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The use of permanent magnets to reduce elasmobranch encounter with a simulated beach net. 1. The bull shark (*Carcharhinus leucas*)

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ABSTRACT

Beach nets are protective nets used to minimize interactions between potentially dangerous sharks and beachgoers. Studies have demonstrated that beach nets are substantial contributors to elasmobranch mortality. One hypothesized solution to reducing this mortality is the use of permanent magnets. The present study examined the effects of grade C8 barium-ferrite ($BaFe_{12}O_{19}$) permanent magnets on bull shark (*Carcharhinus leucas*) behavior, a species frequently entangled in beach nets. To examine this effect, two experiments were conducted: bait and barrier experiments. Log-linear models, more specifically, Poisson regressions were used to test hypotheses pertaining to the effects of treatment type, conspecific density, water visibility, and year on shark behavior. For the bait experiment, the magnetic treatment significantly reduced feeding frequency and increased avoidance frequency, with Poisson regressions also demonstrating that conspecific density was a significant predicator of avoidance and feeding frequencies. For the barrier experiment, the magnetic treatment reduced entrance frequency and yielded an increased avoidance frequency, with Poisson regressions also demonstrating that water visibility was inversely correlated to entrance frequency. This study is the first to demonstrate that *C. leucas* can be deterred by permanent magnets and that magnet efficacy can vary based on situational context. While this study sheds light on the potential for permanent magnets as devices that may reduce *C. leucas* encounters with protective beach nets, research on magnet exclusion properties should be conducted prior to applying this concept to future shark exclusion technologies.

1. Introduction

The bull shark (*Carcharhinus leucas*) is a large coastal shark species found in shallow subtropical and tropical ecosystems around the world (Compagno, 1984). Being a euryhaline species (Thorson et al., 1973; Pillans et al., 2005), *C. leucas* has the ability to tolerate a wide range of salinities and has been found as much as 3 480 km up a freshwater river system (Thomerson et al., 1977; Thorson, 1972). These characteristics and opportunistic feeding habits illustrate the potential for human encounter with this species and thus makes them highly susceptible to anthropogenic mortality. This mortality is concerning due to the k-selected characteristics of this species, such as: (1) low fecundity, producing a litter size that typically ranges from 1 to 13, (2) late age of sexual maturity (i.e. estimated to be 14–15 years for males and 18+ years for females for northern Gulf of Mexico-associated *C. leucas*), and (3) slow growth (Branstetter and Stiles, 1987; Compagno, 1984). Due to its intrinsically low rebound potential, *C. leucas* is listed as being near threatened on the International Union of the Conservation of Nature (IUCN) Red List (Simpfendorfer and Burgess, 2005).

A variety of sources of anthropogenic mortality exist for *C. leucas*; however, one source in particular is beach nets. Beach nets are controversial devices which are responsible for substantial mortality on a wide variety of marine organisms (Dudley and Cliff, 1993; Gribble et al., 1998; Krogh and Reid, 1996; Reid and Krogh, 1992; Van der Elst, 1979). These nets were originally instituted to catch three species of shark; the great white shark (*Carcharodon carcharias*), the tiger shark (*Galeocerdo cuvier*), and the bull shark (*C. leucas*), which were species suspected as being responsible for numerous attacks on beachgoers (Dudley, 1997). Currently, three

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major beach net programs exist: (1) New South Wales, Australia (Hamer, 1993), (2) Queensland, Australia (Anon, 1998), and (3) KwaZulu-Natal, South Africa (Dudley, 1997), which catch up to 2 500 sharks per year (Dudley and Gribble, 1999). More specifically for the focal species of this study, from 1978 to 1990, 772 *C. leucas* were captured by beach nets set off the Natal coast (Cliff and Dudley, 1991). In the New South Wales Program, 728 whaler sharks (*Carcharhinus* spp.) including *C. leucas* were captured between 1972 and 1990 (Krogh, 1994). From 1999 to 2010, 1 043 *C. leucas* were captured in netting and baited drumlines in the Queensland Shark Control Program (Queensland Government, 2010). Although these nets and drumlines have been shown to provide beachgoer safety (Cliff and Dudley, 1991), the shark mortality associated with these nets has had substantial negative impacts on local and migratory shark populations (Dudley, 1997; Stevens et al., 2000; Dudley and Cliff, 1993). Unfortunately, this shark mortality is justified by local governments as safer beaches directly boost tourism and create stable and more reliable local economies (Dudley and Gribble, 1999).

To reduce this mortality, scientists have commenced experimentation with magnetic and electropositive metal stimuli to determine their repellent properties for a variety of applications (Rigg et al., 2009; Brill et al., 2009; O'Connell et al., 2011; Robbins et al., 2011; O'Connell et al., 2014a; O'Connell et al., 2014c). These stimuli are hypothesized to be elasmobranch-specific since elasmobranchs possess an acute and unique electrosensory system known as the ampullae of Lorenzini (Kalmijn, 1982). This sensory system is used to detect minute bioelectric fields emitted from prey and is suspected to be used to detect the Earth's magnetic fields for navigational purposes (Kalmijn, 1982, 1984; Klimley, 1993; Meyer et al., 2005).

