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Location, Location, Location! Evaluating Space Use of Captive Aquatic Species—A Case Study with Elasmobranchs

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Abstract: The space use of captive animals has been reliably used as a tool to measure animal welfare in recent years. However, most analyses of space use focus primarily on terrestrial animals, with very little emphasis placed on the space use of aquatic animals. By comparing the space use of these animals to their natural histories and what would be expected of them physiologically, a general assessment of their overall welfare can be obtained. Using the Zoomonitor program, this study investigated the space use of five elasmobranch species housed in a captive aquatic environment: a blacktip reef shark (*Carcharhinus melanopterus*), a nurse shark (*Ginglymostoma cirratum*), a smooth dogfish (*Mustelus canis*), a bonnethead shark (*Sphyrna tiburo*), and a blacknose shark (*Carcharhinus acronotus*). The exhibit was delineated into five different zones: three represented the animal locations along the X/Y axis ('Exhibit Use'), and two zones were related to the Z-axis ('Depth Use'). The location of each individual on both the X/Y and Z axes was recorded during each observation. Heat maps generated from the Zoomonitor program were used in conjunction with the Spread of Participation Index (SPI) to interpret the data. It was found that while all the individuals used their given space differently, the Exhibit Use was relatively even overall (the SPI values ranged from 0.0378 to 0.367), while the Depth Use was more uneven (the SPI ranged from 0.679 to 0.922). These results mostly reflected what would be expected based on the species' natural histories. However, for the smooth dogfish, the observed Exhibit Use and activity patterns revealed a mismatch between the anticipated and the actual results, leading to further interventions. As demonstrated here, space use results can be utilized to make positive changes to husbandry routines and enclosure designs for aquatic individuals; they are thus an important additional welfare measure to consider for aquatic species.

Keywords: elasmobranch; sharks; space use; ZooMonitor; spread of participation index; animal welfare

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1. Introduction

Although the space use of animals in captivity has been studied both formally and informally for decades, it has only recently been introduced as an indicator of animal welfare [1–3]. Even space use is typically anticipated for captive animals in a good welfare state, as it suggests that the animals do not actively avoid any areas in their habitat and willingly utilize their enclosure to its fullest potential [4,5]. However, it is also important to note that species' natural history or certain physiological elements can also influence activity level and space use [6–8]. In particular, species' natural history must be considered to ensure that enclosures provide appropriate opportunities for species-typical behaviors [9,10]. Both the specific behaviors of the focal subject(s) and the areas in which they display these behaviors are essential to the evaluation of enclosures. Therefore, an indicator of good enclosure design for an animal is whether the animal uses its enclosure in a way that would be expected for its species.

While space-use evaluations have become more commonplace as metrics of welfare in terrestrial animals, they are not yet widely applied to aquatic species, particularly teleosts and elasmobranchs [11]. Consistent considerations in both applications include establishing a behavioral repertoire of species-specific behaviors and an understanding of natural history. Factors that may uniquely affect aquatic animal space use include the chemical parameters and flow of water, the vibration of pumps and other equipment, and the depth of the environment [12,13]. The influence of many of these factors may not be immediately apparent to caretakers, but may be reflected in the enclosure location choices of aquatic animals. Therefore, the consistent documentation of enclosure use for aquatic species could prove to be even more vital to welfare than its use for terrestrial species.

The reliable documentation and quantification of space use for both aquatic and terrestrial animals can be performed quickly and efficiently when using the right tools. The ZooMonitor program [14] is a web application that allows data to be collected on captive-animal behavior and space use with ease. A project can be created based on research needs, and any focal animals can be entered for behavioral data collection. An image of an enclosure can then be uploaded onto the application, and animal location data can be collected at preset intervals by selecting where the individual was in the enclosure image at any given time [5]. Many enclosure-use studies have utilized the ZooMonitor program to collect data on the space use of a variety of terrestrial zoo animals [14–17]; however, few articles have been published about space use in aquatic environments [18].

