FEEDING BEHAVIOR OF LOGGERHEAD AND LEATHERBACK SEA TURTLES: A STUDY TO BETTER UNDERSTAND LONGLINE BYCATCH

by

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This thesis was prepared under the direction of the candidate's thesis advisor, Dr. Jeanette Wyneken, Department of Biological Sciences, and has been approved by the members of her supervisory committee. It was submitted to the faculty of the College of Science and was accepted in partial fulfillment of the requirements for the degree of Master of Science.

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ABSTRACT

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Two species of sea turtle, loggerheads (*Caretta caretta*) and leatherbacks (*Dermochelys coriacea*) are caught frequently as bycatch in longline fisheries. These fisheries use hooks baited with fish or squid. Yet, leatherbacks feed on gelatinous prey while loggerheads are carnivores. I investigated the responses of these two species to bait odors in controlled laboratory experiments to better understand their feeding behavior and why they interact with longlines. Both species initiated feeding behavior in the presence of squid bait odors and just *C. caretta* showed feeding behavior with sardine odors; neither responded to mackerel odors. The turtles are hooked differently on longlines. Loggerheads are usually hooked in the mouth while leatherbacks are usually hooked in the shoulder or flippers. Comparisons of prey attack behavior and accuracy in apprehending a stimulus in the presence of waterborne food odors identified species-specific differences that may predispose the turtles to particular kinds of hooking.

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INTRODUCTION

Fisheries bycatch is a significant source of mortality for sea turtles, sharks, sea birds, and other nontarget species worldwide (Lewison et al., 2004, Wallace et al., 2013). Such mortality is significant and contributes to the decline (and prevents recovery) of these imperiled species (Wallace et al., 2013). Longline fishing occurs in most ocean basins at industrial scales. In 2013, an estimated 10 billion hooks were deployed in longline fisheries worldwide (Fitzgerald, 2013). The main target species are commercially valuable fish such as tuna (*Thunnus* spp.), swordfish (*Xiphias gladius*), and mahi mahi (*Coryphaena hippurus*) (Garrison 2005; Wang et al. 2007; Stokes et al. 2011). A variety of longline configurations are employed in fisheries worldwide. All longline gear is composed of three basic parts: a main line, which can stretch for kilometers; branch lines that clip onto the main line, and baited hooks attached to the branch lines (Kerstetter and Watson, 2006).

Longlines deployed in oceanic waters target pelagic fish while other longline configurations, (bottom, midwater or dermersal longlines), target benthic, pelagic and reef fish (Belda and Sánchez, 2001; Shiode et al., 2005). Pelagic longlines are suspended below the surface and can stretch for over 50 km with thousands of baited hooks (Gilman et al., 2006; Kerstetter and Watson, 2006; Wang et al., 2007). The target species of pelagic longlines are mainly tuna, mahi mahi and swordfish (Belda and Sánchez, 2001; Gilman et al., 2006). Bottom longline gear is similar to pelagic longline gear except that the mainline, called a groundline in this fishery, is anchored so that it lies near or on the bottom of the ocean (Prytherch, 1983). The target species of this fishery include grouper (*epinephelines*), snapper (*lutjanids*), haddock (*Melanogrammus aeglefinus*) and cod (*Gadus* spp.) (Prytherch, 1983). In both configurations, when animals that breathe air are hooked, they are often unable to reach the surface and drown or survive with varying levels of injury from the gear.

Fisheries bycatch represents one of the greatest anthropogenic stressors on marine ecosystems (Dunn et al., 2011). In 2012, U.S. commercial fisheries caught 9.6 billion pounds of seafood (NMFS, 2012). Davis (2002) estimated that one quarter of all fisheries catch worldwide is bycatch. Sharks, seabirds, and turtles are the animals most often caught unintentionally on longlines (Tokai et al. 2008; Wallace et al. 2013). All are migratory megafauna with life history characteristics that make them particularly vulnerable to relatively recent high mortality. Their life history is characterized by delayed maturity and reproduction and low fecundity. Late maturity makes populations especially vulnerable to bycatch because they are immature for a long period of time and so are vulnerable to threats for a long time before having the opportunity to reproduce. Populations are more likely to decline when there are severe losses to juveniles close to and adults of reproductive age (Lewison and Crowder, 2007). As a consequence, detection of bycatch impacts often are delayed and recovery of the population from losses of these stages is often slow (Kaplan, 2005; Lewison and Crowder, 2007; Lewison et al., 2004; Peckham et al., 2007).

Reducing sea turtle bycatch is challenging. Several advances have been made (Alessandro and Antonello, 2009; Gilman et al., 2006; Santos et al., 2012; Shiode et al., 2005; Stokes et al., 2012; Watson et al., 2005) yet additional study is needed to better focus bycatch reduction techniques and enhance understanding of how and why sea turtles are caught. Loggerhead (*Caretta caretta*) and leatherback (*Dermochelys. coriacea*) sea turtles are the species most often caught on longlines (Foster et al., 2012; Lewison et al., 2004; Wang et al., 2007). Published estimates of sea turtle bycatch identified that the U.S. pelagic longline fishing fleets posed a serious threat to loggerhead and leatherback sea turtles (Garrison, 2005). Sea turtles often become entangled in the gear, getting hooked externally (foul hooked) or swallowing the hook (Foster et al., 2012). Mortality from longline bycatch is clearly implicated in the declines of these species in the Atlantic and Pacific Oceans (Lewison and Crowder, 2007; Piovano et al., 2010; Spotila et al., 2000; Wallace et al., 2013).

Sea Turtle Bycatch

Bycatch rates vary widely based on the geographic area where fishing occurs, the type of gear used, and the movement of the turtles in the area. The top three regions for sea turtle bycatch are the Mediterranean Sea, the northwest Atlantic, and the eastern Pacific Ocean (Lewison and Crowder 2007; Wallace et al. 2010). From 1990-2008, there were a reported 6,719 sea turtle interactions with U.S. fisheries in the northwest Atlantic and a reported 2,040 interactions in the eastern Pacific. These interactions ranged from the animals being caught and released to a mortality event (Wallace et al., 2010). Garrison and Stokes (2012) reported an estimated 437.6 loggerhead and 238.5

leatherback interactions in 2011 by the U.S. Atlantic fleet alone. The U.S. Atlantic fleet is only small percentage of the longline fishing effort worldwide where these sea turtle species occur. Of greater concern is that these bycatch numbers are from reported fisheries alone; the actual bycatch numbers are likely much higher due to numerous non-reporting fisheries. Mortality estimates from longline interactions are estimated to range from 17-42% for loggerheads and 8-27% for leatherbacks (Lewison et al., 2004; Swimmer et al., 2013).

Most loggerheads caught as bycatch tend to be hooked in the mouth or internally in the throat or gut (Gilman et al., 2006). In contrast, most leatherbacks captured as bycatch are foul-hooked, or entangled in the gear (Wang et al. 2007; Epperly et al. 2012). Soak times for longline sets can be up to 7 h (Ward and Myers, 2007), however, loggerheads are often hooked within the first 25-40 min of a soak time (Grace et al., 2010). Leatherbacks are most often captured at night (Watson et al., 2004) while loggerheads are most often captured during the day (Ferraroli et al., 2004; Ferreira et al., 2010; Watson et al., 2005). Both species may be attracted to the area of the longline due to visual and chemical stimuli from the baits, gear, or a combination of those factors (Salmon et al., 2008). It is not understood why leatherbacks are generally foul-hooked (Gilman et al., 2006; Salmon et al., 2008).

Worldwide efforts have been made to reduce sea turtle bycatch by fisheries. These include changing the bait types to decrease their appeal to sea turtles. Several studies found that the bycatch of sea turtles decreased significantly with the use of fish bait rather than squid (Foster et al., 2012; Santos et al., 2012). Altering the type of hook used is another mitigation technique. Historically, J-hooks have been used in longline fisheries, though many fisheries globally, and most in the U.S, have switched to circle hooks (Polovina et al., 2003). Circle hooks differ from J-hooks in that the point of the circle hook is angled toward the shaft (Fig 1) while the J-hook point if parallel to the shaft. Circle hooks make it more difficult for sea turtles or other typical bycatch species to be hooked (Cambiè et al., 2012; Santos et al., 2012b; Witzell, 1999). By switching to J-hooks baited with mackerel, leatherback bycatch was reduced by 66% and similarly, by switching to circle hooks baited with mackerel leatherback bycatch was reduced by 65%. Circle hooks with squid bait reduced leatherback turtle catch somewhat less (57%) (Watson et al., 2005). Interestingly, leatherback mouth hookings increased by ~20% when baits were rigged with circle hooks (Epperly et al., 2012). Foul-hookings were still the most common bycatch interaction for leatherbacks with either hook type (Foster et al., 2012; Stokes et al., 2012). Bycatch remains a significant source of interaction for loggerheads and leatherbacks, in spite of the reported reductions by compliant fleets (Wallace et al., 2013).

Time-area-closures are another method that has been attempted to reduce sea turtle bycatch (Gilman et al., 2006). Time-area-closures refers to areas in the ocean that are closed off to industrial fishing during certain periods of time when sea turtle abundance is known to be high, when a large amount of prey is present, water temperatures are favorable to sea turtles, or in areas of upwelling (Curtis and Hicks, 2000). Even with these mitigation techniques in place, sea turtle bycatch poses a high risk to the stability of the species (Wallace et al., 2010). Among the challenges that inhibit novel solutions are our understanding of the factors that attract turtles to an area to be fished and species-specific details of turtle feeding behavior that predispose them to accidental capture. It is unclear if the turtles opportunistically encounter the longlines because they are attracted to warm generally productive waters or if they are attracted to the odors from the baited lines.

Olfaction and Taste in Sea Turtles

Sea turtles are capable of discriminating between different odors and are known to have well developed chemoreceptive senses (Swimmer and Brill, 2006; Endres et al., 2009). Walker (1959) described submerged loggerhead sea turtles with open nostril as they slowly opened and closed their mouths while underwater. He hypothesized that this behavior aided in olfaction by sending water through the nostrils (Walker, 1959). A sea turtle's nasal cavity opens to the environment via the nares; the nasal cavity connects with the mouth via choanae in the primary palate (*Dermochelys coriacea*) or at the posteromedial margin of the partial secondary palate (cheloniids). Water or air enters the nose through nares. The nasal cavity has an olfactory region (Bartol, Soraya Moein and Musick, 2003; Parsons, 1959, 1967).

