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Behavioral responses to weak electric fields and a lanthanide metal in two shark species

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ABSTRACT

The unintentional catch of sharks on hooks intended for other fishes is an economic, environmental and safety concern. Recent research has sought to repel sharks from baited hooks by applying various lanthanide metals and alloys to stimulate the elasmobranch electrosensory system. We present a simplified experimental methodology to test responses of two shark species to a single lanthanide metal. Behavioral responses to prey-simulating, weak electric fields were quantified to establish the sensitivity of the electrosensory system in *Squalus acanthias* (Linnaeus, 1758) and *Mustelus canis* (Mitchill, 1815). Both species detected electric fields <1 nV cm, and responded similarly to other elasmobranchs previously studied. Sharks were then presented with food affixed to treatments of acrylic, stainless steel or neodymium (Nd) metal. *S. acanthias* only fed in groups and fed from Nd significantly less frequently than from either control. *M. canis* was tested both individually and in groups and, when alone, fed less from Nd, however, in groups they fed significantly more often from Nd. These results confirm variability in response to a lanthanide metal both across species and within a species in the presence of competition. Since observed differences are not due to differences in sensitivity, other factors appear to influence behavioral responses and may compromise the effectiveness of lanthanide metals for the reduction of shark bycatch.

1. Introduction

Incidental capture of non-target species can have negative financial impacts on commercial fisheries, cause ecological disruptions by reducing populations, and can undermine fisheries management and conservation efforts (Hall and Mainprize, 2005; Lewison et al., 2004; Mandelman et al., 2008). Fisheries face decreased profitability from non-target species occupying hooks meant for target species, as well as time and monetary losses from damage to fishing gear. Many elasmobranchs (sharks, skates and rays) are vulnerable to fishing pressure due to their K-selected life history characteristics, including slow growth, late maturity, long gestation and low fecundity (Hoenig and Gruber, 1990). Sharks are the major bycatch group in pelagic longline fisheries (Gilman et al., 2007; Mandelman et al., 2008) and several species commonly caught as bycatch are variously listed as, *near threatened*, *vulnerable* or *endangered* by the International Union for Conservation of Nature (IUCN). The US National Marine Fisheries Service (NMFS), has recognized the need to reduce incidental bycatch, which imposes a secondary threat to already substantial reported reductions in shark populations due to targeted fishing (Baum and Myers, 2004; Baum et al., 2003). This study employs a laboratory-based approach to assess a potential method of shark bycatch reduction.

A stimulus that deters elasmobranchs from bait yet has no effect on targeted teleost fishes could provide a viable means of reducing shark bycatch. Elasmobranchs, unlike marine teleosts, possess an exquisitely sensitive electrosensory system that enables them to detect voltage gradients in their environment (Jordan et al., 2009; Kajiura and Holland, 2002; Kalmijn, 1971, 1982). Sharks and rays have demonstrated similar minimum detection thresholds, typically below 1 nV cm^{-1} (Table 1). Lanthanide elements naturally lose electrons and create in seawater a negative charge distribution. The electric fields produced are well within the range of detection by shark electroreceptors. When deployed adjacent to bait, lanthanide metals have been demonstrated to repel sharks and decrease consumption of bait (Brill et al., 2009; Kaimmer and Stoner, 2008; Stoner and Kaimmer, 2008; Wang et al., 2008), conversely, other studies have reported a lack of aversion behavior (Robbins et al., 2011; Tallack and Mandelman, 2009). Unfortunately, differences in methodologies and metal types confound comparisons of results across studies and between species, making it difficult to draw overall conclusions regarding the effectiveness of these metals. It is also unknown if variation across shark species is related to differences in detection capabilities as the

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Table 1
Minimum electrosensory response thresholds of elasmobranchs.

