

THE VISUAL FIELD OF THE BOTTLENOSE  
DOLPHIN (*TURSIOPS TRUNCATUS*)

By

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*(TURSIOPS TRUNCATUS)*

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Abstract: Field of vision (FOV) aids a marine mammal in locating an object and the blind spot within the FOV can impede this ability, possibly leading to harm such as boat strikes (Murayama & Somiya, 1998; Wells et al., 2008). Identifying the FOV of bottlenose dolphins (*Tursiops truncatus*) is an important, but difficult question to study in cetacean biology. Previous attempts have examined the eyes of dead animals to generate potential FOV data based on retinal blind spots (Murayama & Somiya, 1998). But despite a large body of knowledge on vision in some mammals, little is known about bottlenose dolphins' 'practical FOV', defined as the FOV determined from live animals using psychophysical methods. I hypothesized that bottlenose dolphins have blind spots due to selection pressures associated with being both predator and prey in a three-dimensional fluid environment. I predicted blind spots occur in the area along the dorsal fin based on previous research indicating a high number of injuries to this back dorsal area (Wells et al., 2008). I also tested the claims that dolphins cannot see in the frontal area of the rostrum (Starkhammar et al., 2007; Xitco et al., 2004). The primary goal of this study was to determine the practical FOV in bottlenose dolphins and to identify the blind spots using a two-step approach. First, three dolphins from Dolphin Quest: Bermuda were psychophysically trained to give positive acoustic signals to the presence of light stimuli. Second, psychophysical training methods were used to map the dolphins' FOV and determine the location of blind spots in dolphin vision using LED lights at 25 different junction points in a Hoberman sphere, a geodesic dome structure large enough to encompass a dolphin's head (Li et al., 2018). As a result, the three dolphin subjects were able to see anteriorly, but were unable to see in the back dorsal area, which signifies that my hypothesis was supported and the claims made by Starkhammar et al. (2007) and Xitco et al. (2004) were not supported. The knowledge obtained has expanded our comparative understanding of mammalian eye evolution and contributes to conservation applications.

## TABLE OF CONTENTS

Chapter	Page
I. INTRODUCTION .....	1
Visual system evolution.....	1
Bottlenose dolphin vision .....	3
Retinal field of vision .....	4
II. METHODS.....	7
Subjects.....	7
Study area.....	7
Apparatus .....	8
Training.....	9
Hoberman Sphere .....	9
LED Lights Associations .....	10
Experimental Sessions .....	11
Data Analysis .....	13
III. RESULTS .....	15
Qualitative.....	15
Quantitative.....	16
IV. DISCUSSION .....	17
Future studies .....	20
Conservation applications .....	21
V. CONCLUSION .....	24
REFERENCES.....	25

Chapter	Page
APPENDICES .....	32

## LIST OF TABLES

Table	Page
1. Eye Structure.....	32
2. Predicted and observed pattern .....	37

## LIST OF FIGURES

Figure	Page
1. Dolphin Quest overview .....	32
2. Lagoon outline .....	33
3. Waterproof LED light.....	33
4. Attached LED light .....	33
5. Dolphin in Hoberman sphere .....	34
6. Hand signals with LED light.....	34
7. 3-D image of dolphin in sphere.....	35
8. Experimental process.....	35
9. Coloring technique on sphere .....	36
10. Minimum blind spot composite .....	38
11. Maximum blind spot composite.....	39
12. Best of three dolphins composite .....	40
13. 3-D images of M1 in sphere.....	41
14. 3-D images of F1 in sphere.....	42
15. 3-D images of F2 in sphere.....	43
16. Dolphin's visual field .....	44



## CHAPTER I

### INTRODUCTION

#### **Visual system evolution**

The visual system of vertebrates derives from the needs of early lamprey-like ancestors to detect potential predators or prey about 500 million years ago (mya) (Lamb et al., 2008). Vision predates the evolution of bone that would help define the modern vertebrate organism. Within 30 million years after the origin of the proto-vertebrate eye, the first true chordate develops, and with it, the evolution of the primitive vertebrate brain and the ‘neural tube’ that would give rise to the dorsal nerve cord.

Before the origin of the first chordates, two types of light sensitive cells were found in the eyes of our vertebrate ancestors: ciliary and rhabdomeric photoreceptors. Rhabdomeric photoreceptors are common today in invertebrates, whereas the ciliary type is the predominant photoreceptor in vertebrates. However, within the evolution of chordates, comes the ‘reassignment’ of rhabdomeric photoreceptors to the role of projection neurons tasked with sending signals from the ciliary photoreceptors to the early diencephalon of our chordate ancestors (Lamb et al., 2008). Over evolutionary time, the ciliary photoreceptors gave rise to the rods and cones, while the rhabdomeric photoreceptors gave rise to the retinal ganglion cells (RGC). The RGC’s in extant vertebrates are positioned in front of the photoreceptors where they connect to nervous

tissue and bundle into nerve fibers creating the optic nerve that exits out the back of the eye toward the brain. The optic nerve creates an area of decreased sensitivity to light stimuli in the static eye resulting in a retinal blind spot known as the optic disc (Ramachandran, 1992).

Our vertebrate ancestors originated in a marine environment where the vertebrate eye first began to evolve (Fernald, 1988; Holland & Chen, 2001). The metamorphic process of the lamprey eye can be compared to the evolutionary process of the vertebrate eye that occurred over approximately 30 million years (Lamb et al., 2008). As a result of this evolutionary process, optical properties of the eyes of aquatic vertebrates differ from the eyes of terrestrial vertebrates (Table 1). One example is the air-cornea interface that is present in terrestrial vertebrates and provides their eyes with a refractory element responsible for focusing the lens (Fernald, 1988). In aquatic vertebrates, the cornea does not provide image focusing similar to terrestrial vertebrates because there is no variation in refraction between the fluid filled medium of the cornea and the fluid filled medium of surrounding environment (Fernald, 1988). Therefore, the lens needs to be stronger because it is the main source of focusing power for image formation (Fernald, 1988).

Through evolution, most aquatic vertebrates, such as fishes and bottlenose dolphins, evolved single-chambered eyes with spherical lenses that have high refractive power (Fernald, 1988; Land & Fernald, 1992; Cozzi et al., 2017). In comparison, terrestrial vertebrates, like humans, have single-chambered eyes with corneal optics and elliptical lenses (Fernald, 1988; Land & Fernald, 1992; Land, 2005; Breedlove & Watson, 2017). Vertebrates who emerged onto land evolved their visual system by adapting their lens shape and optical properties (Land, 2005). But while most mammals

have evolved to see on land, some have taken a different evolutionary trajectory.

Bottlenose dolphins were once even-toed ungulates and are of the order Cetartiodactyla whose eyes have been shaped over evolutionary time to function again in an aquatic medium (Berta et al., 2015; Dral, 1987; Cozzi et al., 2017; Gunnars & Bruck, 2019).

### **Bottlenose dolphin vision**

The bottlenose dolphin's eyes optimize to both water and air by changing the pupil shape that will result in different reactions to light in both mediums (Rivamonte, 2009). The lens shape in dolphin's eyes is shifted by axial adjustment through an increase or decrease in intraocular pressure that is controlled by contraction of the retractor bulbi muscle (Cozzi et al., 2017; Würsig et al. 2017). This axial adjustment occurs in dolphins because they have a reduced ciliary muscle that is responsible for changing lens shape as shown in terrestrial mammals (Cozzi et al., 2017; Würsig et al., 2017). Dolphins also exhibit eye movement, referred to as saccades, similar to humans, with an exception to the dolphin eye movement that occurs at lower refresh rates while human eye movement occurs at higher refresh rates (Dawson et al., 1981; Tweed, 1997).

Another eye adaptation of dolphins is that they have two areas of high ganglion cell density or high retinal resolution that support their dendrites and optic nerve fibers, which aids in their capability to see identically in both water and air (Dawson & Perez, 1973). Dolphins position themselves laterally while observing an object under water, which is placed posterolateral of their visual field and projected onto the nasal high-resolution part of the retina (Mass & Supin, 2009). When a dolphin observes an object above water, the object is in the ventronasal part of their visual field and projected onto

the temporal part of the retina (Mass & Supin, 2009). While submerged in water, the dolphin's vision is emmetropic, not requiring vision correction (Cozzi et al., 2017; Dral, 1988). Their aquatic vision is influenced by various water properties such as temperature, light, and microorganisms (Mass & Supin, 2009). Conversely, when exposed to air, dolphins exhibit myopic or nearsighted vision (Cozzi et al., 2017; Dral, 1988). Their aerial vision is myopic because of the added refraction to the outer convex corneal surface of their emmetropic lens (Mass & Supin, 2009).

While the location of the practical blind spot in the visual field of dolphins remains uncertain, the literature provides evidence of potential locations. For instance, studies have shown a trend in injuries near the dorsal fin from vessel strikes, which could indicate a potential blind spot area (Wells et al., 2008). Even though injuries from vessels may seem unlikely due to the bottlenose dolphins' sonar ability and swimming agility, it has been observed that unconditioned wild dolphins were more likely to learn to accept food from humans where there is a high presence of vessels and conditioned wild dolphins (Donaldson et al., 2012). Wild dolphins are likely to interact through bow-riding close to the vessel expecting provisions because they have associated the vessel with a reward which could lead to a vessel strike (Donaldson et al., 2012; Durden, 2005). On the other hand, other studies have discussed the possibility of dolphins having a blind spot placed in the epicenter of their rostrum because their sonar ability may compensate for perception rather than their vision (Starkhammar et al., 2007; Xitco et al., 2004).

