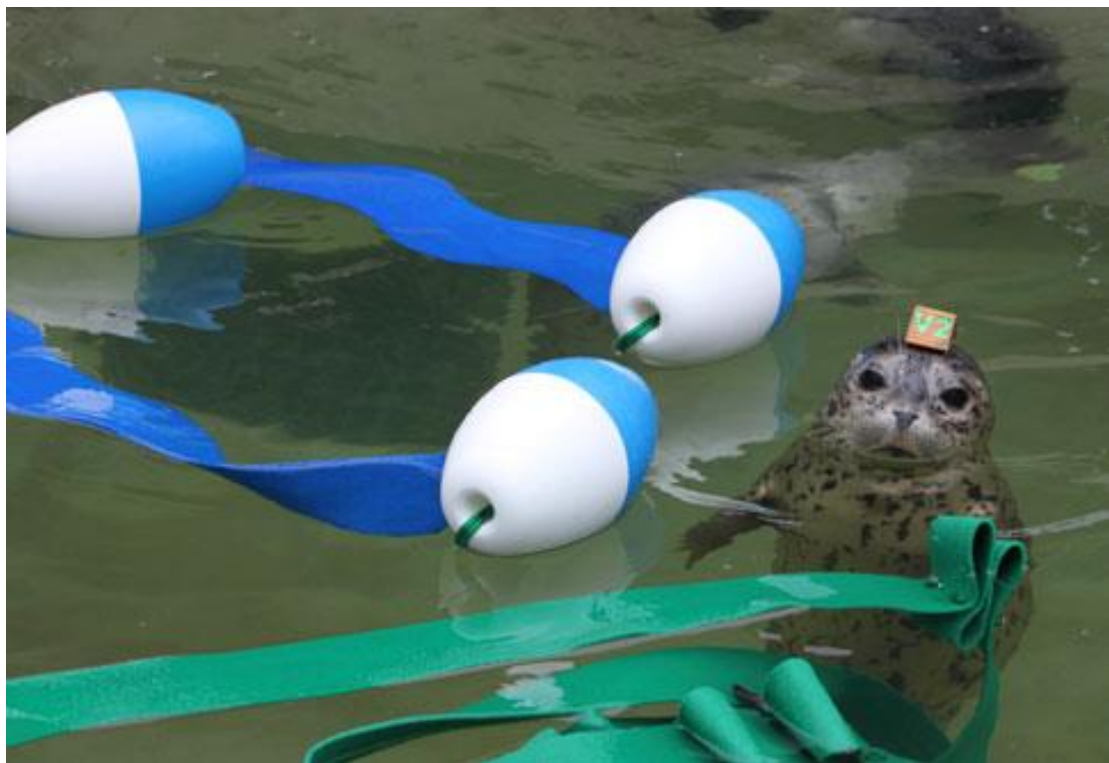
Figure 7. Orphaned harbour seal with environmental enrichment at The Marine Mammal Center of Sousalito, CA, during a research to discover whether enrichment may help to reduce stress and recovery time. Photo: Sarah van Schagen (www.marinemammalcenter.org).

At this point it would be appropriate a summarized and simple review of the main stressful sources listed in the Morgan and Tromborg (2007) paper. The sound — which the pressure levels in nature nowhere near approach the ones recorded in zoos — can affect blood pressure and heart rate when intense and continuous for protracted time and also can be related to elevated levels of physiological and behavioural arousal. An example of a sound source that may affect the animals can be the cages and facility cleaning or the noise related to the increasing number of visitors. The artificially-induced light conditions in closed environments,