Species	Common name	Minimum (nV cm)	Reference
Squalus acanthias	Spiny dogfish	0.2	This study
Mustelus canis	Dusky smoothhound	0.6	
Urobatis halleri	Round stingray	0.3	Jordan et al. (2009)
Pteroplatytrygon violacea	Pelagic stingray	0.3	
Myliobatis californica	Bat ray	0.1	
Dasyatis sabina	Atlantic stingray	0.6	McGowan and Kajiura (2009)
Sphyrna lewini	Scalloped hammerhead	0.4	Kajiura and Holland (2002)
Carcharhinus plumbeus	Sandbar shark	0.5	
Sphyrna tiburo	Bonnethead shark	<1	Kajiura (2003)
Himantura granulata	Mangrove whipray	4	Haine et al. (2001)
Carcharhinus melanopterus	Blacktip reef shark	4	

electrosensory pore number and configuration varies by shark species (Cornett, 2006). Therefore, our goal was to introduce and test a protocol that can be easily replicated with multiple species and employs a single lanthanide metal, neodymium (Nd).

Two small, coastal North Atlantic species that are commonly caught as bycatch were selected for comparison. The piked dogfish, *Squalus acanthias*, is found worldwide (Mecklenburg et al., 2002), typically in large schools. This species sometimes comprises up to ninety percent of catch (Stoner and Kaimmer, 2008), is known to cause gear damage (Ketchen, 1986), and steal baits from hook fisheries including commercial longlines (Stoner and Kaimmer, 2008). Populations of these sharks have reportedly faced serious declines in recent years (Fordham et al., 2006). Although *S. acanthias* is one of the few species previously studied for responses to lanthanide metals, results conflict between individuals from Pacific versus Atlantic populations (Kaimmer and Stoner, 2008; Stoner and Kaimmer, 2008; Tallack and Mandelman, 2009). The dusky smoothhound shark, *Mustelus canis*, overlaps in range distribution and diet with *S. acanthias* in the Western Atlantic and represents an ecologically similar though evolutionarily distant clade of sharks (Compagno, 1984).

We predicted that both species would display high sensitivity to weak, prey-simulating electric fields. When presented with food attached to either a control or Nd metal, we hypothesized that if there is no effect of the lanthanide metal, food would be consumed equally from each treatment. Shark density has been observed to influence behavior (Robbins et al., 2011), therefore, sharks were tested alone and in groups to determine if response to the metal was altered with competition. It has also been suggested that sharks can become habituated to electric fields produced by lanthanide metals, where any reduction in feeding can become less pronounced with increased exposure (Brill et al., 2009). Our lab-based approach allowed us to reliably identify each individual and quantify any changes in response pattern over time.

2. Methods

Four *S. acanthias*, total length (TL) 83–88 cm, and eight *M. canis*, TL 72–96 cm, were captured by trawl and held in captivity for at least one week, until feeding normally, before experimental trials began. All work was conducted under IACUC approval by both Florida Atlantic University (FAU), Boca Raton Florida, and the Marine Biological Laboratory (MBL), Woods Hole, Massachusetts. Throughout all experiments, the water temperatures were maintained within the natural range for the species at 14–16 °C for *S. acanthias* and 17–19 °C for *M. canis*. Salinity ranged from 34 to 35 parts per thousand. Data were transformed as necessary to satisfy assumptions for all statistical analyses and were tested using R version 2.10.1 for Mac (R Development Core Team, 2009).

2.1. Electrosensory experiments

To ensure that any differences in response to electric fields produced by metals were not due to differences in sensitivity, we quantified the detection capabilities of each species to weak dipole electric fields. The experimental apparatus and stimulus generator used were identical to that described in Kajiura and Holland (2002), except that only two dipoles were used (one control and one active). The apparatus was placed on the bottom of the tank and consisted of an acrylic plate with dipoles located 25 cm from an opening for odor delivery. The electric stimulus generator was attached to the plate through underwater electrical cables and 50 cm tygon tubing salt bridges. Electrical currents ranged from 10.5 to 15.5 μA for electrical orientation experiments. Experiments were conducted in a 10 ft diameter round fiberglass tank at the Marine Resources Center at the MBL.