### **Retinal field of vision**

Regarding dolphin field of vision (FOV), the current body of knowledge only addresses retinal FOV for the family Delphinidae. Retinal FOV is different than the practical FOV, which is based on the actual perceptions of living animals, capable of behavioral responses. The retinal FOV was estimated by observing the anatomy of the left eye of a deceased Pacific white-sided dolphin (*Lagenorhynchus obliquidens*) and the right eye of a deceased Dall's porpoise (*Phocoenoides dalli*). However, these estimations do not account for perceptual aspects or eye movement (Dawson et al., 1981; Murayama et al., 1995; Murayama & Somiya, 1998). Another study observed bottlenose dolphin vision, however they only observed the sharpness of the dolphin's vision and not the animal's blind spot (Rivamonte, 2009). From here we see the limitations of determining FOV solely from retinal information *ex situ* as behavioral data is better suited to consider aspects of cognitive processes, perception, and imperceptible eye movements that reduce the effect of retinal blind spots brought on by optic discs (Dawson et al., 1981; Tweed, 1997).

Furthermore, the determination of a functional, real world, blind spot can aid in conservation initiatives. For example, an ongoing project, the tier-1 initiative at Oklahoma State University, using Unmanned Aircraft Systems (UAS, commonly referred to as 'drones') will need to know a dolphin's blind spot in order to capture a hormone sample from the breath of a dolphin's blowhole if the intent is to sneak up on the target animal. Also, as other researchers are engaging in more data tag (D-Tag) deployments on small cetaceans, it is now essential to use visual data to mitigate accidental boat strikes on close approaches (Silva et al., 2017).

The goal of this study was to assess the practical FOV in bottlenose dolphins using psychophysical methods, which involved investigating a relationship between a stimulus and the perception of the subject (Ehrenstein & Ehrenstein, 1999), in such a way in this case, as to give a close to 360-degree representation of the dolphins' practical FOV using light stimuli and vocal responses. Since previous studies have noted a disproportionate amount of scarring on the dorsal fin and back indicating more damage to that region of the body, I predicted that bottlenose dolphins have a blind spot located in this area of their dorsal fin (Wells et al., 2008). Another prediction I chose to test was the claim that dolphins may not be able to see in front of its rostrum (Starkhammar et al, 2007; Xitco et al., 2004).

## CHAPTER II

### METHODS

#### **Subjects**

Three bottlenose dolphins under human care at Dolphin Quest Bermuda (DQB) were tested, one male and two females. The male dolphin was identified as M1 (ten years old), and the two female dolphins were identified as F1 (six years old), and F3 (ten years old), respectively. The subjects lived with ten other dolphins, including three calves. The three dolphins were chosen out of the 13 dolphins on site, based on Dolphin Quest's schedule with their animals, the animals' age, and these animals' general interest with operant tasks. Originally, five dolphins were planned to participate in the study. However, there were two female dolphins that were unable to create an association with the lights once it was combined with the sphere; so they were removed from the study.

#### **Study area**

This study took place in Sandys Parish, Bermuda at DQB, which is housed within the National Museum of Bermuda (Figure 1). DQB has a lagoon divided into six sections: North, South, East, West, a medical pool, and an outer habitat. The specific location of the training and experimental trials varied daily due to ongoing DQB site activity, such as programs that consisted of interactions with guests, which did not impact

the experimental sessions (Figure 2). Location of training and trials was contingent upon amount of daylight, i.e., during midday, the sun shined directly over the west end of the lagoon that potentially could impair the dolphins' vision.

## **Apparatus**

To place lights around the dolphins' head, we used a plastic Hoberman Mega Sphere (Brooklyn, New York; model MS801), which is a waterproof geodesic-like structure (Li et al., 2018) capable of fitting over the dolphin's head to assess its general visual field which allows for consistency of the LED light placement. The sphere expands to 1.37 meters and weighs 4.37 kilograms.

Eighty waterproof LED lights (Shenzhen, China; model KS-SB-005M) (Figure 3) were used throughout the study. The lights have a diameter of 3.8 centimeters and a brightness of 374 lux with the color of the lights set to pure white. High illumination (lux) produces a double-slit pupil in the dolphin that enhances its vision in air allowing it to view in bright lux levels (Rivamonte, 1976, 2009). The light intensity of the ambient light under the shade of an umbrella was measured before each experimental session, by a digital lux meter (Newark, California; model 1330B-V), in order to observe if there was an effect on the dolphin's vision during trials that may contribute to a 'no' response. The apparatus was assembled by screwing 25 lights onto the junction points of each sphere with a one-inch SharkBite 23073A10 Polymer Insulated Suspension Clamp, (Cullman, Alabama; model 23073A10) (Figure 4). Twenty-four attached LED lights had batteries removed so only the test light was triggered with the IR remote during the experimental trials. Battery removal was performed because all lights could be triggered on and off by



a single remote. I was able to change out the experimental lights between presentations away from the dolphin's view, moving the active light to the desired location. A GoPro Hero 5® (San Mateo, California; model CHDHX-502) stationed on a tripod was used to record the experimental sessions for verifying the dolphin's head position after trials.

## **Training**

**Hoberman Sphere** – In consultation with animal care specialists at DQB we began the training process by desensitizing (counter-conditioning) the dolphin subjects to the Hoberman Sphere. The counter-conditioning process consisted of repeatedly presenting the sphere near the dolphin and reinforcing with rewards of fish until it was conditioned and could enter its head into the sphere. Desensitization, in this case, is defined as the dolphin approaching the foreign object without hesitation and stationing (positioning its body) near or in the object for at least five minutes (Domjan, 2014). The sphere sessions began on the staircase platform to allow the dolphins to balance in the sphere (Figure 5). To keep the sphere in place during testing and experimental sessions, it was held by two black straps that were attached to the staircase railings, this was done consistently for all dolphins (Figure 5). An attempt was made in measuring the distance of each dolphin's head from the sphere, but this caused F1 to react differently as she began to not respond to the LED lights while in the sphere. Once this was discovered, the measuring variable was removed and F1 was able to conduct a successful trial. Therefore, the DQB animal care specialist signaled each dolphin to enter the sphere in a straight fashion. If the dolphins were not positioned correctly, the animal care specialist signaled them out so they can readjust and enter again. Video recordings were taken during each experimental session to monitor the consistent head position of the dolphins.

**LED Lights Associations** – Operant training was used to transfer existing hand signals that the dolphins associated with a particular whistle vocalization to a light stimulus instead (Domjan, 2014). As an example of a typical training session, the LED light would turn on, and a DQB animal care specialist would give a visual hand signal for the dolphin to respond with its own vocalization that is associated with the respective visual hand signal (Figure 6). The training was done gradually until the dolphins were able to respond to the light vocally without a visual hand signal. Once this was accomplished the dolphins were able to advance its training with the light and sphere combined. The LED lights were presented close to the sphere, then inside the sphere. Once the dolphins were responding to the light while inside the sphere, the lights were attached onto the junction points of the sphere.

The overall training process consisted of presenting the Hoberman Sphere and LED light association sessions (on average, one of each) per day alongside the DQB programs for each dolphin in the study. The Hoberman Sphere training sessions took a maximum of three minutes for each dolphin, resulting in an overall nine minutes per day. The LED light training sessions took a maximum of two minutes for each dolphin, resulting in an overall six minutes per day. The combined light and sphere sessions took a maximum of five minutes each day per dolphin. These training sessions took an average of 10 – 15 minutes each day depending if all dolphin subjects participated and the training session. Training took about a year and continued into experimental sessions to prevent extinction from occurring. There were days where it was not possible to do a training session, which caused the dolphins to regress. Regression is where the dolphin less reliably gives a conditioned response to a conditioned stimulus (Domjan, 2014).

Staying consistent with training was important so that the subject would not experience regression, which is what occurred with two female dolphins. For example, after one day of no training, one of the females would remove herself from the sphere before the animal care specialist was able to signal the dolphin out. To address these issues, the animal care specialists focused on re-training the dolphin on where regression was occurring.

Throughout the training and experimental sessions, different types of reinforcers were used such as fish and ice cubes. A whistle bridge (10 kHz tone presented by an air blown whistle) was also used to bridge the gap between a behavior and reinforcement to communicate a correct response (Kuczaj & Xitco, 2002).

### **Experimental sessions**

The experimental sessions were done in between DQB program sessions; so the dolphins were tested in different pools away from where the program session was taking place. At least two sessions were completed in the morning and two in the afternoon. The morning sessions worked well since there was not much sunlight. To account for the sunlight in the afternoon sessions, a DQB intern held an umbrella over the testing site during each session.

The Hoberman Sphere was used in its expanded state with all LED lights attached to the junction points and the sphere positioned onto the staircase platform (Figure 5). A DQB animal care specialist signaled a dolphin to station inside the sphere, then the experimental session and video recording began. The first trial of each session was a baseline trial that consisted of an easy to identify light, which was the LED light

positioned in the dolphin's known field of view (FOV), and the dolphin was rewarded for a conditioned vocal response when the light was turned on by remote (Figure 7). The activation of the remote was hidden from the dolphins by obscuring its view of the experimenter's hands with the remote after it was discovered that the subjects would use this cue to reliably vocalize. The second trial involved the first presentation of an experimental light (a light where the dolphin may or may not be able to see it). In this trial the light was placed in a predetermined position. The subject was given a LED light exposure of three seconds to respond or not respond with a vocalization. To ensure that the dolphins had every opportunity to identify the light, experimenters would point out which light would be activated to the dolphins. This ensured that the animals' failure to respond was because they could not see the light illuminate rather than the dolphins not knowing which light would turn on and therefore could not scan the field quickly enough. This process was repeated for the third trial but with a different light position. The session ended with another baseline trial that way the subject began and ended on successful trials to prevent behavioral extinction.