Several studies explored the behavioral responses of sea turtles to potential food odors or tastes. Constantino and Salmon (2003) investigated juvenile leatherback responses to both visual and chemical stimuli. They found that in the presence of a visual stimulus, either alone or in concert with a chemical stimulus, leatherbacks significantly increased diving activity. In the presence of a visual and chemical stimulus presented individually leatherbacks increased biting frequency but when visual and chemical stimuli were presented simultaneously, the leatherbacks did not differ in biting frequency.

Swimmer et al. (2005) investigated the effectiveness of dying squid baits to reduce sea turtle bycatch. They dyed squid bait a blue-red color and presented captive loggerhead and Kemp's ridley sea turtles with both dyed and natural baits. The turtles almost always preferred to bite the unaltered bait. However, field studies showed that dying bait was not an effective means of reducing sea turtle bycatch (Swimmer et al. 2005).

Endres et al. (2009) found loggerhead sea turtles can detect both air and waterborne chemical stimuli from food odor. Piovano et al. (2012) investigated the responses of large juvenile and adult loggerheads to two longline baits, mackerel (*Scomber scomber)* and squid (*Ilex argentines*) presented in colored cloth bags to determine if loggerheads were attracted to the baits even when shape was uniform. They found that squid bait elicited more biting behavior than did mackerel and that younger loggerheads were more likely to bite at the bags than older turtles.

The goals of my studies were to investigate (i) whether loggerhead and leatherback sea turtles are attracted to longline bait odors, (ii) if the odor alone released feeding behavior, (iii) responses to the different odors, and to (iv) determine if feeding behavior traits can explain the species-specific nature of bycatch. Based upon the Constantino and Salmon (2003) study, I hypothesized that the turtles would increase flipper stroke rate, biting and diving frequency if the bait odors are releasers for feeding behavior. I hypothesized that loggerheads would have greater accuracy when biting a target than leatherbacks.

Questions

1. Do loggerhead and leatherback sea turtles show attraction to longline bait odors?
2. Do longline bait odors release feeding behavior in loggerhead and leatherback sea turtles?
3. Do the two sea turtle species respond similarly to different longline bait odors?
4. How do the two species differ in the ways they approach synthetic "food-like" targets?
5. Do the two species differ in their responses to moving or stationary target in the presence of bait or food odors?

MATERIALS AND METHODS

Collection and maintenance

Hatchling loggerhead and leatherback turtles were collected upon emergence from Boca Raton, Juno Beach, Hillsboro and, Boynton Beach, Florida and transported in a covered Styrofoam™ cooler with damp sand at the bottom to Florida Atlantic University's Marine Lab at Gumbo Limbo Environmental Complex. Ten loggerheads and 5 leatherbacks that were morphologically normal from were selected from each clutch (~10% of the clutch). Each turtle was measured weekly; straight carapace length and width (SCL and SCW) to the nearest 0.1mm with vernier calipers, and weighed to the nearest 0.1g using an electronic scale. The turtles were monitored daily to ensure that they were swimming and feeding normally. Normal feeding behavior in hatchling loggerhead sea turtles involves the animals actively searching for food at the surface or on the bottom of their holding tank, diving towards the food and snapping at food or bubbles (at the surface). Hatchling leatherbacks pause briefly in their swimming when they detect food, orient towards the food and bite at it.

All turtles went through a 5-10 day quarantine process before entering the colony to ensure that they were healthy. Any signs of sluggish swimming or diving behavior or failure to feed designated the animals as abnormal and precluded them from this study. Only when the turtles passed quarantine and were feeding normally were used in this study.

Loggerheads were kept in tanks with open flow through seawater at 25-29°C and were kept in tanks that hold 9-30 turtles. Loggerheads were held individually in flow-through baskets (19.5cm x 12.7cm x 12.7cm). Loggerheads received weekly tank cleaning and disinfection.

Leatherbacks were housed individually in tanks filled with filtered seawater, maintained at 23-25°C. Because leatherbacks do not recognize barriers such as tank walls, a 1.0cm^2 Velcro^{TM} patch was attached to their carapace with a drop of cosmetic grade cyanoacrylate cement. The patch served as the attachment site for a monofilament tether that was approximately 16-20 cm in length. The tethers allowed the turtles to swim and dive in any direction but prevent abrasions from repeated contact with sides or bottom of the tank.

Both species were kept on a 12h:12h light:dark light cycle with light supplied by overhead UVA/UVB fluorescent "reptile lights" located 0.5m above the water.

Test Odor Preparation

In order to infer if loggerheads and leatherbacks are attracted to logline bait odors I created odor solutions and tested turtle responses to odors solutions using the same protocols as Constantino and Salmon (2003). Chemical stimuli for these trials were made from baits commonly used for pelagic longline fishing: squid (*Illex illecebrosus*), mackerel (*Scomber scombrus*), and sardines (*Sardinia aurita*). The baits were bought frozen from commercial bait suppliers. The fish and squid bait were the same species are used commonly in longline fisheries. Baits were kept frozen and separated into smaller amounts that were appropriate for each experiment. Chemical stimuli, (odor solutions), were prepared by soaking 120g of thawed bait in 1L of filtered seawater Initially baits were soaked in seawater for 1h or 7h to create 360 g*min/L and 50,400g*min/L solutions. Lion's mane jellyfish (*Cyanea capillata*) was also prepared by homogenizing the jellyfish in a blender to compare the turtles' behavior in the presence of a natural prey item to that of the bait odors. The odor solutions and homogenized jellyfish were stored and frozen in 20 cc aliquots; an aliquot was thawed for each trial to water temperature.

Behavioral Measurements

To identify if a bait odor was attractive to sea turtles and if any was more attractive than the other, the responses of each turtle was measured in a standardized test tank (after Constantino and Salmon 2003). Turtles were removed from their normal holding tanks and placed in a test tank. The test tanks were round plastic pools (150 cm diameter x 28 cm deep) that were externally marked to divide the tanks into quarters (after Constantino and Salmon 2003) (Fig. 2). An aquarium filter (Skilter™ Power Filters, Model 250) without filter material was used to introduce control and water-borne odor stimuli into the test tank via the outflow. To ensure that the odor plumes reached the turtles, the odor plume was mapped prior to testing using food coloring.

Turtles were allowed to acclimate to the test tank for 30 min before trials began. Loggerheads were fitted with a small nylon-lycra harness with a thin 130-140 cm long monofilament tethered that was anchored to the center of the tank above the water; leatherbacks were kept on their tether which was anchored to the center tank support (Fig. 2). Each experiment began with a 10 min control during which 20cc of seawater, with no odor stimulus, was introduced into the filter. The responses of the turtles:

snapping, stroke rate and diving behavior were recorded. Immediately following the control period, 20cc of odor solution was introduced into the filter. The odor used was determined randomly using a random numbers table. Pools were cleaned in-between trials with freshwater and 0.12% chlorohexidine solution to remove any remaining odor after each trial and to disinfect the test pool and then rinsed with fresh water.

Each animal's reaction to the stimulus (diving, change in stroke rate, or snapping) was recorded by direct observation and by a Sony HDR-DX 160 Handycam^{TM} (60 fps). Diving and snapping counts were recorded during both control and experimental periods. Stroke rate was measured as the number of fore flippers strokes/min and was measured during minutes 1, 5 and 10 for both control and experimental periods.

Each turtle was tested just once. A single odor was presented to each of 63 leatherbacks and 60 loggerheads of 2-3 weeks of age. Twenty leatherbacks were tested with squid odor, 20 were tested with sardine odor, and 23 were tested with mackerel odor. Twenty loggerheads were tested with each bait odor for a total of 60. Ten loggerheads and 10 leatherbacks were tested with lion's mane jellyfish as a control to observe normal response to a natural prey odor.

Bait Odor Trial Data Analyses

The total numbers of snaps and dives per turtle were compared between the control and experimental periods. Stroke rate was analyzed by comparing strokes per min during the last min of the control period to those during the first min of the experimental period. I focused on this particular period because the stroke rate remained the same during the control period and changed briefly during the first minute of the experimental period after the odor was introduced. Soon after the introduction of the odor, stroke rate returned to its normal baseline rate. Each turtle served as its own control so turtles that received the same treatment were analyzed using Wilcoxon Signed Rank Tests. In order to compare the responses between species a Mann Whitney U was used (Zar, 1998). P values of ≤ 0.05 were considered significant. All tests were performed using Minitab 16 (Minitab, Inc).

Bite Accuracy Trials by Species

To determine how the species differed in their prey attack behavior and accuracy, I conducted "visual approach trials" in which turtle behavior in the presence of a synthetic "food" model was measured. Trials were conducted in a rectangular (85cm x 60cm x 57 cm) tank (Fig. 3) filled with 222 L of filtered seawater. A mirror measuring 63.5 x 76 cm was placed at a 45° in the tank to allow concurrent observation of the lateral and ventral views of the animal. Loggerheads were harnessed and leatherbacks were tethered similarly to the odor trials except the tether was 20(± 2) cm in length. Turtles were tested individually. Each turtle was given a 30 min acclimation period then 20 cc of filtered seawater or the bait odor stimulus was added to the water surface and a standardized visual stimulus was immediately lowered into the water (Fig 4). The visual stimulus represented an odor-free "simulated prey item" for the turtle. A small and a large stimulus were tested. A lead fishing weight (#3 "split-shot" lead weight, 1cm diameter) was used as the small visual stimulus. Loggerheads responded to this stimulus but no leatherback responded to the lead weight; consequently the small stimulus was presented to loggerheads alone. A plastic jellyfish (11cm in diameter, 12cm in maximum length, 22cc vol.) served as a large visual stimulus (previous studies showed that leatherbacks responded to the plastic jellyfish (Constantino and Salmon, 2003).

For both loggerhead and leatherback turtles, bite performance was measured in several ways: (i) total bites during control or experimental period (defined as Total Bite Performance), (ii) total bites at the visual stimulus, (iii) total successful bites (a bite in which the turtle's mouth made contact with the target), and (iv) initial bite success. Additionally, I quantified if the bite response that was elicited by a stationary or moving visual stimulus. For loggerheads, I compared if the turtles differed in their responses to the two stimuli.

Between trials, the test tank was drained and cleaned with fresh water and VedCo™ D-256 disinfectant solution and rinsed with freshwater before refilling the tank with filtered seawater.