An odor stimulus (squid rinse) was injected through the odor delivery tube and one dipole was activated to initiate the trial. Once a shark oriented and attempted to bite at the active dipole, it was switched off and the other dipole was activated. Food rewards were occasionally placed next to an active dipole to positively reinforce searching behavior. Trials were recorded with a SONY Handycam DCR-HC40 NTSC mini-DV video camera positioned directly above the experimental plate.

For these experiments *S. acanthias* were tested with a group of 4 individuals present in the tank. Any shark was free to respond to the active dipole during these trials. Trials were run two times per day for a total of 28 trials. Trials with individuals were attempted, however, *S. acanthias* did not feed in isolation. Individual trials were successful with *M. canis*, and sharks were tested individually in the experimental tank after an acclimation period of at least 30 min. Each individual was tested every other day for a total of 5 trials per shark.

Video sequences of each biting response of a shark to an electrode were captured and individual frames extracted using iMovie HD version 6.0.4 (Apple Computer Inc.). The still frame that immediately preceded the initiation of an orientation toward the dipole was used to measure the position of the shark with respect to the center of the dipole. To calculate the strength of the electric field, E, at the point of orientation a line was drawn on the image from the center of the dipole to the closest side of the shark's head. The length of the line and the angle relative to the dipole axis were measured using ImageJ (NIH: http://rsb.info.nih.gov/ij).

The log of E was compared between species for all orientations while controlling for multiple observations within species and for each individual using a linear mixed effects model. The minimum electric field strength that elicited a response from each individual was compared between species using a one-way ANOVA. The maximum orientation distance for each individual was compared between species using an ANCOVA with applied current strength at the time of orientation as a covariate. To determine if any differences were associated with body size in *M. canis* (range 72–96 cm), minimum E and maximum orientation distances were compared with total length by linear regression.

2.2. Metal experiments

Both species were presented with food attached to control treatments or samples of Nd metal to test whether the sharks consumed food equally from all treatments. The experimental apparatus consisted of three 40 cm^2 clear acrylic plates connected side-by-side with small cable ties. Each plate had a 2.5 cm^2 acrylic platform in the center with a 20 cm diameter circle drawn on the plate around each platform (Fig. 1). The distance between platforms on adjacent plates was 40 cm. A hole in the center of each platform was threaded to accept a nylon bolt, which was used to affix a 2.5 cm square sample of either acrylic (control), stainless steel (control), or Nd (test metal, 99.5%, CSTRAM Advanced Materials Co. Shanghai, China; Fig. 1). Fresh frozen squid were thawed and cut into 1 cm wide rings and were tied closely to the metal or acrylic with 4 lb test fishing line. Only the mantle was used to ensure that food pieces were as uniform as possible. The position of the test metal and controls was randomized.

To begin a trial, the joined plates with metals, controls, and food attached were placed on the bottom of the experimental tank. As soon as a shark removed a piece of food from any of the treatments, the plates were pulled out of the tank, the food was replaced, the order of metals/controls was randomly changed and the plates were placed back in the water for the second trial within the session. This process was done as quickly as possible (1–2 min) to prevent the sharks from losing interest in searching for food while the plates were out of the water. Sessions continued until either all prepared food was consumed or the shark(s) showed no interest in the food or experimental plates for 5 min. Choices (eating from control or test metal) were noted on data sheets and shark behavior was recorded using the video camera positioned over the tank.

S. acanthias was tested only in a group of 4 sharks. To reduce handling stress they were not moved at any time throughout these experiments. Sharks participated in one to two sessions per day for a total of 13 sessions, each consisting of 5 to 13 trials. *M. canis* was tested both individually and in groups. Individuals participated in one session every other day with at least 30 min acclimation time in the experimental tank, for a total of 3 sessions and 30 trials each. In groups of four, sharks were tested twice per day every other day for a total of 8 sessions with up to 27 trials in each session. One additional session was conducted on the final day of testing with only the three sharks that had eaten the fewest food pieces and contributed the lowest number of choices to the group data set.