For the present study, we aimed to examine *C. leucas* behavior towards grade C8 barium-ferrite ($BaFe_{12}O_{19}$) permanent magnets, or materials that produce a magnetic flux (*G*) that is orders of magnitude greater in strength than what elasmobranchs typically encounter with geomagnetic fields. More specifically, we assessed the utility of permanent magnets as *C. leucas* repellents by: (1) conducting a bait experiment to examine if *C. leucas* is sensitive to permanent magnetic fields and (2) conducting a small-scale barrier experiment that aimed to determine if a permanent magnetic barrier can manipulate the swimming patterns of interacting *C. leucas*. It was hypothesized, for both bait and barrier experiments, that the magnets would overstimulate the electrosensory system of interacting *C. leucas* and therefore elicit repellent responses away from magnet-associated baits and barriers. Besides basic behavioral data, additional data pertaining to biological (i.e. conspecific density) and environmental (i.e. water visibility) variables were collected to determine the conditions which yield optimal magnetic repellency. It is hypothesized that because of intraspecific competition (Polis, 1981), high conspecific density would reduce repellent success. Also, since the extent of an elasmobranchs' visual range is directly related to water visibility properties, it is hypothesized that low visibility conditions may result in an increased reliance on electrosensory cues and thus may maximize the effectiveness of magnetic repellents.

This paper is the first in a series of four describing the effects of permanent magnets on elasmobranch species which are frequently captured in beach nets. The subsequent papers will explore the effects of permanent magnets on other elasmobranch species, including the great white shark (*C. carcharias*), great hammerhead shark (*Sphyrna mokarran*), and tiger shark (*G. cuvier*).

2. Methods

This study was conducted during the months of January–March from 2011 to 2013 in North Bimini, Bahamas off the docks of Bimini Big Game Resort and Marina and Bimini Blue Water Marina. Over the course of 28 days, two different experiments were conducted: (1) the bait experiment and (2) the barrier experiment. To identify individual sharks throughout each experiment and to ensure one shark was not responsible for all behavioral interactions, short term identification characteristics were used, such as: shark size, shark sex, presence/absence of a tag, shark color, presence/absence of fin damage, and presence/absence of scars. All research that was conducted abided to the rules and regulations of the assigned Bahamas Department of Marine Resources permit (MAF/FIS/17).

2.1. Bait experiment

At the study location, three different apparatus were deployed, (1) the control (C), (2) the procedural control (PC) and (3) the magnetic (M). The control apparatus consisted of a 1 m^2 observation zone constructed out of polyvinyl chloride (PVC). The procedural control apparatus was similar in construction to the control apparatus; however, one clay brick (215 × 102 × 67 mm) that was similar in shape, size and color to that of the magnetic treatment was attached to the center of the apparatus. Lastly, the magnetic apparatus consisted of one grade C8 barium-ferrite ($BaFe_{12}O_{19}$) permanent magnet (152 × 102 × 51 mm) placed in the center of the observation zone (Fig. 1). In the center of each treatment zone, a mesh bag containing 0.18 kg of great barracuda (*Sphyraena barracuda*) was placed to provide olfactory and gustatory cues to attract *C. leucas*. Mesh bags were used to prevent the quick removal of bait by teleosts. Once each apparatus was baited, treatment arrangement was randomized to eliminate the possibility of side preference based behavior and all three apparatuses were simultaneously deployed. Upon deployment, apparatus were spaced by a minimum distance of 1 m to ensure the strong magnetic fields (exceeding the ambient magnetic field, 0.25–0.65 G) associated with the magnetic apparatus did not overlap with the control and procedural control apparatus (Fig. 1; see O'Connell et al., 2010 for flux distance). Once in position, the following behaviors were recorded: visit, avoidance, feeding, and no reaction (Table 1). If any one of the baits was removed during a trial, the trial was immediately terminated. Each apparatus was then rebaited and a new trial was conducted.

Throughout each trial, two additional variables were measured, water visibility and conspecific density, to determine their potential effect on *C. leucas* behavior towards the magnetic treatments. To measure water visibility, prior to and after each trial, the horizontal extent of water visibility was measured with an HD 1080p Go Pro camera using the dock columns as a reference. After completion of a trial, the video was reviewed and the mean visibility distance for each trial was computed. Also, during each behavior, shark quantity was recorded using topside observation techniques. After experimentation, behavioral data were then placed within the appropriate conspecific density and water visibility category for each trial.

2.2. Barrier experiment

Using the southernmost dock at the Bimini Big Game Resort and Marina, the barrier apparatus was deployed between four dock pillars. The pillars were separated by a distance of 6 m, with pillars serving as the boundary between treatment zones: (1) control (C), (2) procedural control (PC), and (3) magnetic (M) (Fig. 2). The boundary produced by the pillars was approximately 2 m and was termed the treatment separation zone.

To construct the barrier, all three treatments were randomly assigned to an inter-pillar section. The control zone did not consist of any experimental manipulation. However, to construct both the procedural control and magnetic zones, a nylon surface rope was

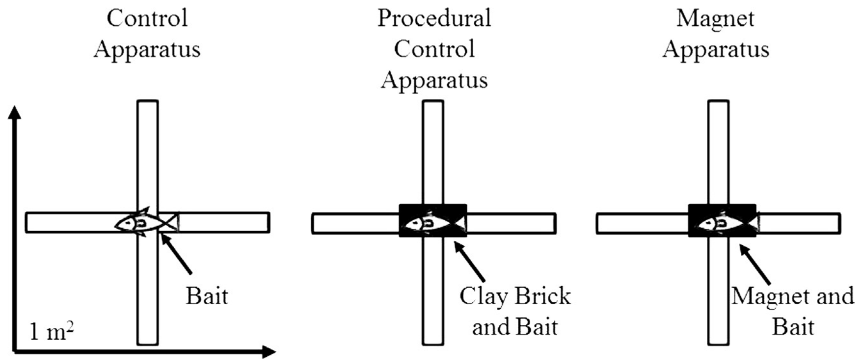

Fig. 1. The bait experiment. For this experiment, there were three, 1 m^2 apparatus. The control apparatus, the procedural control apparatus that contained a clay brick that was similar in shape, size and color to the grade C8 barium-ferrite ($BaFe_{12}O_{19}$) permanent magnet used for the magnet apparatus. In the center of each apparatus was one piece of bait that was identical in species and similar in shape and size.