which are often not corresponding the normal ones, and may alter the melatonin and serotonin ratio or suppress the circadian activity. If we focus on the fact that almost all mammals are macro-osmatic (they largely depend on olfactory cues), even the smell may be considered as a source of stress, such as the ones that comes from the cleaning products, from forced proximity to humans, conspecifics or possible predators. They are mostly related to increased blood pressure, production of long-lasting changes in anxiety-like behaviour or increase in defensive behaviours. The temperature plays a fundamental role in the animal life, and any variation (intended as both increase or decrease) in level may be considered as a possible source of stressor, depending on the animal that we are taking in consideration. Regarding this precise point, this author suggests the consultation of the given literature for more interesting information concerning the principal responses and reactions to temperature variation (Welch, 1992; Mortola and Frappell, 2000). Anyway, looking back on Morgan and Tromborg (2007) work, temperature principally affects the behaviours of the animals. High temperature has been often described as a source of discomfort and distress while low temperatures and cold result in a higher frequency of stereotypical behaviour, even more, prolonged and irregulated shift on thermal levels may be related to abnormal growth rate and altered sexual behaviour and maturation. Moreover, one of the greatest stressors in captivity is the restriction of movement due to small cages or environments in general which is often related to abnormal behaviour, stereotypic locomotion or increase in agonistic behaviour and impaired growth rate. On the other hand, increasing cage size or absence of retreat space may be stressful for prey animals that are hunted in open spaces. In captivity, the opportunity to move away from one another or from human passers-by is often negate due to the architecture of the buildings in which the animals are hauled that led in a possible forced proximity to humans. Regarding this, the authors says that zoos, parks and aquariums normally increase visitor-animal interaction to promote empathy and sense of connection needed to improve attitudes with respect to conservation (this was true in this author's personal experience as well), but that forced proximity or contact can be deleterious to animal well-being. In fact, the human's presence appears to reduce species-typical behaviour, and in some cases, overall activity. An interesting and recent study on visitor effects on harbour seals and California sea lions were conducted by Vere (2018) in a park in California, and she discovered that the sea lions showed no significant changes in behaviour while seals showed increased feeding behaviour and vigilance. This is to explain that the proximity of humans is not always a source of stress, it depends on the life history of the animal and it surely depends on the species, for example, seals are well known for being much more bashful and vigilant and compared with sea lions (personal experience

and observation). Indeed, the effect of possible contact with humans varies depending on the nature of that contact and animal's past experiences (Hemsworth, 2003), moreover, positive interactions can result in improved well-being and they are often searched out by animals. In this list it cannot go unmentioned the routine husbandry events, often associated with human caretakers, that even if they aim to give more variables to the animals they keep, is often really difficult to avoid certain kinds of daily routines. For example, repeated events such as cage-cleaning may be a source of distress, or restricted feeding and foraging opportunity with an inflexible or unaccommodating daily schedule. The food is substantially different from what the animals would eat in nature in many situations and for many species, and the portion of daily activity for search and consumption of food in captivity is minimal or absent and it requires minimal effort. Some authors have discovered that the frustration of appetitive behaviour results in locomotor stereotypies as animals attempt to search for food in a restricted environment (Morgan and Tromborg, 2007). For example, post-feeding oral stereotypic behaviours and tusk rubbing in walruses has been widely recognized (Dittrich, 1987; Steenkamp, 2003), probably reflecting natural molluscivorous diet in wild (Mason, 2010). Moreover, the predictable availability of food in some cases appears to generate abnormal behaviour like stereotyped pacing and other repetitive locomotor activity that seems to increase as feeding times approach (Vickery and Mason, 2004; Morgan and Tromborg, 2007). In fact, the predictability of captive life may be stressful even if the animals tend to choose predictability over unpredictability when a choice is given (Gliner, 1972).

AIM OF THE WORK

The general aim of the study is to evaluate the effect of some variables, some of which may be potential stressors, on the physiology of respiration in three adult female walruses, housed in managed care facilities. More specifically, the aim of the present study is to find the relation of these potential stressors with respiratory frequency. As already described (1.4 chapter), variations in respiration rate in certain situations may be an indicator of acute stress. The variables that were considered in the research are variables that cannot be controlled by the animal, in fact, as we know, greatest stressors for captive mammals are those over which the animals have no control and form which they cannot escape (Morgan and Tromborg, 2007). Taking as a reference some studies, observations and reviews (Dittrich; 1987; Porges, 1995; Morgan and Tromborg, 2007; Mason, 2010; De Vere, 2018) conducted on pinnipeds and other animals, the variables analyzed in this study are: time of the day, level of public (low/medium/high), presence / absence of environmental enrichment, pre-feed/ post-feed / non-feed and body mass. The temperature and the light conditions were not considered in the study, because they were kept almost constant. Moreover, no less important, it would be interesting to provide, through the present work, useful insights for future research perspectives, such as the construction of a detailed respiratory rate pattern to be able to estimate the metabolic rates where respirometry is of difficult application. The present work is to be considered valid for the subjects and the study environment, the possible application to the population and other individuals will be discussed below.