Loggerhead Bite Accuracy Tests

The lead weight was affixed to a piece of 5.4kg strength (12lb test) monofilament line and lowered to approximately 5 cm below the water surface field of view of the turtle. The line suspending the stimulus was held taut with a 170g weight to keep the stimulus steady in the water. A trial began when 20cc of filtered seawater (control) or 20cc of squid odor (test solution), prepared according to the methods above, was introduced into the test tank from above via 20cc syringe. A subset of turtles was tested with a seawater control then with the test odor. Because the control consistently resulted in lack of response, it was discontinued after. Ten loggerheads were tested with a control and squid odor solution; 13 were tested with squid odor alone. If a turtle received the control treatment, they were also tested with squid odor. The seawater control was always introduced before the test odor. After introduction of the control or test solution, the visual target was lowered into the test tank. Behavior was recorded for 1 min once the turtle bit at the visual stimulus or 3 min if the turtle did not bite at the stimulus during the first min. If the odor treatment was delivered after the control odor, the target was lifted out of the water, squid odor was introduced into the tank, and then the visual target was then lowered back into the tank.

All animals were tested with a stationary and moving visual stimulus to ascertain if a moving target changed the turtle's responses. A moving stimulus was created by slowly jiggling the line that the stimulus was attached to in order to make it sway a few cm in the water.

The plastic jellyfish model (Fig. 4) was used as a visual target for 10 loggerheads using a seawater control and squid odor. The jellyfish model was attached to the middle of a tether, 20 cm in length, and was weighed down with a sinker weight. The upper surface of the jellyfish model was approximately 3 cm below the water surface. The odors were delivered in the same manner as trials performed with the lead weight target. A trial was concluded once the animal made an attempt to bite the visual target. If the turtle did not try to bite at the visual target, trials were concluded after 3 min.

Leatherback Bite Accuracy Tests

The visual target for leatherbacks was a plastic jellyfish model. Homogenized lion's mane jellyfish was used as the odor stimulus to elicit feeding behavior in leatherbacks (after Constantino and Salmon 2003). A trial began when 20cc of filtered seawater or 20cc of thawed homogenized lion's mane jellyfish odor was introduced into the test tank. If a turtle received the control treatment, they were also tested with lion's mane odor. The control was always introduced before the odor. After introduction of the control or odor, the visual target was lowered into the test tank. Behavior was recorded for 1 min once the turtle bit at the visual stimulus or for 3 min if the turtle did not bite at the stimulus. The treatments were delivered in the same method as for loggerheads. All animals were tested with a stationary and moving visual stimulus to ascertain if there was a preference for one over the other. Thirteen leatherbacks were tested with a sea water control and jellyfish odor, and 10 with lion's mane jellyfish odor alone.

Statistical Analyses

All variables (total bite performance, total bites at the visual target, total successful bites, initial bite success, and bite response to moving vs. stationary targets) were compared between control and experimental periods using Wilcoxon Signed Rank tests (Zar, 1998). Stroke rate changes and bites/test period were compared between loggerheads and leatherbacks using a Mann Whitney U. P values of ≤ 0.05 were considered significant. All analyses were performed using Minitab 16 statistical software.

RESULTS

Odor Trials

Differences in counts of each behavior were compared between the last min of the control period and the first min of the experimental periods. Table 1 summarizes those results. When stroke rate decreased, stroke amplitude also appeared to decrease however the amplitude could not be measured and so it simply noted here.

Leatherbacks

In the presence of squid odor, leatherbacks increased snapping significantly, diving did not change, and they significantly decreased stroke rate (Fig 5) during the first min of the experimental period. With sardine odor, neither snapping nor stroke rate (Fig. 6) changed but diving increased significantly. When mackerel odor was tested, snapping increased significantly but diving and stroke rate (Fig.7) did not change. In the presence of lion's mane jellyfish odor, snapping increased; the number of dives and stroke rate (Fig. 8) did not change.

Loggerheads

When loggerheads were given squid odor, snapping and diving increased, while stroke rate decreased significantly (Fig. 9). With sardine odor, loggerheads snapping increased, diving did not change, and stroke rate decreased (Fig. 10). In the presence of mackerel odor, there was no change in snapping and diving, however stroke rate decreased significantly (Fig 11). In the presence of lion's mane jellyfish, snapping and diving increased significantly while the stroke rate decreased (Fig 12).

Comparisons of Species

When comparing the responses of leatherbacks and loggerheads with squid odor, loggerheads showed a greater increase in snapping ($U=308.5$, $p<0.05$) and diving ($U=293.0$. $p<0.05$), and decreased stroke rate more ($U=495.5$, $p= 0.02$) than leatherbacks. In the presence of sardine odor, loggerheads showed a greater increase in snapping ($U=276.5$, $p<0.05$) and decreased stroke rate more ($U=548.5$, $p<0.05$) than leatherbacks. Both loggerheads and leatherbacks increased diving in the presence of sardine odor but did not difference significantly ($U=447.5$, $p=0.27$). With mackerel odor, there was significant difference in diving ($U=501.0$, $p=0.91$) or snapping ($U=508.5$, $p=0.96$) between the species. Loggerheads slowed their stroke rate more than leatherbacks ($U=687.5$, $p<0.05$). In the presence of lion's mane jellyfish odor, the number of snaps ($U=46.0$, $p=0.39$) and change in stroke rate ($U=70.0$, $p=0.07$) did not differ significantly but the number of dives ($U=28.5$, $p=0.05$) differed in that loggerheads dove more than leatherbacks.

Bite Accuracy Trials

During the control periods, the turtles seldom showed any response to the visual target; just one leatherback and one loggerhead bit at the lead weight while two loggerheads bit at the jellyfish model. Consequently, only experimental period results were informative in assessing target approach behavior and bite accuracy of the turtles. Table 2 summarizes the results of these trials. Both species bit the jellyfish model (large target), however neither species enthusiastically attached. Just 6 of 10 loggerheads bit and they approached somewhat tentatively and mostly bit the tentacles (37 bites, mode=5, 2-15). Twelve of 27 leatherbacks bit the model, however they mostly bit the bell portion (147 bites, mode=7, 1-31). When presented with the small target, no leatherback showed any interest and none bit it. In contrast loggerheads enthusiastically bit at the small target, 17 of 23 turtles (199 bites, mode=5, 3-20).

Total bite performance differed between species. Loggerheads bit more often during the experimental period (Fig. 13). Loggerheads showed no preference for biting small vs. large targets (Table 2). There was no difference between total bite performance for loggerheads and leatherbacks tested with the plastic jellyfish (Table 2). Leatherbacks were not tested with the small target.

In terms of bites directed at the target, loggerheads did not differ in how many times they bit at lead weight and the plastic jellyfish (Table 2). Loggerheads bit at the small target significantly more often than leatherbacks bit at the jellyfish target (Fig. 13). Loggerheads and leatherbacks did not differ in the number of bites directed at plastic jellyfish stimulus (Table 2). Neither first bite success nor total bite success differed in any measure between species (Fig. 14, Fig. 15, Table 2).

When presented with a stationary vs. moving target, loggerheads showed no preference ($U=430$, $p=0.28$) (Fig. 16). Leatherbacks bit at stationary targets more often than moving ones ($U=252.5$, $p=0.05$). Loggerheads were more likely to bite at a moving target than leatherbacks ($U=456$, $p=0.005$).

DISCUSSION

Odors from longline baits elicited behavior associated with feeding-related behavior in both loggerhead and leatherback sea turtles. This is the first demonstration that bait odor alone can elicit behavior associated with feeding. While conducting this study, I identified previously undescribed species-specific feeding behavior. In both species, feeding behavior starts decrease in stroke rate was is an early or starting part searching behavior. When both species detected an odor, they reduced the amplitude of their flipper stroke and slowed swimming movements dramatically. The odor resulted in a change in swimming characteristics, hence my classification of it as part of searching. Constantino and Salmon (2006) described snapping and diving by leatherbacks as part of feeding behavior. I found that in both loggerheads and leatherbacks snapping often occurred next and was the strongest indication that an animal was attempting to eat. Diving was feeding-related behavior in both species. Most dives associated with odors were directed toward a target. Although the test pools were uniform blue in color, the surface was embossed with shapes. The turtles that dove and bit appeared to select an embossed area as their target. In the second series of experiments, that provided visual targets in conjunction with large and small targets the turtles tended to bite the target as well as unintended targets such as their reflections in the mirror or bubbles when bait or natural food odors were introduced. Dives were directed at the target in many cases however some dives were escape dives away from the target.

While all bait and prey odors produced responses in both loggerheads and leatherbacks, those responses differed in detail. Both species responded to squid odor by increasing snapping and slowing their swimming. Loggerheads diving more compared with the control period, Sardine odor was the only one in which the number of dives increased for most leatherbacks (three increased their diving behavior). Leatherback stroke rate slowed the most with squid odor. Mackerel odor resulted in the most snapping (18 turtles), followed by squid (9 turtles), and lion's mane jellyfish odors.

Loggerhead turtles showed greater change in most measures of feeding in response to the bait odors than leatherbacks. Squid produced the greatest increase in the diving followed by lion's mane (12 loggerheads with squid, 4 with lion's mane). Loggerhead stroke rate decreased with sardine (19 loggerheads), squid (17 loggerheads), mackerel (17 loggerheads) and lion's mane (4 loggerheads). Squid odor resulted in the greatest increase in snapping (15 loggerheads) followed by lion's mane (7 loggerheads).

Both species of sea turtles showed greater change in behavior (snapping and diving for leatherbacks and all 3 recorded behavior for loggerheads) with squid than fish odors. This is consistent with the observation that sea turtles are hooked more often on longlines baited with squid (NMFS, 2011; Santos et al., 2012) than lines baited with fish. Foster et al., (2012) showed that the use of mackerel in conjugation with circle hooks reduced loggerhead bycatch by 87-88% and leatherback bycatch by 63-74%. Santos et al. (2012) also found reduced loggerhead sea turtle bycatch with the use of mackerel bait. Loggerhead sea turtle bycatch was reduced more than leatherback bycatch. In my study, leatherbacks were more likely to snap in the presence of mackerel odor than loggerheads. The reduction in sea turtle bycatch with fish baits correlates with the results of this study.

