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I Can Beat You One Handed: Spiny Lobster Self Defense after the Loss of an Antenna

Amy Parsons

THE FLORIDA STATE UNIVERSITY
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I CAN BEAT YOU ONE HANDED:

SPINY LOBSTER SELF DEFENSE AFTER THE LOSS OF AN ANTENNA

By

Amy Parsons

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The members of the Committee approve the thesis of Amy Parsons defended on December 02, 2003.

William F. Herrnkind
Professor Directing Thesis

Gregory M. Erickson
Committee Member

Robert H. Reeves
Committee Member

Approved:

Timothy S. Moerland, Chairman, Department of Biological Science

The Office of Graduate Studies has verified and approved the above named committee members.

I dedicate this to my Mother, Penny Parsons.
Thank you for all that you have done.

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ABSTRACT

Crustaceans release (autotomize) a limb grasped by a predator or conspecific, often as an escape tactic. However, there are potential fitness costs over the time needed to regenerate a missing limb. If anti-predatory defensive structures are lost, the individual risks further serious injury or death. The Caribbean spiny lobster, *Panulirus argus*, uses two long, armored, mobile, spinous antennae to defend against predators such as the gray triggerfish, *Balistes capriscus*. The loss of one or both antennae potentially leaves it highly vulnerable to attack unless the lobster has compensatory behavior to offset the weapon loss. I tested the ability of *P. argus* to defend itself against *B. capriscus* after loss of one and both antennae and evaluated how lobsters behaviorally compensated. Single sub-adult lobsters, both unrestrained and tethered, were pitted against adult triggerfish in large open seawater arenas. Triggerfish presented with a choice between intact lobsters and those missing an antenna strongly preferred to attack the latter. All lobsters with no antennae were quickly debilitated but those with one antenna were unexpectedly comparable to lobsters with both antennae in their ability to thwart triggerfish attack. That is, the differences in timing and frequencies of injury and mortality were not statistically significant, although the data suggest a trend for higher vulnerability after loss of one antenna. Additionally, the overall frequencies of particular defensive actions by lobsters missing an antenna closely resembled those of intact lobsters. The tail-flip escape action was infrequent and occurred mainly in the last part of trials in which a lobster was defeated. By comparison, successfully defending lobsters, with either one or two antennae, stood their ground and more consistently made effective, timely antennal counter actions in response to triggerfish predatory actions. Free ranging and tethered lobsters defended similarly and with similar success despite constraint of the former. Caribbean spiny lobsters with a single antenna can partially compensate for weapon loss potentially providing a survival advantage, thus allowing them to continue to move about over open terrain where this species commonly forages and migrates.

INTRODUCTION

Marine crustaceans commonly lose and regenerate appendages. Aggressive encounters, predatory attacks and human handling typically induce autotomy (self-release) presumably facilitating escape. Most limbs regenerate after one or several molts (Robinson et al., 1970; McVean, 1976; Davis, 1981; Berzins & Caldwell, 1983; Reichman, 1984; Bildstein et al., 1989; Harris 1989; Lawton, 1989; Juanes & Smith, 1995; Smith, 1995; Bergmann et al., 2001). For example, male fiddler crabs, *Uca pugilator,* frequently lose the enlarged major chela to predators such as the white ibis, otters, or blue crabs (Robinson et al., 1970; Bildstein et al., 1989). Blue crabs, *Callinectes sapidus*, lose appendages to both conspecifics and interspecific predators (Smith, 1995). In addition, limb loss caused by human handling is the most frequently seen injury among commercially fished crustaceans, usually involving the loss of chelipeds or periopods (Norman, 1995; Bergmann et al., 2001). In the case of stone crabs, *Menippe mercenaria*, the chelae are removed by inducing autotomy and the crab is released with the expectation that it will survive and regenerate the claws for another harvest (Lindberg and Marshal, 1984).

Theoretically, there is reduced fitness from losing the functional contribution of a limb. The more important a limb is to survival, the more costly that loss becomes (Reichman, 1984). The loss of a walking leg to a decapod theoretically should be less costly (to fitness) than the loss of one of the specialized chelipeds used for feeding, courtship, aggression, or defense. The remaining legs act redundantly until regeneration, whereas a lost feeding appendage reduces growth or gamete production (Reichman, 1984; Hunt & Lyons, 1986; Bilstein et al., 1989; Juanes & Smith, 1995). The functional loss of a limb used also for sexual display may decrease fecundity even if the individual survives. Male fiddler crabs, which signal females and defend the nesting burrow with the oversized cheliped (Bildstein et al., 1989), cannot function in a sexually competitive manner if it is lost. Furthermore, the claw of older crabs may not regenerate sufficiently, thus ending its individual fitness potential.

While the scenarios above can be reasonably inferred, few studies have estimated fitness loss by tracking the fate of individuals after loss of a defensive limb. Instead, most studies have focused on metabolic costs of limb replacement. In general, a smaller size at maturity from lengthier intermolt periods is a consequence of limb replacement because metabolism must be shunted into limb regeneration rather than somatic growth (Bennett, 1973; Davis, 1981; Hunt & Lyons, 1986). Because body size (volume) in crustaceans determines the number of eggs produced by females and with success in attracting or defending mates by males (Berzins & Caldwell, 1983), widespread limb loss has the potential of decreasing both population recruitment potential and genetic diversity of future generations (Davis, 1981; Berzins & Caldwell, 1983; Reichman, 1984; Harris 1989; Juanes & Smith, 1995). In addition, injured individuals may become more susceptible to disease (Juanes & Smith, 1995).

However, the greatest fitness cost may occur if limb loss reduces anti-predator defense. It is unknown how effectively an injured individual thwarts predators until a limb can be regenerated. Because autotomy is evolutionarily widespread and persistent, it is likely crustaceans accommodate limb loss by compensating behaviorally sufficient to survive most predatory encounters. For example, *Gonodactylus bredini*, an aggressive stomatopod, conceals itself and become less aggressive, avoiding potentially damaging conspecific fights (Berzins & Caldwell, 1983). When attacked, the land crab *Gecarcinus quadratus* initially counterattacks by "attack autotomy", clamping down on the predator, releasing its clenched chelipeds as a distraction, and then fleeing. A second encounter without its chelae induces its immediate retreat (Robinson et al., 1970). Some species take advantage of passive dilution and selfish herding in large groups thus reducing the probability of being attacked (Bilstein et al., 1989; Juanes & Smith, 1995; Childress & Herrnkind, 2000). However, some predators single out an injured individual (Bilstein et al., 1989; Juanes & Smith, 1995). Alternatively, if a group remains together during defense, mortality may be less likely for those missing a limb. For example, a triggerfish is less effective attacking an injured spiny lobster in an aggregation as compared to when it is solitary (Herrnkind et al 2001, unpublished data). But how effective are compensatory defensive behaviors of a solitary lobster at preventing mortality after weapon loss and how do they work?

Anti-predator defense and antenna loss in the spiny lobster, *Panulirus argus*.

The Caribbean spiny lobster, *Panulirus argus,* has long, paired, spinous antennae with powerful basal musculature that swivel to cover most of the body. Antennae are used mainly for defense such as warding off piscine predators especially the gray triggerfish, *Balistes capriscus* and queen triggerfish, *B. vetula.* Given the opportunity, triggerfish are capable of biting through the carapace anywhere on the body (Voss et al., 1994; Herrnkind et al., 2001; Barshaw et al., 2003; Parsons, personal observation). Although a spiny lobster's carapace alone may initially deter triggerfish from biting through to the internal organs, successive attempts eventually penetrate. Tethered spiny lobster *Palinurus elephas,* for example, rapidly succumb to triggerfish predation if both antennae are removed (Barshaw et al., 2003).

Spiny lobster antennae may be autotomized when grasped and held or they may be bitten off at some point along their length thus providing an opening to attack by a predator. Wild *P. argus* are commonly found missing one or both antennae, especially in heavily fished areas (Davis and Dodrill 1980). Recreational divers inflict very high injury rates of antennal autotomy while trying to extract lobsters from crevices (Davis & Dodrill, 1980). Commercial fishing adds further damage to undersized lobsters when removing them from traps (Davis, 1981; Murphy & Kruse, 1995). In 1977, 40.3 % of largely late juvenile and pre-adult lobsters sampled in Biscayne Bay, Florida were missing limbs. Mortality from injuries was about 22%, while natural mortality was estimated at 34.8% per year (Davis, 1981). It is generally unknown how much of that mortality is due to predation. Because handling injuries caused significantly reduced growth of mainly juvenile lobsters, the U. S. National Park Service set aside lower Biscayne Bay as a refuge where lobsters may not be caught.