The schedule of reinforcement for the trials occurred continuously but with variable reinforcers, which consisted of changing the type or amount of reward given. These reinforcers were balanced out accordingly throughout the trials by the DQB animal care specialists. For the duration of the experimental sessions, the four trials were around 10-15 seconds long and the three inter-trial intervals were about another 5-10 seconds, this resulted in an average total of one minute and 30 seconds (Figure 8). This timing schedule accounted for changing the light into a new position during a session and rewarding the dolphin. An experimental session consisted of these four trials and after a

session was done for one subject, these steps were repeated for the other two subjects. The experimental sessions were completed until all 25 lights were tested twice for each dolphin. If a dolphin responded to a light once and then did not respond to it a second time, this light was tested a third time, and a 'best two out of three' approach was taken in the analysis.

### **Data Analysis**

For descriptive data visualization, 'heat map' images were created through Solidworks to exhibit the "best of three" responses to the 25 light positions on the Hoberman sphere, which is an icosidodecahedron (Systemes, 2020). The sphere was used as a 3-D model along with a 3-D dolphin model in Solidworks ("Dolphin", 2014; Navigation, 2017; Systemes, 2020). The triangles and pentagons of the Hoberman sphere were broken up into three and five equal parts respectively and were colored at the vertices of these shapes to demonstrate the positive or negative responses. (Figure 9).

I used the Observation Oriented Modeling (OOM) statistical software package to compare a predicted pattern to the pattern of observations from this study (Grice, 2011). I chose OOM because it contains analyses that have more of an individual approach than traditional statistics by focusing on each subject and providing insight on how one subject may differ from another. One of the analyses is the pattern analysis: concatenated orderings, which tests a predicted pattern of observations chosen by the experimenter across several orderings (predicted pattern shown in Table 2) (Grice, 2011). The predicted pattern depended on the light positions that were placed around the dolphin's head and what previous literature may indicate about a dolphin's ability to see objects in

those areas. In the pattern analysis, the Percent Classification Correct (PCC) index shows the percentage of actual observations that were correctly classified relative to the predicted pattern (Grice et al., 2012). The actual observations of yes and no responses were randomized 1,000 times and the PCC values were compared between the randomized trials and actual observations. There is also a probability statistic, chance value (c-value), that determines whether or not the randomized data consistently match a pattern (Grice et al., 2012).

## CHAPTER III

### RESULTS

#### **Qualitative**

Each of the subjects had blind spots occur in the posterior area of their head, which included the dorsal fin and back area (labeled as 1 in the minimum blind spot composite, Figure 10). All subjects were able to see in the area in front of their rostrum (labeled as 1 and 2 in the maximum blind spot composite, Figure 11). The light positions that received two or three 'yes' responses occurred horizontally across the sphere lining up with the lateral eyes of the dolphins (shown in green in the best of three dolphins composite, Figure 12). The light positions that received two or three 'no' responses occurred below the right side of the head, dorsally above the blowhole, and posteriorly towards the dorsal fin (labeled as 1 and 2 in the best of three dolphins composite, Figure 12). M1 had blind spots occur directly above his head in the area of his blowhole as well as in the area below his head (labeled as 1 and 2, respectively, Figure 13). The area that M1 was able to see occurred horizontally around the sphere as shown in figure 12. F1 had a blind spot occur on the right lateral side and one positioned in the dorsal area towards her left lateral side close to where her blowhole is located but not directly over it (labeled as 1 and 3, respectively, Figure 14). Despite these blind spots, F1 was able to see in the frontal and left lateral area. F2 had blind spots occur directly above her head in the area

of her blowhole as well as within the area below her head, and both areas were angled towards the right (labeled as 1 and 2, respectively, Figure 15). Similar to M1, F2 was able to see horizontally across the sphere.

### **Quantitative**

In the predicted pattern the dolphins were not expected to see, light #6, the light directly in front of their rostrums, (Starkhammar et al., 2007; Xitco et al 2004). I also expected that the dolphins would not see Lights #19-25, which were positioned around the dorsal fin and back region of the dolphin. Lights #1-5 and #7-18 were positioned either anteriorly or laterally of the dolphin's eyes, and so I predicted that they would be able to see these light positions. More than half of the observations of the three dolphins matched the projected behavior (PCC: overall = 72%, M1 & F1 = 76%, and F2 = 64%). The randomized trials from the overall data showed that not 1 out of 1000 trials met a minimum PCC of 34.67% or a maximum PCC of 69.33% (c-value < 0.001). The randomization of M1's data was able to match the prediction 40 times out of 1000 trials (c-value = 0.04; random PCC: max = 84%, min = 36%). F1's randomized data was able to match the prediction 20 times out of 1000 trials (c-value = 0.02; random PCC: max = 76%, min = 28%). Lastly, F2's randomized data was able to match the prediction 130 times out of 1000 trials (c-value = 0.13; random PCC: max = 72%, min = 24%).



## CHAPTER IV

### DISCUSSION

Studies that have observed the retinal field of vision have not been able to make precise claims about a practical FOV in dolphins due to the inability to measure perception in dead animals that lack the eye twitch necessary to compensate for optic disc interference in visual processing (Gunnars & Bruck, 2019; Murayama & Somiya, 1998). Analogous to the bottlenose dolphin, the pacific white-sided dolphin has an optic disc located where the retina meets the optic nerve which would correspond to a retinal blind spot around 12 to 17 degrees from the fixation point (Figure 16) (Murayama & Somiya, 1998; Spector, 1990). Information on the nature of the actual FOV from these data is incomplete because it is based on a non-moving eye fixating in only one direction without eye twitch. Assumptions of where the blind spots could occur depend on what the organism is fixating on and how far its optic nerve is to that fixation point (Ramachandran, 1992). However, in the practical field of vision study I have completed, it can be established where the actual blind spots lie within the bottlenose dolphins' FOV.

The FOV of all three bottlenose dolphins revealed blind spots in its posteriodorsal area of their body (Figure 10). Furthermore, all subjects were able to respond to the LED light positioned in front of the rostrum, challenging assumptions made by Starkhammar et al. (2007) and Xitco et al. (2004). On an individual basis, M1

and F2 were unable to see in the area below the rostrum as well as directly above the blowhole (Figures 12 and 14). However, these blind spot areas for F2 were angled more towards the right (Figure 14). F1 was unable to see in the lateral area of her right side and in the dorsal area of her left side (Figure 13).

The results indicated that my hypothesis regarding a dorsomedial blind spot, suggested by Wells et al. (2008), was supported, but I failed to find support for the hypothesis made by Starkhammar et al. (2007) and Xitco et al. (2004) regarding anterior blind spots. The results have demonstrated that in fact all three dolphins are capable of observing in front of their rostrum, which provides evidence that they do not need to rely on echolocation to identify what is in front of them. This finding could be explained by the two areas of high ganglion cell density within the bottlenose dolphins' eyes that are responsible for both binocular and lateral vision (Dral, 1987). The two areas of high ganglion cell density are also common across most cetaceans, such as the false killer whale, pacific white-sided dolphin, and beluga whale (Murayama & Somiya, 1998). Comparatively, the results also indicated a consistent pattern of 'no' responses to LED lights that were positioned in the area of the dorsal fin (see Figure 10). The common pattern of vessel strikes occurring near the dolphins' dorsal fin has implied that this is an area where they cannot see, which has been supported from the observed results (Marks et al., 2020; Wells et al., 2008).

The composite images portrayed the responses of all three subjects. The minimum blind spot composite showed the maximum field of vision for all the subjects and the area shown in red was where they all could not see (Figure 10). The maximum blind spot composite showed the minimum field of vision for all subjects; so if any of the subjects

could not see a certain light it was shown in red (Figure 11). The best of three dolphins composite shows a combined view of the minimum and maximum blind spot composites by presenting two or three 'yes' responses in green and two or three 'no' responses in red (Figure 12). The minimum blind spot composite would be considered most useful out of the three composites since it provides an accurate representation of the blind spot by showing the consensus between all subjects. The maximum blind spot composite acts more as a representation of the maximum blind spot areas the bottlenose dolphin may have. Out of the three images, the composites of the maximum blind spot and the best of three dolphins were closely similar to each other because they showed more of the 'no' responses than the minimum blind spot composite. Overall, all of the composite images show that the dorsal fin area is where a bottlenose dolphin cannot see (Figures 10, 11, and 12).

I expected that the results would be more uniform across all subjects, however the visual field variations observed for each individual may suggest that the field of view has natural interindividual variation or that the dolphin's may have had variations in its ability to respond to the stimuli consistently. M1 was by far the most consistent dolphin in the study with regard to training and performance in the sphere. He was able to station in the sphere for the longest period of time and had the most consistent response to the lights. He was the first to make the correct association between the vocalization and the light, and he consistently did not make mistakes on any baseline lights. One should weigh his data more strongly than those of F1 and F2. However, since F1 and F2 were able to reliably whistle for lights that M1 could not, especially in the lateroventral area, indicates

that F1 and F2's lower head position (as a feature of their smaller size) may have aided them in improving FOV in lower areas around the head.