Both species showed attraction to one or a few odors from commonly used longline baits when presented alone. The reason that the turtles are hooked on longlines likely reflects other factors in addition to odor attraction. The two species have very disparate diets (Bolten, 2003) and might not be found in the same parts of the water column under normal circumstances (Bailey et al., 2012; Stewart et al., 2013; Vander Zanden et al., 2014). Longline fishing often takes place in areas of high productivity (Dunn et al., 2011; Wallace et al., 2010) where many fish species are present. Highly productive areas can coincide with areas of upwelling, or convergence zones that result in nutrient rich waters, which attract many types of marine fauna (Olson et al., 1994). Fishers tend to use these naturally productive regions to increase their chances of catching their intended targets. Areas of high productivity are also used by loggerhead and leatherback sea turtles (Polovina et al. 2001, Polovina 2006, Kobayashi et al. 2008) and so may place them in the same areas as longline deployments. Additionally abundance of chemical stimuli from baits may attract the turtles to areas of active fishing. As suggested by these observations, turtles may bite at the longline baits instinctively because they present a suspended visual target in the water.

The habitat of juvenile leatherbacks is largely unknown; incidental captures and strandings indicate that they have a pelagic lifestyle (Eckert 2002; Jones et al., 2012). Juvenile leatherbacks may be found in both convergence zones and areas of upwelling where there is an abundance of jellyfish and other potential prey items (Olson et al., 1994). Interestingly, this study shows that leatherbacks increase feeding-related behavior when odors from longline baits are present. My observations demonstrate that the leatherback may not forage exclusively on gelatinous prey as has been previously thought (Constantino and Salmon, 2003; Heaslip et al., 2012; Houghton et al., 2006) when alternative prey are available and accessible.

There have been efforts to reduce sea turtle bycatch in fisheries worldwide (NMFS, 2011; Wallace et al. 2013). The most common method is to change the bait and hook type to decrease bycatch. Many fisheries have switched from J-hooks to circle hooks (Santos et al., 2012b). Circle hooks with no or minimal offset make it more difficult for sea turtles or other typical bycatch species to become hooked (Stokes et al. 2012; Cambiè et al., 2012; Santos et al., 2012; Witzell, 1999). By switching to J-hooks baited with mackerel, the proportion of leatherback bycatch was reduced (Foster et al., 2012). Circle hooks with squid bait also reduced the proportion of leatherbacks caught, but not as drastically as with fish bait (Watson et al., 2005). Interestingly, leatherback mouth hookings increased by ~20% when baits were rigged with circle hooks. Foul-hookings were still the most common for leatherbacks with either hook type (Epperly et al., 2012; Foster et al., 2012; Stokes et al., 2012). These results suggest that the increase in proportion of mouth hooking with circle hooks may be caused by the reduced propensity for a circle hook to snag. Based upon my observation that leatherbacks often miss smaller targets and have to make multiple approaches, I hypothesize that leatherbacks that with the hook barb contained within the bait the turtles were not becoming foul-hooked. Instead they could back up and reapproach the baited hook to successfully bite and ingest the bait, becoming hooked in the mouth

When the responses of two species to large and small targets, there were species-specific differences. Leatherbacks only bit the larger target, completely ignoring the small target. Further, they only bit the bell portion of the target and bit a few times. This behavior is consistent with feeding strategies for maximizing energy intake via high volumes of low calorie prey (Heaslip et al. 2012, (Fossette et al., 2012). This test was of just a single small target. The turtles behaved as if it wasn't there. Small prey items likely are not energetically "worth while" unless they are highly concentrated and abundant.

I found that loggerheads bit at both large and small visual targets. While they vigorously approached the small target with the mouth open, they slowly approached the large target, often while in a tucked position. This may have been due to the size of the plastic jellyfish in relation to the turtle. The jellyfish was almost the same size or larger than most of the loggerhead turtles tested. When they bit it, they ignored the bell and attached only the tentacles, effectively, dealing with a smaller target. In general, loggerheads tended to bit more different kinds of targets. After the introduction of a food odor into the tank, loggerheads would usually bite at the first object that moved; this was often their own reflection in the mirror present in the tank. However, if they did bite at the jellyfish they would bite at it more than leatherbacks did.

I expected loggerheads to be much more successful at biting at visual targets than leatherbacks but found that this was not the case. Both species successfully bit at the target approximately half of the time. While comparing success with two different kinds of targets is of somewhat limited value, the comparison allows some insights into accuracy or effectiveness in prehending the visual stimulus that is the "preferred target" type.

Since leatherbacks were so unsuccessful when eating in the lab I expected poor first bite success with the plastic jellyfish model. Instead I found they were at least as successful as loggerheads this may be due to the size of the plastic jellyfish. The jellyfish model was much larger and easier to see than the food that the animals are accustomed to and may offer an explanation for why they were more successful at biting it than their food. Interesting future directions may include testing leatherback response to a visual target smaller than the jellyfish model that still elicits feeding behavior to see if they are still as successful at biting the target.

During bite accuracy trials it was often necessary to move or jiggle the target to get the turtles' attention. I then tested if the turtles had a preference for a moving or stationary target. Loggerheads showed no preference for a moving target versus a stationary target, especially with the lead weight, because the size was comparable to their food. Their reaction to the plastic jellyfish was intriguing because most of the turtles assumed a defensive tuck position (Witherington, 2002) when the jellyfish was introduced into the tank. The loggerheads were less likely to bite at the plastic jellyfish than the small lead weight and only the turtles that did not assume a tucked position bit the jellyfish model. The turtles would sometimes bite at the target while still moving or wait for it to stop. Leatherbacks bit at a stationary target more often than a moving target. Typically, they would see the target move, watch until it stopped moving, and then approach it. The same was often true for loggerheads; they would notice the target while it was moving and then wait until it was stationary to bite. The fact that the target sometimes needed to move initially for the turtles to notice it and bite it is potentially significant. Perhaps once a prey odor is present, the prey needs to move in order for the turtles to locate it. This result may contribute to our understanding of why sea turtles get hooked on longlines. Baited hooks are almost always exposed to moving water while suspended in water columns and would thereby provide both odor cues and visually alert sea turtles to the target. Due to the abundance of odors present in the areas where longline fishing occurs this may elicit feeding behavior in the turtles.

Another factor to consider in this study is the age of the turtles tested. All turtles in this study were 2 weeks and 6 weeks of age. I noted change in their feeding ability in the first few weeks and therefore did not test turtles until they were at least 2 weeks old. When turtles first begin eating they will often crisscross their tank searching for the food and take some time to orient and dive towards it. By the age of 2 weeks the turtles are orienting and diving towards their food in a quick and concise manner that is considered to be normal feeding behavior. It is possible that repeating these observations with turtles that are older will refine or alter the results of this study, especially if turtles improve motor coordination with age. Maturation of motor skills is well documented in young passerine birds (Barraud, 1961) as well as shorebirds (Buckley and Buckley, 1974). Both of these studies showed that fledgling and juvenile birds spend more time searching for food and have to make more attempts at obtaining food than adults.

When a loggerhead detects an attractive odor, they will often pause briefly and look around, using their back flippers to orient. Once they find their intended target, they swim and dive towards it with power strokes. They will then open their mouth before reaching the target item with their foreflippers angled upwards. This angling of the flippers might be a characteristic that is more commonly observed in hatchling and neonate loggerhead sea turtles because they will be living in sargassum (Witherington et al., 2012) at this stage in their life and will be approaching their prey from above. Loggerheads often successfully bite food that is offered to them on the first bite. This behavior contrasts starkly with the feeding behavior of leatherbacks in our care. When leatherbacks encounter food odor, they will slow or stop their swimming behavior completely. They then look around their surroundings and orient using both their fore and back flippers, in the direction of the food odor. When they observe their intended target, they perform a distinctive wiggle where they move back and forth laterally using their foreflippers. They then swim towards their prey and open their mouth when they are almost on their target. However, unlike loggerheads, leatherbacks often miss their food while being fed and have to back up, using their foreflippers, and readjust their position before re-approaching the food. To do this they rotate their foreflippers so the blade leading edge is perpendicular to the water's surface is elevated and depressed to slowly themselves backwards. Due to the fragile nature of leatherbacks (Miller et al., 2009) and their inability to recognize barriers, they are tethered while in our laboratory and during these tests. It is possible that this behavior is an artifact of being tethered and might not be representative of how leatherbacks maneuver in the wild.

In summary, this study is the first to show that specific odors from longline fishing baits elicit feeding behavior by leatherback and loggerhead sea turtles are in the absence of visual cues. Further, the numbers of feeding-related responses to longline bait odors. Squid odor elicited to most feed-related behavior in both species while mackerel bait elicited the fewest. These results are consistent with fisheries bycatch data that find more sea turtles are caught with squid bait and fewer are caught on mackerel. The presentation of bait odor in combination with a visual target resulted in increased biting, strong evidence of motivation to feed, even on novel prey.

APPENDIX A: FIGURES

Figure 1. Shows the differences in J-hooks (pictured on the left of each box above) and offset circle hooks. Circle hooks differ from J-hooks in that the point of the hook is directed toward the shaft the offset increases target fish catch without increasing turtle bycatch (Stokes et al. 2012).

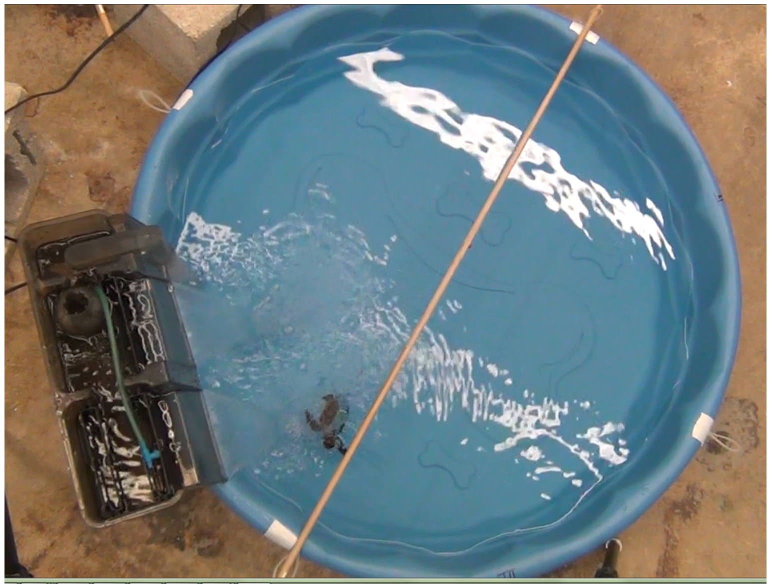

Figure 2. Test tank with quarters indicated by external white markings so that turtle location could to assigned during odor response trials. Turtles were on tethers attached to wooden dowels across the middle of the test tank. The filter was placed in a randomly selected quadrant of the tank. The filter did not alter the turtle's behavior.

