International Journal of Comparative Psychology, 2013, 26, 75-82.

Correlations of Swimming Patterns with Spinal Deformities in the Sand Tiger Shark, *Carcharias taurus*

Erin E. Tate
The Florida Aquarium Center for Conservation, U.S.A.
The University of Tampa, U.S.A.

Paul A. Anderson
The Florida Aquarium Center for Conservation, U.S.A.

Daniel R. Huber
The University of Tampa, U.S.A

Ilze K. Berzins
The Florida Aquarium Center for Conservation, U.S.A.

Spinal deformities among captive sand tiger sharks, *Carcharias taurus,* are unfortunately common, and abnormal swimming behavior due to constrained aquarium space has been hypothesized to contribute to the development of this condition. Public aquaria across the United States were surveyed for number, condition (healthy vs. affected), and total length of resident *C. taurus* specimens and for dimensions of their aquaria. They were also asked to record 10 minute video segments of individual *C. taurus* swimming in lateral view. Total length of sharks, regardless of condition, averaged 225 ± 5 (mean ± SE) cm. Aquarium shapes varied widely, but aquaria held median volumes of $1.03 \text{ X } 10^6$ L, and were a median of 4.6 m in depth and 20.7 m in greatest horizontal distance. The greatest horizontal distance of aquaria was negatively correlated with disease prevalence of resident populations in a logarithmic fashion ($r = 0.72$). Behaviorally, sharks were assessed for total time and percentage of time spent swimming in a specific direction (clockwise, counter-clockwise, or linear), in a glide, and tail-beat duration. Regardless of condition, *C. taurus* spent a median of 98.9% of time swimming and 0.62% of time gliding. Healthy sharks spent a median of 0.67% gliding versus a median of 0% for afflicted sharks ($p = 0.036$), suggesting an increased swim-to-glide ratio among the latter group. All sharks swam asymmetrically in either a clockwise or counter-clockwise direction for a median of 99.7% of observed time. Affected specimens had tail beat durations of 3.37 ± 0.23 s vs. 2.72 ± 0.10 s for healthy sharks ($p = 0.005$). The increase in swim-to-glide ratios and inordinate time spent swimming asymmetrically for all affected sharks support the hypothesis that swimming patterns induced by captive exhibits may contribute to spinal deformities in *C. taurus* due to more stress placed on the spine. Large, complex aquarium designs are recommended in the planning of new exhibits to discourage stereotypical swimming behavior and also to provide sufficient length for sharks to complete natural swimming repertoires. Comprehensive behavioral enrichment activities that encourage complex movement are also recommended as well as considerations such as even weight distribution of the animal during capture, sourcing of appropriately aged sharks, and nutritional supplementation.

The authors are grateful to the participating aquaria, as well as their husbandry and veterinary staffs: Adventure Aquarium, Aquarium of the Pacific, Downtown Aquarium in Denver (Landry's), Dynasty Marine Associates, Jenkinson's Aquarium, Kattegat Centre, Moody Gardens, Mystic Aquarium and Institute for Exploration, National Aquarium in Baltimore, New England Aquarium, New York Aquarium, North Carolina Aquarium on Roanoke Island, Omaha's Henry Doorly Zoo, Ripley's Aquarium, Sea World of Orlando, Sea World of San Antonio, The Seas Aquarium at Epcot (Walt Disney World), South Carolina Aquarium, Tennessee Aquarium, and Underwater Adventures at Mall of America. This study was sponsored by The Association of Zoos and Aquariums Conservation Endowment Fund, The Disney Worldwide Conservation Fund, The Bernice Barbour Foundation, and The Jacarlene Foundation. P. Anderson was supported by The Spurlino Foundation and an anonymous donor. W. Price advised E. Tate's scholarship at the University of Tampa in the context of this study. Correspondence concerning this article should be addressed to Erin E. Tate, The Florida Aquarium Center for Conservation, 701 Channelside Drive, Tampa, Florida, 33602, U.S.A. (Etate07@gmail.com).