Late juvenile and adult Caribbean spiny lobsters are highly nomadic and migratory across shelter-less terrain (Herrnkind, 1980). During mass migrations they form queues, single file lines of up to 60 or more individuals, which travel up to 10 or more kilometers a day, moving in daylight as well as darkness (Herrnkind, 1969; Kanciruk & Herrnkind, 1978; Herrnkind et al., 2001). Hundreds of thousands of lobsters may move during these episodic events. When not traveling, they peacefully share shelters or pile atop one another in the open to rest when shelter is unavailable, as do rock lobster, *Jasus edwardsii* in New Zealand (Kelly et al. 1999). The aggregations may be an effective defensive tactic to guard against predation, by combining antennal weaponry that cover each other's vulnerable body parts and to distract the predator from singling out a target (Herrnkind, 1969; Dehn, 1990; Eggleston & Lipcius, 1992; Herrnkind et al. 2001). While in dens or cornered against a structure they rest against and upon each other with antennae pointing outward and overlapping. When a queue is threatened, the leader pirouettes while the line of followers spiral in an ever-tightening circle. The end result is a tightly packed radial clump of lobsters with antennae facing every direction above and to the side with their vulnerable abdomens toward the center. This dense forest of moving, spine-laden weapons may be a daunting barrier to an attacking triggerfish (Herrnkind et al. 2001).

Two percent of migrants become separated from queues and wander solitarily (Herrnkind et al 1972). Because migratory routes often trace through stretches without shelter, a straggling lobster has to rely on its own defensive prowess. Simply escaping the immediate area is likely insufficient to avoid highly mobile, swimming predators (Barshaw et al., 2000). Herrnkind (in Kanciruk, 1980) photographed and reported a successful queen triggerfish attack on a solitary migrant. Isolated, exposed lobsters need to defend effectively until the predator loses interest, the lobster finds shelter, or conspecifics arrive.

Because crustacean, especially spiny lobster, limb loss and regeneration is so widespread, one expects a selective advantage for compensatory behaviors to reduce predation pressure until the limb is replaced. That is, the animal needs to "assess" its susceptibility to predation and compensate behaviorally to counter its increased vulnerability (Dehn, 1990; Lima & Dill, 1990; Bouskila & Blumstein, 1992). This study evaluates the manner and effectiveness by which individual Caribbean spiny lobsters of migratory size defend against individual gray triggerfish when exposed in the open during daylight under three conditions; i.e., both antennae intact, one antenna intact, and both antennae missing. I predicted that *P. argus* missing one or both antennae display new or specialized patterns of behavior or alter the frequency of particular defensive actions. I expected that compensatory tactics are ineffective for antenna-less individuals and only partially effective for lobsters with one antenna and significantly less effective than intact cohorts. I expected escape by tail-flipping to play an important role in the defensive tactics of a single lobster, regardless of antenna number. Therefore, I also compared between tethered and free-moving lobsters during predatory triggerfish confrontations to evaluate antennal defense *per se* when constrained to one location.

METHODS

Test Facilities

At the Keys Marine Laboratory on Long Key, Florida, large, 5 m x 5 m x 1 m deep, concrete-lined outdoor arenas with free flowing seawater from the Gulf of Mexico were used to stage encounters between lobsters and triggerfish. These arenas were large enough for complete freedom of movement for all animals. The sides were sloped outward and made slippery to the lobsters with aluminum sheeting to prevent the lobsters from using the walls as a defensive structure. The triggerfish could approach from any direction even when the lobster was near a wall. The observer was positioned on a shaded tower 3 m above the arena out of view of the animals.

Animal Handling, Care, and Training

Triggerfish

Gray triggerfish were captured from natural rock reefs in 10-20 m depth in the Gulf of Mexico by squid-baited barbless hooks. Swim bladder gas pressure was immediately released by inserting a hypodermic needle. Ten triggerfish (~ 20 cm to 30 cm total length; mean, 26cm) were held individually in large (~0.5 cubic meter), flow-through cages with shading at the top. Their daily diet consisted of squid and lobster. When not being used for trials, the fish took turns in a large spare arena for social contact and exercise. Fish were fasted 36 hours before a trial to encourage predatory behavior. When all trials were complete, the fish were released back into the Gulf of Mexico.

Before trials began, the triggerfish were fed only live lobster for two weeks to assure that all individuals were capable of subduing a lobster because there was no way to know their individual prior experiences with lobster prey. Additionally they were acclimated to the arena and to handling. The fish were handled using small-mesh, soft fabric nets. Training ended when all triggerfish killed and ate a lobster and they remained calm when captured and transported in the net.

Lobsters

Lobsters ranging in size from ~55 to 75 mm Carapace Length (measured from between the rostral horns to the back edge of the carapace) were captured from 2-3 m depth near Long Key by divers using hand nets then held in 2 m dia. shaded tanks with cement block shelters and flow-through sea water. Their daily diet was chopped squid and shrimp. All lobsters were used once then released back into the Gulf.

Each antenna was removed after inducing autotomy by firmly holding the antenna near the base while the lobster tail flipped. Autotomy was performed one day before a trial to allow the lobster to adjust and to avoid discharging hemolymph that might attract the fish. No mortality was caused by this procedure. When introduced to the arena, the lobsters were allowed 10 minutes to settle before a trial began.

Tethering

To tether a lobster so it could pirouette freely and exhibit the full range of defensive antennal actions, a chain of fishing snap swivels secured by a wire around the cephalothorax was connected to an eye on the center of a fiberglass rod affixed to the arena floor. The swivel chain also allowed about 10 cm radius of movement. This arrangement resembled that used in other studies (Barshaw et al 2003, Herrnkind, unpublished).

Videotaping and analysis

All trials except 'Tasters Choice' (described below) were videotaped from the arena-side tower using a high resolution, Sony Handycam™ mini digital video camera with zoom-telephoto lens fitted with a polarizing filter. This allowed close-up recording so the fish or lobster filled the frame, as well as wide-angle perspectives. The camera microphone permitted simultaneous voice recording of key comments to assure thorough and accurate information. Behavioral data were subsequently transcribed from the videotapes into Excel computer format using an editing type Sony digital cassette editing tape deck, with stop-frame and other manipulations, to obtain details of acts and timing unavailable from voice tape recordings or written notes alone. All triggerfish predatory actions and corresponding defensive actions during encounters were coded according to the descriptive categories in Table 1. These actions are essentially the same as those developed by Herrnkind (unpublished) and Barshaw and colleagues (Barshaw et al 2003 and K. Lavalli, personal communication). Additional data on proximity and spatial aspects were also drawn from the tapes.

Statistics

I used 1-way ANOVA to test significances of arcsine, square-root transformed data among and between treatments. When a transformed data set did not have normally distributed residuals, the Welch's ANOVA was performed.

Trials: Outcomes and Compensatory Actions

Free Ranging Lobsters

To determine whether *P. argus* exhibits compensatory behavior after the loss of one or both antennae, I compared the outcomes, behavioral frequencies, and durations of fish antagonistic actions paired with lobster defensive reactions for Intact (both antennae), Missing Antenna (one antenna removed), and No Antenna (both antenna removed) individuals. Survival status and the location and number of any injuries that puncture the exoskeleton were quantified for each test group to estimate relative effectiveness in ability to thwart triggerfish predation.

A single, untethered free ranging lobster (CL = 70mm, +/- 10mm) with both antennae (Intact), missing an antenna (MA), or no antennae (NA) was pitted against one randomly chosen triggerfish for each lobster antennal group. The antenna(e) number for each of 60 trials (20 trials each) was randomly determined to limit sequential exposure of the same type of lobster per fish. Ten MA lobsters had the right antenna removed and the remaining 10 had the left removed. All antennae were trimmed to 15 cm. Antennae length can influence defensive advantage more so than body size when comparing the lobsters (Barshaw et al., 2003). I did not include data after any Intact or MA lobster lost half or more of its antenna length when comparing behavioral frequencies between groups. An Intact lobster with a severely damaged antenna, for instance, might gradually exhibit the defensive tactics of a lobster with only one antenna, thus obscuring behavioral differences.