MATERIALS AND METHODS

1 INDIVIDUALS

I measured respiratory frequency in three adult female Pacific walrus *Odobenus rosmarus divergens* (Figure 8), raised in managed care and housed in the 'Artico' department at Avanqua Oceanogràfic Ágora in Valencia, Spain, in the current study. All were born in the wild and arrived together to the park when they were few months old and still not weaned. At the time of the study, they were fed on a diet composed principally of herrings (*Clupea harengus* - Linnaeus, 1758), capelin fish (*Mallotus villosus* - Müller, 1776), squids (*Loligo vulgaris* - Lamarck, 1798), mussels (*Mytilus galloprovincialis* - Lamarck, 1819) and edible jelly (Table, 1). They were normally fed by hand and the composition of the diet, such as quantities and percentage of each food item were determined by the husbandry staff and veterinarians. A supplement in vitamins (Aquavits) was provided daily, with the first meal in the morning.

Table 1. Individuals information at the beginning of the study.

Animal ID	Weight (kg)	Age (years)	Sex
26005389	900	16	F
26005390	783	16	F
26005388	665	16	F

Figure 8. Individuals.

2 CHARACTERISTICS OF THE STUDY AREA

The walrus exhibition pool consisted of two sections (Figure 9). The first one is the land area (4), called 'beach' and is a normal smooth basement where the animals can haul-out to rest and is the zone in which the keepers and trainers usually feed them, making the public able to watch. The second area (5) is the aquatic one, filled with sea water and without topographical features, which is the one where all the observations for the study were conducted. There were more sections and facilities on the backstage (Figure 2), out of the view of visitors, which is the reason why they are not considered in the study, such as the medical pool (1), the 'scale' area where the animals were weighed (6), the 'shower' area where the walruses were sometimes hauled out to sleep (2) and the veterinary section (3). In all the described sections, the animals could be trained and fed by their trainers. A brief summary of the total volumes and surfaces of the pools is presented below (Table 2).
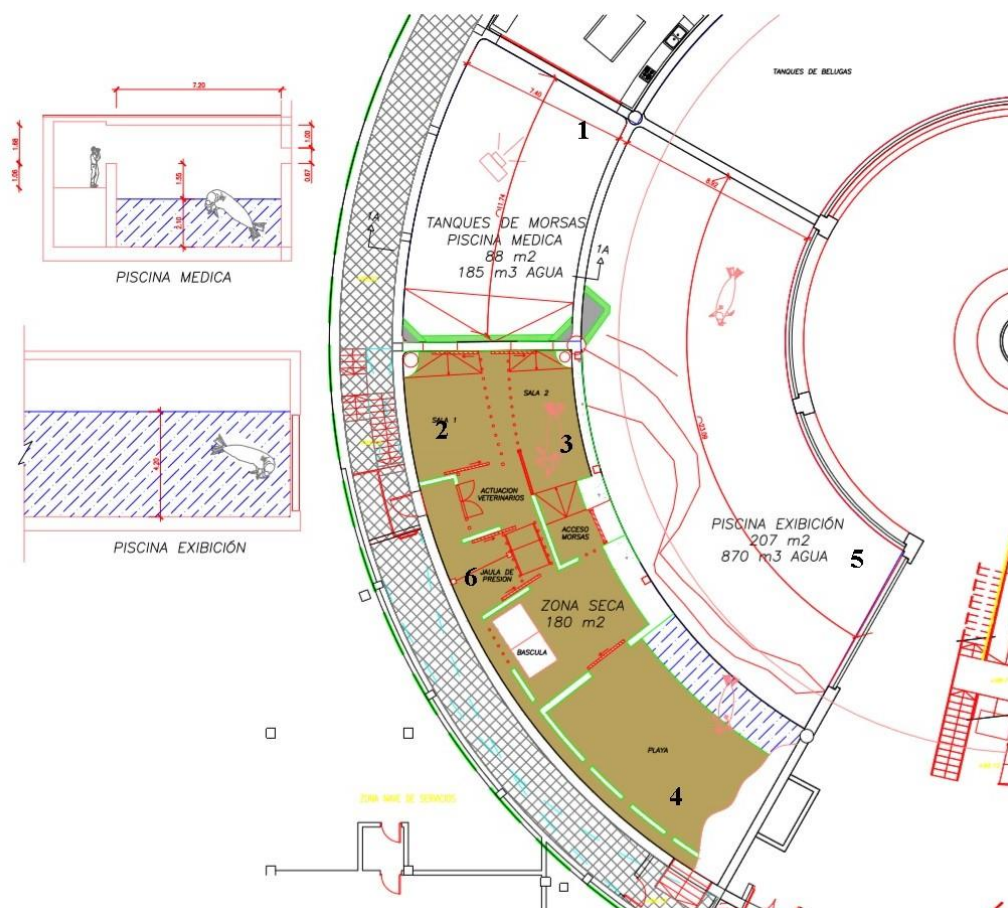
Figure 9. Walruses pools and facilities divided into areas.