The space-use data collected from ZooMontitor can be easily evaluated using a variety of post-occupancy evaluations. Post-occupancy evaluations (POEs) were originally used to determine how effectively space was used in occupied industrial buildings [19,20]. POEs involve assessing the utilization of a given space, as well as interviewing individuals who use the area being evaluated and gaining insight into their level of satisfaction with the space. The insight gained from these evaluations would historically be used to steer architectural changes in how buildings were designed [20]. However, in recent years, POEs have found additional practical applications in studies of animal enclosure use [21]. All POEs usually involve dividing a given space into zones, and then running analyses based on how those zones are used in relation to the entire space [11]. Many different POEs that can be used to interpret how an animal explores its enclosure and interacts with the resources within it [11]. Brereton discusses four main methods that are used to evaluate space use in captive animal species: zone occupancy, Dickens' [22] Spread of Participation Index (SPI), Plowman's [23] Modified Spread of Participation Index, and Vanderploeg and Scavia's [24] Electivity Index. Each of these methods evaluates unique aspects of enclosure use. For example, zone occupancy is used to report the percentage of time a specific zone is in use, whereas SPI is used to determine how evenly a given space is used. Both the Modified SPI and the Electivity Index can be used to determine how resources in space are utilized. The evaluation method chosen ultimately depends on which variables are examined in the study [25]. In addition, while all of these methods have their own merits, very few of them have been used to assess aquatic populations [11].

The lack of quantifiable data on welfare outcomes in aquatic populations has driven the formation of the Association of Zoo and Aquariums' (AZA) Aquatic Collection Sustainability Committee, with the expressed goal of encouraging the proper consideration, documentation, and assessment of welfare indicators in aquatic collections [26]. With that goal in mind, this study aims to raise awareness of the importance of documenting space-use data on captive aquatic species, and of how this information can then be utilized to improve welfare outcomes.

2. Materials and Methods

2.1. Subjects

There were five focal subjects in this study: a female bonnethead shark *(Sphyrna tiburo*), a female blacknose shark (*Carcharhinus acronotus*), a male blacktip reef shark (*Carcharhinus melanopterus*), a female smooth dogfish (*Mustelus canis*), and a female nurse shark (*Ginglymostoma cirratum*). All individuals resided together with other animals in a mixed-species exhibit.

2.2. Exhibit

Data collection took place at the SEA LIFE Michigan Aquarium. The focal individuals resided in the Ocean Exhibit, which had a volume of 473,000 L and a depth of 7.3 m (Figure 1). This exhibit is designed to mimic conditions of ocean ecosystems, with dissolved oxygen concentration held at 98%, salinity held at 29–30 ppt, temperature held at 24–25 °C, and a photoperiod of 14:10. In addition to the five focal individuals, the Ocean Exhibit is also home to two green sea turtles (*Chelonia mydas*), roughly 250 teleost fish (including golden trevallies (*Gnathanodon speciosus*), tangs (*Naso* sp.), a Goliath grouper (*Epinephelus itajara*), among other assorted tropical marine species, and two dozen other elasmobranchs, including cownose rays (*Rhinoptera bonasus*) and southern stingrays (*Hypanus americanus*). With the exception of the blacktip reef shark, all individuals in this study were the only individuals of their species in this exhibit. The male blacktip reef shark was specifically chosen for data collection, as he was the easiest to reliably differentiate from the other conspecifics.