A trial ended either when a triggerfish lost interest for 15 minutes or when a lobster lost an eye (interrupts reaction to attacker), three legs on one side (severely limits Pirouetting), or was mortally wounded (became unresponsive). Such debilitating injuries within minutes lead to death from triggerfish attack. These injuries, along with mortal wounds, were recorded as a “kill” regardless of whether the lobster actually died. Any other damage to the carapace, i.e. broken antennae tips, the loss of a rostral horn, non-lethal punctures and tears, were simply grouped as injuries throughout this study unless otherwise specified. Surviving lobsters were removed from the arena, allowed to recover then released. Most lobsters recovered from limb and eye loss, as well as single bites to the telson and abdomen.

Tethered Lobsters

Tethered lobsters (CL = 73mm, +/- 10mm) were used to further explore the role of fleeing (Walk, Tail Flip) in the absence of conspecifics or shelter.

Intact lobsters were used for 17 trials, MA lobsters for 16, and NA lobsters for 13. The trials were run identically to those with free ranging lobsters except that the lobster was tethered in the center of the arena. The lobsters could Lunge and Tail Flip to the limit of the tether but could not Walk away (Table 1).

Lobsters without antennae necessarily rely only on the carapace to ward off puncturing bites. If escape is more important to a lobster without antennae, I expected more and faster kills by the triggerfish in the tethered trial. If escape does not play a large role for lobsters in an open area, I expected defensive patterns comparable to those of free ranging lobsters. Therefore, I compared the tethering data with those obtained from untethered lobsters.

Taster’s Choice – Triggerfish selectivity for fewer antennae.

If faced with more than one lobster, a triggerfish may be able to detect vulnerability of a prey (i.e., reduced defensive capacity) through visual inspection or by cues from a lobster’s response to its approach. If so, this potentially leads to increased predatory attacks on lobsters that have lost an antenna either from more frequent attacks or greater persistence on the part of a predator. Additionally, group defense may become less effective, further placing emphasis upon the lobster’s ability to defend itself. Tasters Choice was designed to test whether triggerfish selectively attack lobsters missing an antenna if given a choice and to document the behaviors of the predator.

For 29 trials, two tethered lobsters were placed 1.5 meters apart at the ends of a fiberglass rod affixed to the arena floor, well away from the arena walls so the fish was able to visually inspect the lobsters from all angles. The lobsters were far enough apart that they could not contribute to, or interfere with, each other's defense against the fish. A lobster with one antenna was always paired with an Intact lobster of the same size (+/- 3mm CL). All antennae were trimmed to 15 cm, though only the right antenna was removed from MA lobsters. The placement of the two rods was always the same but I switched sides of MA and Intact lobsters each trial. This prevented a fish from exhibiting a bias for a particular side of the arena rather than for a lobster. At the beginning of the trial, a fish was introduced by net into the arena between the two lobsters. The trial ended with a "kill" or until the fish did not attack after a 15 minute lapse.

For 16 trials, fish attention to a lobster was estimated by recording its proximity to a lobster when Approaching and Circling, in addition to whether any Bites took place (Table 1). A higher frequency (1-way ANOVA) of any or all of these actions directed at one lobster indicates a bias for that individual.

Table 1. Description of behavioral actions by triggerfish and lobsters. The following behaviors are capitalized in text.

Fish Actions

Approach
The fish swims toward the lobster within 2 antennae lengths yet out of reach of the antennae.

Attack
The fish moves directly toward the lobster within one antenna length but does not try to bite the lobster.

Bite Attempt
The fish tries and fails to close its mouth on part of the lobster from within one antenna length.

Bite
The fish's mouth closes on part of the lobster; injury may or may not occur.

Circle
The fish swims continuously around a lobster for at least 270^{o} from its starting point and no more than 2 antennae lengths from the lobster.

Clockwise or Counterclockwise: Direction the fish swims around a lobster with both antennae intact or both missing. While swimming, the fish usually becomes positioned at the anterior region of a lobster with both antennae as the lobster tries to face the fish while Circling. Antennae perpendicular to the anterior block the fish from swimming to the side of the lobster when within antennae range.

The fish rapidly swims around lobsters without antennae and does not tend to remain positioned at one location more than any other. No antennae block the fish from swimming at the side of the lobster. The lobster often does not rotate fast enough to face the fish at all times.

Away (from the antenna): When swimming around a lobster with one antenna, the fish swims away from the side with an antenna, starting at the anterior end of the lobster. The fish usually remains positioned at the anterior end while the lobster rotates with the fish, or stays near the side without an antenna. The fish is often within antenna range.

Towards (the antenna): When swimming around a lobster with one antenna, the fish swims toward the side with the antenna, starting at the anterior end of the lobster. The fish will usually remain at the anterior end of the lobster. The remaining antenna forms a barrier, preventing the fish from swimming along that side.

Table 1 - continued.

Lobster Actions

Point
The antenna of the lobster moves at, or is held in, the direction of the fish. No contact is made.

Parry
When the tip or side of the antenna makes contact with any part of the fish, including when the antenna is held stationary against the fish (pushing).

Lunge
The lobster's antennae are swept together rapidly in front of the lobster and the body rapidly moves forward at the fish, by the use of the legs and/or the rapidly undulating telson. This movement is about one lobster body length; the antennae may or may not make contact.

Cross Over
A lobster missing one antenna swings the remaining antenna across the midline of the body to confront an attacker approaching from the antenna-less side. Often the lobster tilts sideways, leaning the antenna-less side against the substrate.

Pirouette
The lobster rotates around its body axis more than a half circle.

Table 1 - continued.

Rear Back
The lobster lifts its anterior, standing mostly on its rear legs. The antennae are pointed backwards along the cephalothorax and abdomen. The telson may extend out behind the lobster but it is usually curled underneath. Extreme cases may cause the lobster to lie nearly on its back.

Tail Flip
The rapid flexion of the extended abdomen, one or more times that results in propelling the lobster to a new location.

Walk
The lobster uses only its legs to move itself to another location. It may move forwards or backwards.

RESULTS

Typical Encounter Described

During a typical encounter, with a lobster in the open, a triggerfish moves close but initially stays out of antennae range perhaps to visually inspect the lobster. The fish hovers above or beside the lobster or repeatedly Approaches the lobster (see Table 1 for action descriptions), then begins Circling. Over time, the intensity and frequency of these actions escalate. A lobster typically responds by Pointing and shifting its body to face the fish. Antennal Pointing is frequently maintained during a Pirouette.

A fish may then begin a series of Attacks, close-in maneuvers within antennal range. The fish makes swift maneuvers, rapidly changing direction or position in the water column, often swimming sideways or upside down. Doing so sometimes provides an opening for a Bite or Bite Attempt. The lobster counters with Parries or Lunges at the fish that deflect the Attacks. Eventually persistent Attacks result in successful Bites that penetrate the carapace or remove a limb or part of an antenna. Areas that received most attention were the eyes, antennae, legs, and posterior region. Once the triggerfish landed a hard bite, the lobster sometimes began Walking and occasionally Tail Flipping. The fish quickly chased down the lobster and resumed Attack.

The fish-lobster interactions may be a long series of nonstop, rapid actions, or a series of multiple bouts with brief pauses (up to several minutes each). During pauses, the fish retreats or hovers about 1-2 meters away. A successful fish, having bitten a vulnerable area, Attacks and Bites repeatedly until consuming the internal organs and abdominal musculature.

Free Ranging Lobsters

Antennal Injury and Mortality

Triggerfish bit off pieces of antennae from 55% of the Intact lobsters and 64% of MA lobsters, but biting and dragging did not cause autotomy. The amount of antenna bitten off different for MA (23.4%) and Intact lobsters (10.6% x 2) (Welch ANOVA: $F = 4.81$, $df = 1$, $F= 65.90$, $p < 0.032$). NA lobsters were injured (90%) or killed (85%) at higher rate than either Intact (25% mortality/ 45% injured) or MA lobsters (50% mortality/ 74% injured). Survival of Intact and MA lobsters was not statistically different (Figure 1) (One-Way ANOVA: $F =2.71$, $df =38$, $p < 0.108$). Intact lobsters suffered less frequent injuries than MA and NA lobsters (One-Way ANOVA: $F = 5.29$, $df = 2, 57$ $p < 0.0078$). Both MA and Intact lobsters survived more than NA lobsters (One-Way ANOVA: $F = 9.16$, $df = 2, 57$ $p < 0.0004$).