Symmetry in the responses should also potentially be seen as an indicator of reliability as neither dolphin in this study is known to have visual impairments (however, they were not tested for this directly). M1 does have the most symmetrical response indicating a potentially more reliable FOV. Variations in the performance of F1 and F2 could be due to the consistency of each subjects training. There were days where one subject was unable to participate in training while others participated in training, which impacted F2 the most and caused regression. This resulted in more training time, mainly on Hoberman sphere desensitization, for F2 since she is known to have decreased motivation around the staircase platform. A greater sample size could corroborate my findings and possibly remove some of the variation in the results.

### **Future studies**

Further research should consider investigating color vision of bottlenose dolphins using these methods that I have developed. There have only been two studies that I have been able to locate that have attempted to observe color vision in bottlenose dolphins, but each tested only one bottlenose dolphin (Griebel & Schmid, 2002; Madsen, 1976). Both of these studies consisted of the subject swimming up to a target (physical object the dolphins were trained to touch with its rostrum) to station awaiting the presentation of the stimulus, then responding to the stimulus by swimming towards the test field (stimulus) (Griebel & Schmid, 2002) or pressing a paddle (Madsen, 1976). Due to buoyancy, these methods result in an inconsistent stationing since the dolphin drifts slightly back and

forth while waiting for the stimulus. The use of a platform as well as a Hoberman sphere could mitigate these issues by providing a consistent station for the dolphin and the attached stimulus on the sphere could be presented easily. Furthermore, this is the first study I am aware of to show that dolphins are capable of detecting LED lights despite their flicker rates. In the field of dolphin research, it can be difficult to obtain an ideal sample size; so performing more rigorous color vision studies could provide a better estimate on whether color vision is possible or not.

Additionally, future studies could improve previous methods as well as providing a solid foundation of color vision data. One study has noted that there have been both confirmations and denials on the presence of cone cells in bottlenose dolphins (Dawson & Perez, 1973). In addition, Griebel & Schmid (2002) have noted that pinnipeds are capable of discriminating color and compared pinnipeds with cetaceans because both have experienced a gene deletion of their shortwave-sensitive cone photoreceptor cell (Hofmann & Palczewski, 2015). Similar to the double-slit pupil in bottlenose dolphins, a small slit appears in the pupils of pinnipeds during daylight where their rods and cones could still function and could explain why they are capable of color vision (Griebel & Schmid, 2002; Rivamonte, 2009). Although, there have been spectral sensitivity and immunocytochemistry studies conducted on pinnipeds that show they have a functional cone, so their color vision is a result of signals between their rods and cones. Thus, more research is needed to determine if bottlenose dolphins also have a color vision system based on this potential input from rods and cones as shown in pinnipeds (Griebel & Schmid, 2002). And this design is well suited to explore that question.

### **Conservation applications**

Due to insufficient knowledge on the practical field of vision and location of the bottlenose dolphins blind spot and consequences relating to boat strikes as well as potential UAS effects (both beneficial and detrimental), it was vital to establish this information. These data will now be applied to the development of next generation UASs where information regarding the FOV will allow cryptic flight near the blowhole regions of these animals for hormone collection *in situ* (Bruck, 2020). The revolutionary use of UAS and non-invasive techniques could help by allowing for untainted, stress-hormone data to be collected in wild animals.

The knowledge of the blind spot will also provide further evidence to support wildlife management policies on the proper distance kept by oceanic vessels (i.e. fishing boats and recreational boats) and the general public to avoid harming these wild cetaceans. Marine Mammal Commission (MMC) and the National Marine Fisheries Service (NMFS) provide a distance that large vessels need to have when approaching various marine mammals (Lusseau, 2003; Spradlin et al., 2001). However, in the study Lusseau (2003) conducted, they found that 70% of the vessels violated the distance regulations indicating further enforcement is needed by these organizations. Informing MMC and NMFS of the blind spot around the bottlenose dolphins' dorsal fin could refine the regulations they have in place, as well as inform both recreational boaters and fisheries of this blind spot so that more caution is taken. One of the main causes of mortality in wild dolphin populations is due to vessel strikes and human interactions, which are noted in regions of Florida, Western Australia, and New Zealand (Donaldson et al., 2012; Marks et al., 2020; Wells et al., 2008).

Additionally, a non-anthropogenic source that impacts this area of the dolphin are caused by shark attacks and conspecifics (Cockcroft et al., 1989; Heithaus, 2001; Lee et al., 2019). An important note, Lee et al. (2019) observed these attacks on the Indo-Pacific bottlenose dolphin (*Tursiops aduncus*), which are smaller in proportion to the common bottlenose dolphin (Hale et al., 2000). The evolutionary stasis on the dorsal area of the bottlenose dolphin's field of vision has had a negative impact towards their population-level survivability (Donaldson et al., 2012; Heithaus, 2001; Marks et al., 2020; Wells et al., 2008). A possible explanation for shark mortality could be due to the dolphin's viewing preference in which it prefers to look at objects laterally with one eye under water, resulting in not being alert to an incoming attack (Dral, 1972). For this reason, further investigation is needed on the bottlenose dolphin's viewing preference while under water to see if there is also a preference towards objects that are positioned above water, such as vessels or a UAS.

## CHAPTER V

### CONCLUSION

Previous studies making conjectures about the visual field of the bottlenose dolphin did so without data to support their assertions (Starkhammar et al., 2007; Xitco et al., 2004). Through training and experimentation, a functional analysis for a dolphin's blind spot now exists. While there is a degree of uncertainty around exactly how far that blind spot extends laterally, confidence exists for the posterior estimation (Figure 10). This refutes the claims made by Xitco et al. (2004) that dolphins have an anterior blind spot compensated for by echolocation.

These data indicate that approaches from behind dolphins either by recreational vessels or by research vessels for the purposes of hormone sampling or D-Tagging need to be avoided or considered with great care. Furthermore, future attempts at hormone sampling by drone should consider a rear approach for the best opportunity to stay out of the dolphin's visual range. This study also verifies that dolphins are capable of perceiving LED lights and therefore has implications for the effects of light pollution on marine mammals as well as paves the way for possible future studies in color vision using this, or a similar methodology.



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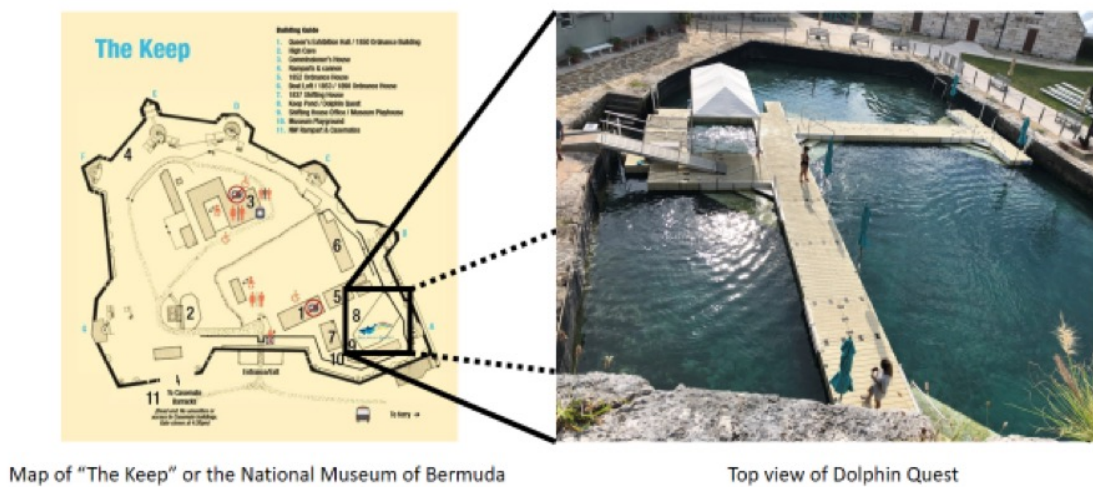
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## APPENDICES

Eye structure			
Trait	Human	Dolphin	Fish
Binocular vision	Yes	?	Barreleye yes. Most others no
Color vision	Yes	?	Most teleost species
Lens shape	Elliptical	Spherical	Spherical

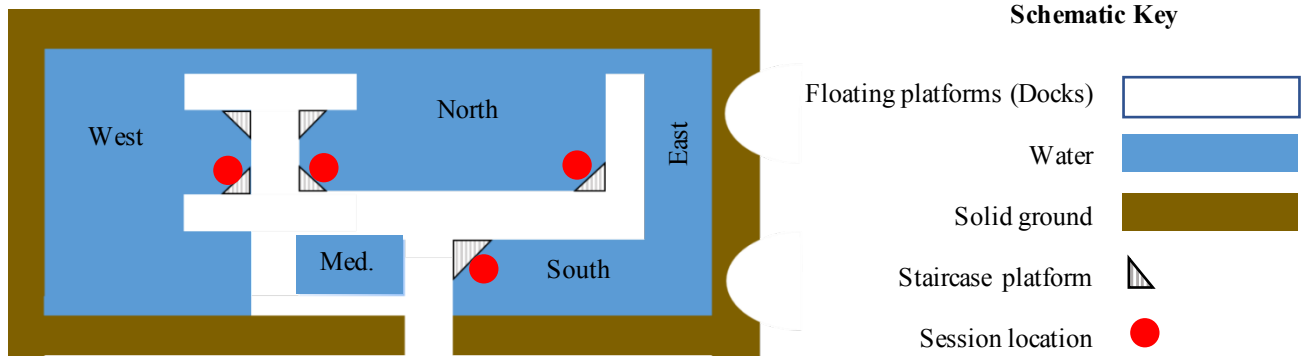
*Table 1.* Eye structure – Different eye structure traits and its presence on a human, dolphin, and fish. (Breedlove & Watson, 2017; Cozzi et al., 2017; Fernald, 1988; Land, 2005; Land & Fernald, 1992).