Table 2. Total volumes and surfaces of the water areas.

Pools and water areas	Volume (m3)	Surface (m2)	Depth (m)
Exhibition	528	220	4
Beach	8	75	0,24
Medical pool	340	85	3
Total	876	380	/

3 SAMPLING METHODOLOGY

Evaluation of the respiratory frequencies and variables

Respiratory rate (breaths · min^{-1}) was determined visually, without any manipulation of the animals and only while they were in water due to the difficulties on evaluating proper measures while hauled-out. The observation of the animals started the first of May and lasted till the 31 of July. When fed, observations lasted for three minutes (Bertelsen et al., 2006), one for each animal. The data were taken randomly through the day, but not daily, one measure for each animal in the 15 minutes prefeed and one in the 15 minutes post feed. At least half an hour after a feeding session, two breathing rate values for each animal were captured for the 'non-fed' measures, in observation sessions that lasted normally ten to fifteen minutes (Franks et al., 2010). All the respiratory frequencies have been evaluated by observing the exhalation and the nostrils while they emerged from the water to breath. Rare episodes of apnoea were observed and signed as 0 (breaths/min) in the dataset. Data regarding environmental enrichment were taken only as presence/absence in the tank or outside or both. The visitor presence was evaluated by counting the people around the pool while monitoring the animals and summarized into four categories: 0 when 0; 1 when 1 to 25; 2 when 25 to 50; 3 when more than 50 (Table 3). The body mass (kg) was determined weekly using a Mettler Toledo scale, as a normal routine in the park. The date and the hour were noted down for each observation.

Table 3: Here is shown a portion of 26005389's dataset. Under the voice Treatment, 'C' is unfed, 'B' is prefeed and 'A' is post feed. Under the voice Enrichment presence, 'YES' means presence and 'NO' means absence.

Date	Animal ID	Breath frequency (breaths/min)	Treatment	Public level	Body mass (kg)	Hour	Enrichment presence
01/05/2018	26005389	1	C	2	890	14:00	YES
	26005389	3	C	2	890	14:00	YES
	26005389	4	C	1	890	17:45	YES
	26005389	4	C	1	890	17:45	YES
02/05/2018	26005389	2	B	1	890	15:30	NO
	26005389	4	A	1	890	16:00	NO
03/05/2018	26005389	5	B	1	890	10:10	NO
	26005389	3	A	1	890	10:40	NO
	26005389	3	B	1	890	15:50	NO
	26005389	5	A	1	890	16:20	NO
	26005389	3	B	1	890	15:50	NO
	26005389	7	A	1	890	16:20	NO
06/05/2018	26005389	3	C	1	890	17:10	NO
	26005389	4	C	1	890	17:10	NO
	26005389	4	B	1	890	11:25	NO
	26005389	5	A	1	890	11:55	NO
	26005389	4	B	1	890	17:00	NO
	26005389	4	A	1	890	17:30	NO
07/05/2018	26005389	6	B	1	890	10:55	NO
	26005389	6	A	1	890	11:25	NO
	26005389	3	B	1	890	13:45	NO
	26005389	2	A	1	890	14:15	NO

4 DATA AND STATISTICAL ANALYSIS

During the experiment, a total of 375 measures of breathing frequency were collected. The relationship between the dependent variable (breathing frequency) and experimental covariates animal, body mass, enrichment (yes/no), treatment (no food/before feeding/after feeding), and visitor state (low/medium/high), time of day, was analyzed using linear-mixed effects models (lme, R: A Language and Environment for Statistical Computing, R Foundation for Statistical Computing, version 3.3.3, 2016). The individual animal was treated as a random effect, which accounted for the correlation between repeated measurements on the same individual (Littell et al., 1998). Best models were chosen by the AIC statistics against nested models. In this study, P-values ≤ 0.05 were considered as significant and $P \leq 0.1$ were considered a trend. Data are presented as the mean $\pm$ standard deviation (s.d.), unless otherwise stated.