attached between the remaining pillars. Once secured, 305 mm diameter polyform buoys, five per treatment zone, were attached to the mainline at 1.5 m intervals to help suspend the vertical columns that contained the experimental treatments. The 3.05 m long vertical columns were constructed out of 95 mm diameter flex pipe. Flex pipe was used to increase rigidity of the columns and prevent entanglement of interacting animals. For the procedural control treatment, 152 × 102 × 13 mm foam sham magnets were attached at 0.66 m intervals on each vertical column and terminated with a clay brick (215 × 102 × 67 mm) to secure the column to the substrate. Sham magnets were covered in black duct tape to make them visually identical to the magnets. For the magnetic treatment columns, 152 × 102 × 13 mm grade C8 barium-ferrite magnets were placed at 0.66 m intervals, with a larger grade C8 barium-ferrite magnets (152 × 102 × 52 mm) placed at the end of the column to secure the column to the substrate. Five vertical columns per treatment were deployed per trial (Fig. 2). To alleviate the possibility of side-preference based behavior, treatment placement was randomized for each trial.

Once deployed, one 12.7 mm (diameter) × 1 m (length) piece of polyvinyl chloride (PVC) was placed 1 m down current from each treatment zone. These markers were used to create an observation zone, standardizing the locations of recordable behaviors. Markers were only placed down current of the columns, since sharks would approach from this direction due to the flow direction of the olfactory stimulus. Once sharks approached, if any part of a shark's body crossed over the observation zone, the associated behavior(s) were recorded.

Additionally, two equal-sized great barracuda (*S. barracuda*) or wahoo (*Acanthocybium solandri*) and two Tournament Master Chum® menhaden blocks were placed upcurrent of each treatment zone in order to attract elasmobranchs towards the apparatus. If any bait was removed, the remaining bait was detached and two new baits were redeployed to alleviate any potential preference-based behavior. Once the olfactory stimuli and barrier were deployed and sharks entered the observation zone, four behaviors were recorded: visit, avoidance, entrance and no reaction (Table 1).

In addition, throughout each trial, two additional variables were measured, water visibility and conspecific density, to determine their potential effect on *C. leucas* behavior towards the magnetic treatments. To measure water visibility, prior to and after each trial, the horizontal extent of water visibility was measured with an HD 1080p Go Pro camera using the dock columns as a reference. After completion of a trial, the video was reviewed and the mean visibility distance for each trial was computed. Also, during each behavioral interaction towards the magnetic treatment, shark quantity was recorded using topside observation techniques. After experimentation, behavioral data were then aggregated within the associated conspecific density and water visibility category for each trial.

During experimentation, the behavior of other species, including teleost species, tarpon (*Megalops atlanticus*) and bar jacks (*Caranx ruber*), and one elasmobranch, the nurse shark (*Ginglymostoma cirratum*), were also observed. Reactions of these fish were recorded, similar to techniques used for *C. leucas*.

Table 1
Behavioral ethogram. This table describes the bull shark (*Carcharhinus leucas*)-associated behaviors for both bait and barrier experiments.

Behavior	Definition of behavior
Bait experiment behaviors	
Visit	Shark swam within an observation zone
Avoidances	Shark abruptly changed direction, such as a sudden turn and/or acceleration away, after visiting an observation zone
Feeding	Shark was observed to bite or remove bait from apparatus
No secondary interaction	Shark visited an observation zone, but did not avoid or feed
Barrier experiment behaviors	
Visit	Shark swam within an observation zone
Avoidances	Shark abruptly changed direction, such as a 45°, 90° or 180° turn and/or acceleration away, after visiting an observation zone
Entrances	Shark visited an observation zone and swam through the PVC pipes
No secondary interaction	Shark visited an observation zone but did not avoid or enter

2.3. Statistical analysis

2.3.1. Log-linear model: Poisson regression

Data collected throughout experimentation was in the form of frequencies (i.e. counts) for *C. leucas* and non-target species (i.e. *G. cirratum*, *M. atlanticus*, and *C. ruber*). However, the data pertaining to *C. leucas* were multi-dimensional, where the effects of several variables and the interactions between these variables were of interest. Therefore, the traditional Chi-square analysis, which was used for non-target species, was inefficient at detecting potential multi-dimensional effects on *C. leucas* behavior and thus, log-linear models (Poisson regressions) were used (McCullagh and Nelder, 1989; Dobson and Barnett, 2008). Additionally, Poisson regressions were also appropriate for *C. leucas* data since the experimental data for both the bait and barrier experiments were from a multinomial event (e.g. bait experiment – three secondary behavioral possibilities: avoidance, feeding, and no reaction; barrier experiment – three secondary behavioral possibilities:

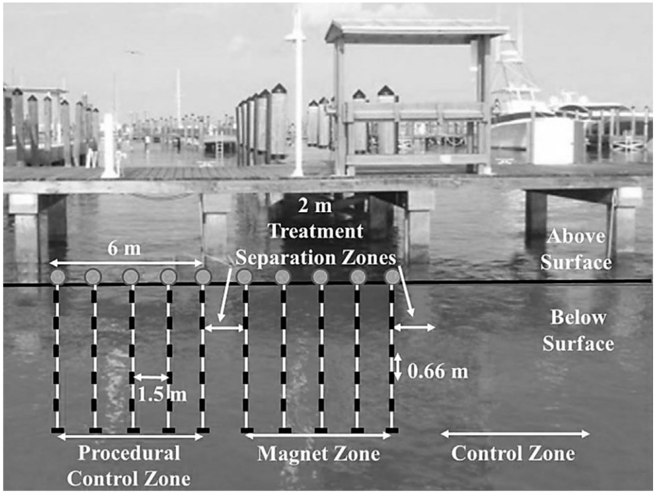

Fig. 2. The barrier apparatus. The five vertical columns on the left represent the procedural control zone, the five in the center represent the magnet zone, and the remaining equal-sized region is the control zone. Each column is separated by 1.5 m. Zones were separated by a cement partition (dock pillar), separating the two zones by a distance of 2 m and is termed the treatment separation zone. The black squares on the vertical columns represent the experimental treatments, with the larger, horizontally-oriented, rectangles representing the larger treatments which served as anchors.

avoidance, entrance, and no reaction); however, analyses pertaining to "no reaction" were not conducted since this behavior is not relevant to assess elasmobranch magnetic field repellency and since "no reaction" is the complement event. A multinomial distribution is the joint distribution of Poisson random variables, conditional upon the total frequencies in those three categories (Dobson and Barnett, 2008). Thus we apply a Poisson regression where the link function is the logarithm.

$$\log(\mu_i) = \log(n_i) + \boldsymbol{x}_i^T\boldsymbol{\beta} \quad (1)$$

where i is observation index (ith trial), μ_i is the expected value of the ith response variable (i.e. $E(Y_i)$), Y_i is the frequencies of avoidances or those of feedings in the ith trial of the bait experiment and the frequencies of avoidances or those of entrances in the ith trial of the barrier experiment, n_i is the total visits in the ith trial, with $\log(n_i)$ being the offset term, $\mathbf{x}_i$ is the vector of candidate explanatory variables at the ith trial (e.g. treatment type, year, conspecific density, water visibility, and associated interaction terms), T is the transpose operation and $\boldsymbol{\beta}$ is the vector of coefficients that correspond to the $\mathbf{x}_i$.

Using analysis of deviance (ANODEV), we evaluated Poisson regressions (e.g. McCullagh and Nelder, 1989; Hyun et al., 2007). A null model was used to begin the forward selection process, of which subsequent models were created adding one or several explanatory variables. In addition to deviance, we also used other model selection criteria: e.g. Akaike Information Criteria (AIC), and behavior of the deviance residuals of a model using a quantile–quantile (Q–Q) plot (See Supplementary Fig. 1). The form of deviance residuals for the Poisson regression is:

$$\mathrm{RD} = \mathrm{sign}(Y_i - \mu_i)\sqrt{2\left(Y_i{*}\log\left(\frac{Y_i}{\mu_i}\right) - Y_i + \mu_i\right)} \quad (2)$$

where μ_i is the expected value of the ith response variable and Y_i is the frequencies of avoidances or those of feedings in the ith trial of the bait experiment and the frequencies of avoidances or those of entrances in the ith trial of the barrier experiment (McCullagh and Nelder, 1989).

2.3.2. Chi-Square analysis

In addition, the basic behavioral data pertaining to *G. cirratum* and teleost species, *M. atlanticus* and *C. ruber*, individual Chi-square tests were warranted to determine if any associations between behavior and treatment type existed.

3. Results

3.1. Bait experiment

After ten days, a total of 34 trials were conducted. Throughout the trials, a minimum of 14 different sharks were identified using a short-term identification technique. Using the apparatus as a comparative measure, sharks ranged in size from 1.75 to 2.75 m. Throughout experimentation, sea surface temperature was 23.11 °C ± 1.11 (mean ± standard deviation), salinity was 35.44 ppt ± 0.37, water visibility was 7.625 m ± 1.099, and conspecific density ranged from 1 to 8; however, water visibility was excluded as a covariate since minimal variability was observed throughout experimentation.

3.1.1. Bait experiment: avoidance

When focusing solely on the logarithm of avoidance frequency, the best fit model included the main effects of treatment type and conspecific density (T + De) and contained the lowest AIC of 171.66 (Table 2). When referring to model A4, the magnetic treatment (2.012, $t = 5.056$, $P < 0.001$; Table 3) and water visibility (0.083, $t = 1.791$, $P = 0.073$; Table 3) had a significantly positive and correlative effect on avoidance frequency (Fig. 3a). In addition, in comparison to the procedural control treatment, the magnetic treatment had a greater influence on avoidance frequency.

3.1.2. Bait experiment: feeding

When focusing solely on the logarithm of feeding frequency, the main effects of treatment and density, and the interaction between treatment and density (T + De + T*De) were significant. For feeding

Table 2
Analysis of deviance (ANODEV) table for the bait experiment. The response variables are the logarithm of avoidance and feeding frequencies and the explanatory variables are T (treatment) and De (conspecific density). Selected model for avoidance ratio and feeding ratio were A4 and B5, respectively, based on a combination of deviance (D), Akaike Information Criteria (AIC), and *P*-values. 1 in the linear form denotes intercept. Significant models for main effects ($P \le 0.05$) and interaction terms ($P \le 0.1$) are in bold.