Note – not a direct translation from "The Keep" map

*Figure 1.* Dolphin Quest overview – Outline of the National Museum of Bermuda and overview of the Dolphin Quest lagoon.





*Figure 2.* Lagoon outline – Outline of all five lagoons of Dolphin Quest. Red dots signify where the training and experimental sessions took place. \*Note: the outer habitat is separated by a wall, which is to the right of the East and South pool.



*Figure 3.* Waterproof LED light – LED light with the IR remote, the pure white light was used for the study.



*Figure 4.* Attached LED light – LED light screwed onto the junction point of the Hoberman Sphere with the black plastic clamp.



*Figure 5.* Dolphin in Hoberman sphere – A demonstration of M1 in the Hoberman sphere.



*Figure 6.* Hand signals with LED light – Sequence of images of a hand signal given while the LED light is turned on.

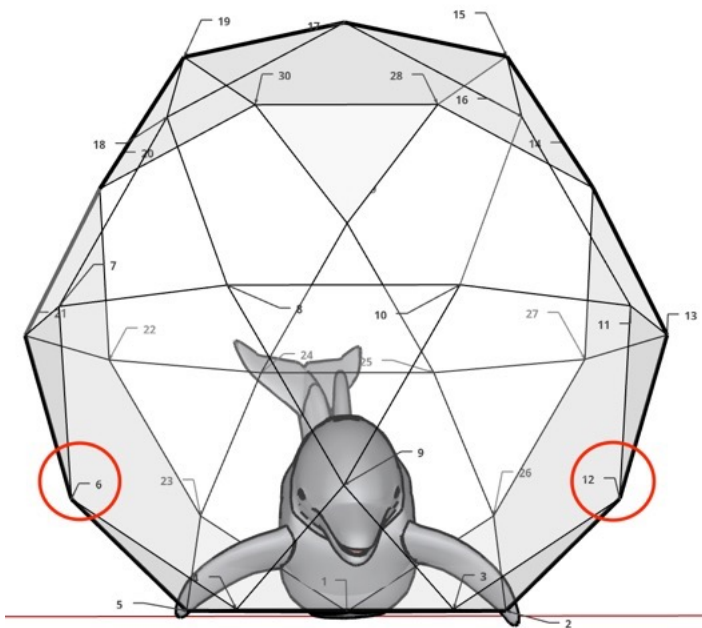


Figure 7. 3-D image of dolphin in sphere – Baseline lights are circled in red.

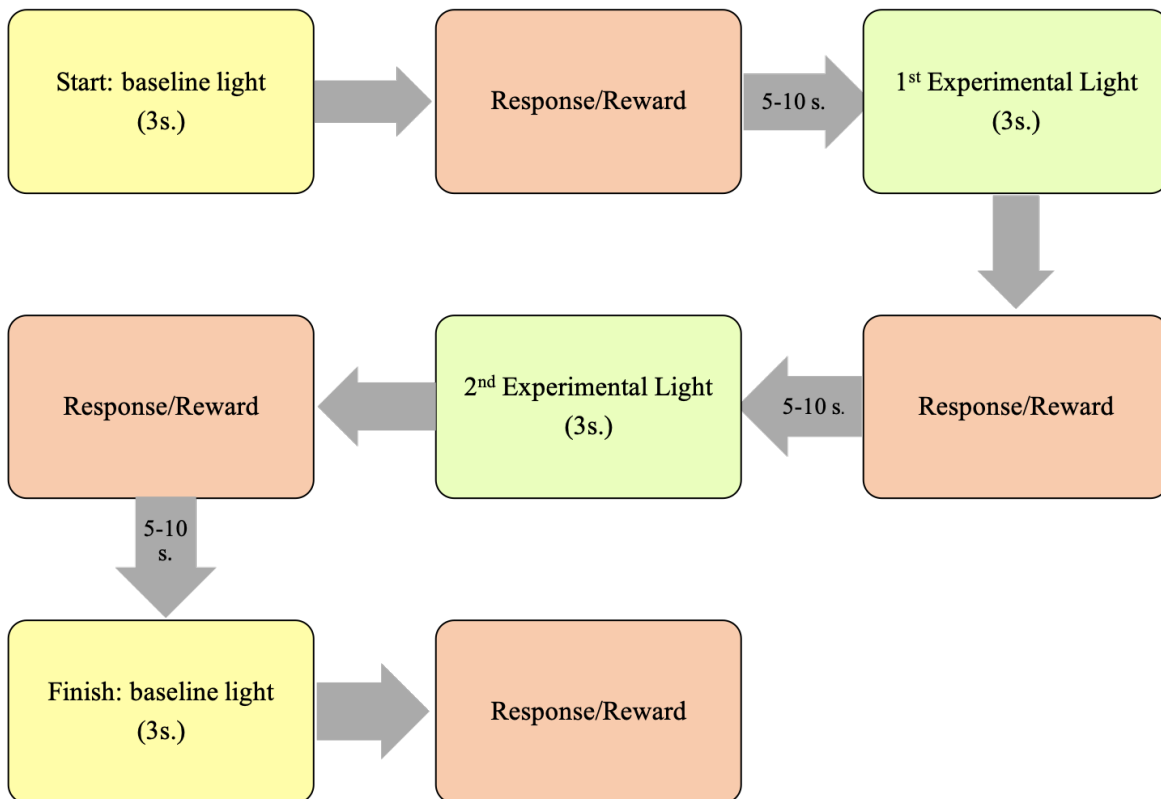
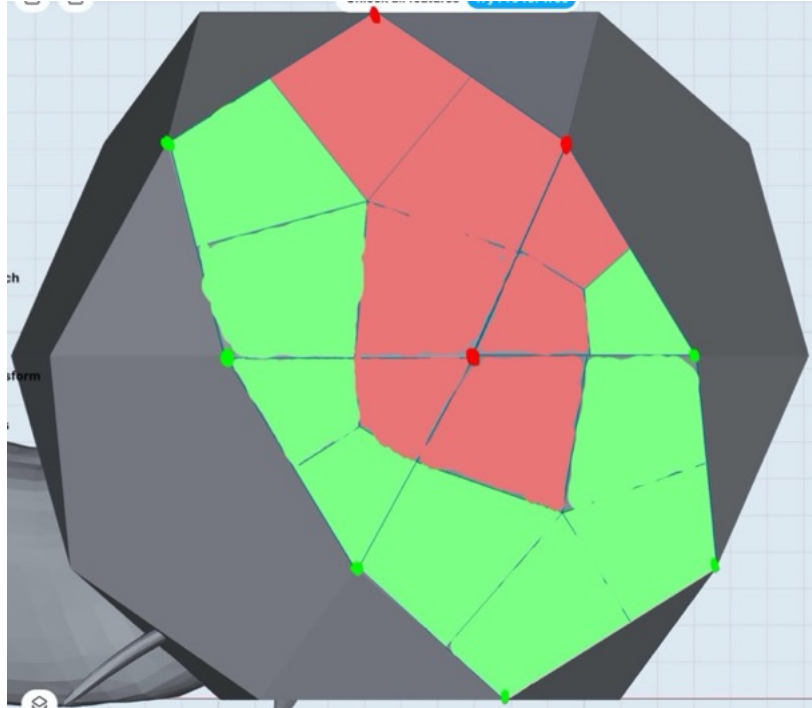