Fish Actions

The array and distribution of Triggerfish actions toward MA and Intact lobsters were similar but both differed from NA lobsters (Table 2). Bites and Attempted Bites on NA lobsters were more frequent, while Circling was less frequent than in MA and Intact trials (Table 2, Figure 2).

<u>Winner/loser comparison</u>. Fish made fewer Approaches but more Bites, with a trend for more Attempted Bites, on losing MA lobsters than on successfully defending MA lobsters (Table 3a, Figure 3). Similar results were seen for Intact lobsters, in addition to more frequent Attacks and Bite Attempts on losing individuals (Table 3b, Figure 3b). The overall tactics used by fish engaging an Intact or MA lobster were similar regardless of the eventual success of the fish (Figure 2).

<u>First/last quarter of bout</u>. As time within a trial progressed, triggerfish tactics shifted during confrontations with MA lobsters. During the last quarter of a trial against MA opponents, triggerfish escalated the frequency of Bites, which were rarely accomplished during the first quarter (Table 4; Figure 4a).

Lobster Actions

Overall, MA and Intact lobsters responded similarly to triggerfish actions. However, lobsters missing both antennae Lunged and Reared Back more than their Intact and MA cohorts. NA lobsters Tail Flipped most but the other evasive action, Walking, did not differ statistically from Intact and MA individuals (Table 2; Figure 2).

<u>Winner/loser comparison</u> (see Table 3 and Figure 3a-b). Failing MA lobsters Pointed less but Parried and Reared Back more than successful cohorts. The same was observed for failing Intact lobsters, in addition to a higher frequency of Tail Flips and less Walking. No difference was seen between Intact and MA lobsters.

Cumulative Lobster injuries and survival by antennae number.

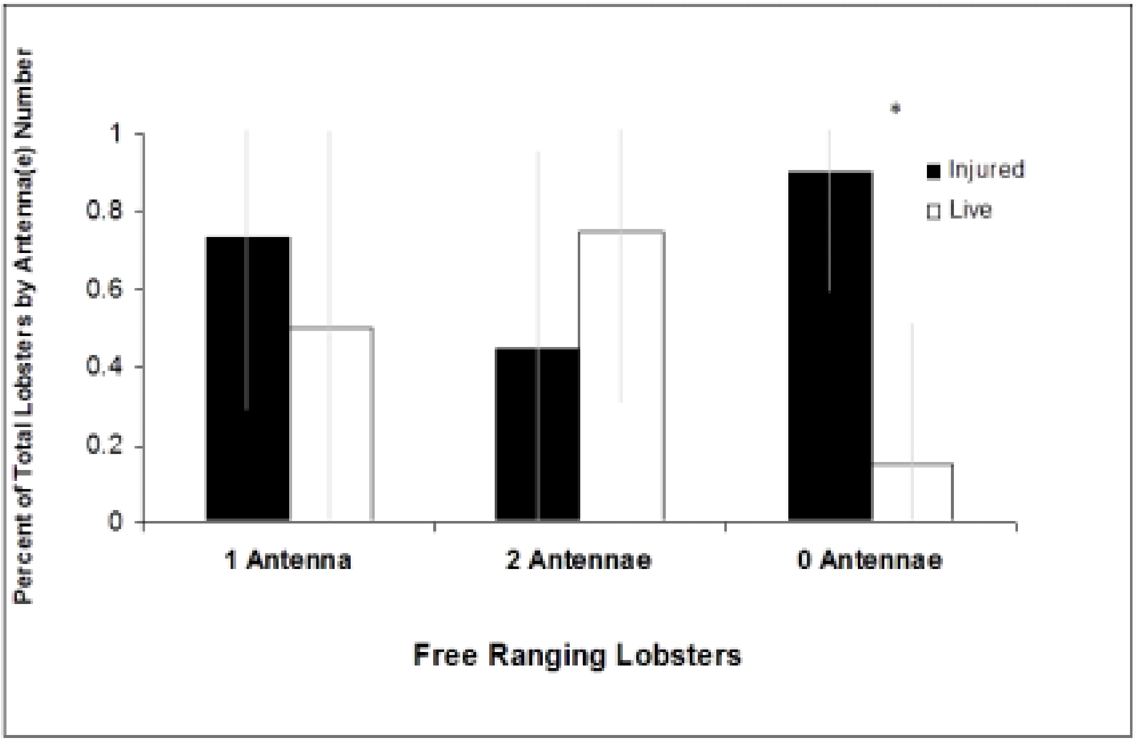

Figure 1. Lobster injuries and survival after facing a triggerfish according to antennae number. Only lobsters without antennae showed significant difference from the other antennal groups. Injuries are both lethal and non-lethal. Surviving lobsters may be injured. N=20 each. *p < 0.05.

Table 2. Actions that differ when comparing lobsters without antennae to lobsters with one or both antennae.

No differences were seen between lobsters with one antenna and those with both antennae overall. Df = 2,57. Fish = (f), Lobster = (l)

	Source	**F**	**p <**	**fish (f)/lobster (l)**
1-Way ANOVA:	Bite Attempt	19.29	0.0001	(f)
	Bite	14.81	0.0001	(f)
	Lunge	11.89	0.0001	(l)
Welch ANOVA:				
	Circle	6.03	0.0055	(l)
	Tail Flip	21.76	0.0001	(l)
	Rear Back	3.43	0.043	(l)

Overall actions of fish and free ranging lobsters (1, 2, 0 antennae).

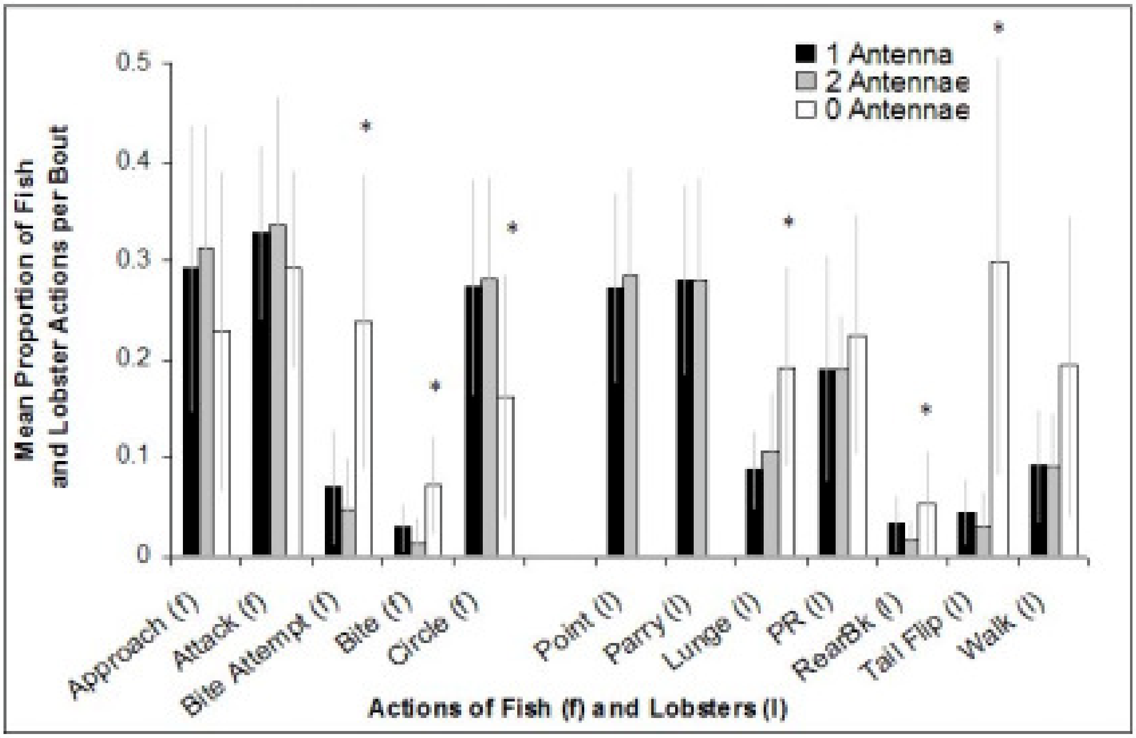

Figure 2. Fish treated lobsters with antenna(e) the same. One or more lobster actions are In response to a single fish action. Only lobsters without antennae differed in behavior and how they were treated by fish. N = 20 each. Error bars show standard deviation. *$p < 0.05$.