Number	Linear form	*D*	*Df*	Δ*D*	Δ*df*	*P*-value	AIC
Avoidance frequency							
A1	Null	144.44	96	NA	NA	NA	229.84
A2	**1 + T**	**83.40**	**94**	**61.04**	**2**	**<0.001**	**172.8**
A3	**1 + De**	**138.10**	**95**	**6.34**	**1**	**0.01**	**225.5**
A4	**1 + T + De**	**80.25**	**93**	**3.15**	**1**	**0.08**	**171.66**
A5	1 + T + De + T*De	77.89	91	2.36	2	0.31	173.3
Feeding frequency							
B1	Null	99.59	96	NA	NA	NA	168.8
B2	**1 + T**	**75.33**	**94**	**24.27**	**2**	**<0.001**	**148.53**
B3	1 + De	99.26	95	0.34	1	0.56	170.46
B4	1 + T + De	74.56	93	0.76	1	0.38	149.77
B5	**1 + T + De + T*De**	**67.54**	**91**	**7.02**	**2**	**0.03**	**146.74**

Abbreviations: 1 = *y*-axis intercept, T = treatment, De = density, *D* = residual deviance, *df* = residual degrees of freedom, Δ*D* = change in residual deviance between former model and model being considered, Δ*df* = change in residual degrees of freedom between former model and model being considered, *P*-value = indicates the level of significance of the explanatory variable added, AIC = Akaike Information Criterion, a model selection criterion.

Table 3
Selected models for the bait experiment. Coefficients, standard errors, *t* statistic and *P*-values of explanatory variables for best models A4 and B5 for the logarithm of avoidance and feeding frequencies, respectively, in the bait experiment. Significant models for main effects ($P \leq 0.05$) and interaction terms ($P \leq 0.1$) are in bold.

Model	Explanatory variable	Coefficient	Standard error	*t*	*P*-value
Avoidance frequency					
A4	**Intercept**	**−3.17**	**0.43**	**−7.42**	**<0.001**
	Magnet	**2.01**	**0.39**	**5.06**	**<0.001**
	Procedural control	0.30	0.51	0.59	0.55
	Density	0.08	0.05	1.79	0.07
Feeding frequency					
B5	**Intercept**	**−1.24**	**0.37**	**−3.35**	**<0.001**
	Magnet	**−4.07**	**1.58**	**−2.58**	**0.009**
	Procedural control	**−1.56**	**0.61**	**−2.55**	**0.01**
	Density	−0.10	0.09	−1.08	0.28
	Magnet: density	0.39	0.27	1.48	0.14
	Procedural control: density	**0.33**	**0.13**	**2.44**	**0.01**

frequency, model B5 outperformed the other models and contained an AIC of 146.74 (Table 2). The coefficients and associated *P*-values with the selected model demonstrate that the magnetic and procedural control treatments were significantly negative (−4.07, $t = -2.58$, $P = 0.009$ and −1.56, $t = -2.55$, $P = 0.01$, respectively; Table 3), with the magnetic treatment having a greater influence on feeding frequency. In addition, the interaction between the procedural control treatment and conspecific density was significantly positive (0.327, $t = 2.435$, $P = 0.015$). This finding demonstrates that feeding frequency is inversely correlated with the effects of both

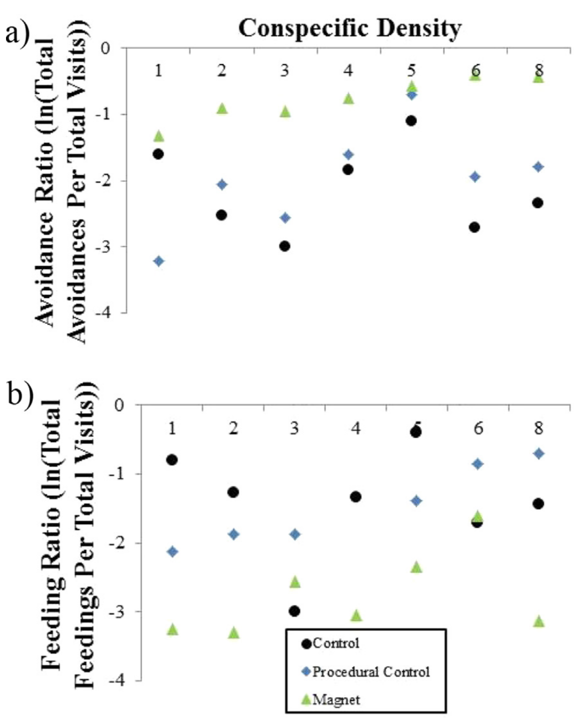

Fig. 3. Graphical representation (ln (total frequency of behavior/total visits)) for the best fit models during the bait experiment pertaining to bull shark (*Carcharhinus leucas*) behavior. For both behaviors, data were transformed to (ln (total behavior + 1)/total visits) at each conspecific density level to improve the interpretability of the data. a) The best fit model (A4) pertaining to the logarithm of avoidance ratio and significant predictor variables, treatment type and conspecific density. b) The best fit model (B5) pertaining to the logarithm of feeding ratio and significant predictor variables, treatment type, conspecific density and the interaction between treatment type and conspecific density.

magnetic and procedural control treatments, whereas feeding frequency was positively and significantly correlated to the interaction between conspecific density and the procedural control treatment (Fig. 3b).