Spinal deformities have been documented in both captive and wild-caught cartilaginous and bony fish (Heupel, Simpfendorfer, & Bennett, 1999; Hoenig & Walsh, 1983). Sand tiger sharks *(Carcharias taurus)* maintained in human care have been known to develop spinal deformities with some prevalence; Berzins, Whitaker, March, and Hutchins (1998) and Berzins, Walsh, and Richards (2002) reported 33 cases, representing 1/3 of *C. taurus* held in in human care at that time (American Elasmobranch Society, 1997; Anderson, Huber, & Berzins, in press). The deformity is described as a lateral and/or dorso-ventral spinal curvature (kyphoscoliosis) that develops between the pectoral fins and the cranial dorsal fin (Berzins et al., 1998). Hypothesized etiological factors include abnormal swimming patterns due to inadequate aquarium size or design, capture and/or handling-induced trauma, dietary deficiencies, genetic factors, musculoskeletal disease, biomechanical abnormalities, and abnormal growth patterns (Berzins & Walsh, 2000; Preziosi et al., 2006). Anderson et al. (in press) and Noaker, Huber, Anderson, and Berzins (2010), which present a more in-depth discussion of other facets of this disease, discovered that capture, handling, nutrition, and the biomechanical properties of spinal tissue were correlated with the deformity.

Most sharks are either facultative or obligate ram ventilators, requiring constant forward motion to maintain respiration (Gruber & Keyes, 1981). This presents husbandry challenges to public aquaria maintaining sharks in human care as aquaria must be designed to be large enough to accommodate constant swimming motion by large animals. Klay (1977) described the swimming repertoire of sharks to include cruising, rest or glide, recovery, and turning stages. Klay calculated that shark species commonly kept in human care need an average linear swimming space of 14 body lengths, or approximately 20 m for a shark with an average adult length of 140 cm, to conduct a normal swimming repertoire composed of all of the above stages. Klay hypothesized that most shark aquaria in existence at the time were of limited size and thus 1) didn’t provide sufficient distance to enable sharks to carry out full swimming cycles, and 2) necessitated excessive turning. Powell, Wisner, and Rupp (2004) and Choromanski (2004) expanded on Klay’s findings and added that ram ventilators such as *C. taurus* would benefit the most from aquarium designs that included gentle currents, long stretches between rocky outcrops, and aquarium shapes to improve swim-to-glide ratios over the common cylindrical design found in many aquariums. These hypotheses suggest that behavior of *C. taurus* in human care may either be a causative or exacerbating factor with regard to the development of spinal deformities in *C. taurus*. The objective of this aspect of the study is therefore to evaluate correlations between shark size, aquarium dimensions, swimming patterns, and the occurrence of spinal deformities in *C. taurus.*

Method

Surveys

A survey kit was sent out to U.S. public aquaria with *C.taurus* in their collections. Surveys requested information on total length (from tip of the snout to tip of the upper caudal lobe in a natural position) of *C.taurus* specimens, presence or absence of spinal deformities, photos and radiographs for verification of said deformities, and aquarium dimensions (shape, volume, length, width, and height). As part of a two-stage survey, we also requested information regarding animal history (sex, morphological data at as well as date of acquisition, location and method of capture, and onset of deformity if the animal in question is affected) and blood samples for hematological analysis. These aspects of the survey are discussed in-depth in Anderson et al. (in press). Survey kits also included a Sony Handycam (Model No. DCR-HC52, Minato, Tokyo, Japan) and MiniDV videotapes. Participants were asked to record 10-minute segments of individuals swimming in lateral view. Aquarists were asked to clean exhibit glass prior to filming, to shut off aerators, and to cease other aquatic activity in order to provide optimum visibility and to capture normal, uninterrupted behavior.

Materials and Procedure

Returned videotapes were played back on a JVC GR-D850 camcorder connected to a portable Philips LCD flat screen television (Amsterdam, Netherlands). An ethogram of swimming behavior was constructed from qualitative observations of 20 individuals on videotape. Behaviors were subsequently scored and quantified by one observer using JWatcher software (V. 1.0, Blumstein Lab at University of California Los Angeles and The Animal Behaviour Lab, Macquarie University, Sydney Australia). All observations were completed in a random order over a span of 3 months.