Table 3. Free ranging lobster success vs. failure to survive.

a) Comparison of differences between the success and failure of free ranging lobsters to survive a trial for a) 1-antenna lobsters and b) 2-antennae lobsters. All tests used One-Way ANOVA. df = 1,18.

a) MA lobster Success vs. Failure to Survive

Source	F	p <	fish (f)/lobster (l)
Approach	11.83	0.0029	(f)
Bite	10.16	0.0051	(f)
Point	14.64	0.0012	(l)
Parry	6.67	0.019	(l)
Rear Back	7.58	0.031	(l)

b) Intact lobster Success vs. Failure to Survive

Source	F	p <	fish (f)/lobster (l)
Approach	16.01	0.0008	(f)
Attack	5.96	0.025	(f)
Bite Attempt	7.45	0.014	(f)
Bite	12.21	0.0026	(f)
Point	12.46	0.0024	(l)
Parry	5.42	0.032	(l)
Rear Back	11.22	0.0036	(l)
Tail Flip	12.00	0.0028	(l)
Walk	7.31	0.015	(l)

Actions based on lobster success or failure to survive a trial with one antenna.

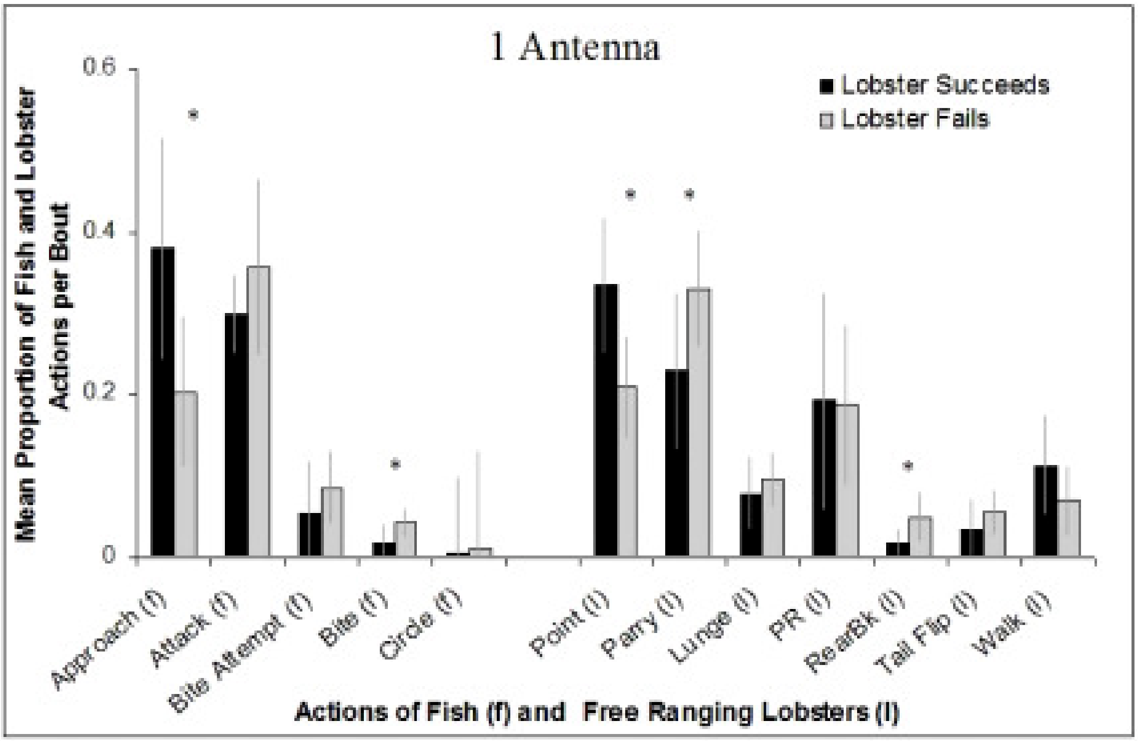

Figure 3a. When comparing bouts based on lobster survival, failing lobsters were bit more by a triggerfish while successful lobsters kept the fish out of antennae range. N= 10 each. Error bars show standard deviation. *p < 0.05.

Actions based on lobster success or failure to survive a trial with two antennae.

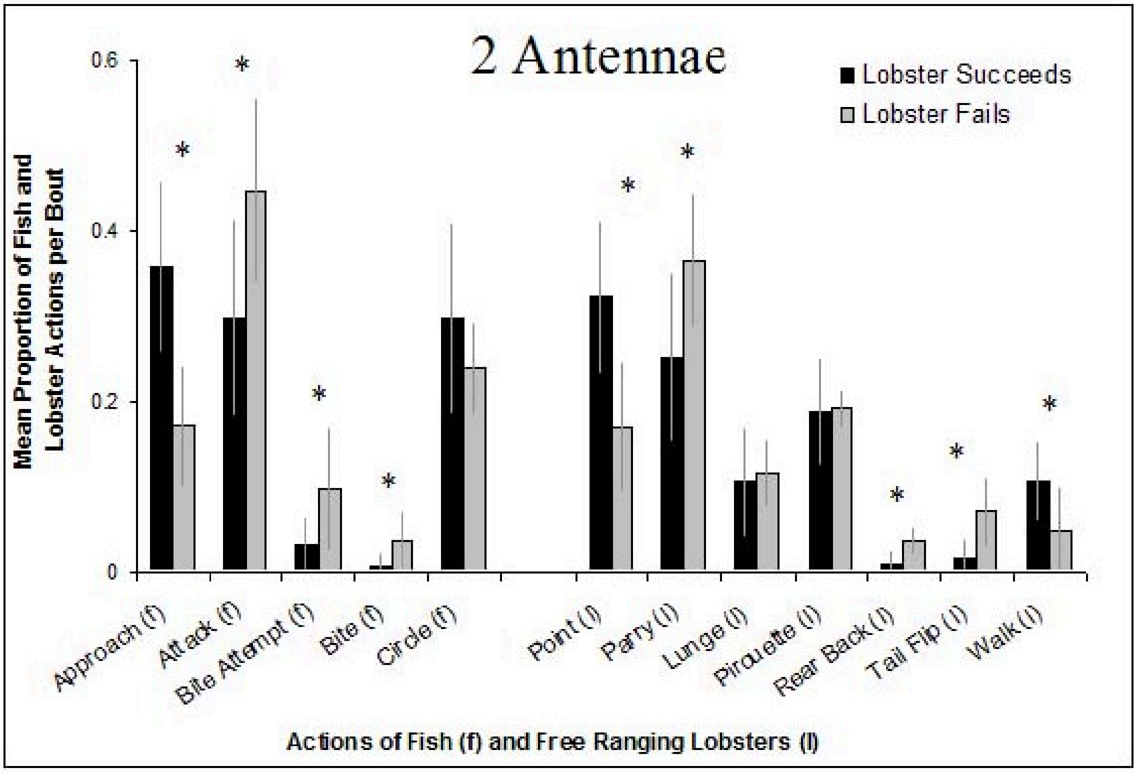

Figure 3b. If the fish gets past the antennae, lobster success decreases. The lobster is more likely to try to put distance between itself and the fish by leaving the immediate area. N= 14 each. Error bars show standard deviation. *$p < 0.05$.

Table 4. Differences when comparing the first and last quarters of a trial for 1-antenna and 2-antennae, free-ranging lobsters.

Analysis by One-Way ANOVA except where indicated. df = 1,26. N= 14 (MA), 13 (Intact).

MA Lobsters			
Source	**F**	**p <**	**fish (f)/lobster (l)**
Bite	16.35	0.0004	(f)
Point	4.53	0.043	(l)
Rear Back	5.70	0.025	(l)
Intact Lobsters			
Rear Back	5.95	0.026	(l) (Welch ANOVA)
Intact vs. MA Lobsters (last quarter)			
Lunge	7.98	0.0092	(l)

Mean comparison of actions during the first and the last quarter of trials: 1 antenna.