The number of times food was consumed from each control and metal was compared to the prediction of equal consumption from all three treatments using Pearson's Chi Squared tests for *S. acanthias* (group only), *M. canis* individual and *M. canis* group trials. Contingency tables allowed comparisons by individual and by treatment position on the plate. The percentage of food consumed from each of the treatments was calculated for each individual, arc sine transformed, and compared with ANOVA and Tukey post-hoc tests.

Approaches to control/metal were also counted and compared from video recordings. An approach was defined as any time a shark's head entered within the 20 cm diameter circle drawn around the treatment platform. An approach was counted only if the shark's snout was initially aimed toward the platform followed by a change in behavior such as swimming direction or speed, with no food removed before exiting the circle. This criterion eliminated glancing passes where the shark swam through the edge of the circle without demonstrating any interest in the food item.

To test for changes in response over time we employed linear regression to compare the percentage of food removed from Nd across consecutive sessions. Any video sequence where more than one shark was over the acrylic plate array at the time of food removal was not included in analyses. This occurred in only 3 and 9% of all group trials conducted for *S. acanthias* and *M. canis* respectively.

3. Results

Electrical detection capabilities were similar for both species, however, response to a lanthanide metal, Nd, differed. Furthermore, within a species, responses to this metal could be reversed when sharks were alone or in groups.

3.1. Electrical response

In total, 166 dipole orientation responses were analyzed and compared (55 *S. acanthias*; 111 *M. canis*). Both species showed high sensitivity to weak electric fields that are similar to those recorded for other elasmobranch species (Table 1). No significant differences were found between species for responses to dipole electrodes (median response: *S. acanthias* = 14 nV cm^{-1}, *M. canis* = 29 nV cm^{-1}; Linear multilevel regression, Table 2). We also found no significant differences between species in the minimum electric field strength (mean ± standard error: *S. acanthias* = 1.5 ± 1.0 nV cm^{-1}, *M. canis* = 2.8 ± 2.7 nV cm^{-1} ANOVA: $F_{1,10} = 0.83$, $p = 0.38$) and maximum orientation distance (mean: *S. acanthias* = 30 ± 7 cm, *M. canis* = 26 ± 5 cm, ANCOVA: $F_{2,9} = 1.04$, $p = 0.39$) for each individual. Over 80% of responses for each species were to stimuli <100 nV cm^{-1} (Fig. 2). No significant relationship was found with body size in *M. canis* for minimum electric field strength (Linear regression: $R^2 = 0.25$, $p = 0.12$) or maximum orientation distance (Linear regression: $R^2 = -0.15$, $p = 0.62$).

3.2. Metal experiments

A total of 140 choice trials were analyzed for *S. acanthias* in groups, 240 for *M. canis* tested individually, and 212 for *M. canis* in groups. The hypothesis that food would be consumed equally from the acrylic, stainless steel, and Nd metal was rejected for all experiments; however, different patterns were observed (Fig. 3). *S. acanthias*