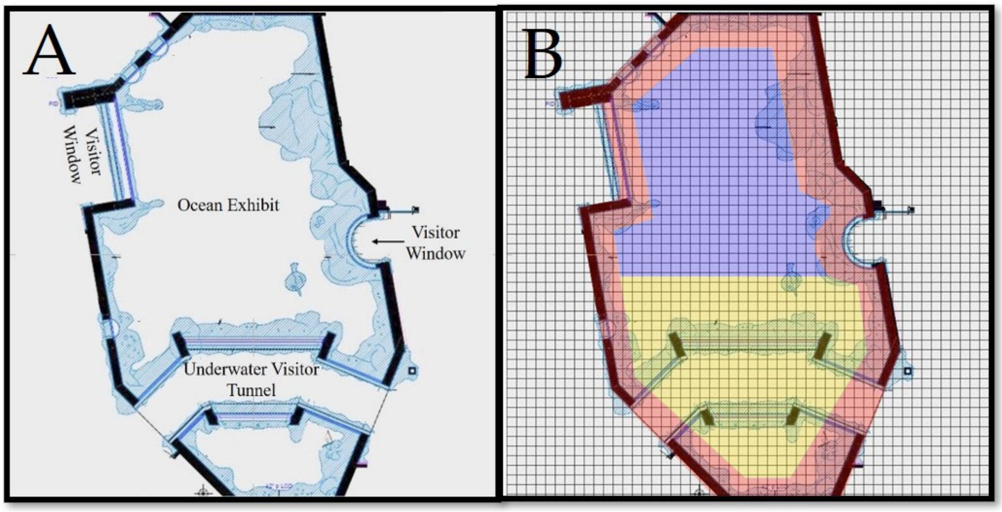

Figure 1. (**A**) The 2-D map of the Ocean Exhibit used to collect the Exhibit Use data. The thick black lines represent the perimeter of the exhibit, whereas the blue shades represent vertical rock formations within the tank. The 'underwater visitor tunnel' was a submerged glass tunnel for visitors to walk through, over which the exhibit animals could swim. (**B**) Map with zones indicated, and the 50 × 50centimeter grid used to ensure the zones were of equal size. Zone 'A' is colored in yellow, Zone 'B' is blue, and Zone 'C' is red.

2.3. Data Collection

Data were collected from 13 December 2018 to 18 June 2019, and data collection sessions were conducted one to two times a week. To ensure well-represented data and attempt to prevent selection biases, every week, a random number generator was used to determine both the weekdays and the time of day that data would be collected. Data were recorded using a tablet with the ZooMonitor program, which allows users to easily input the location of an individual at predetermined intervals [14]. Two observers collected data: one aquarist from SEA LIFE Michigan and one university student studying animal behavior. Prior to data collection, the observers conducted several practice sessions where both observers would record location of an individual simultaneously in order to determine whether results were consistent. Following these practice sessions, an inter-observer reliability test was conducted, which yielded nearly perfect similarity (>90%) in data collection from both observers. Both observers continued to collect data throughout the observation period.

Observational sessions for each individual lasted ten minutes, and focal scan sampling of location was performed at one-minute intervals [27]. If the focal individual was not visible at the one-minute interval, no data were recorded. All focal individuals were recorded once per observation day, and the order in which individuals were observed was also randomized each day of data collection via a random number generator.

2.4. Data Analysis

The data collected from ZooMonitor were used to generate heat maps for all individuals using Microsoft Excel's 3D Map feature. A 2-D map of the exhibit was uploaded into the Zoomonitor program to allow documentation of animal location along the X/Y axis during observations (hereafter referred to as Exhibit Use; Figure 1A). A 50 × 50-centimeter grid was then placed over the exhibit map in order to divide the enclosure into three equal sections of 245 cm^2 (Figure 1B). The area of each zone was calculated by hand using the over-laid grid. The zones were designated as the front of the exhibit (zone 'A', colored in yellow on the map), the back of the exhibit (zone 'B', colored in blue), and the perimeter of the exhibit (zone 'C', colored in red) (Figure 1B). The exhibit was split into equal 'zones' in order to determine whether space use was relatively even overall throughout the exhibit. Even though the zones were equal in size, they were unique in composition. Notably, zone 'A' included the visitor tunnel, which is a large viewing area for guests to walk through. Zone 'B' had far fewer views to offer guests and more open space. Zone 'C' included the rock formations along the perimeter of the exhibit. In addition, the animal depth (Z-axis) was also documented by recording whether the animal was located in the upper 50% or lower 50% of the water column at the time of the observation.