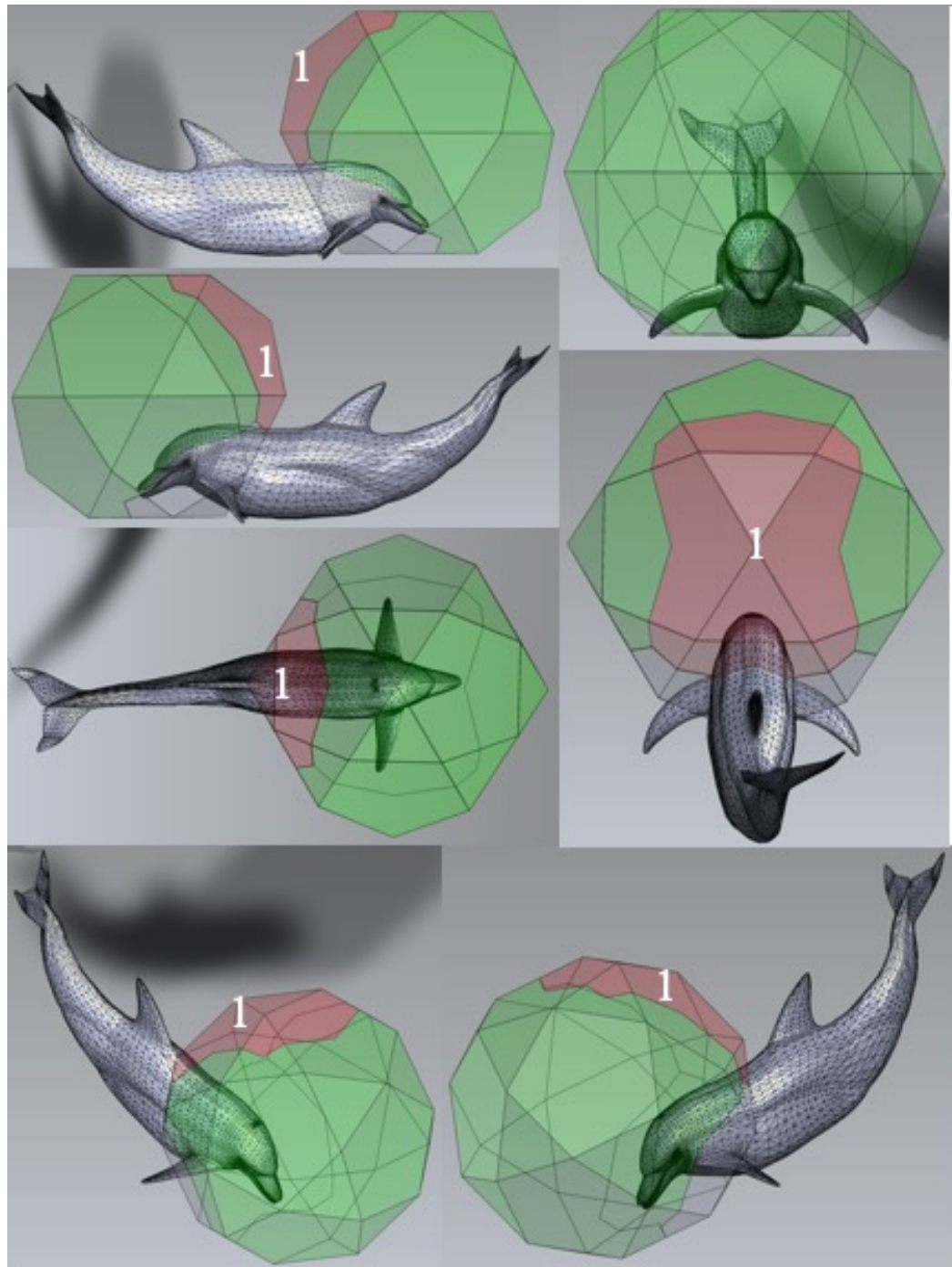
Figure 8. Experimental process – A diagram of the experimental process.



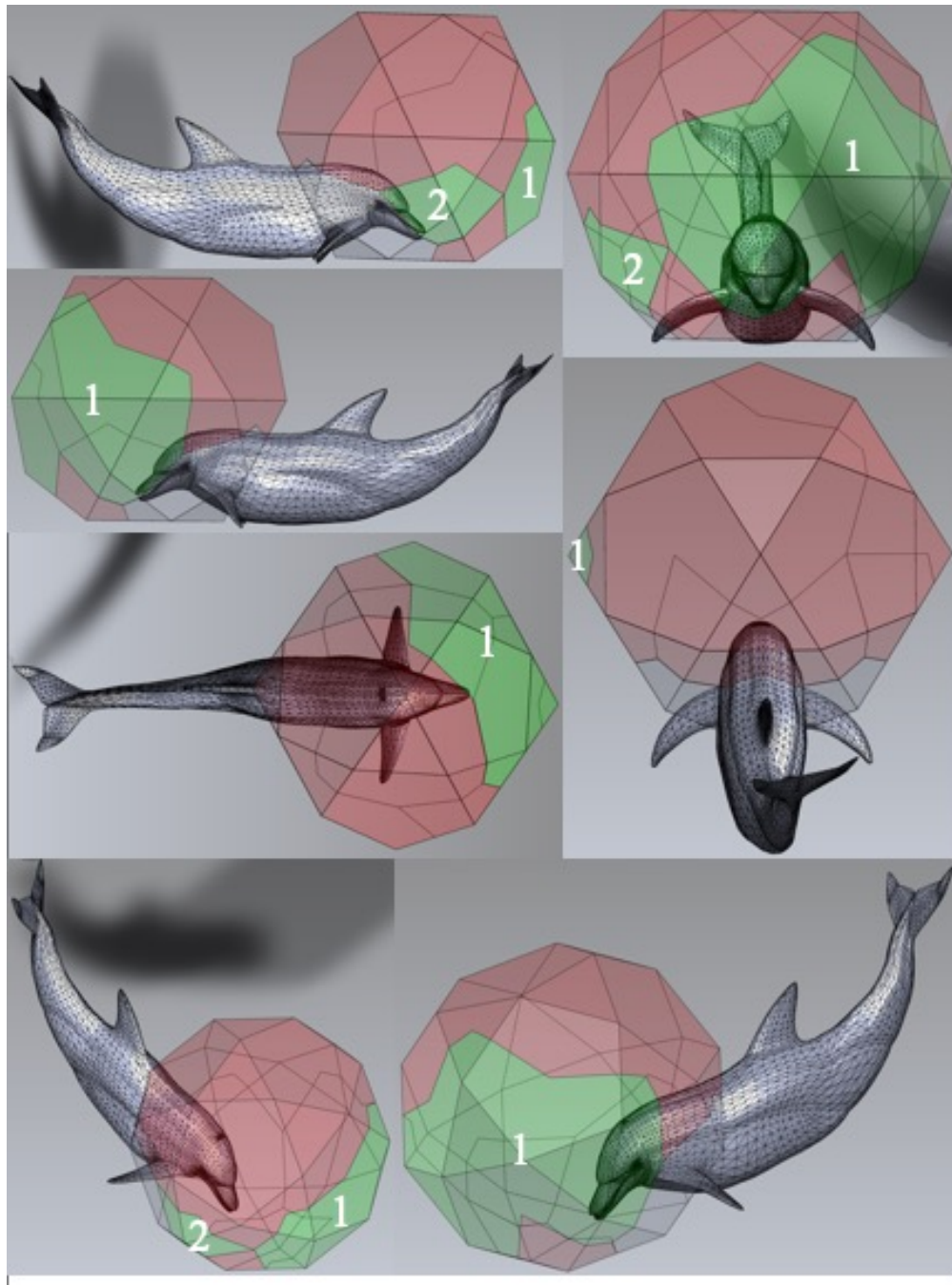
*Figure 9.* Coloring technique on sphere – The coloring technique done on the sphere in order to map out the responses of each subject. This provides a visual image of the possible location of the blind spot. The ‘yes’ responses were represented in green, ‘no’ responses in red, and the area that the dolphin laid on was left blank since it was not used at all.

		RESPONSE	
		Yes	No
Light #	1	F1 F2	M1
	2	F1	M1 F2
	3	M1 F1 F2	
	4	M1 F2	F1
	5	M1 F1 F2	
	6	M1 F1 F2	
	7	M1 F1 F2	
	8	M1 F1 F2	
	9	M1 F1 F2	
	10	M1 F1 F2	
	11	M1	F1 F2
	12	M1	F1 F2
	13	M1 F1 F2	
	14	F1	M1 F2
	15	M1 F1	F2
	16	M1 F1	F2
	17	M1 F1	F2
	18	M1 F2	F1
	19	M1 F1	F2
	20		M1 F1 F2
	21		M1 F1 F2
	22	M1 F2	F1
	23		M1 F1 F2
	24		M1 F1 F2
	25		M1 F1 F2

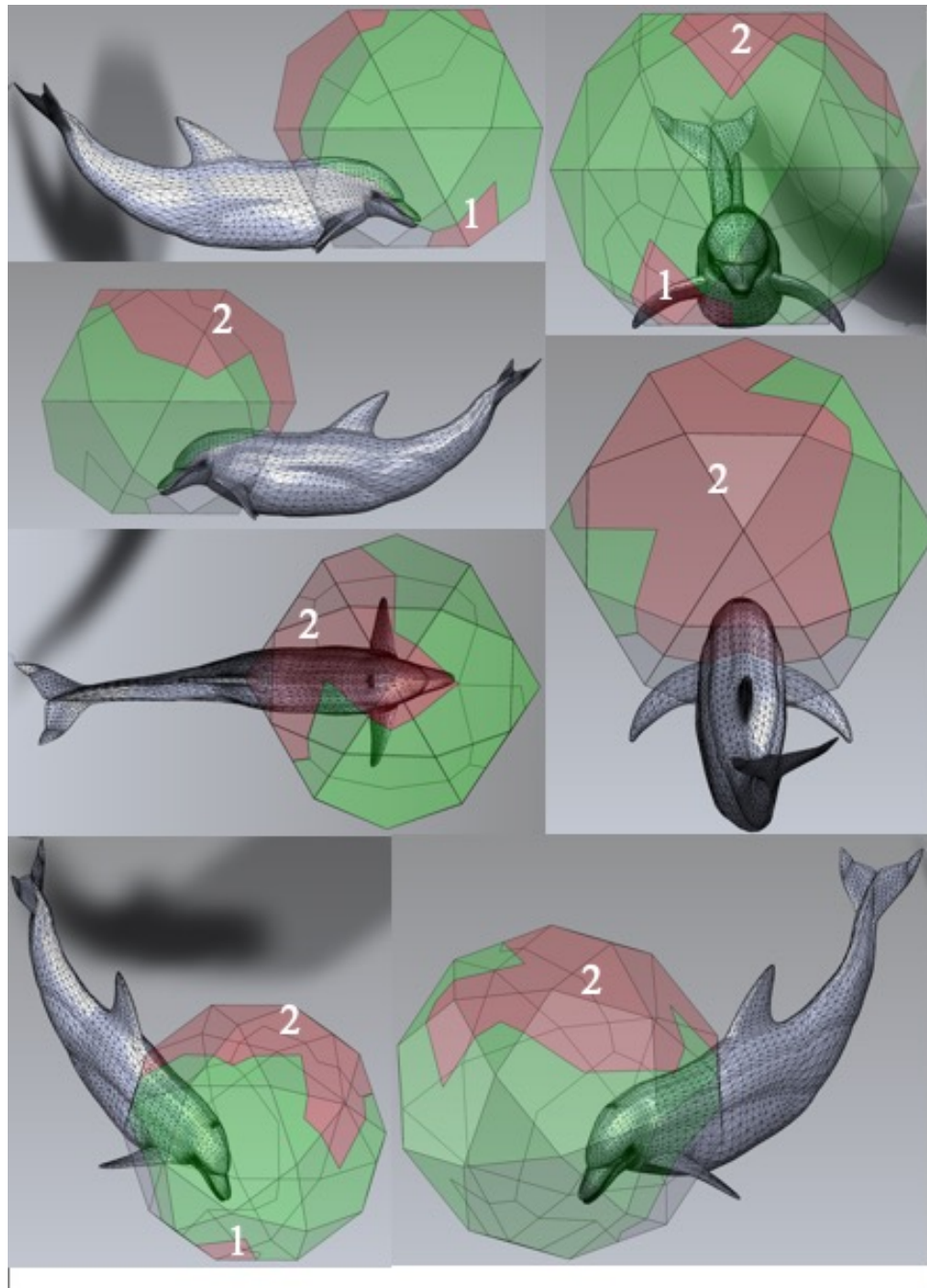
*Table 2.* Predicted and observed pattern – Boxes highlighted in grey are the predicted pattern. Observed responses of M1, F1, and F2 are shown.