3.2. Barrier experiment

A total of 44, 30 min trials were conducted over the course of eighteen days. For the first study year (January–March 2011), a minimum of fourteen different sharks were identified using short term identification characteristics and post-hoc video analysis. For the second study year (November 2012), a minimum of four different sharks were identified; however, it could not be determined if these four sharks were different sharks compared to the first year. For analysis purposes, these sharks were considered new sharks. Using the inter-column distance as a reference, it was estimated that sharks ranged from 2 to 3 m in total length. Throughout experimentation, sea surface temperature was 22.6 °C ± 0.58 (mean ± standard deviation), salinity was 35.57 ppt ± 0.28, water visibility was 6.188 m ± 3.02 and conspecific density ranging from 1 to 9.

3.2.1. Barrier experiment: avoidance

When focusing solely on avoidance frequency, the main effect of treatment type (T) was significant, whereas all other candidate variables were not significant and thus dropped from the model. For avoidance frequency, model C2 outperformed all the other models and contained the lowest AIC of 186.68 (Table 4) indicating that treatment type is a significant predictor of avoidance behavior. When referring to model C2, the magnetic treatment (3.527, $t = 8.473$, $P < 0.001$; Table 5) and procedural control treatment

Table 4
Analysis of deviance (ANODEV) table for the barrier experiment. The response variables are the logarithm of avoidance and entrance frequencies and the explanatory variables are T (treatment), De (conspecific density), V (water visibility), and Y (year). Selected models for avoidance and entrance ratios were C2 and D8, respectively, based on a combination of deviance (D), Akaike Information Criteria (AIC), and *P*-values. 1 in the linear form denotes intercept. Significant models for main effects ($P \leq 0.05$) and interaction terms ($P \leq 0.1$) are in bold.

Number	Linear form	*D*	*Df*	Δ*D*	Δ*df*	*P*-value	AIC
Avoidance frequency							
C1	Null	362.48	47	NA	NA	NA	452.46
C2	**1 + T**	**92.70**	**45**	**269.78**	**2**	**<0.001**	**186.68**
C3	1 + Y	362.40	46	0.08	1	0.78	454.38
C4	1 + De	360.85	46	1.63	1	0.20	452.83
C5	1 + V	362.04	46	0.43	1	0.51	454.03
C6	1 + T + Y	92.40	44	0.29	1	0.59	188.38
C7	1 + T + De	90.38	44	2.32	1	0.13	186.36
C8	1 + T + V	92.19	44	0.50	1	0.48	188.17
Entrance frequency							
D1	Null	241.36	47	NA	NA	NA	382.95
D2	**1 + T**	**107.24**	**45**	**134.12**	**2**	**<0.001**	**252.83**
D3	1 + Y	240.96	46	0.40	1	0.53	384.55
D4	**1 + De**	**224.24**	**46**	**17.13**	**1**	**<0.001**	**367.83**
D5	**1 + V**	**219.35**	**46**	**22.01**	**1**	**<0.001**	**362.94**
D6	1 + T + Y	106.57	44	0.67	1	0.41	254.16
D7	**1 + T + De**	**91.12**	**44**	**16.12**	**1**	**<0.001**	**238.71**
D8	**1 + T + V**	**85.66**	**44**	**21.58**	**1**	**<0.001**	**233.25**
D9	1 + T + V + Y	84.36	43	1.29	1	0.25	233.95
D10	1 + T + V + De	85.39	43	0.28	1	0.59	234.98
D11	1 + T + V + T*V	82.87	42	2.79	2	0.25	234.46

Abbreviations: 1 = *y*-axis intercept, T = treatment, De = conspecific density, V = water visibility, Y = year, *D* = residual deviance, *df* = residual degrees of freedom, Δ*D* = change in residual deviance between former model and model being considered, Δ*df* = change in residual degrees of freedom between former model and model being considered, *P*-value = indicates the level of significance of the explanatory variable added, AIC = Akaike Information Criterion, a model selection criterion.

Table 5
Selected models for the barrier experiment. Coefficients, standard errors, t-values and *P*-values of explanatory variables for best models C2 and D8 for the logarithm of avoidance and entrance frequencies, respectively, in the barrier experiment. Significant explanatory variables ($P \leq 0.05$) for each model are in bold.

Model	Explanatory variable	Coefficient	Standard error	*t*	*P*-value
Avoidance frequency					
C2	**Intercept**	**−4.16**	**0.41**	**−10.19**	**<0.001**
	Magnet	**3.53**	**0.42**	**8.47**	**<0.001**
	Procedural control	**1.06**	**0.49**	**2.18**	**0.03**
Entrance frequency					
D8	**Intercept**	**−0.31**	**0.13**	**−2.29**	**0.02**
	Magnet	**−2.25**	**0.29**	**−7.80**	**<0.001**
	Procedural control	0.04	0.12	0.37	0.71
	Visibility	**−0.09**	**0.02**	**−4.61**	**<0.001**

(1.061, $t = 2.175$, $P = 0.03$; Table 5) had a significantly positive and correlative effect (Fig. 4a), with the magnetic treatment having a greater influence on avoidance frequency than the procedural control treatment.