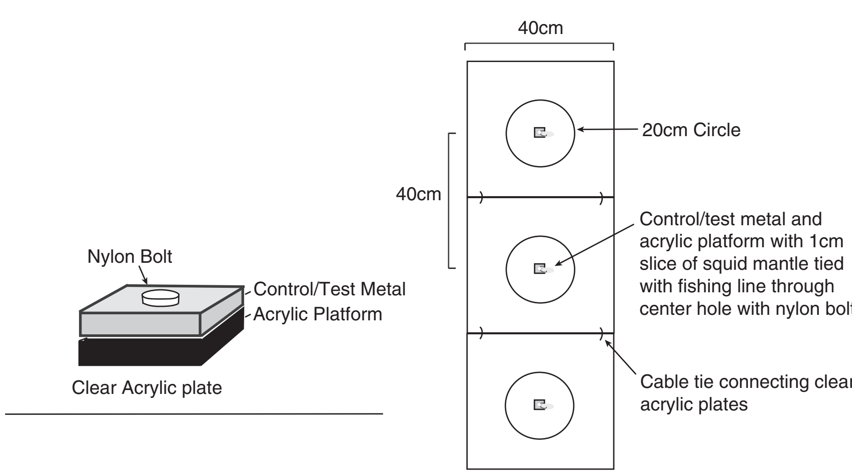

Fig. 1. Experimental apparatus for metal experiments. A black acrylic platform was bonded to the clear acrylic plate with a threaded hole in the center to secure the nylon bolt. The control (acrylic or stainless steel) or test metal (neodymium) was held in place on top of the platform by the bolt so the three samples could be easily rearranged between trials. Three plates were attached together by small cable ties so they would lie flat on the bottom of the tank. A 1 cm wide piece of squid mantle was attached to the apparatus with 4 lb clear monofilament line tied through the hole in the center of the control/metal.

Table 2
Multilevel regression of the log of the electric field strength at the point of orientation. No significant differences were found between species, right or left dipoles, or with initial current. SE = standard error, DF = degrees of freedom.

Parameter	Value (SE)	DF	p-value
Intercept	−0.15 (0.87)	151	0.86
Squalus acanthias vs. *Mustelus canis*	−0.28 (1.60)	10	0.87
Dipole (R or L)	−0.03 (0.10)	151	0.73
Current	−6071.46 (126994.73)	151	0.96

consumed food from Nd significantly less frequently than from the two control treatments regardless of its position on the plate or the individual eating (Pearson's Chi Squared: $X^2_2 = 16.51$, $p<0.001$; position $X^2_4 = 4.38$, $p = 0.36$; individual $X^2_6 = 8.07$, $p = 0.23$). Although there was some individual variation (Fig. 4b), when tested alone, *M. canis* ate food from Nd significantly less often than from controls (Pearson's Chi Squared: $X^2_2 = 10.83$, $p<0.01$). However, when in groups, *M. canis* ate food from Nd significantly more frequently than from controls regardless of either the position of the metal on the plate or the individual feeding (Pearson's Chi Squared: $X^2_2 = 14.08$, $p<0.01$; position $X^2_4 = 4.47$, $p = 0.35$; individual $X^2_{14} = 16.80$, $p = 0.27$). The low percentage of food removed from Nd by *S. acanthias* and *M. canis* tested individually was similar and significantly lower than the percentage removed by *M. canis* in groups (ANOVA, $F_{2,17} = 17.95$, $p<0.0001$; Tukey post-hoc test, *S. acanthias* and *M. canis* individual $p = 0.43$, *S. acanthias* and *M. canis* group $p<0.001$, *M. canis* individual and *M. canis* group $p<0.001$).

Distinct patterns also existed in approaches to Nd versus controls. Over 50% of all observed approaches for both species were directed towards Nd. Sharks would enter the 20 cm circle around the metal and typically turn away and quickly exit the circle or sometimes attempt to bite without successfully directing the strike at the food, before exiting. Both *S. acanthias* (tested in groups only) and *M. canis* (when tested individually) showed a relatively high level of curiosity, approaching Nd in over 35% of trials. However, when *M. canis* was tested in groups, approaches to Nd were only observed in 14% of trials.

No significant differences in the percentage of food consumed from Nd were observed over consecutive trials (linear regression: *S. acanthias* $R^2 = 0.07$, $p = 0.18$, *M. canis* individual $R^2 = 0.10$, $p = 0.08$, *M. canis* group $R^2 = 0.17$, $p = 0.15$, Fig. 4a–c).

4. Discussion

The use of electrical stimuli to reduce shark bycatch in hook fisheries is a promising recent avenue of research. Results from previous studies indicate variability in shark responses (Brill et al., 2009; Kaimmer and Stoner, 2008; Robbins et al., 2011; Stoner and Kaimmer, 2008; Tallack and Mandelman, 2009; Wang et al., 2008). This study confirms variability in both inter and intraspecific responses to a lanthanide metal using a standardized set of experimental conditions and metal type. Despite a similar electrical sensitivity between *S. acanthias* and *M. canis*, observed behavioral response to the lanthanide metal differed dramatically.