The heat maps generated by Zoomonitor display individual data points as colored dots, and the density of data points at a given location is determined by color [5,28]. Blues and greens indicate a low density of data points, whereas yellows and reds indicate a higher density. The number of data points in each of the three zones for all five individuals was determined following data collection. As all zones chosen were of equal size, if the focal animals used all exhibit space effectively, they were observed in each zone evenly.

The effectiveness of enclosure use for the animals in this study was measured using Dickens' Spread of Participation Index (SPI) [22]. This method of analysis was chosen as it compares evenness of space use for individuals [11]. As our primary goal was to simply determine how the animals in the Ocean Exhibit used their space, and because all three zones chosen for this study were of the same size, this index was determined to be the most appropriate. Moreover, even though space use in aquatic populations is extremely understudied, this method has been used previously to evaluate space use in aquatic habitats [11].

The equation for SPI is as follows:

$$\frac{M(nb - na) + (Fa - Fb)}{2(N - M)}$$

where M is the mean frequency of observations in all pre-determined zones, N is the total number of observations, nb and na is the number of zones with observations less than or greater than M, respectively, and Fb and Fa are the number of observations in those zones [22]. A value of 0 indicated perfectly even space use, whereas a value of 1 indicated highly uneven space use. Two SPI values were calculated: one for the Exhibit Use (XY-axis), and a separate value for Depth Use (Z-axis). The index values ascertained from all individuals were then compared to each other and to what would be expected of the species in its natural environment.

3. Results

In total, 1214 observations were recorded in total for all the individuals, with an average of 243 observations recorded for each individual. There were 30 days of data collection in total, with observation times ranging anywhere from 8AM to 4:15PM. The overall number of data points for each individual in each of the zones is displayed in Table 1. These values were used to calculate the SPIs for all the individuals.

Table 1. Total number of data points in each zone and calculated SPI values for all five focal individuals. The 'Exhibit Use' section compares evenness for the front, back, and perimeter zones (i.e., XY-axis), whereas the 'Depth Use' section compares evenness for the upper and lower water columns (i.e., Z-axis). The ♦ symbol indicates the species with the most even space use, whereas the ♦♦ symbol indicates the species with the most uneven space use.

	Exhibit Use					Depth Use			
	Number of Data Points in Each Zone					Number of Data Points in Each Zone			
Individual	**A**	**B**	**C**	**Total**	**SPI**	**Upper Water Column**	**Lower Water Column**	**Total**	**SPI**
Blacktip reef shark	85 (35.9%)	78 (32.9%)	74 (31.2%)	237	0.0378 ♦	199 (84.0%)	38 (16.0%)	237	0.679 ♦
Bonnethead shark	104 (42.6%)	94 (38.5%)	46 (18.9%)	244	0.217	234 (95.9%)	10 (4.1%)	244	0.922 ♦♦
Blacknose shark	54 (20.4%)	73 (27.7%)	137 (51.9%)	264	0.278	242 (91.7%)	22 (8.3%)	264	0.833
Smooth dogfish shark	72 (31.2%)	33 (14.3%)	126 (54.5%)	231	0.318	221 (95.7%)	10 (4.3%)	231	0.913
Nurse shark	110 (46.2%)	107 (45.0%)	21 (8.8%)	238	0.367 ♦♦	30 (12.6%)	208 (87.4%)	238	0.761

A range of Exhibit Use SPIs was determined for all five individuals, which varied from 0.0378 (indicating very even space use) to 0.367 (indicating less even space use). The nurse shark had the most uneven space use (SPI = 0.367), followed by the smooth dogfish and the blacknose shark. The individuals with the most even Exhibit Use were the bonnethead shark and the blacktip reef shark (SPI = 0.0378; Table 1).

For the Depth Use, the SPI values ranged between 0.679 and 0.922. The individuals that had the most even relative space use for these zones were the blacktip reef shark and the nurse shark. The individuals with the most uneven space use were the blacknose shark, the smooth dogfish, and the bonnethead shark (Table 1).