RESULTS AND GRAPHICS

The multivariate analysis, including animal as a random factor, indicated that only treatment (before feeding/after feeding) warranted inclusion in the model, while the number of visitors, presence of enrichment, the time of the day and body mass did not affect the f_R. A post-hoc Tukey test indicated that there was no difference in f_R without food and before feeding, and these two treatment periods were pooled and the final model was (c^2=4.79, 1 df, P = 0.029): f_R = 3.55 + 0.46 * after feeding, showing that f_R increased by 13% after feeding. For mass-corrected f_R (sf_R) the equation was: f_R/M_b = 0.0047 + 0.00059 * after feeding (c^2=4.88, 1 df, P = 0.027).

Table 4. Animal ID, mean breathing frequency (f_R), body mass ($M_{b,}$). Superscripted numbers are the number of repeated measurements

Animal ID	f_R (breaths * min^{-1})	M_b (kg)
26005389	3.7 ± 1.6^{126}	906 ± 28^{12}
26005390	3.0 ± 2.2^{126}	787 ± 11^{12}
26005388	4.3 ± 1.4^{123}	665 ± 9^{13}

Graphics

As long as there are no differences within animals, we may not consider the uneven number of samples and we can summarize the distribution of the treatments in the following boxplot graphics (Figure 10).
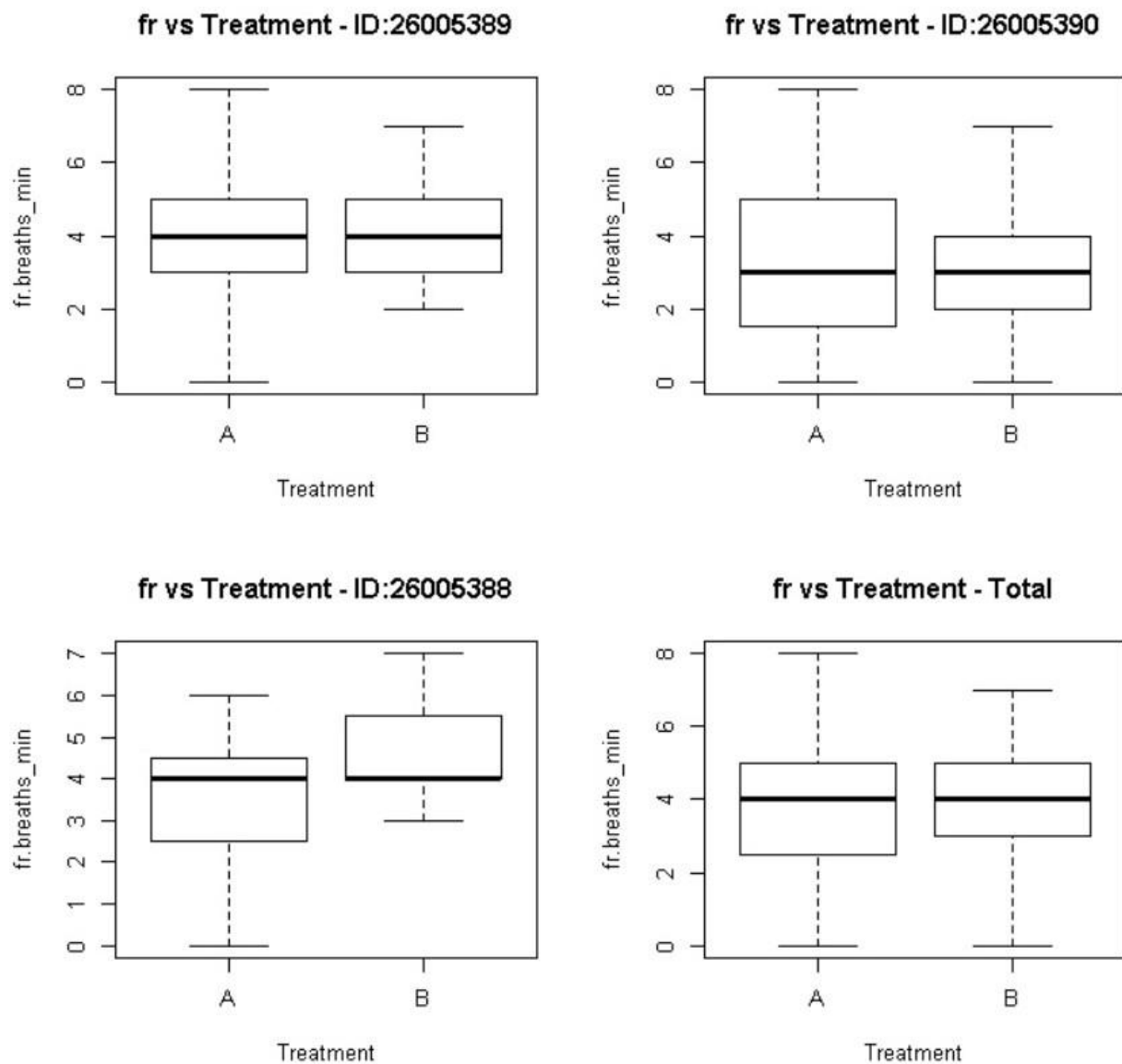
Figure 10. On the *x*-label A indicates the after feeding treatment and B indicates the before feeding treatment, with the frequencies as *y*-label.