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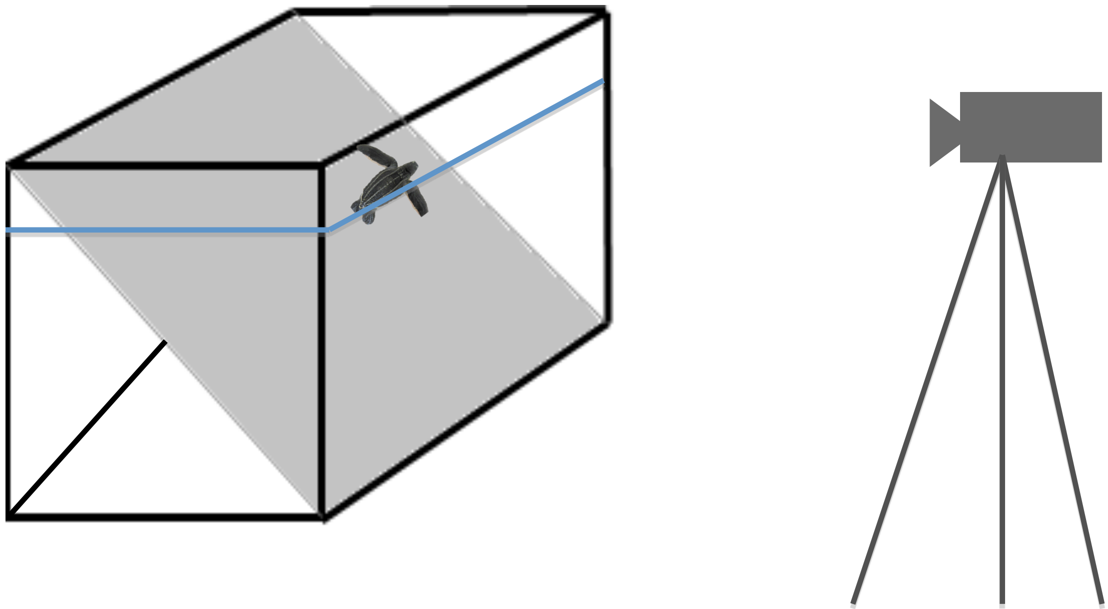

Figure 3. Test tank for visual approach trials with mirror (in grey) at a 45 angle in the tank. This allowed us to view the animals' ventral and lateral movements at the same time.

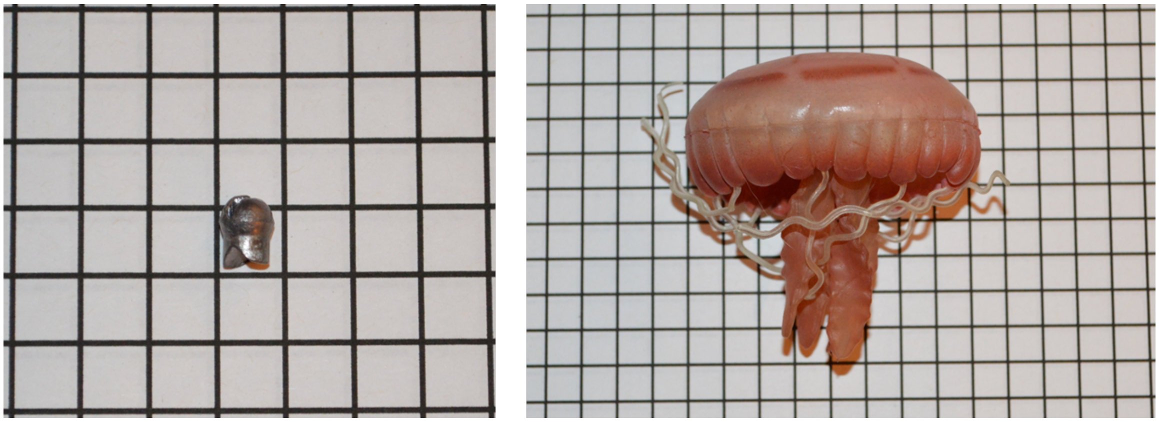

Figure 4. Lead weight visual stimulus (on left) and plastic jellyfish model used in visual approach trials. Photos show the visual stimuli against a 1cm x 1cm grid.

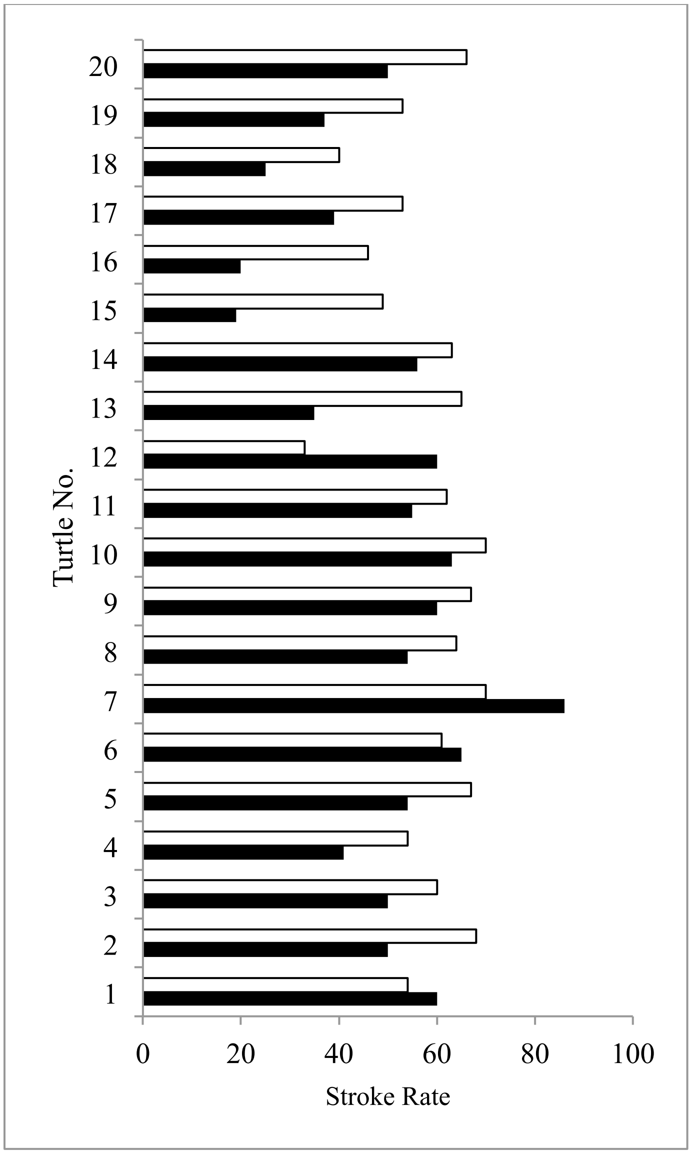

Figure 5. Comparisons of leatherback stroke rate with squid odor during the last min of the control period (open bars) to the first min of the experimental period (black bars). Stroke rate slowed significantly (see text) in 16 of 20 turtles after the odor was introduced.

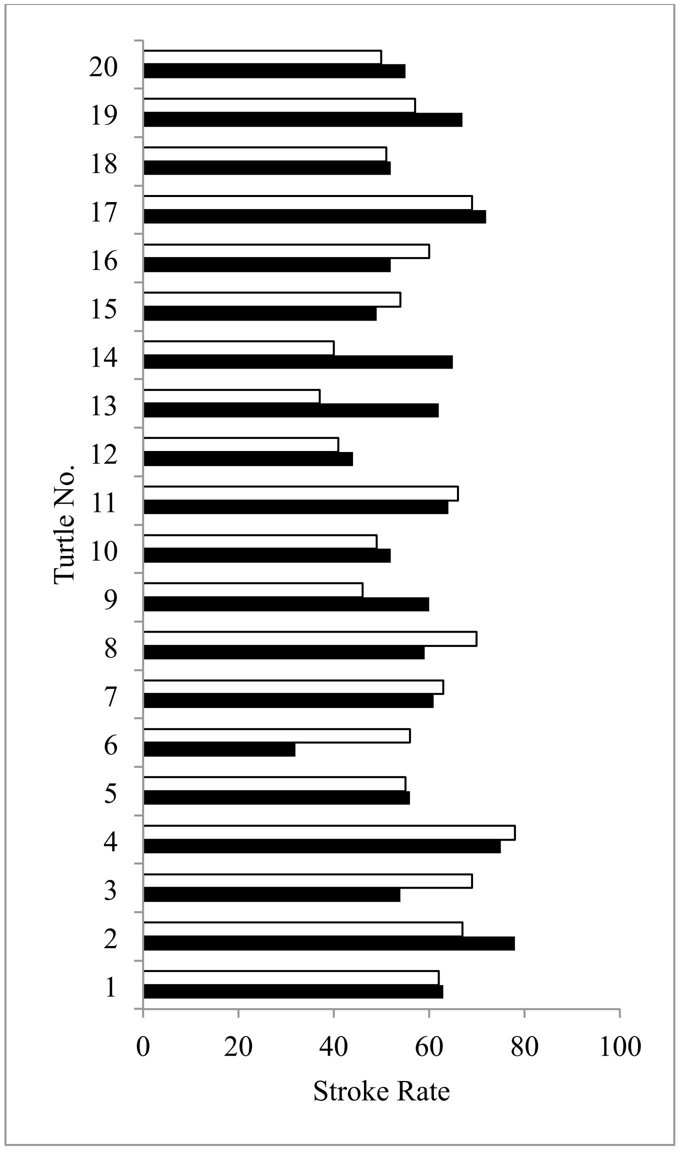

Figure 6. Comparisons of leatherback stroke rate with sardine odor during the last min of the control period (open bars) to the first min of the experimental period (black bars). Just 6 of 20 turtles decreased their stroke rate when the odor was introduced.