3.2.2. Barrier experiment: entrance

When focusing solely on the logarithm of entrance frequency, the main effects of treatment type and water visibility (T + V) were significant. For entrance frequency, model D8 outperformed all the other models and contained the lowest AIC of 233.25 (Table 4) indicating that both treatment and water visibility (T + V) are significant predictors of entrance behavior, whereas the remaining explanatory variables (i.e. conspecific density and year) were not and thus dropped from the model. When referring to model D8, the magnetic treatment (-2.247, $t = -7.801$, $P < 0.001$; Table 5) and water visibility (-0.088, $t = -4.609$, $P < 0.001$; Table 5) were both significantly negative suggesting that entrance frequency is inversely correlated with the effect of both these significant variables (Fig. 4b). Furthermore, these results illustrate that the magnetic treatment had the greatest influence on entrance frequency.

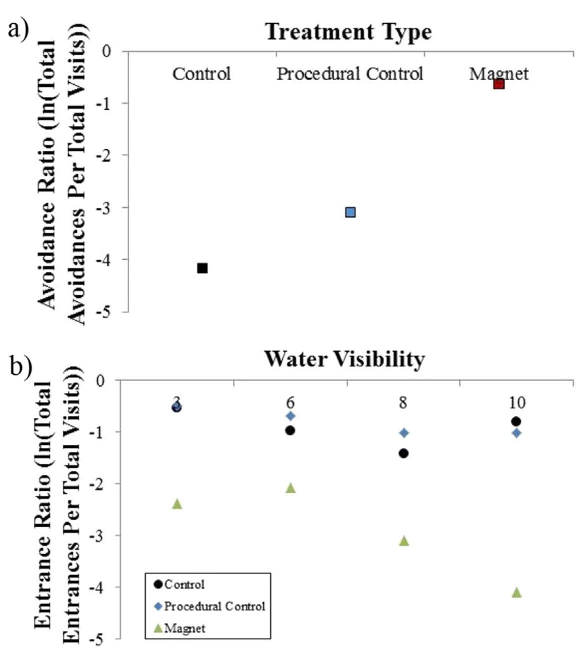

Fig. 4. Graphical representation (ln (total frequency of behavior/total visits)) for the best fit models during the barrier experiment pertaining to bull shark (*Carcharhinus leucas*) behavior. a) The best fit model (C2) pertaining to the logarithm of avoidance ratio and significant predictor variable, treatment type. b) The best fit model (D8) pertaining to the logarithm of entrance ratio and significant predictor variables, treatment type and water visibility. For entrance ratio, all data were transformed to (ln (total entrances + 1)/total visits) at each water visibility level to improve the interpretability of the data.

3.3. Nurse sharks

It was estimated that six different *G. cirratum* interacted with the barrier apparatus but, it was difficult to monitor individual sharks throughout experimentation due to high animal density. One, two, and three initial visits were made towards the control, procedural control, and magnetic treatment zones, respectively. There were insufficient data to determine side preference based on initial visits using a chi-square analysis. However, the behavior of *G. cirratum* was associated with the treatment zone, avoiding the magnetic treatments a significantly greater number of times compared to the control treatments ($C = 4$, PC = 8, $M = 14$; $\chi^2 = 5.85$, d.f. = 2, $P = 0.05$), and entering through the control treatments a significantly greater number of times compared to the magnetic treatments ($C = 50$, PC = 36, $M = 19$; $\chi^2 = 13.77$, d.f. = 2, $P = 0.001$).

3.4. Teleosts

A total of 15 *M. atlanticus* and ~40 *C. ruber* interacted with the apparatus. The total number of *C. ruber* could not be accurately counted as the movement of one *C. ruber* school was only one brief event resulting in the inability for observers to precisely count each fish. No aversion behaviors were observed and an even quantity of the school swam through each treatment zone. However, the behavior of *M. atlanticus* could be quantified. *M. atlanticus* did not exhibit a preference for a particular treatment zone based on initial visits ($C = 3$, PC = 5 $M = 7$, $\chi^2 = 1.60$, d.f. = 2, $P = 0.45$). In addition, no avoidance behaviors were observed and entrance behavior was not significantly associated with treatment zone ($C = 27$, PC = 41, $M = 39$; $\chi^2 = 3.22$, d.f. = 2, $P = 0.20$).

4. Discussion

The aims of this study were to determine the effects of permanent magnets on *C. leucas* behavior and examine how both conspecific density and water visibility may influence magnetic repellent efficacy. The results are the first to show the successful manipulation of *C. leucas* swimming and feeding behavior towards a magnetic barrier and baited apparatus, respectively, with indications that behavior is significantly influenced by situational context (i.e. variations in conspecific density or water visibility).

4.1. Basic behavioral observations

For both the bait and barrier experiments, as hypothesized, the magnetic treatment had a significant impact on *C. leucas* behavior (Figs. 3 and 4). More specifically, for the bait experiment, avoidance frequency was highest towards, and feeding frequency was lowest towards, the magnetic treatment (Table 3). For the barrier experiment, avoidance frequency was highest, and entrance frequency was lowest, towards the magnetic treatment zone (Table 5). These findings are consistent with previous studies that demonstrate that the Australian blacktip shark (*Carcharhinus tilstoni*), grey reef shark (*Carcharhinus amblyrhynchos*), and the lemon shark (*Negaprion brevirostris*), are sensitive and deterred from permanent magnets (Rigg et al., 2009; O'Connell et al., 2011). However, these entrance-related findings suggest that *C. leucas* enters through the magnetic region fewer times in comparison to the procedural control region and thus these findings differ from a previous study pertaining to the great white shark (*C. carcharias*; O'Connell et al., 2014a). Since experimental designs were nearly identical between the studies, behavioral differences towards the experimental treatments may be directly related to the feeding ecology of the interacting sharks. For example, studies demonstrate that adult *C. carcharias* are highly reliant on vision for prey capture (Strong, 1996), illustrating the importance of vision to this species and suggestive as to why the visual stimuli provided by the procedural control columns were sufficient to elicit behavioral modification. In contrast, *C. leucas* is typically associated with high turbidity environments such as freshwater, estuarine and other coastal environments (Curtis et al., 2013; Heupel and Simpfendorfer, 2008) and thus, this species may rely more heavily on their electrosensory system, rather than their visual system, when foraging and navigating. With a heightened reliance on electroreception due to their frequent occurrence in turbid environments, this may yield a heightened sensitivity to magnetic fields, thus making magnetic stimuli more effective on this species and providing potential for future bycatch reduction and swim pattern manipulation applications.