The graphic "fr vs Treatment – total" shows a symmetric distribution of the measures with low dispersion around the median in the before feeding ("B") treatment, while the distribution is asymmetric with more dispersion in the after feeding ("A") treatment. The higher dispersion in the upper limit of the after feeding treatment, that ranges for higher values of respiration frequencies, supports the results that we obtained by the model. The presented f_R data are not mass-corrected, and the differences in the boxplots 26005388 and the others suggests a possible high correlation with body mass.

DISCUSSION

In this study, I am presenting mean values of f_R that ranged between 3.0±2.2 and 4.3±1.4 breaths per minute while the animals were active in water. The animals of this study are used to be in almost constant visual contact with visitors. They are grown in managed care and the number of visitors present did not seem to affect their f_R. The same seems to happen with the environmental enrichment presence and is not likely to have a negative impact. As this, the time of the day is not affecting their respiration rates even if we know that the basal metabolism varies through the day. Is good to mention again that the facility where they are housed is indoors, and that the temperature and the light conditions (mostly artificial) are kept almost constant. It is possible that those conditions may play a role on the regulation of their metabolism. For the body mass, more measures are needed to make this variable significant, or it may not be significant, but anyway, we already know that it correlates well with the breathing frequencies in mammals, and then, we need to consider that smaller individuals tend to show higher rates if compared to bigger ones. For the feeding state, we discovered that after feeding treatment showed an increase on mean f_R rates of about 13% in comparison to before feeding. This can be explained in many ways. First of all, we already know that oral stereotypic behaviours such as tusk rubbing and food searching on the bottom of the pools in walruses, due to the natural molluscivorous diet, has been widely recognized after feeding session (Dittrich, 1987; Steenkamp, 2003; Mason, 2010). This allows us to think about the fact that if they actively spend more time underwater then they emerge more times to breathe in a given period of time, due to a physical effort or simple stereotyped swimming. As already mentioned, the predictable availability of food can affect the locomotor activity like stereotyped pacing as feeding times approach (Vickery and Mason, 2004; Morgan and Tromborg, 2007). Anyway, this remains unclear for the population that we considered in this study, as it seems that there may be no differences between before feeding and non-feed, and as such, it is of the opinion of this author that they are not likely to anticipate feeding times. Even more, we know that those animals are almost always fed by hand, and that the nature of contact with the human caretaker is often positive and can result in improved well-being and they are often searched out by the animals (Hemsworth, 2003). Then, we can speculate the fact that they are likely stay in a sort of excitation the first minutes after a feeding session, because it brings not only food, which is the primary reinforcement used in training, but variability, traduced in different contacts and activities with the keepers, like playing. Thus, it seems logical to think that those results are the