4. Discussion

Overall, these results display a relatively expected level of space use for all five focal individuals, given their unique natural histories. The non-quantitative view of the heat maps showed that each animal uses their given space uniquely, with some sharks preferring certain areas over others. All five individuals in the study were observed in all three of the aforementioned zones, although the degree to which a zone was utilized varied by individual. For example, while the blacktip reef shark appeared to prefer certain areas of the exhibit (such as the cluster between zones A and C of the exhibit; Figure 2C), the overall Exhibit Use was extremely even (SPI = 0.0378; Table 1).

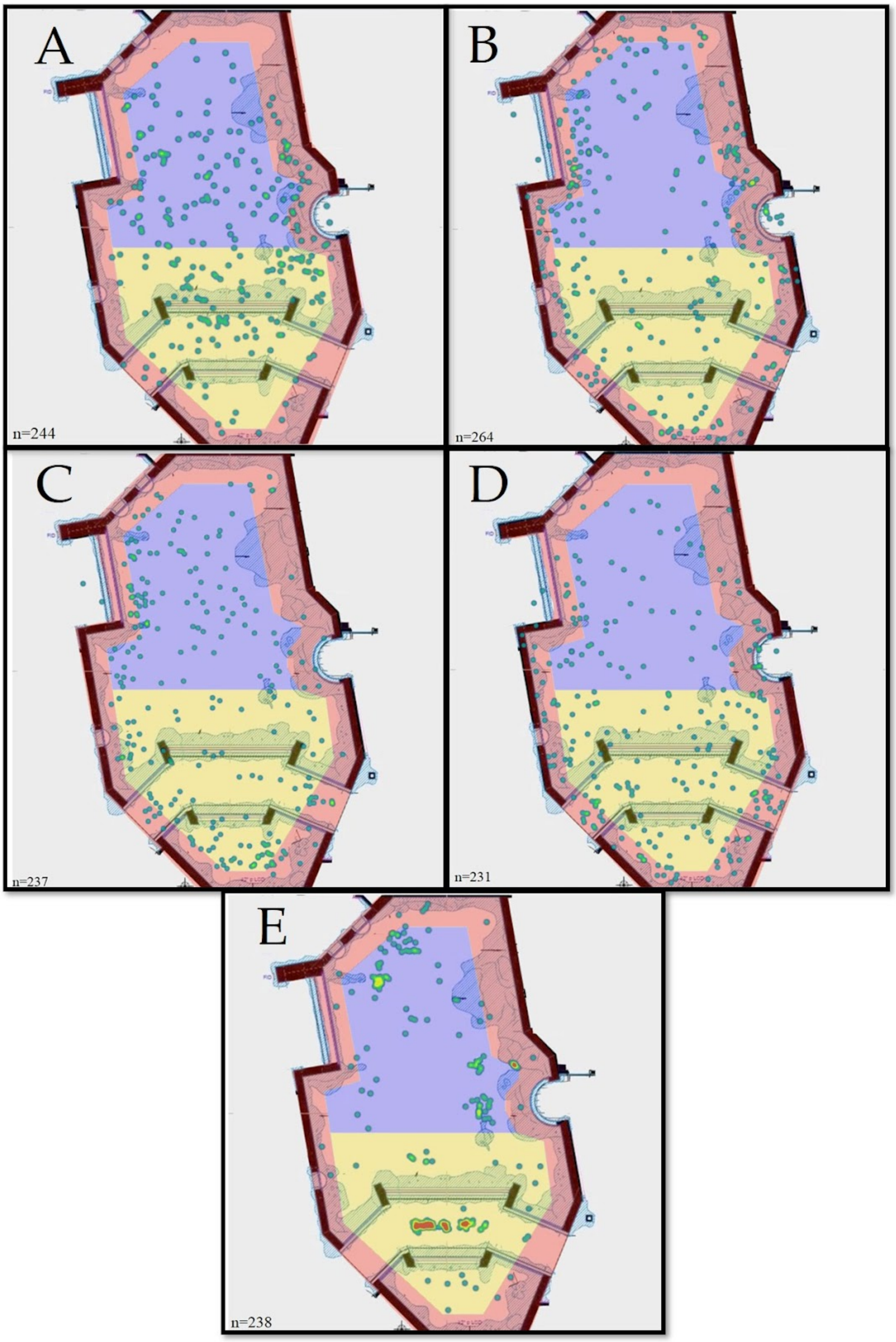

Figure 2. Heat maps generated for the Exhibit Use of all five individuals. The heat maps are labeled as follows: (**A**) bonnethead shark; (**B**) blacknose shark; (**C**) blacktip reef shark; (**D**) smooth dogfish; and (**E**) nurse shark. Zone 'A' is colored in yellow, zone 'B' is blue, and zone 'C' is red. Blue and green dots represent 1–2 data points, whereas reds and yellows represent large clusters of data points (3 or more).

As previously stated, when examining Exhibit Use, it is important to consider the physiology and natural history of an animal. The individual who had the most uneven Exhibit Use, the nurse shark, had an SPI of 0.367 (Table 1). The heat map for this individual (Figure 2E) shows that the nurse shark was indeed observed in all three zones, but preferred very distinct areas within the exhibit (shown by the clusters of red in the figure). Notably, the areas with the greatest concentration of observations of the nurse shark were above the viewing tunnel. Following the data collection, it was discovered that this preferred location was also near a high-flow pump. While several factors could have influenced her preferences, a possible explanation could also lie within the natural history of her species. Importantly, unlike the other shark species in this study (with the exception of the smooth dogfish), nurse sharks are not obligate ram ventilators, meaning they do not have to continually move in order to supply their body with oxygen [29–32]. Nurse sharks instead use a specialized organ, called a buccal pump, to move water over their gills while remaining motionless [31,33]. Thus, nurse sharks are typically considered to be highly sedentary because they have a higher cost for metabolic activity compared to other shark species [8]. With this in mind, it is possible that by positioning herself near the high-flow pump, the nurse shark in this study achieved even greater oxygen exchange with minimal effort. In addition, it was unsurprising that the nurse shark had a high SPI value