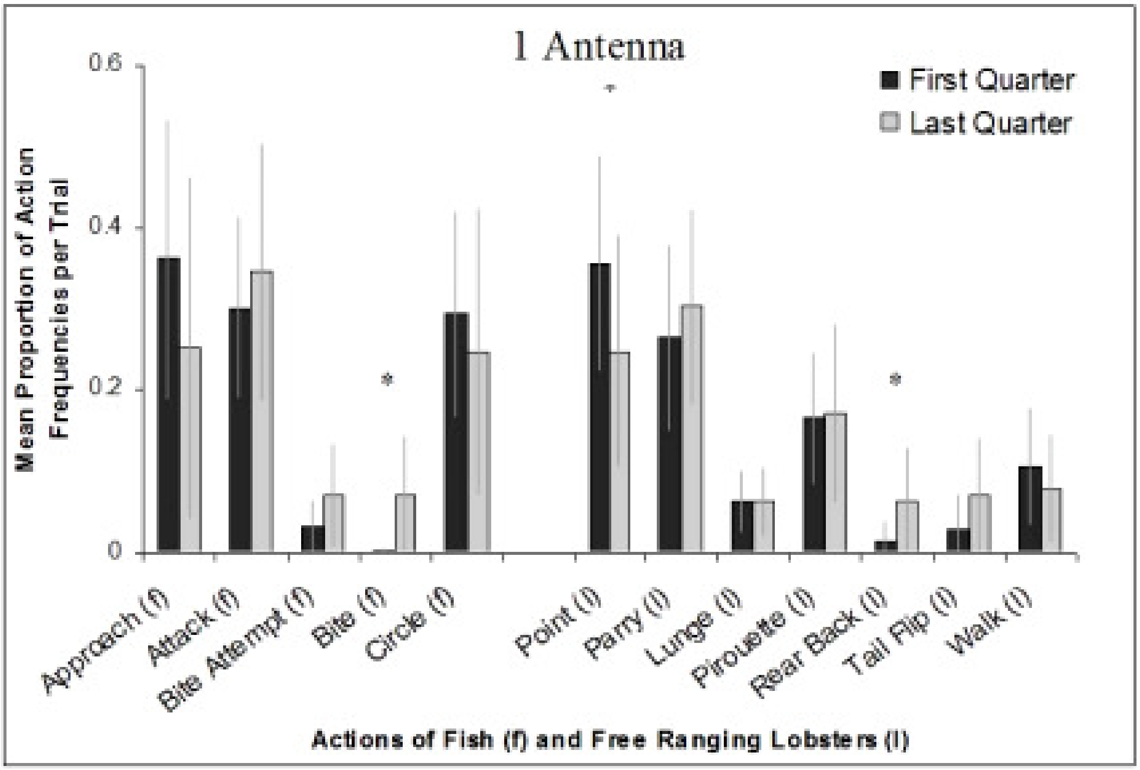

Figure 4a. Triggerfish tactics changed as the trial progressed. N= 14 each. Error bars show standard deviation. *p < 0.05.

First/last quarter of bout (see Table 4 and Figures 4 a-c). Towards the end of the trial, failing MA lobsters Pointed less, and Reared Back more frequently yet Tail Flipping did not change. Failing Intact lobsters only increased Rearing Back during the last quarter of the trial. Intact lobsters showed a higher frequency of Lunging than MA lobsters.

Lobster response to particular fish actions (see Table 5a,b and Figures 5a-e). To better discriminate the cause of changes in lobster behavior, I examined lobster actions to particular fish actions. Intact and MA lobsters exhibited statistically similar responses to each fish action. When a fish Approached an Intact or MA lobster, it usually encountered Pointing. Losing MA lobsters tended to Reared Back more often than successful defenders. All lobsters were more likely to Parry an Attacking fish. **(Amy, this past sentence is not clear)** When compared to successful lobsters, failing MA lobsters were less likely to Pirouette, favoring to Rear Back instead. A Bite Attempt nearly always resulted in a lobster Parrying the fish. MA lobsters also Tail Flipped and Walked in response to this action more than those lobsters with two antennae. A Bite also resulted in a high frequency of Parrying and Tail Flipping by the lobsters while MA lobsters tended to Rear Back as well. Intact and MA lobsters responded to by Pointing and Parrying at Circling triggerfish, often coincident with Pirouetting. This did not change with success or failure to survive a bout. However, successful MA lobsters Pointed more often than successful Intact lobsters. Losing MA lobsters Lunged less frequently and more often Reared Back as compared to losing Intact cohorts.

Circling direction

I analyzed whether fish Circled around symmetric NA or Intact lobster either Clockwise or Counterclockwise (Figure 6). Both directions were equally likely around NA lobsters but biased towards Counter Clockwise for Intact lobsters (1-Way ANOVA: df = 1,36, F= 14.75, $p > 0.0005$) (Table 6). However, MA lobsters were Circled mostly Away (1-Way ANOVA: df = 1, 36, F= 18.89, $p > 0.0001$) from the remaining single antenna regardless of whether it was on the right or the left side of the lobster. Yet, when this asymmetry was considered, the data showed no Clockwise or Counter Clockwise bias. Otherwise, both successful and unsuccessful Intact and MA lobsters behaved similarly (Table 6).

Mean comparison of actions during the first and the last quarter of trials: 2 antennae.

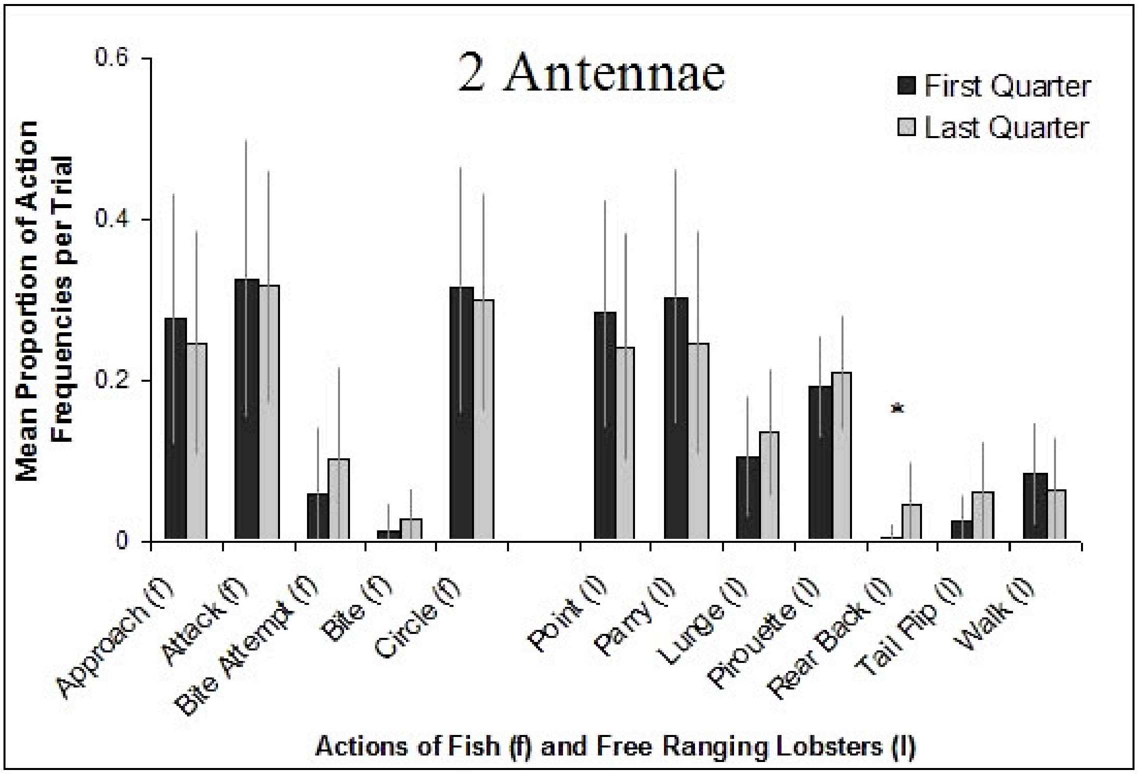

Figure 4b. Little changed as time progressed. The beginning of a trial looks very much like the end. N = 13. Error bars show standard deviation. *p < 0.05.

Comparison of 1 antenna (MA) and 2 antennae (Intact) actions during the first and the last quarter of trials.