4.1. The piked dogfish conundrum

Laboratory based studies on *S. acanthias* have provided conflicting results for responses to lanthanide metals both across populations, and now within a population (Stoner and Kaimmer, 2008; Tallack and Mandelman, 2009). Stoner and Kaimmer (2008) reported a reduction in Pacific spiny dogfish feeding from baits "protected" by a mischmetal alloy containing primarily cerium (64.02%), and lanthanum (34.22%), and found statistical differences even with food deprivation. In the Atlantic, however, Tallack and Mandelman (2009) only observed a reduction in consumption of food protected by a similar alloy one hour after feeding, and no reduction when the sharks were deprived of food for 2 days or longer. Conversely, despite a similar group size, in the present study Atlantic spiny dogfish exposed to a pure sample of Nd exhibited clear selectivity, avoiding food associated with this metal relative to controls.

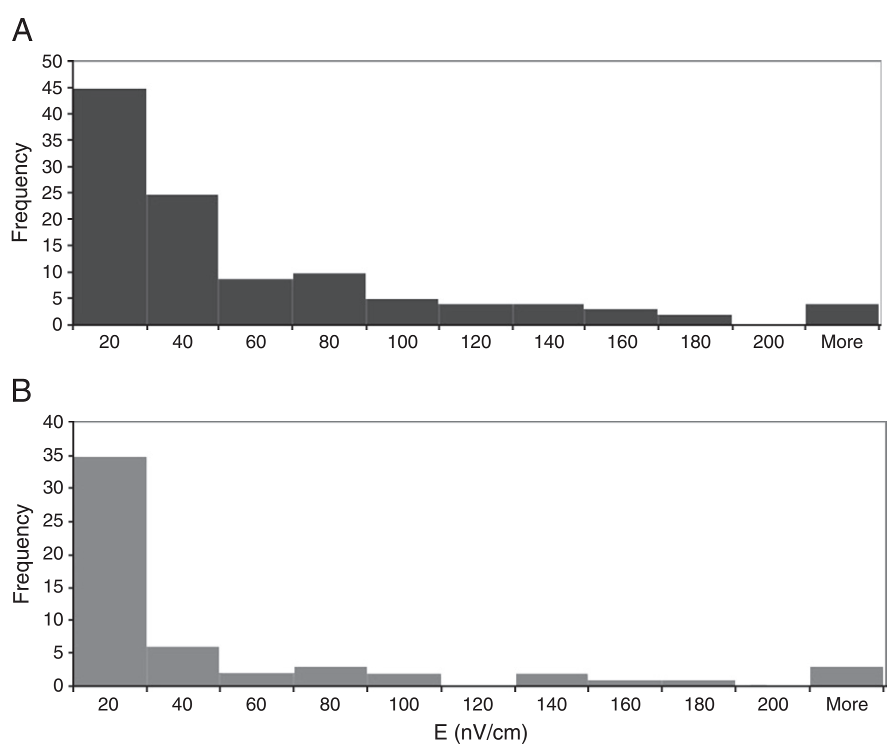

Fig. 2. Percentage of responses to weak electric fields in (A) *Squalus acanthias*, and (B) *Mustelus canis*. Fifty-five responses were analyzed *S. acanthias* and 111 for *M. canis*.