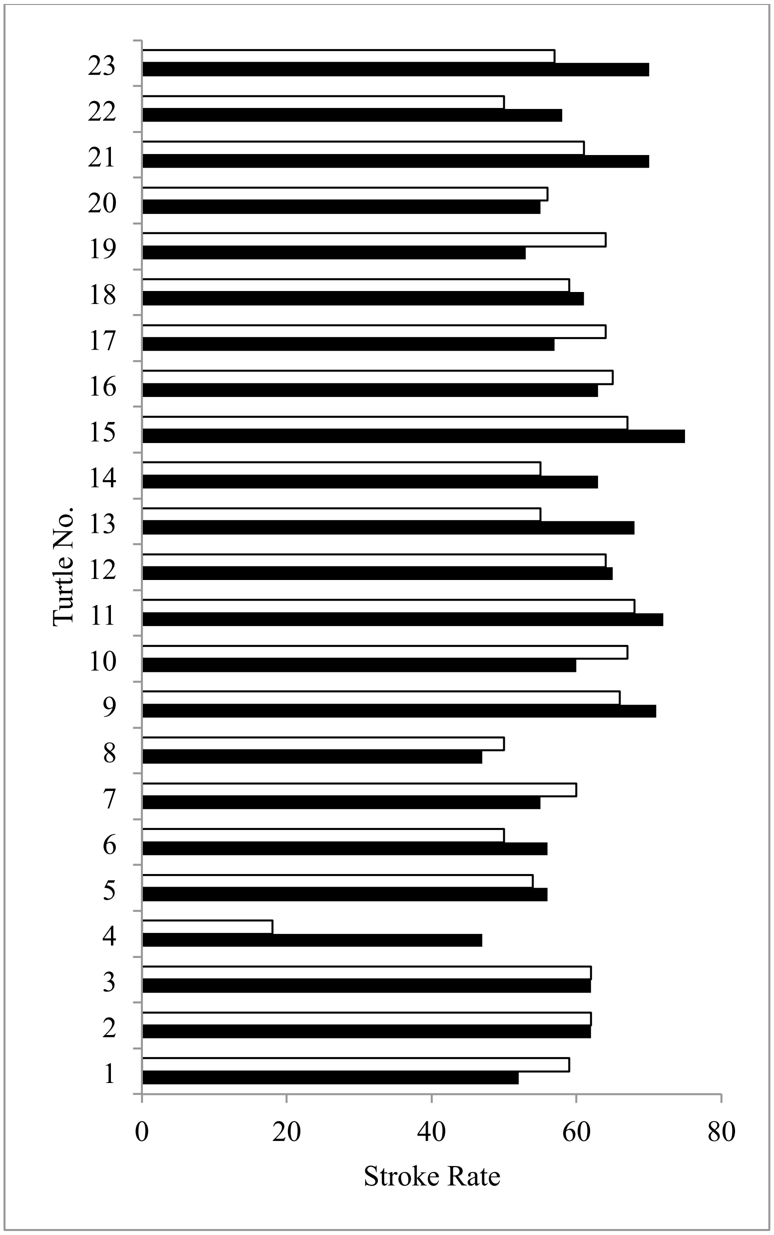

Figure 7. Comparisons of leatherback stroke rate with mackerel odor during the last min of the control period (open bars) to the first min of the experimental period (black bars). Stroke rate did not slow significantly (see text) after the odor was introduced; just 7 of 23 turtles decreased their stroke rate when the odor was introduced.

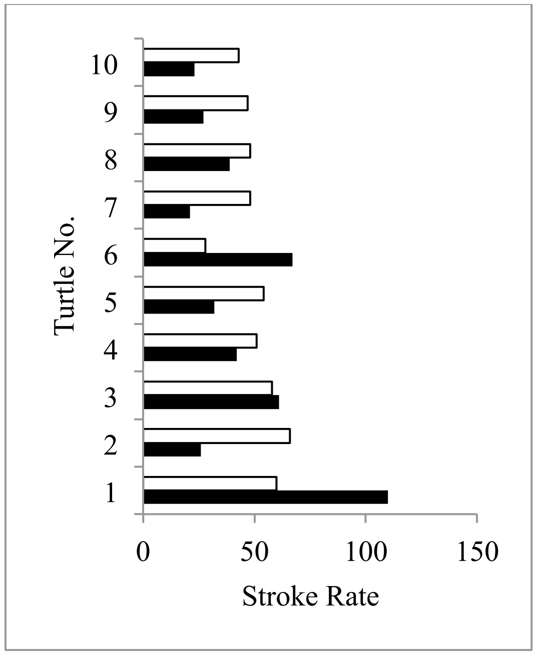

Figure 8. Comparisons of leatherback stroke rate with lion's mane jellyfish odor during the last min of the control period (open bars) to the first min of the experimental period (black bars). Stroke rate did not slow significantly (see text) after the odor was introduced 7 of 3 turtles slowed. 7 out of 10 turtles decreased their stroke rate when the odor was introduced.

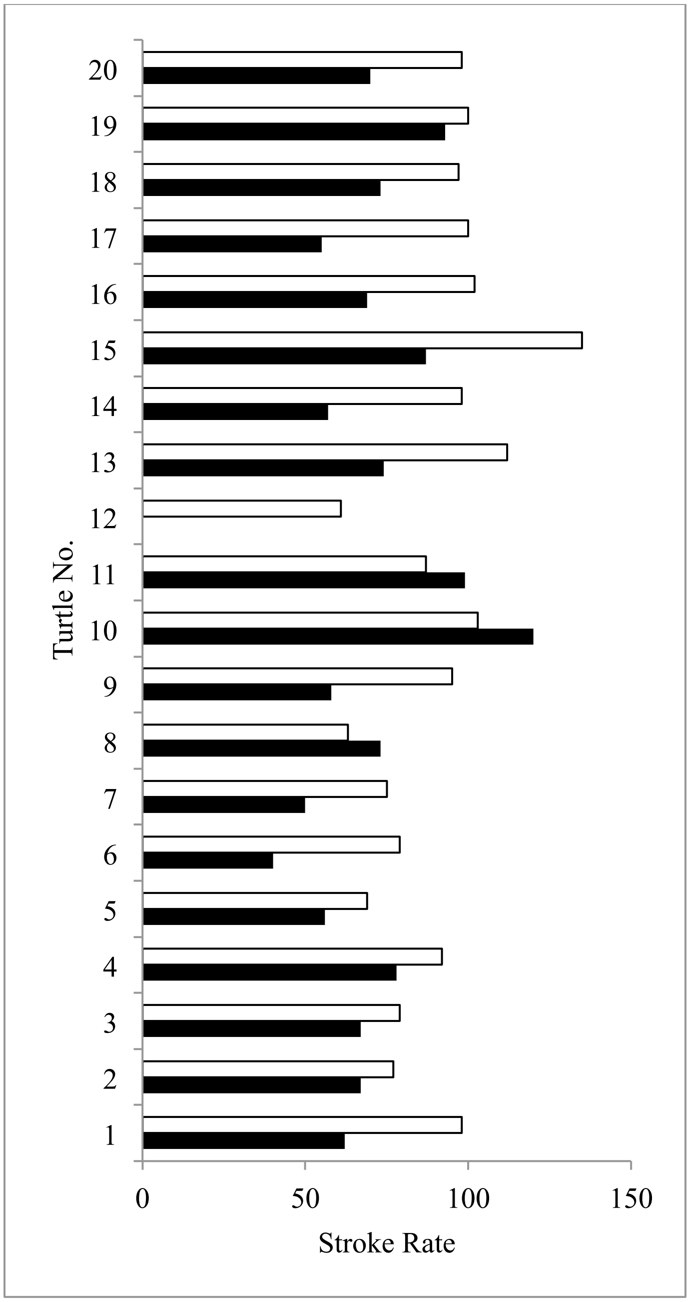

Figure 9. Comparisons of loggerhead stroke rate with squid odor during the last min of the control period (open bars) to the first min of the experimental period (black bars). Stroke rate slowed significantly;17 out of 20 turtles decreased their stroke rate when the odor was introduced.

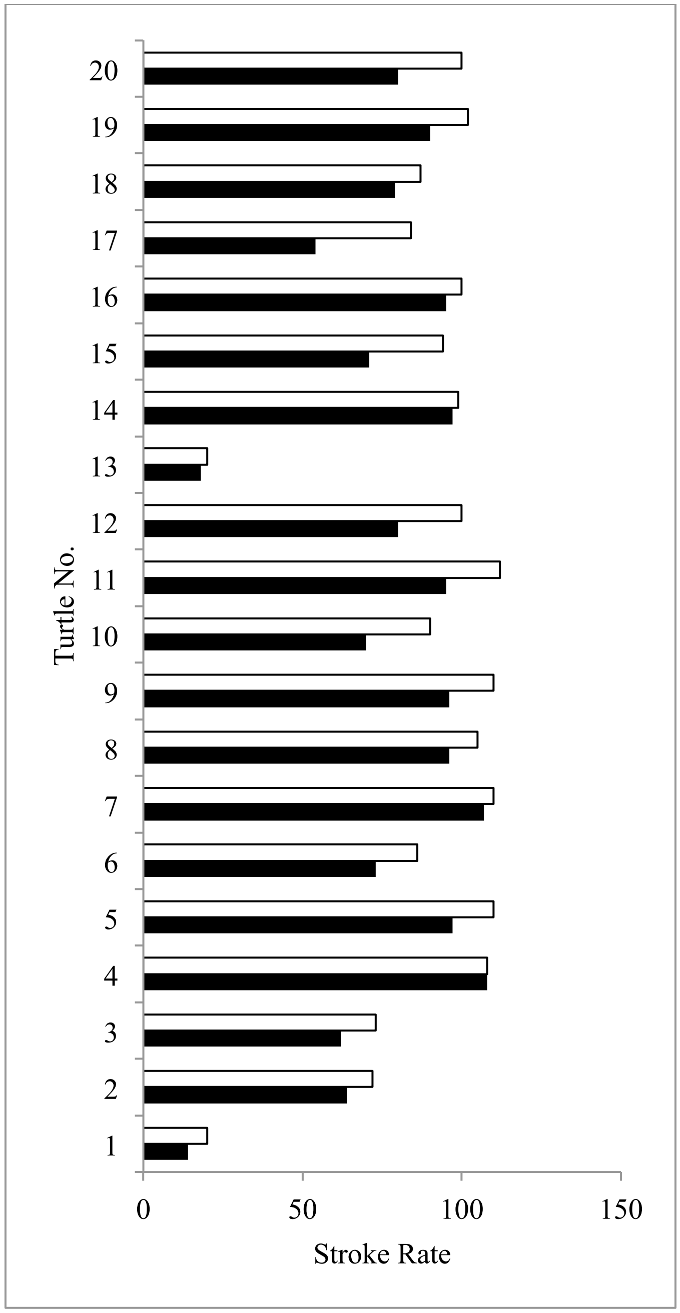

Figure 10. Comparisons of loggerhead stroke rate with sardine odor during the last min of the control period (open bars) to the first min of the experimental period (black bars). Stroke rate slowed significantly (see text) in 19 of 20 turtles after the odor was introduced. 20 out of 20 turtles decreased their stroke rate when the odor was introduced.