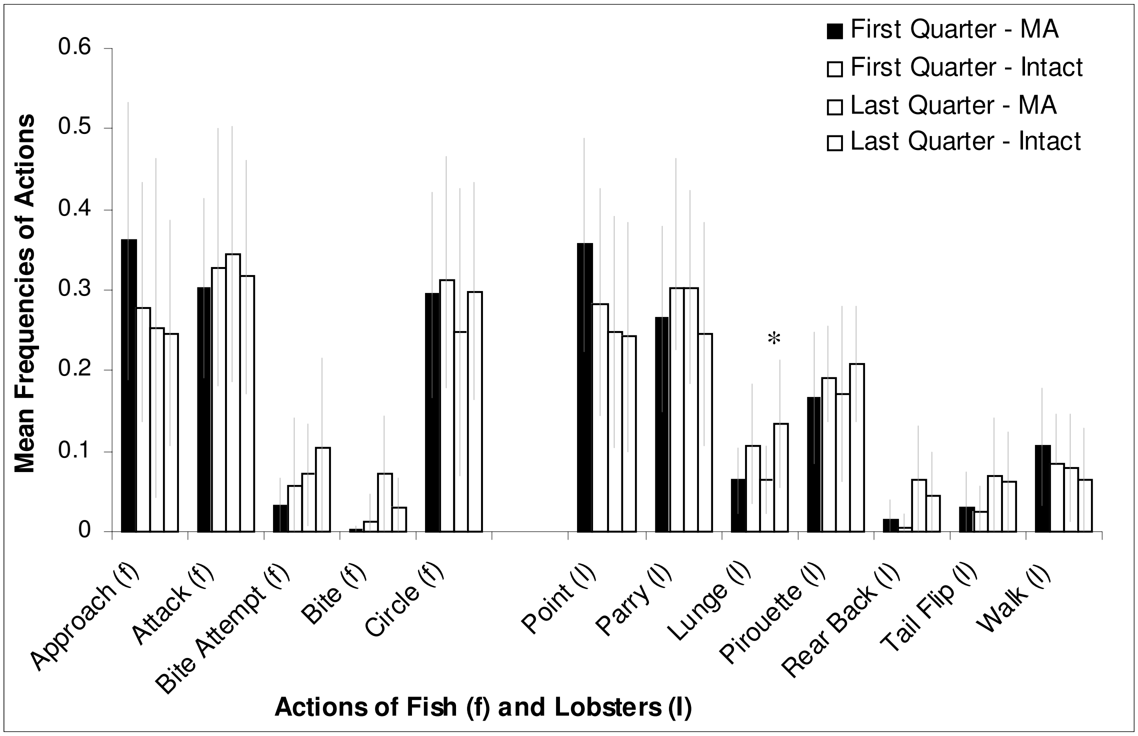

Figure 4c. Intact lobsters lunged more frequently than MA lobsters near the end of the trial. N = 14 (MA), and 13 (Intact). Error bars show standard deviation. $*p < 0.05$.

Table 5. Comparison of the success and failure of free-ranging lobsters to survive a trial in reaction to a fish action.

a) 1 Antenna survival comparisons. 2 antennae lobsters were not shown to be different whether they succeeded or failed. **b)** Comparison of 1 antenna and 2 antennae lobsters survival. 1-Way ANOVA except where indicated. df = 1,18.

a) **1 Antenna Lobsters, Free-ranging**

	Source	F	p <	
Per Attack:	Pirouette	5.79	0.027	
	Rear Back	7.67	0.017	(Welch ANOVA)
Per Bite Attempt:	Tail Flip	6.58	0.020	
	Walk	5.79	0.027	
Per Bite:	Rear Back	8.67	0.0087	
Per Circle:	(Point	4.31	0.052)	

b) **2 Antennae vs. 1 Antenna, Free-ranging**

	Source	F	p <
Per Attack:	Pirouette	4.90	0.045
Per Circle	Point	6.34	0.019
(Survived)	(Parry)	3.97	0.058
Per Circle:	Lunge	5.32	0.038
(Failed to Survive)	Rear Back	6.48	0.024

Lobster actions per fish approach according to survival success and antennal number.

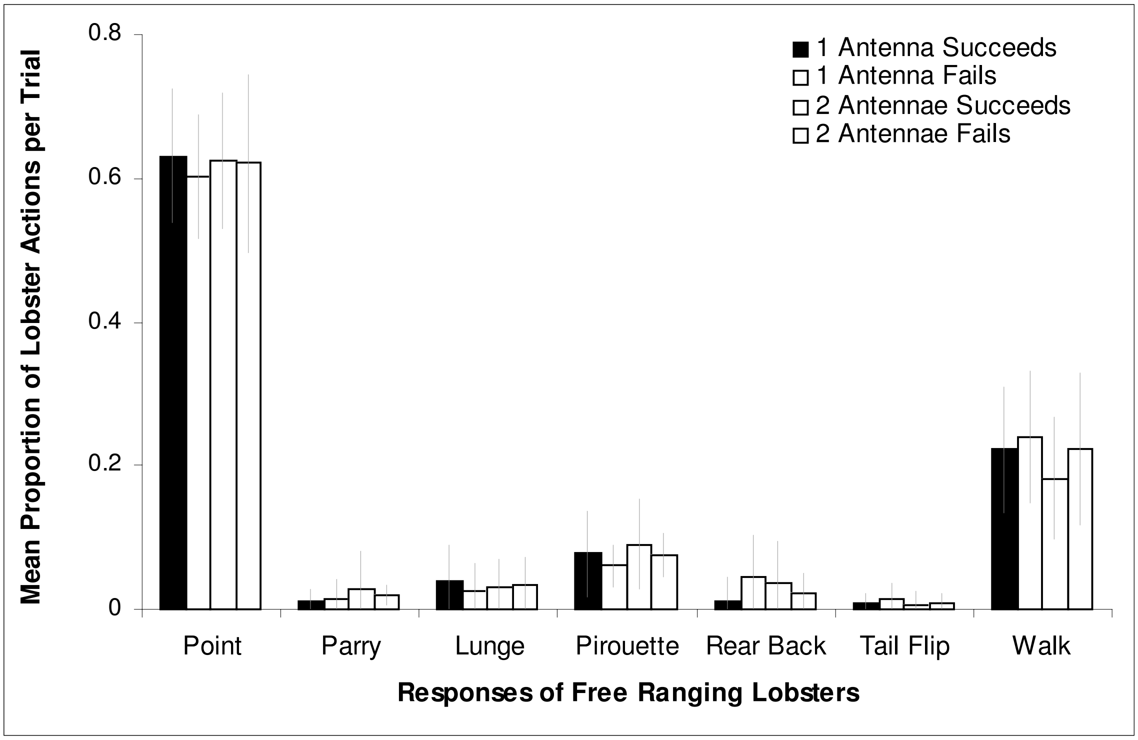

Figure 5a. Lobsters were most likely to Respond to an Approach by Pointing. Succeed: n= 10 (1 antenna) and 15 (2 antennae). No differences seen by antennae number. Fail: n= 10 (1 antenna) and 5 (2 antennae). Error bars show standard deviation.

Lobster actions per fish attack according to survival success and antennae number.