for depth and was most often found in the lower water column (Table 1), because nurse sharks are primarily a benthic species [33,34] and characteristically spend most of their time resting on the seafloor [29]. These results reinforce the importance of taking natural history elements into account when evaluating space-use results, as uneven space use may not necessarily be a cause for welfare concern in some species.

While both nurse sharks and smooth dogfish are known to be primarily sedentary [8,35], blacktip reef sharks, bonnethead sharks, and blacknose sharks are considered obligate ram ventilators, who must therefore must move continuously in order to receive oxygen [31,36,37]. These three species are therefore typically considered highly exploratory (compared to the smooth dogfish and nurse shark), and, indeed, the SPIs and the heat maps of these species reflected this: all three individuals utilized their exhibits relatively evenly (Table 1). In addition, these three species are generally pelagic, and tend to appear in the open water [34]. It is therefore unsurprising that the data for depth show that these individuals tended to prefer the upper water column.

The notable exception to the species-appropriate Exhibit Use results was the smooth dogfish. Although smooth dogfish are buccal-pumping sharks and can frequently be found at rest [35,38], the smooth dogfish in our experiment appeared to be continuously moving throughout the exhibit and was never observed to be motionless throughout the data collection period. This is uncharacteristic of what would be expected physiologically [30]. In addition, she also had the second-most uneven Exhibit Use. The Depth Use SPI revealed even more startling information: the dogfish again had the second-most uneven space use, but the vast majority of the observations recorded her as being in the upper water column. As smooth dogfish are primarily benthic [39], these results were particularly troubling. Taken together, this information drove the creation of an additional study focused solely on the dogfish, whose space-use and behavior were more thoroughly examined [18]. Interestingly, it was noted that the perimeter of the exhibit (where she spent a disproportionate amount of time) seemed to encourage her to display stereotypical swimming behaviors. This drove a the implementation of a combination of interventions by animal husbandry staff, which ultimately resulted in more even space use, a reduction in stereotypical behaviors, and an increase in species-appropriate behaviors for this dogfish [18]. Without the initial data collection on the dogfish's basic space use, however, this welfare concern, and the resulting improvement in the animal's well-being, would not have been addressed.