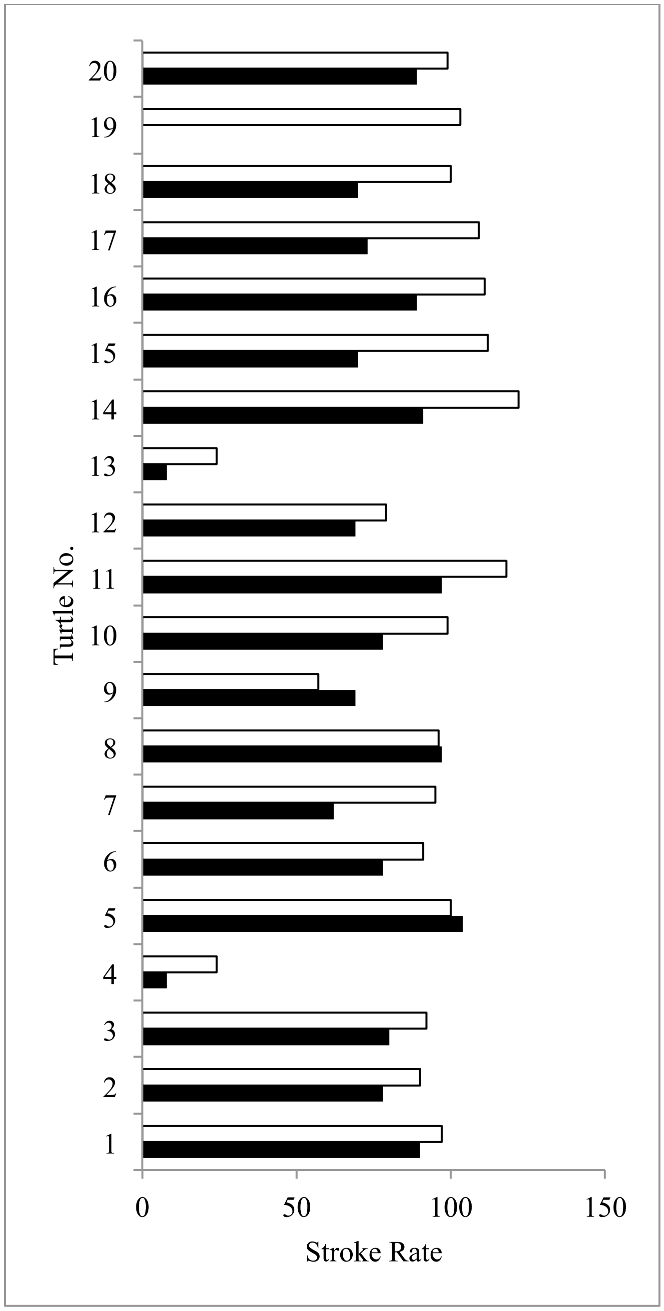

Figure 11. Comparisons of loggerhead stroke rate with mackerel odor during the last min of the control period (open bars) to the first min of the experimental period (black bars). Stroke rate slowed significantly (see text) in 17 of 20 turtles after the odor was introduced.

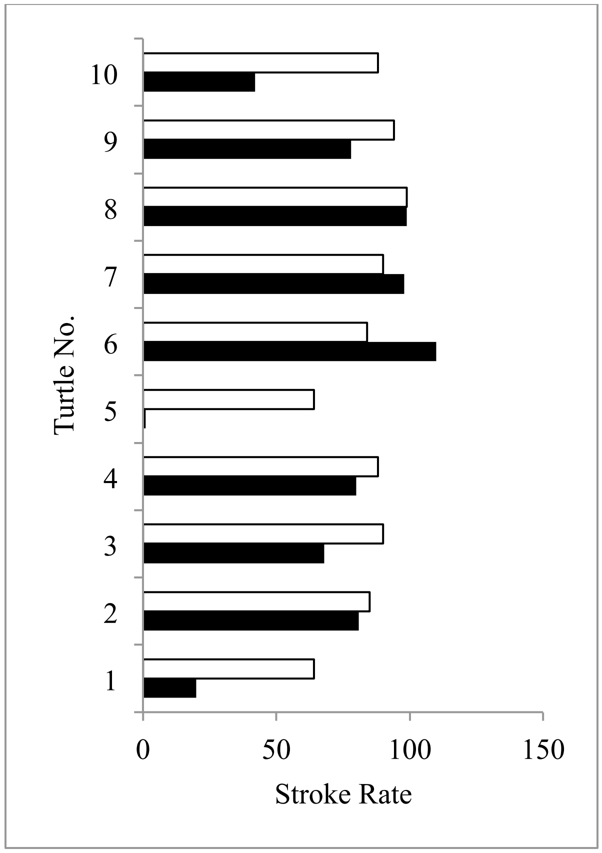

Figure 12. Comparisons of loggerhead stroke rate with sardine odor during the last min of the control period (open bars) to the first min of the experimental period (black bars). Stroke rate slowed significantly (see text) in 8 of 10 turtles after the odor was introduced.

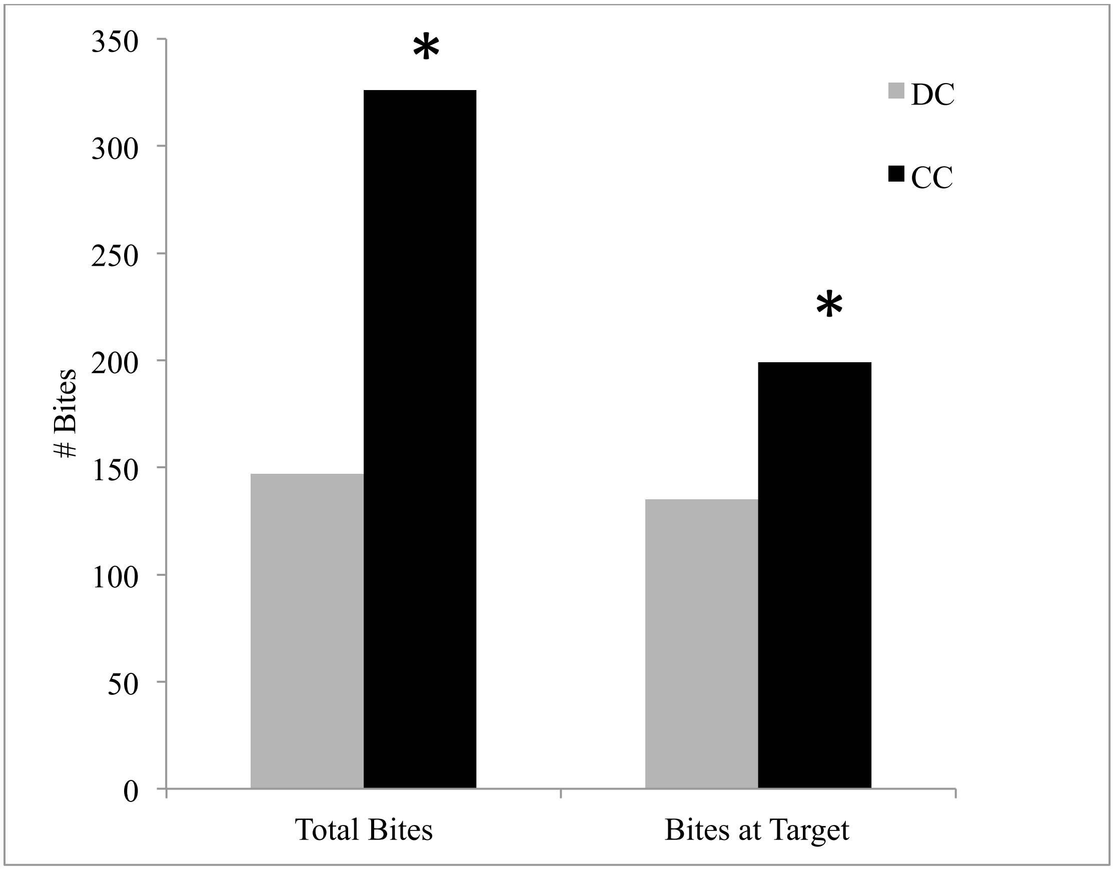

Figure 13. Comparisons of the total overall bites and number of bites at the target for loggerhead (grey bars) and leatherback sea turtles during bite accuracy trials. Loggerheads bit significantly more overall (p=0.02, U=430) and at their visual target (p=0.05, U=411.5) than leatherbacks.

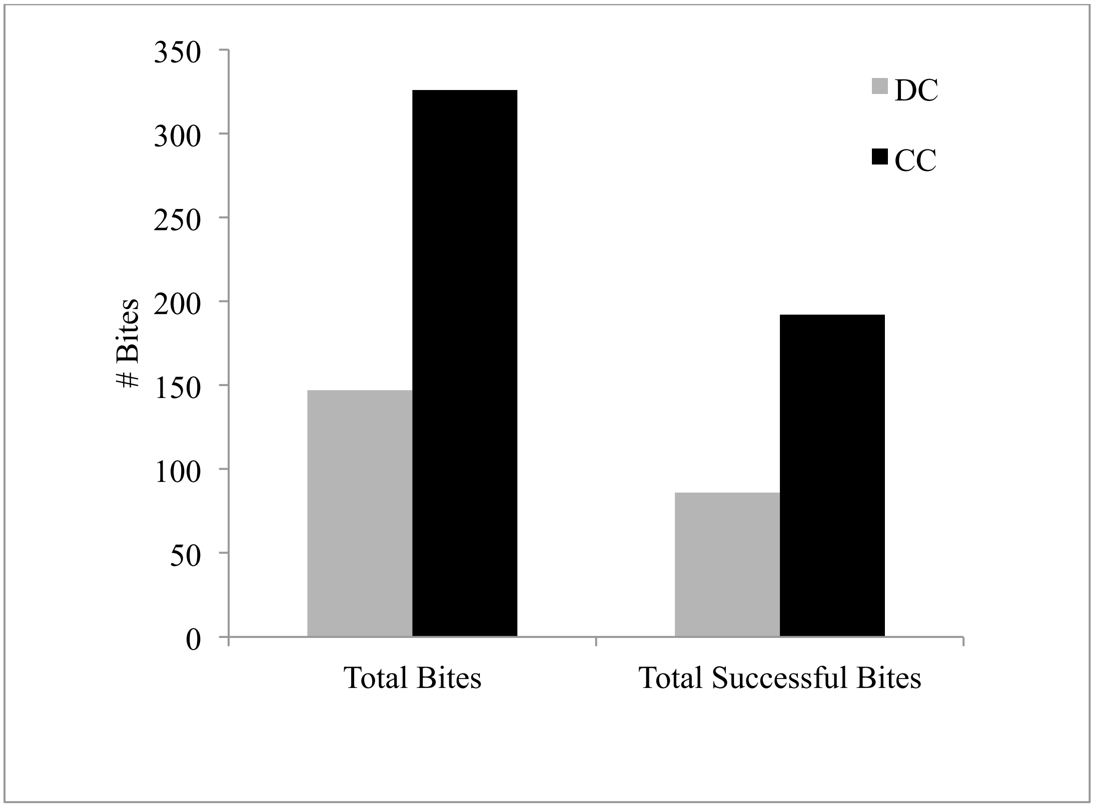

Figure 14. Shows the total number of bites compared to the total successful bites for loggerhead (grey bars) and leatherback (black bars) sea turtles. Both species were successful approximately half the time and there was no significant difference ($p=0.66$, $U=118.5$) in the accuracy of the species in these trials.