*Figure 10.* Minimum blind spot composite – Composite that represents the minimum blind spot area based on the results from each of the three dolphins. Each of the three dolphins were unable to see within this red area (1). If all subjects had a ‘no’ response that region was colored red.  
 Top left: right lateral view. Middle top left: left lateral view. Middle bottom left: aerial view.  
 Bottom left: right angled view. Top right: frontal view. Middle right: rear view. Bottom right: left angled view.

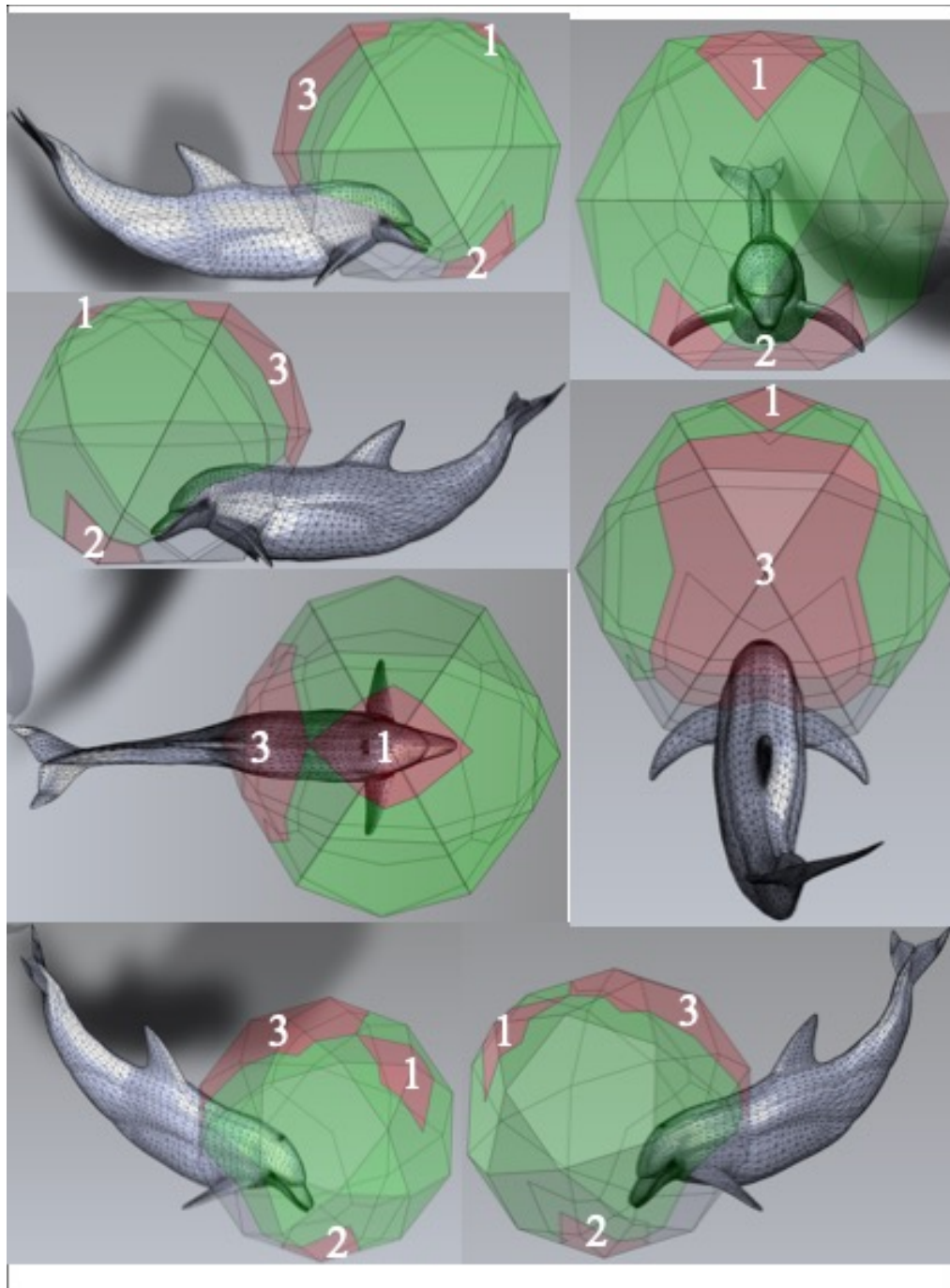


*Figure 11.* Maximum blind spot composite – Composite that represents the maximum blind spot area on the results from each of the three dolphins. Each of the three dolphins were able to see within this green area (1 and 2). If any of the subjects had a ‘no’ response that region was colored red. Top left: right lateral view. Middle top left: left lateral view. Middle bottom left: dorsal view. Bottom left: right angled view. Top right: frontal view. Middle right: rear view. Bottom right: left angled view.

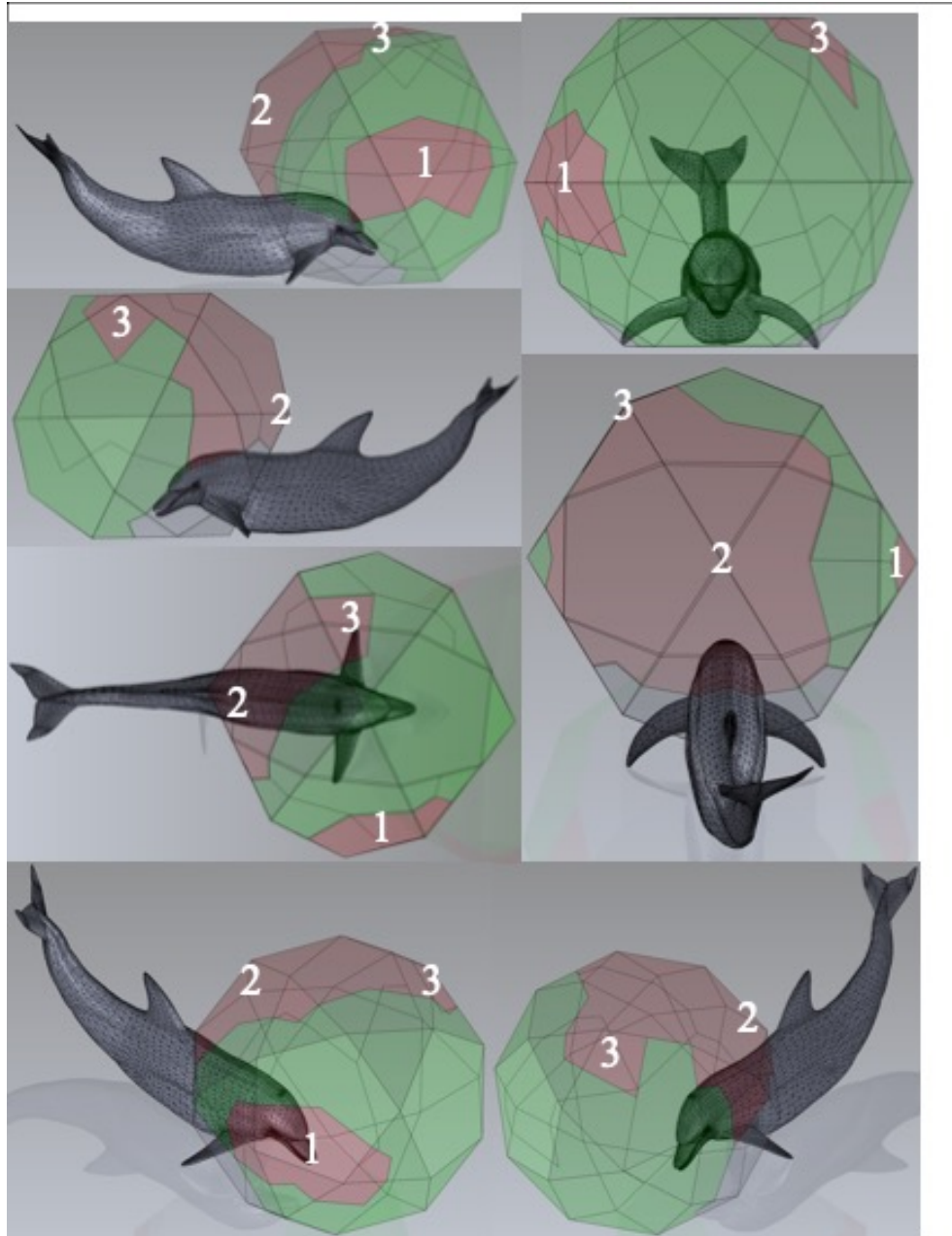


*Figure 12.* Best of three dolphins composite – Composite that represents the field of vision based on the best two out of three responses from the three dolphins. If a light position got two or three ‘yes’ responses it was colored green and if a light position got two or three ‘no’ responses it was colored red. Top left: right lateral view. Middle top left: left lateral view. Middle bottom left: dorsal view. Bottom left: right angled view. Top right: frontal view. Middle right: rear view. Bottom right: left angled view.