normal consequence of the physiology of digestion, with higher metabolic rates and then higher f_R rates. Furthermore, the mean f_R in the current study agreed well with results from previous reports in wild animals (Stirling and Sjare, 1988; Born and Knutsen 1990*a*; Bertelsen et al., 2006). The measures taken in those studies comes from resting animals or before anaesthesia, then, it seems that there is not a noteworthy difference in the mean breathing frequencies between a resting animal and an active one. Bertelsen et al. (2006) obtained a mean value of 3.3 ± 0.3 breaths per minute on resting wild animals, mean values of 3.9 breaths per minute were obtained by Born and Knutsen (1990a) and 4.5 breaths per minute by Stirling and Sjare (1988) before anesthesia. Obviously, it must be taken in consideration the physiological state of the animal. Is reasonable to think that a sick individual is likely to respond differently in comparison to a healthy one. Even more, Bertelsen et al. (2006) says that in his field work the animals were not disturbed by the presence of the researcher, and that they did not even react to the application of electrodes to measure the hearth rate. The lower heart rates and breathing frequencies that he took, according to the other mentioned studies, support his view. The results that we obtained by animals kept in managed care seems to give strength to this theory, but still, we cannot exclude that the presence of visitors and people in general can be a potential source of stress, and that the alteration in breathing frequencies are much more closely related to acute stress than chronic (Morgan and Tromborg, 2007) and for now, we cannot define which kind of possible stressor the public presence might be due to its situational nature. Thus, we must consider many variables in any one given situation of contact with an animal — either in the nature or in managed care — like the eventual presence of calf or new born, the physiological state of the animal, the circumstances, and life history. On the other hand, in many scenarios the public may play as a source of distraction, and the contact, intended as the simple presence of the people around the pool can potentially be positive. To conclude, it is necessary to mention that the managed care parks aim to reach the highest level on animal welfare and that those organizations spend a lot of resources and efforts to get this target. In the past few years the knowledge concerning this topic has improved as has public sensitivity. In addition, it is important to say that the results obtained in this study can potentially be useful for future researchers and studies and that more attention need be paid in certain situations. Even if this work gives clues that supports the possibility that the presence of people is not considerable as a stressor, it is of the opinion of this author that it remains difficult to answer to the question: "Is this species affected negatively by the presence of humans?".

CONCLUSIONS

As previously showed, it seems that there are no noteworthy differences on the respiratory frequencies between resting and active walruses. First of all, it is beneficial to be aware that the quantity of data in concerned literature is poor, and therefore, we cannot confirm this hypothesis quite yet. And then, another interesting research prospective would be the construction of a detailed respiration pattern for the different activities of those animals through the day. This would allow us to make more solid conclusions and mostly, to be able to build a model to estimate the metabolic rates. In essence, the visitor level, the enrichment presence and the time of the day, seems not to affect the respiration rates of the walruses housed at the at Avanqua Oceanogràfic Ágora in Valencia, Spain. And for now, it is right to accept the fact that those variables may not be considerate as a source of stress in those animals, or better, we can say that they do not affect this particular component of the physiological response to stress. A component, which seems to be affected by the feeding state. The possibility that the frequencies are affected as a result of the behavioral component of stress response is yet to be evaluated, even if it seems a reasonable view. For this reason, it would be of invaluable interest to pursue research in this particular field, by monitoring the behaviors of those animal over the same conditions and following the same treatments. It appears clear that some work still needs to be done and for the moment, it is untimely to say that the differences that have been discovered reflect stress, but rather a normal consequence of digestion. Until now, we cannot pinpoint exactly what is occurring and thus more attention is needed. To conclude, the present study provides novel data concerning the respiratory frequencies of walruses and the methodology presented here, provides a simple way of performing active monitoring without any manipulation of the animal by the researcher. This suggests that the technique would be applicable under the same condition in another park as-well. More so, the fact that we treated the subjects of this study as a random factor, allows us to speculate about the entire walrus population under managed care over the same conditions, in any park. In fact, we are dealing with variables concerning physiology, such as differences in respiration rates related to metabolism and digestion, variables, that are unlikely to change for different individuals in the same health conditions. This said, we can consider our individuals as random walruses of a certain size. If we think about the possibility that any one of those walruses could be a part of the given population, then we can apply the results of this study to them as well.

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