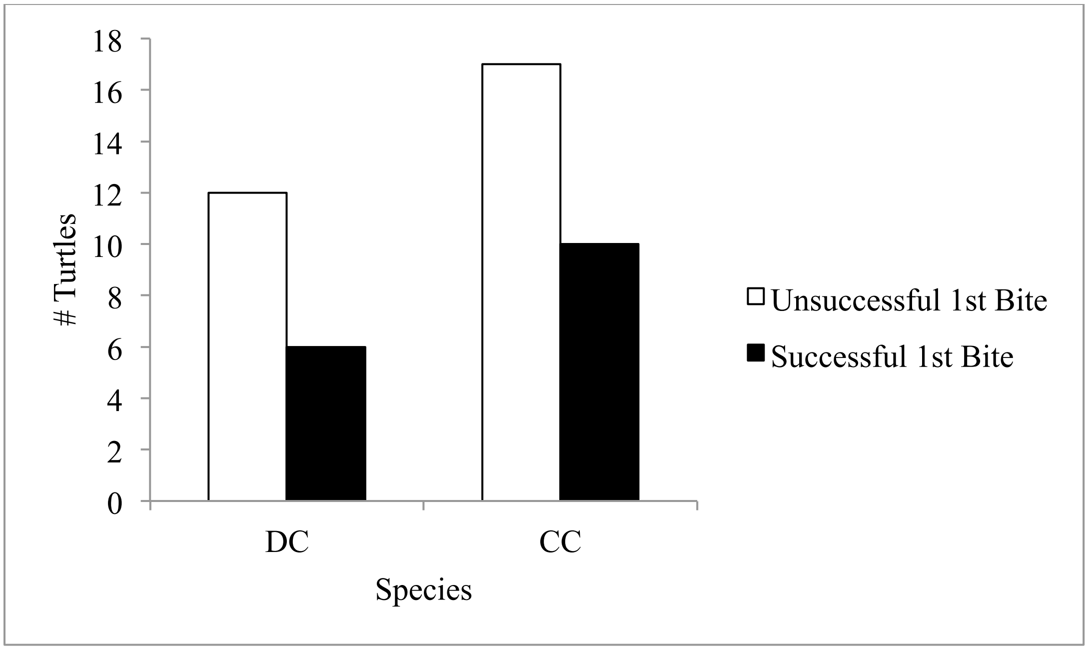

Figure 15. Shows the number of leatherback (DC) and loggerhead (CC) sea turtles that were unsuccessful (open bars) or unsuccessful (black bars) on their first attempted bite. There was no significant difference between the species (p=0.47, U=118.5), both were successful approximately half the time.

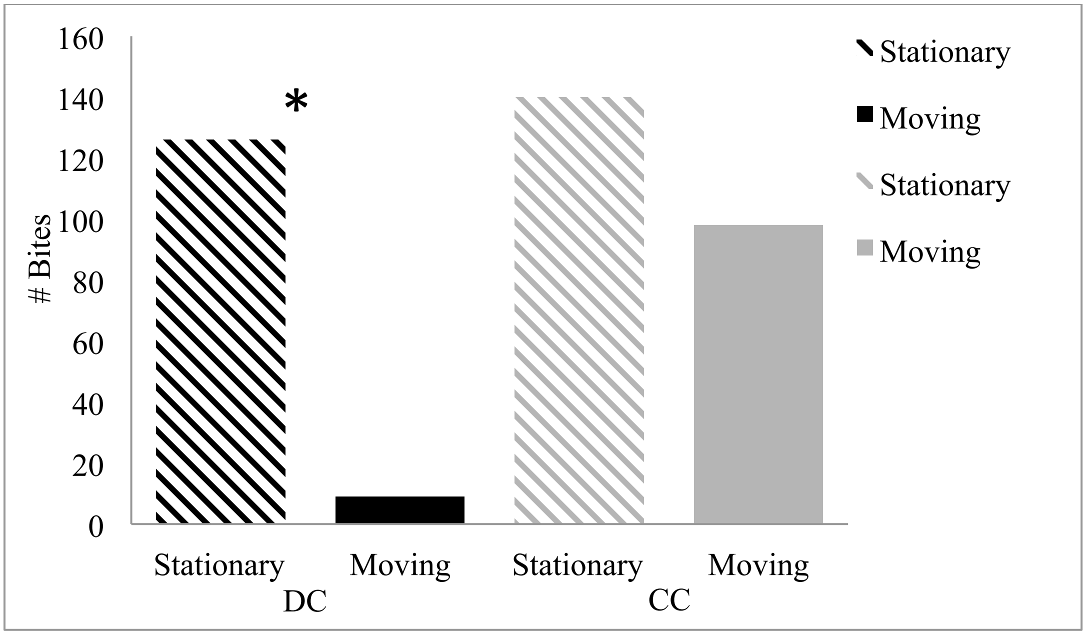

Figure 16. Compares the preference for a moving or stationary target for leatherback (DC) and loggerhead (CC) sea turtles. Leatherbacks showed a preference for biting at a stationary target (p=0.05, U=252.5) while loggerheads showed no preference (p=0.28, U=430).

APPENDIX B: TABLES

Table 1. Bait Odor Response Trials

		Leatherbacks			Loggerheads		
Odor		Snaps	Dives	Stroke Rate	Snaps	Dives	Stroke Rate
Squid	Change in Behavior	+1-23	+2-4	-7-30	+2-50	+1-15	-10-17
DC=20, CC=20	Wilcoxon Sign Rank Test	T=45.0, p<0.001	T=3.0, p=0.97	T=35.0, p<0.05	T=120.0, p<0.001	T=85.5, p<0.05,	T=15.0, p<0.001
No. Δ, ↓, ↑		11,0,9	13,5,2	0,16,4	5,0,15	7,1,12	0,17,3
Sardines	Change in Behavior	+2-4	+1-23	-2-24	+1-95	+1-11	-2-30
DC=20, CC=20	Wilcoxon Sign Rank Test	T=45.0, p=0.70	T=55.0, p<0.001	T=121.5, p=0.74,	T=105.0, p<0.001	T=23.0, p=0.07	T=0.0, p<0.001
No Δ, ↓, ↑		14,3,3	10,0,10	0,8,12	6,0,14	13,0,7	1,19,0

Mackerel	Change in Behavior	+1-17	+1-10	-1-11	+2-21	+1-5	-1-12
DC=20, CC=20	Wilcoxon Sign Rank Test	T=42.0, p=0.01	T=58.0, p=0.20	T=157.0, p=0.92	T=50.5, p=0.06	T=23.0, p=0.07	T=10.0, p<0.001
No Δ, ↓, ↑		14,1,8	10,4,9	2,8,13	9,3,8	13,1,6	0,17,3
Lion's Mane Jellyfish	Change in Behavior	+2-30	+3-10	-9-40	+2-55	+2-5	-4-63
DC=20, CC=20	Wilcoxon Sign Rank Test	T=33.0, p=0.02	T=32.5, p=0.13	T=19.0, p=0.21	T=28.0, p=0.01	T=10.0, p=0.05	T=8.5, p=0.05
No Δ, ↓, ↑		2,1,7	1,3,6	0,7,3	3,0,7	6,0,4	1,8,1

Table 1. Bait Odor Response Trials For Leatherbacks and Loggerheads. The change in behavior (increase +, decrease -) for each type odor is shown as a range of change during the entire test period vs. the control period for snaps and dives. Change in stroke rate (strokes/min) was calculated as the differences between the last min of the control period and first min of the experimental period. Wilcoxon Ranked Sign Test results are shown for each odor type is shown, $p \leq 0.05$ were considered significant. The number of turtles that showed no change (No Δ), a decrease (↓), or increase (↑) in recorded behavior for control to experimental periods are shown above. Leatherbacks sample sizes by odor are squid: n=20; sardine n=20, mackerel n=23; lion's mane jellyfish: n=10. Loggerhead sample sizes by odor are squid: n=20; sardine: n=20; mackerel: n=20; lion's mane jellyfish: n=10.

Table 2. Bite Accuracy Trial Results

Total Bite Performance		
CC_{LW} vs. DC	U=430, p=0.02	CC ↑
CC_{JF} vs. DC	U=158.5, p=0.43	No Change
Bites at Target		
CC_{LW} vs. DC	U=411.5, p=0.05	CC ↑
CC_{JF} vs. DC	U=145.5, p=0.73	No Change
CC_{LW} vs CC_{JF}	U=71, p=0.09	No Change
First Bite Success		
CC_{ALL} vs. DC	U=118.5, p=0.47	No Change
CC_{LW} vs. DC	U=72, p=0.15	No Change
CC_{JF} vs. DC	U=54, p=0.10	No Change
Overall Success		
CC_{LW} vs. DC	U=84.5, p=0.66	No Change
CC_{JF} vs. DC	U=155.5, p=0.49	No Change
CC_{LW} vs CC_{JF}	U=85, p=0.25	No Change

Table 2. Bite Accuracy Trials. Comparisons between leatherbacks with loggerheads during the experimental periods. Twelve of 27 leatherbacks bit, 17 out of 23 loggerheads bit with the small lead weight, and 6 out of 10 loggerheads bit with the jellyfish model. Mann Whitney tests, $p \leq 0.05$ was considered significant. Loggerheads (n=23) tested with the lead weight: CC_{LW} ; Loggerheads (n =10) tested with the jellyfish model: CC_{JF} ; all Loggerhead bite success (see text): CC_{ALL}; All leatherbacks (DC, n=27) were tested with the jellyfish model.

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