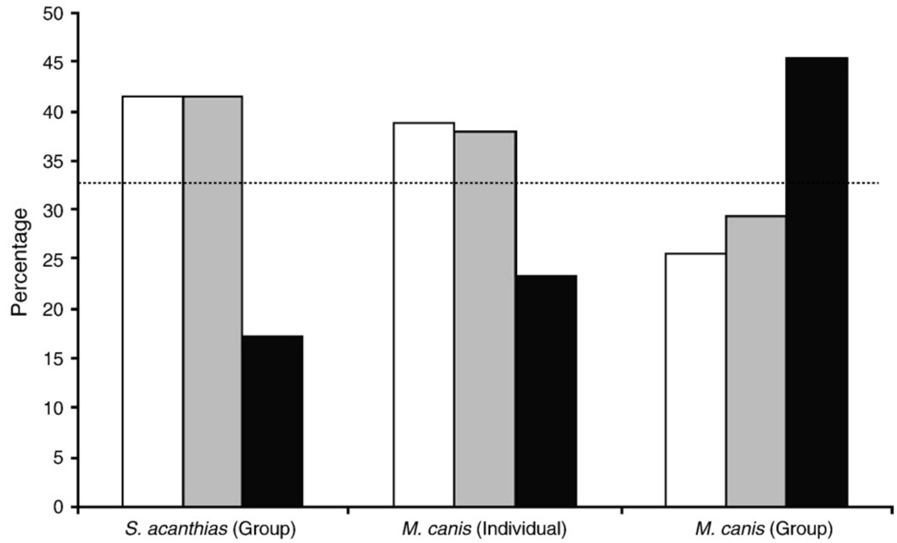

Fig. 3. Percentage of food consumed from Acrylic (white), stainless steel (gray), and neodymium metal (black). The dotted line indicates the predicted percentage if food was consumed equally from all treatments.

Differences between these findings may be dependent on the type of metal used, feeding motivation, and/or the number of conspecifics present to influence feeding behavior. Although it is possible that pure Nd is a more successful deterrent, other factors are likely to be important in understanding the variability in response within this species and are relevant to predicting responses in the field. For example, in this study, *S. acanthias* was held in captivity and fed to satiation three times per week before experiments began. Although these sharks did not eat for over one week during our attempts to test them individually, they displayed generally slow responses to food, a high degree of investigation of food options (indicated by the number of approaches not resulting in consumption), and participated in a low number of trials per session before loss of interest. This behavior more closely resembles behavior Tallack and Mandelman (2009) observed when *S. acanthias* was satiated, suggesting that hunger level and pre-experiment feeding regimen are important factors to consider. The behavior of *S. acanthias* sharply contrasted that of *M. canis* tested in groups of the same size. It is possible that the threshold for the number of sharks required to facilitate competitive feeding behavior is higher in *S. acanthias* than in *M. canis*. Spiny dogfish found schooling in the wild typically number in the hundreds, and forage in "packs" attacking schools of fish (McMillan and Morse, 1999). Even with a five-fold increase in group size, from 3 to 15 in the same sized tank, Tallack and Mandelman (2009) did not observe differences in feeding behavior or responses to the cerium/lanthanum alloy. The similarities in preference for controls (Fig. 3) and approach behavior we observed between *S. acanthias* (in groups of four) and *M. canis* tested individually support the conclusion that the group size tested for *S. acanthias* was not large enough to facilitate competitive feeding behavior.

4.2. Competitive feeding behavior

The introduction of additional sharks had profound effects on our results for *M. canis*. When examining another carcharhiniform, the Galapagos shark (*Carcharhinus galapagensis*), Robbins et al. (2011) observed that animals became less selective and consumed the most easily available or closest bait when three or more sharks were present. Instead of a decrease in selectivity, we observed a transition from sharks avoiding food affixed to Nd to preferring it in the presence of conspecifics. Individual sharks were significantly less likely to eat from Nd, preferring controls, and spent more time investigating their options when they were alone in the tank. When in groups, however, sharks were significantly more likely to feed from Nd than either control and we observed fewer approaches to any treatment that did not result in food removal. A potential explanation