Analysis. We selected the following behavioral measures to analyze from the video tapes: total time and percentage of time spent swimming in a specific direction while energy was exerted to produce momentum (clockwise, counter-clockwise, linear), time spent gliding, and full tail-beat duration (a combination of the right and left tail beat, starting from the middle of the body and returning to the middle). We calculated percentages as a proportion of total time the animal was in sight during the recording.

Aquarium/Prevalence Correlation. We computed and reported descriptive statistics for total length of sharks and aquarium dimensions. We then constructed a correlation between the longest horizontal distance of aquaria containing a mixed population of at least three (healthy and/or afflicted) animals and the proportion of populations presenting with spinal deformities.

Descriptive statistics were then computed, and we assessed measures for normality using the Kolmogrov-Smirnov method. We tested raw data for measures that demonstrated normal distributions; data demonstrating non-normal distributions were transformed prior to testing. Data sets between healthy sharks and those presenting with spinal deformities were assessed for heterogeneity of variance using the F-test, and *t*-tests were run between healthy and deformed sharks for all measures reported, assuming equal variances only if F-test results did not support heterogeneity of variance between groups. Two-tailed *p* values are reported.

Results

Total lengths of sharks were reported from 43 healthy and 15 affected specimens distributed among 14 institutions, but did not differ between the two groups of animals ($t = 0.06$, $df = 56$, $p = 0.953$). Regardless of condition, total body lengths ranged from 101 to 292 cm, with a mean of 225 ± 5 (mean ± SE) cm.

Sixteen aquarium dimensions were reported from 14 institutions. Aquaria varied widely in shape, and included four cylinders, three ellipses, three rectangles, two kidney-shaped aquariums, and one each of aquaria described as a triangle, dumbbell, donut, or other polygon. Aquaria ranged in volume from 1.51×10^5 L to 2.16×10^7 L, with a median of 1.03×10^6 L. Aquaria ranged in depth from 1.4 to 12.8 m, with a median of 4.6 m. The longest horizontal distance of aquaria ranged from 8.23 to 61.8 m, with a median of 20.7 m.

The longest horizontal distance of aquaria was negatively associated with disease prevalence in a logarithmic fashion ($r = 0.72$):

$$y = -0.339 \ln x + 1.3538 \qquad (1)$$

where y = disease prevalence (as a proportion) and x = horizontal distance (m). That is, aquaria with smaller lengths or diameters had populations of *C. taurus* with higher prevalence of spinal deformity. For example, the aquarium with the smallest diameter of 12.2 m demonstrated a disease prevalence of 75% of its population, while the aquarium with the longest length of 37.8 m demonstrated a disease prevalence of only 27% of its population (Figure 1).