4.2. Conspecific density

During the bait experiment, treatment type, conspecific density, and the interaction between the two were significant predictors of the feeding frequency (Table 2). The main effect of conspecific density resulted in an overall decrease in feeding frequency; however, this effect was not significant ($P = 0.279$ in Table 3). The interaction between the treatment type and conspecific density was nonparallel, resulting in a significant outcome (Fig. 3b). More specifically, the interaction between the procedural control treatment and conspecific density resulted in a significant increase in the feeding frequency (Table 3). These findings may be explained by intraspecific competition (Polis, 1981; Stiling et al., 1984), where an increase in conspecific density has the capacity to drastically alter the behavior of interacting organisms (i.e. increase in feeding frequency).

Furthermore, although there was an increase in feeding frequency in relation to the interaction between the magnetic treatment and conspecific density, this relationship was not significant ($P = 0.138$ in Table 3). These findings are not consistent with the results of Brill et al. (2009) and Robbins et al. (2011) which reported a behavioral change in interacting elasmobranchs to magnetic and electropositive metal repellents with increasing conspecific density. Therefore, although there are inconsistencies between studies, these inconsistencies may be explained by magnetic field sensitivity: varying on the species-level, varying with situational context, and/or varying based on other biological and/or environmental variables.

4.3. Water visibility

During the barrier experiment, the overall effect of water visibility was sufficient to significantly alter entrance frequency (Table 4). Future studies may find it pertinent to focus solely on turbidity rather than water visibility. Water visibility incorporates light intensity that can be directly influenced by depth in the water column and light intensity shifts associated with the time of day. Since most elasmobranchs are equipped with an intra-ocular light-reflecting structure known as the tapetum lucidum (Gruber and Cohen, 1985), light is augmented during periods of low light conditions. Therefore decreases in water visibility that are not directly correlated with high turbidity, may not have such an inhibitory effect on vision capabilities as originally presumed for this study. Using this concept, although future studies should not neglect water visibility, turbidity may be a more pertinent factor in magnetic repellent success and should be more thoroughly studied to understand what environmental parameters influence repellent success and what locations may yield the most successful application of these repellents.

4.4. Habituation

Additionally, although not statistically analyzed, throughout the bait and barrier experiments, there were no observable signs of habituation. In contrast, a previous study examining the effects of magnetic stimuli on the lemon shark (*N. brevirostris*) demonstrated that repeated exposure to the stimuli after a period of 1 h led to rapid habituation (O'Connell et al., 2011). The current study differs in that magnetic effectiveness did not change with time, as interacting sharks were continually observed to avoid magnet-associated treatments. One potential explanation for these differing findings is that the present study was conducted in the wild, where *C. leucas* had the capability to avoid and remain out of the range of the magnetic fields. In O'Connell et al. (2011), the study was conducted in an outdoor pen where the swim patterns of experimental animals were restricted, leading to constant exposure to the magnetic fields over a short duration. Secondly, during the present barrier experiment, the vertical columns containing magnets are not permanently affixed and thus rotate with any sort of water turbulence (e.g. waves and currents). Thus upon each interaction, *C. leucas* may be exposed to differing magnetic field strengths which can be hypothesized to prolong habituation.

4.5. Additional species

Besides *C. leucas*, a variety of additional species were observed to interact with the barrier, including the nurse shark (*G. cirratum*), the tarpon (*M. atlanticus*), and the bar jack (*C. ruber*). Results from the barrier experiment illustrate the elasmobranch-specific nature of magnetic repellents, where *G. cirratum* behavior was modified and teleost (i.e. *M. atlanticus* and *C. ruber*) behavior was not observably modified by the magnetic treatment regions. These results are supported by previous studies (Stoner and Kaimmer, 2008; Rigg et al., 2009; O'Connell et al., 2014b) demonstrating that interacting teleosts did not exhibit any significant trends in behaviors towards magnetic and electropositive metal repellents. This information provides implications for the potential utility of magnets for future applications that focus solely on elasmobranch capture or bycatch reduction.

5. Conclusion

Successful demonstration of using baits and a small scale barrier containing grade C8 barium-ferrite permanent magnets to repel *C. leucas* in this study provides a foundation for continued research on other predatory elasmobranchs (i.e. *C. carcharias* and *G. cuvier*). In addition, results illustrate the need to monitor environmental and biological variables throughout future studies as inter-trial behavioral variation occurred towards deterrent stimuli. With a continued focus on these variables and deterrent effectiveness, in addition to future research examining the exclusion properties of magnetic barriers, it may soon be understood if any logistical and practical applications of these technologies exist.

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Appendix A. Supplementary data

Supplementary data related to this article can be found at http://dx.doi.org/10.1016/j.ocecoaman.2013.12.012.

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