Given that the space use of aquatic animals is an understudied aspect of zoo and aquarium welfare, future studies could be performed in many directions. The use of the Dickens' SPI index was appropriate to address the goals of the current study, but its utility is relatively limited, as it only provides an indication of the evenness of space use [25]. Our results indicated that specific areas of the exhibit were in fact preferred by certain individuals. Therefore, one important avenue for future analysis could involve the determination of the biologically relevant aspects of an exhibit (such as pump locations, viewing windows, hiding spaces, etc.) based on species' natural history, and the relation of those variables to individual space use using Plowman's Modified SPI or Vanderploeg and Scavia's Electivity index [23,24]. These indices are useful, as they provide information about whether specific locations (in both the X/Y and Z axes) within an exhibit are over- or under-utilized by animals [25]. Unfortunately, due to limited prior knowledge regarding the exact composition of the exhibit at the time of the data collection, these more inclusive analyses were not run for this dataset. It is also worth noting that since the current study observed five different species, a 'one-size-fits-all' analysis of resource utilization would not have been appropriate. All five species in this study have a unique natural history, and therefore have different biological preferences. These preferences likely result in different resource utilization by each species, which would have impacted how the zones were defined and what the expected values for the time spent in those zones would have been. For researchers interested in incorporating these indices in the future, it may be most effective to focus on a single species at a time for analysis, and to relate the space use to what would be biologically expected for that species based on its natural history. Nonetheless, we encourage researchers to consider utilizing these indices in the future, as they can provide even more detailed information relating to animal preferences and welfare.

This study initially aimed to simply determine whether all the focal individuals properly utilized the exhibit space provided. Even though these results are somewhat limited in their application, they highlight the fact that elasmobranchs *do* utilize their space differently based on their biological context, which was previously only anecdotally noted. By utilizing ZooMonitor software to collect data on the space use of captive animals, caretakers can therefore gain an understanding of the preferences of and potential causes of stress for animals that may not immediately be apparent. As space-use studies in aquatic species are relatively rare in comparison to equivalent studies of their land-dwelling counterparts [11], studies such as these can give important insight into the movement patterns and habitat choices of elasmobranchs and other fishes in captivity. By conducting comprehensive space-use analyses on aquatic populations, animal husbandry professionals can gain insight into changes in activity for individuals, the effects of visitors on space use, areas of the exhibit that show indications of being preferable or uninviting for resident animals, how individuals may alter their space use in relation to one another or seasonally, and many other applications. This information could be particularly useful for species involved in a Species Survival Plan (SSP) [40]. The IUCN states that, currently, 37% of all shark and ray species are endangered to some extent [41], which makes successful captive breeding programs even more essential to the continuation of these species. By learning how elasmobranchs are inclined to use space, animal caretakers can optimize exhibit design and overall welfare for individuals whose genetic diversity is of utmost importance, ultimately supporting conservation interests.

Continued space-use studies on captive aquatic populations can not only positively affect the focal individuals (as in the smooth dogfish in this study), but can also help to respond to the AZA Aquatic Collections Sustainability Committee's call to document, address, and improve the welfare and wellbeing of aquatic populations [26]. We therefore encourage other facilities to take an increased interest in the space use of their aquatic species, and suggest utilizing the ZooMonitor program as an important tool for enhanced aquatic animal management.

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Institutional Review Board Statement: As the data collection was purely observational and no external variables were added to the animals' enclosure, ethical review and approval were waived for this study.

Informed Consent Statement: Not applicable.

Data Availability Statement: Data are available upon request.

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