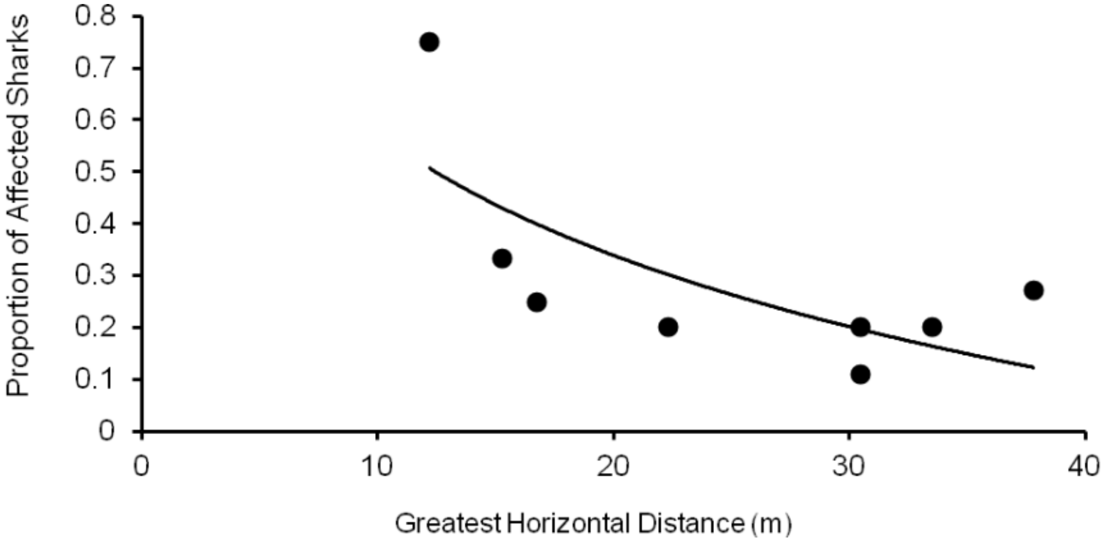

Figure 1. Greatest horizontal distance of aquaria vs. proportion of captive *Carcharias taurus* populations presenting with spinal deformities.

Videotapes were returned for 40 captive *C. taurus* distributed among 10 institutions. Thirty-one sharks were healthy, while 9 were diagnosed with spinal deformity via gross appearance and/or radiography. An ethogram was created from behavioral observations (Table 1). All *C. taurus*, regardless of condition, spent a median of 98.9% of time swimming and 0.62% of time gliding. Healthy specimens spent a median of 0.67% gliding versus a median of 0% for specimens with spinal deformities (t = 2.17, df = 38, p = 0.036). Regardless of condition, individuals swam asymmetrically (clockwise or counter-clockwise) a median of 99.7% of time, while linear swimming was negligible (0%). Finally, specimens with spinal deformities had tail-beat durations of 3.37 ± 0.23 s vs. 2.72 ± 0.10 s for healthy sharks (t = 2.96, df = 38, p = 0.005).

Table 1

Ethogram of locomotion in the captive sand tiger shark, Carcharias Taurus

Linear Swim	Carchariniform swimming pattern along a straight trajectory. Body is parallel with exhibit floor/water surface. Caudal fin undulates equally at 45° from median on each side of the body. Pectoral fins are angled out and may be angled down at approximately 30°.
Counter-clockwise Swim	Shark continuously swims in counter-clockwise direction. Undulation of caudal fin is continuous but uneven on the left and right sides of the body, > 45° to the left and < 45° to the right. Pectoral fins are angled out and may be angled down at approximately 30°.
Clockwise Swim	Shark continuously swims in clockwise direction. Undulation of caudal fin is continuous but uneven on the left and right sides of the body, > 45° to the right and < 45° to the left. Pectoral fins are angled out and may be angled down at approximately 30°.
Glide	Shark stops undulating the caudal fin; caudal fin positioned directly behind the body. Pectoral fins are angled out and down at approximately 15°. No momentum is generated.
Right Tail-Beat	Caudal fin undulates > 0° to the right of the body during swimming. Tail-beat ends when caudal fin is in line with the body at 0°.
Left Tail-Beat	Caudal fin undulates > 0° to the left of the body during swimming. Tail-beat ends when caudal fin is in line with the body at 0°.

Discussion

The results reported here suggest a relationship between aquarium length and the prevalence of spinal deformities among captive *C. taurus* populations. Aquaria less than 20 m in length held populations with greater than or equal to a 25% prevalence rate. Evaluating these results in the context of Klay's (1977) recommendations, a captive sand tiger shark with an average length of 225 cm requires a minimum linear swimming length of 31 m. Only 38% of aquariums with reported dimensions approached this requirement.

The aquarium length deficiencies encountered in the survey are informative in light of measured swim-to-glide ratios. Klay(1977) and Powell et al. (2004) suggests swim-to-glide ratios ranging from 1:1 to 1:2. However, in our study gliding was a rare phenomenon throughout the entire behavioral data set. Furthermore, sharks with spinal deformities spent significantly less time gliding than did healthy sharks; all sharks, regardless of condition, spent essentially 100% of their time swimming asymmetrically. We therefore hypothesize that the excessive proportion of active, asymmetrical swimming places undue lateral stress on the vertebral column, potentially contributing to scoliosis.