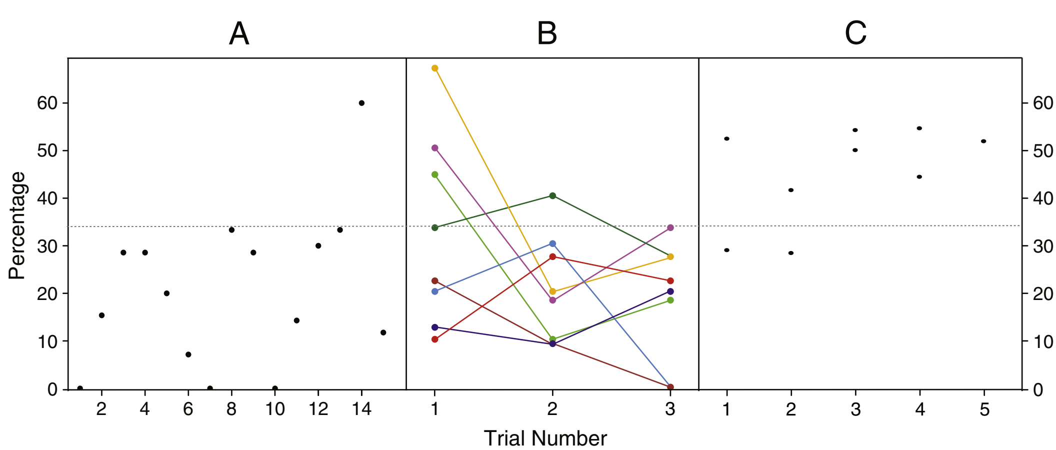

Fig. 4. Percentage of food consumed from neodymium metal across consecutive trials in (A) *Squalus acanthias*, (B) *Mustelus canis* tested individually, and (C) *M. canis* in groups. Individuals in B are distinguished by different colors. The gray dotted line indicates the expected percentage if food was consumed equally from all 3 materials.

for this dramatic shift in behavior could be that in the face of perceived competition from other nearby sharks, individuals were driven to take the food they could most easily locate. Although each treatment provided visual and olfactory cues that might help the shark to locate the food, only the Nd also provided an electrosensory cue. Electric fields provide directional information that sharks can use to accurately locate prey items and this sense is thought to be the most important in directing the strike once prey is within close range (Kalmijn, 1972, 1982). The additional sensory information may have helped sharks to locate food associated with Nd more readily, leading them to ignore any irritation caused by the strength of the electric field to quickly consume the food before a competitor approached. Due to these lab results and those of Robbins et al. (2011) in the field, the potential success of this metal type as a repellent would likely be enhanced with more solitary species that are not as likely to experience similar competitive influences.

4.3. Influence of experience

Whereas some studies have reported a decrease in the effectiveness of deterrents with time and experience (Brill et al., 2009; Robbins et al., 2011), we, like Rigg et al. (2009) did not see a significant pattern. Because we tested *M. canis* in groups after their individual tests it could be suggested that the sharks were already desensitized to the field produced by the lanthanide metal before group trials began. If sharks were desensitized, a resulting indifference to food located near Nd or controls could be expected after an initial aversion. However, we saw no indication of desensitization throughout individual tests. Although no significant trend was found, sharks exhibited greater variability during their first exposure, and then were less likely to eat from Nd during subsequent trials (Fig. 4b). Therefore, the dramatic difference in preference between individual and group tests in *M. canis* is attributed to the presence of additional sharks.

4.4. Conclusions and suggestions for future work

Our results support evidence that sensitivity to electric fields is comparable across all elasmobranchs (Haine et al., 2001; Jordan et al., 2009; Kajiura, 2003; Kajiura and Holland, 2002; McGowan and Kajiura, 2009). However, despite similar electrosensitivities, behavioral responses to electric fields produced by Nd varied between the two species examined in this study. Furthermore, avoidance of food located near Nd could be reversed within a species (*M. canis*) when individuals were tested in small groups. Thus, Nd may be a more successful repellant in hook fisheries where solitary shark species comprise a large component of the bycatch. A better understanding of the role of hunger level and the presence or absence of competition in both lab and field situations will likely improve predictions of how a shark will respond to deterrents that target the electrosensory system.

Acknowledgments

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