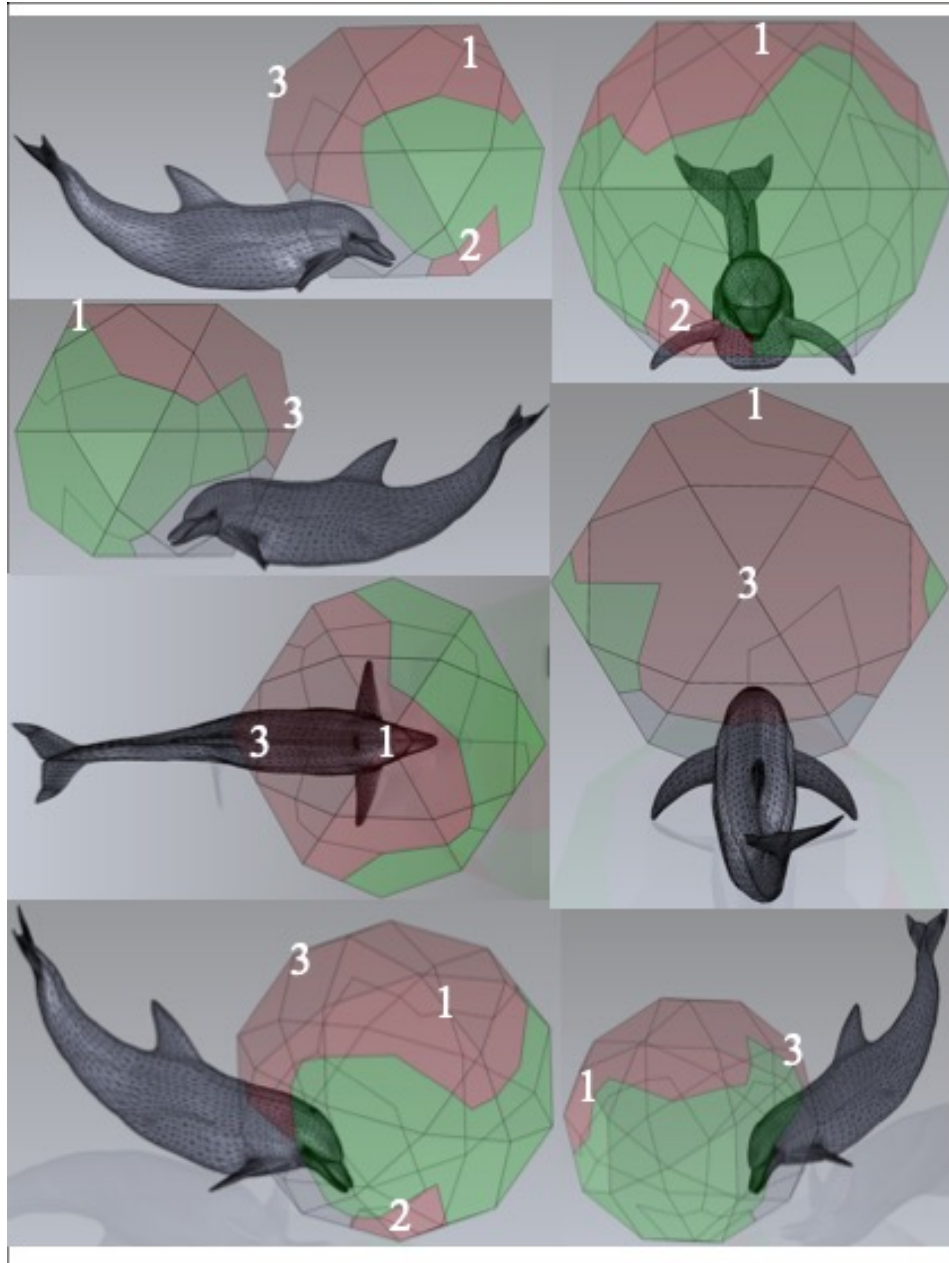


*Figure 13.* 3-D images of M1 in sphere – Green depicts the areas of two or three ‘yes’ responses and red depicts the areas of two or three ‘no’ responses. The top and bottom red areas (1 and 2, respectively) were predicted to be visible, however M1 did not support that prediction. The data from M1 supports the prediction that the area towards his dorsal fin and back (3) would be a blind spot. Top left: right lateral view. Middle top left: left lateral view. Middle bottom left: dorsal view. Bottom left: right angled view. Top right: frontal view. Middle right: rear view. Bottom right: left angled view.

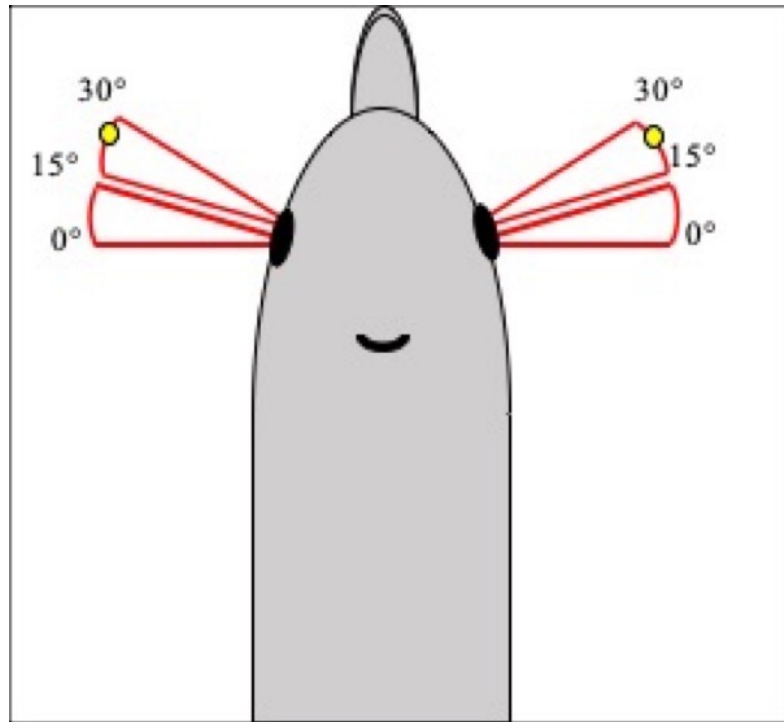


*Figure 14.* 3-D images of F1 in sphere – Green depicts areas of two or three ‘yes’ responses and red depicts areas of two or three ‘no’ responses. The red area in the lateral view of the right side (1) was predicted to be visible, and F1 did not support this prediction. The red area towards the rear (2) was predicted to be a blind spot and F1 supported this prediction. The red area noted dorsally towards the left lateral side (3) was predicted to be visible, and F1 did not support this prediction.

Top left: right lateral view. Middle top left: left lateral view. Middle bottom left: dorsal view. Bottom left: right angled view. Top right: frontal view. Middle right: rear view. Bottom right: left angled view.



*Figure 15.* 3-D images of F2 in sphere – Green depicts areas of two or three ‘yes’ responses and red depicts areas of two or three ‘no’ responses. The top and bottom red areas (1 and 2, respectively) were predicted to be visible, and F2 did not support this prediction. The red area towards the rear (3) was predicted to be a blind spot and F2 supported this prediction. Top left: right lateral view. Middle top left: left lateral view. Middle bottom left: dorsal view. Bottom left: right angled view. Top right: frontal view. Middle right: rear view. Bottom right: left angled view.



*Figure 16.* Dolphin's visual field – The visual field of a deceased dolphin which does not consider eye movement. Each cone (outlined in red) extends to 15°. The blind spot (yellow circle) is positioned 12°-17° from where the fixation point would be. (Murayama & Somiya, 1998; Spector, 1990)

## VITA

Tabitha Sally Gunnars

Candidate for the Degree of

Master of Science

Thesis: THE VISUAL FIELD OF THE BOTTLENOSE DOLPHIN (*TURSIOPS TRUNCATUS*)

Major Field: Integrative Biology

Biographical:

### **Education:**

Completed the requirements for the Master of Science in Integrative Biology at Oklahoma State University, Stillwater, Oklahoma in December, 2020.

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