Afflicted sharks demonstrated longer tail-beat durations, suggesting slower swimming. This quantitatively confirms qualitative observations of loss of forward speed in affected animals, described by Preziosi et al. (2006). This behavioral change is not likely a behavioral response to nociception of the injury. Elasmobranchs lack populations of unmyelinated sensory axons in nerves entering the spinal cord; these types of axons are the predominant type responsible for signaling the occurrence of nociceptive stimuli and tissue injury (Rose, 2002; Snow, Plenderleith, & Wright, 1993). It is thus considered that elasmobranchs lack the neural structures for processing nociceptive information. Alternatively, slower swimming speed may result from disruption of the biomechanical properties of the tissues involved in swimming. Another possibility may be the result of a less than optimal hydrodynamic configuration where a crooked body would not generate the proper lift and forward translation as that of a straight body moving through the water column. Afflicted sharks also demonstrated higher body condition factors (K, after Anderson & Neumann, 1996) than healthy sharks despite no significant differences in dietary intake mass (Anderson et al., 2012). This increased weight per unit length may result from lower activity budgets, symptomatic of metabolic decline, and may place an extra weight-burden on an already compromised vertebral column.

Consistent swimming in one circular direction with no gliding behavior to break the swimming cycle is a repetitive and unvarying behavior and as such, resembles stereotypic behavior (Mason, Clubb, Latham, & Vickery, 2007). It is reminiscent of locomotor stereotypies documented in terrestrial mammals (e.g., pacing, Clubb & Vickery, 2006), birds (e.g., route tracing, Keiper, 1969), and aquatic mammals (e.g., circle or pattern swimming, Grindrod & Cleaver, 2001; Hunter, Bay, Martin, & Hatfield, 2002; Kastelein & Wiepkema, 1988, 1989). Stereotypical behavior often signals an elevated stress state (Cabib, 2006). Alternatively, it may develop as a coping mechanism to help the animal manage in a stressful environment (Novak, Meyer, Lutz, & Tiefenbacher, 2006). In either case, it is often considered a behavioral symptom of suboptimal animal welfare (Mason, 1991b; Mason et al., 2007). Unfortunately, some stereotypies can be directly self-injurious (e.g., hair-pulling in primates, Novak et al., 2006) and even indirectly self-injurious. For example, horses that display the locomotory stereotypical behaviors of weaving and stall-walking develop painful back conditions (Mason, 1991a). We hypothesize that the repetitive circular swimming behavior observed by *C. taurus* is an example of an indirectly self-injurious, locomotory stereotypical behavior. Causation of stereotypical behavior is probably multifaceted, and a thorough discussion of the topic is beyond the scope of this study. However, some hypotheses point to captive situations in which the animal is housed in an environment with low stimulus input and/or physical restraint (Mason, 1991b). The authors hypothesize that the development of stereotypical swimming behavior in *C. taurus* may be instigated by these conditions.

Thus, public aquaria are encouraged to build large aquariums for shark holding and exhibition. For the average size adult captive sand tiger shark (225 cm), the length of aquaria should be at least 31 m long to enable animals to exhibit species-typical swimming cycles as described by Klay (1977). Increasing enclosure size has been shown to reduce locomotory stereotypies in other animals as well, such as canaries (Keiper, 1969) and primates (Chamove, 1989; Draper & Bernstein, 1963). Involvement of husbandry staff in aquarium design is also encouraged to ensure the space will be adequate for the optimal welfare of the animals as emphasized by Powell et al. (2004). Aquarium shapes and habitats should be designed to discourage stereotypical circular swimming and to encourage more complex swimming patterns; for example, figure-eight aquarium designs may encourage sharks to change directions in circular swimming, or habitats may be constructed in an aquascape that disrupts the circular swimming track – these types of aquarium designs have shown success in improving swim-to-glide patterns as highlighted by Choromanski (2004). These strategies may be considered environmental enrichment strategies; in monkey enclosures, the addition of trellises to walls, leaf cover to cage bottoms, and complex branching systems in the interior of enclosures reduce stereotypies and lead to a higher percentage of expression of wild-type behaviors by resident primates (Chamove, 1989).

Behavioral enrichment strategies can also lead to the reduction of stereotypical behavior. Among aquatic mammals with stereotypies, feeding enrichment strategies reduce stereotypical circular or pattern swimming. These strategies include variation in the amount, type, timing, and position of food offered; variation in the animal handler providing the food; and novel presentations of food in ice blocks, buoys, tethered to line (Grindrod & Cleaver, 2001), and buried in substrate (Kastelein & Wiepkema, 1989). Behavioral training, where animals are conditioned to perform a behavior for a reward, also reduces locomotory stereotypies in Steller sea lions (Kastelein & Wiepkema, 1988). A. Smith and S. Delano (Mystic Aquarium, pers. comm.) noted a change in behavior from circular swimming to complex swimming patterns in *C. taurus* upon the presentation of frozen blocks of water mixed with fish blood.

To reduce the occurrence of this disease among the captive population of *C. taurus,* we recommend a comprehensive health and husbandry management plan. This plan includes the recommendations here regarding aquarium design, environmental and behavioral enrichment, as well as recommendations developed in Anderson et al. (in press) that address considerations such as even weight distribution of the animal during capture and restraint, sourcing of wild caught sharks of appropriate age, and supplementation of the diet with vitamins C and E, potassium, and zinc.

References

American Elasmobranch Society. (1997). The 1997 International Captive Elasmobranch Census.

Anderson, P. A., Huber, D. R., & Berzins, I. K. (2012). Correlations of capture, transport, and nutrition with vertebral deformities in captive sandtiger sharks, *Carcharias taurus. Journal of Zoo and Wildlife Medicine. 43(4),* 750-758. doi: 10.1638/2011-0066R1.1

Anderson, R. O., & Neumann, R. M. (1996). Length, weight, and associated structural indices. In B. R. Murply & D. W. Willis (Eds.), *Fisheries techniques* (pp. 447-482). Bethesda, MD: American Fisheries Society.

Berzins, I. K., & Walsh, M. T. (2000). *Sandtiger shark (Carcharias taurus) scoliosis data and sample collection guidelines*. Presented at the 31st Annual Conference of the International Association of Aquatic Animal Medicine, Boston, MA.

Berzins, I. K., Walsh, M., & Richards, M. (March, 2002). *Spinal deformities in captive sand tiger sharks (Carcharias taurus).* Proceedings of the 27th Annual Eastern Fish Health Workshop, Mount Pleasant, SC.

Berzins, I. K., Whitaker, B., March, G., & Hutchins, G. M. (1998). *Preliminary evaluation of spinal deformities in the Sandtiger shark (Odontaspsis taurus*). Presented at the 29th Annual Conference of the International Association for Aquatic Animal Medicine, Tampa, FL.

Cabib, S. (2006). The neurobiology of stereotypy II: The role of stress. In G. Mason & J. Rushen (Eds.), *Stereotypic animal behavior: Fundamentals and applications to welfare, 2nd ed.* (pp. 227-255). Oxford, UK: CAB International. doi:10.1079/9780851990040.0000

Chamove, A. S. (1989). Environmental enrichment: A review. *Animal Technology, 40,* 155-178.

Choromanski, J. M. (2004). Quarantine and isolation facilities for Elasmobranchs: Design and construction. In M. Smith, D. Warmolts, D. Thoney, & R. Hueter (Eds), *The Elasmobranch husbandry manual: Captive care of sharks, rays, and their relatives* (pp. 43-51). Columbus, OH: Special Publication of the Ohio Biological Survey.

Clubb, R., & Vickery, S. (2006). Locomotory stereotypies in carnivores: Does pacing stem from hunting, ranging or frustrated escape? In G. Mason & J. Rushen (Eds.), *Stereotypical animal behavior: Fundamentals and applications to welfare, 2nd ed* (pp. 58-85). Oxford, UK: CAB International. doi:10.1079/9780851990040.0000

Draper, W. A., & Bernstein, I. S. (1963). Stereotyped behavior and cage size. *Perceptual and Motor Skills, 16,* 231-234. doi:10.2466/pms.1963.16.1.231

Grindrod, J. A .E., & Cleaver, J. A. (2001). Environmental enrichment reduces the performance of stereotypic circling behaviour in captive common seals *(Phoca vitulina). Animal Welfare, 10,* 53-63.

Gruber, S., & Keyes, R. (1981). Keeping sharks for research. In A. D. Hawkins (Ed.), *Aquarium systems* (pp. 373-402). New York: Academic Press.

Hoenig, J. M., & Walsh, A. H. (1983). Skeletal lesions and deformities in large sharks. *Journal of Wildlife Diseases*, *19* , 27-33

Heupel, M. R., Simpfendorfer, C. A., & Bennett, M. B. (1999). Skeletal deformities in elasmobranches from Australian waters. *Journal of Fish Biology, 54,* 1111-1115. doi:10.1111/j.1095-8649.1999.tb00861.x

Hunter, S. A., Bay, M. S., Martin, M. L., & Hatfield, J. S. (2002). Behavioral effects of environmental enrichment on harbor seals *(Phoca vitulina concolor)* and gray seals *(Halichoerus grypus). Zoo Biology, 21,* 375-387. doi:10.1002/zoo.10042

Kastelein, R. A., & Wiepkema, P. R. (1988). The significance of training for the behaviour of Steller sea lions *(Eumetopias jubata)* in human care. *Aquatic Mammals, 14,* 39-41.

Kastelein, R. A., & Wiepkema, P. R. (1989). A digging trough as occupational therapy for Pacific walruses *(Odobenus rosmarus divergens)* in human care. *Aquatic Mammals, 15,* 9-17.

Keiper, R. R. (1969). Causal factors of stereotypies in caged birds. *Animal Behavior, 17,* 114-119. doi:10.1016/0003-3472(69)90119-5

Klay, G. (1977). Shark dynamics and exhibit design. *Drum and Croaker, 171,* 29-32.Mason, G. J. (1991a). Stereotypies: A critical review. *Animal Behavior, 41,* 1015-1037. doi:10.1016/S0003-3472(05)80640-2

Mason, G. J. (1991b). Stereotypies and suffering. *Behavioural Processes*, *25,* 103-115. doi:10.1016/0376-6357(91)90013-P

Mason, G., Clubb, R., Latham, N., & Vickery, S. (2007). Why and how should we use environmental enrichment to tackle stereotypic behaviour? *Applied Animal Behaviour Science*, *102,* 163-188. doi:10.1016/j.applanim.2006.05.041

Noaker, D., Huber, D., Anderson, P., & Berzins, I. K. (2010). Biomechanics of spinal deformities in captive sandtiger sharks *Carcharias taurus*. *Florida Scientist, 73 (S1),* 37.

Novak, M. A., Meyer, J. S., Lutz, C., & Tiefenbacher, S. (2006). Deprived environments: Developmental insights from primatology. In G. Mason & J. Rushen (Eds.), *Stereotypical animal behavior: Fundamentals and applications to welfare. 2nd ed.* (pp. 58-85). Oxford, UK: CAB International. doi:10.1079/9780851990040.0000

Powell, D. C., Wisner, M., & Rupp, J. (2004). Design and construction of exhibits for elasmobranchs. In M. Smith, D. Warmolts, D. Thoney, & R. Hueter (Eds), *The elasmobranch husbandry manual: Captive care of sharks, rays, and their relatives* (pp. 53-67). Columbus, OH: Special Publication of the Ohio Biological Survey.

Preziosi, R., Gridelli, S., Borghetti, P., Diana, A., Parmeggiani, A., Firoavanti, M. L., & Berzins, I. (2006). Spinal deformity in a sandtiger shark, *Carcharias taurus* Rafinesque: A clinical pathological study. *Journal of Fish Diseases*, *29,* 49-60. doi:10.1111/j.1365-2761.2005.00684.x

Rose, J. D. (2002). The neurobehavioral nature of fishes and the question of awareness and pain. *Reviews in Fisheries Science, 10,* 1-38. doi:10.1080/20026491051668

Snow, P. J., Plenderleith, M. B., & Wright, L. L. (1993). Quantitative study of primary sensory neurone populations of three species of elasmobranch fish. *Journal of Comparative Neurology*, *334,* 97-103. doi:10.1002/cne.903340108