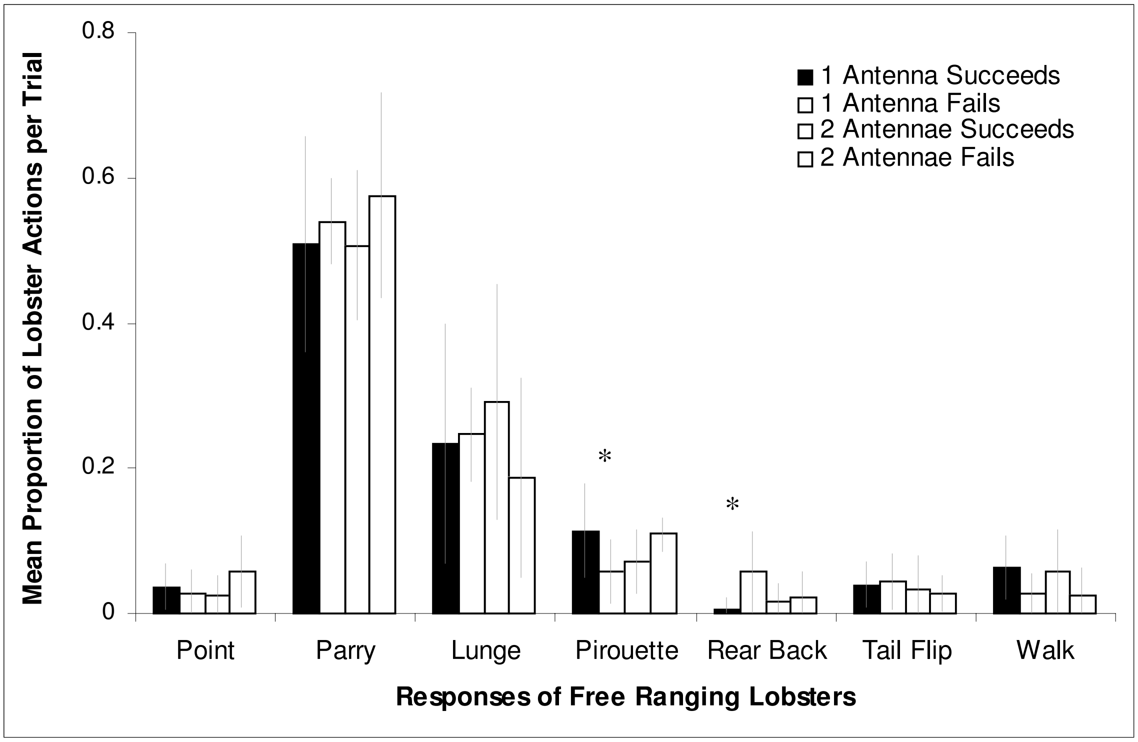

Figure 5b. All lobsters were most likely to respond to an Attack by Parrying the fish. Successful 1 antenna lobsters Pirouetted more frequently and Reared Back less. Lobsters with both antennae responded the same regardless of success. Succeed: n= 10 (1 antenna) and 15 (2 antennae). Fail: n= 10 (1 antenna) and 5 (2 antennae). Error bars show standard deviation. *$p < 0.05$.

Lobster actions per fish Bite Attempt according to survival success and antennae number.

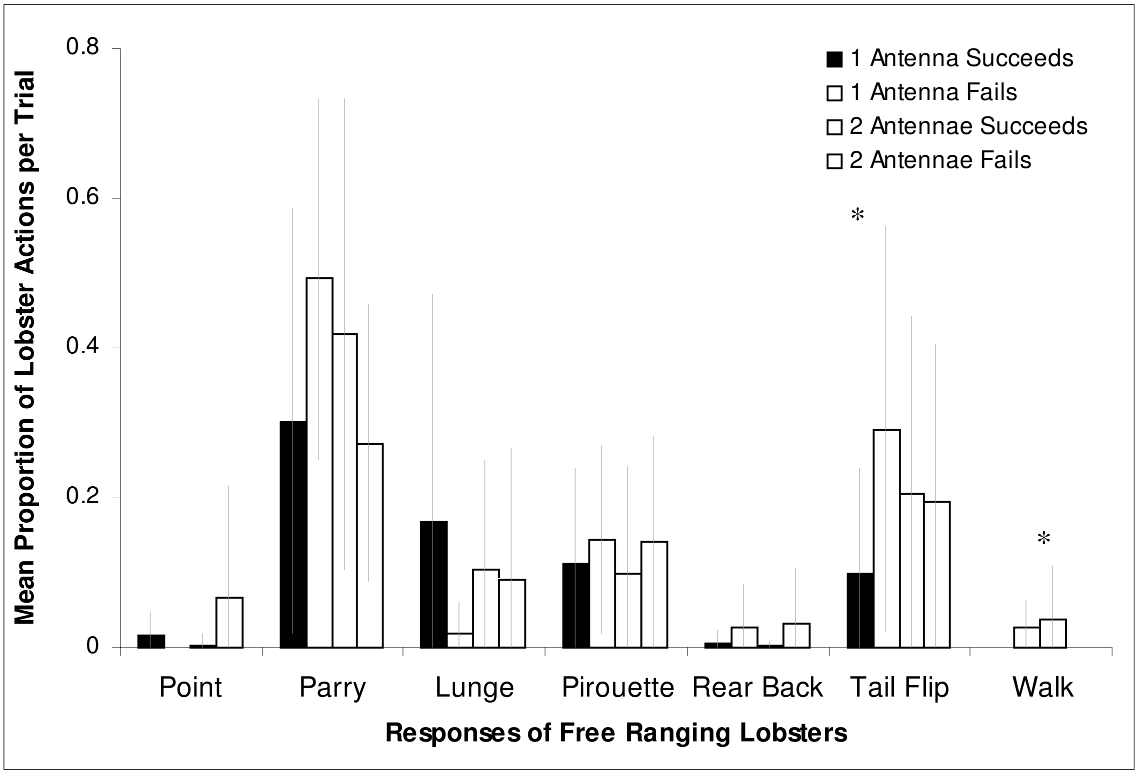

Figure 5c. Lobsters Parried Bite Attempts most frequently. Tail Flips increased when lobsters were failing. Walking benefited lobsters with 2 antennae more than those missing an antenna. Succeed n= 10 (1 antenna) and 15 (2 antennae). Fail n= 10 (1 antenna) and 5 (2 antennae). Error bars show standard deviation. *$p < 0.05$.

Lobster actions per fish Bite according to survival success and antennae number.

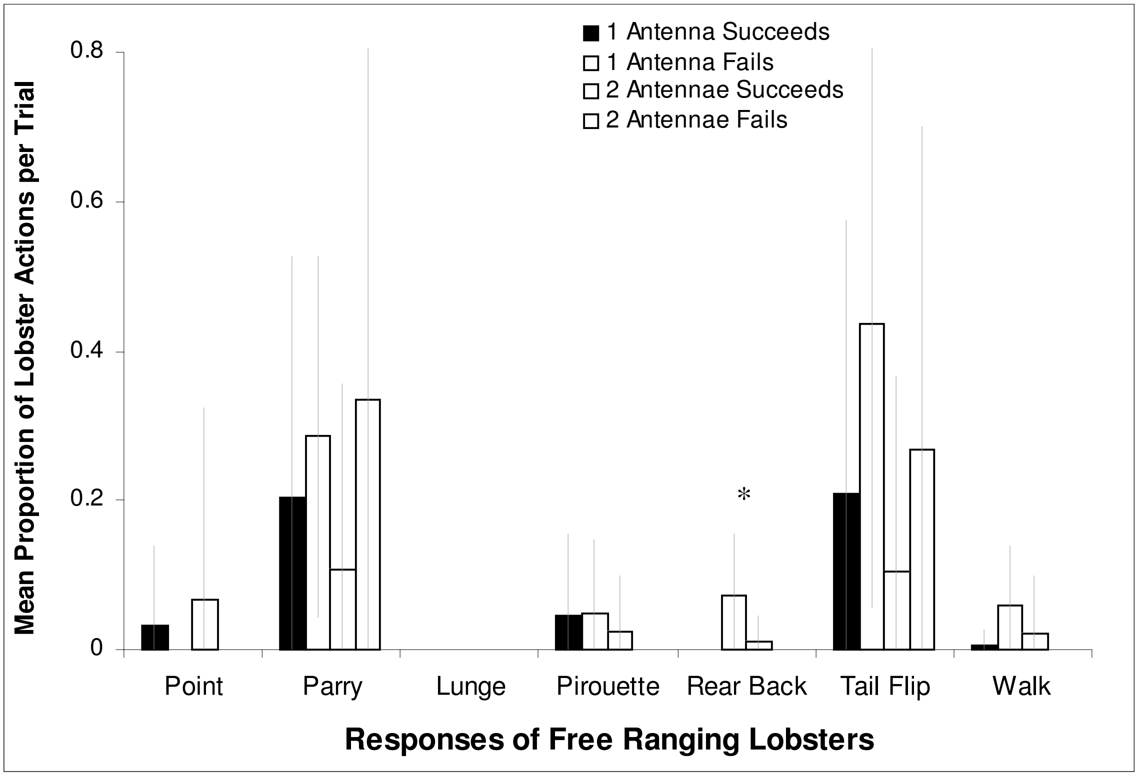

Figure 5d. Lobsters responded to a Bite with a Parry or Tail Flip. Rearing Back was associated mostly with failing lobsters with a single antenna. Succeed: n= 10 (1 antenna) and 15 (2 antennae). Fail: n= 10 (1 antenna) and 5 (2 antennae). Error bars show standard deviation. *$p < 0.05$.

Lobster actions per fish Circle according to survival success and antennae number.

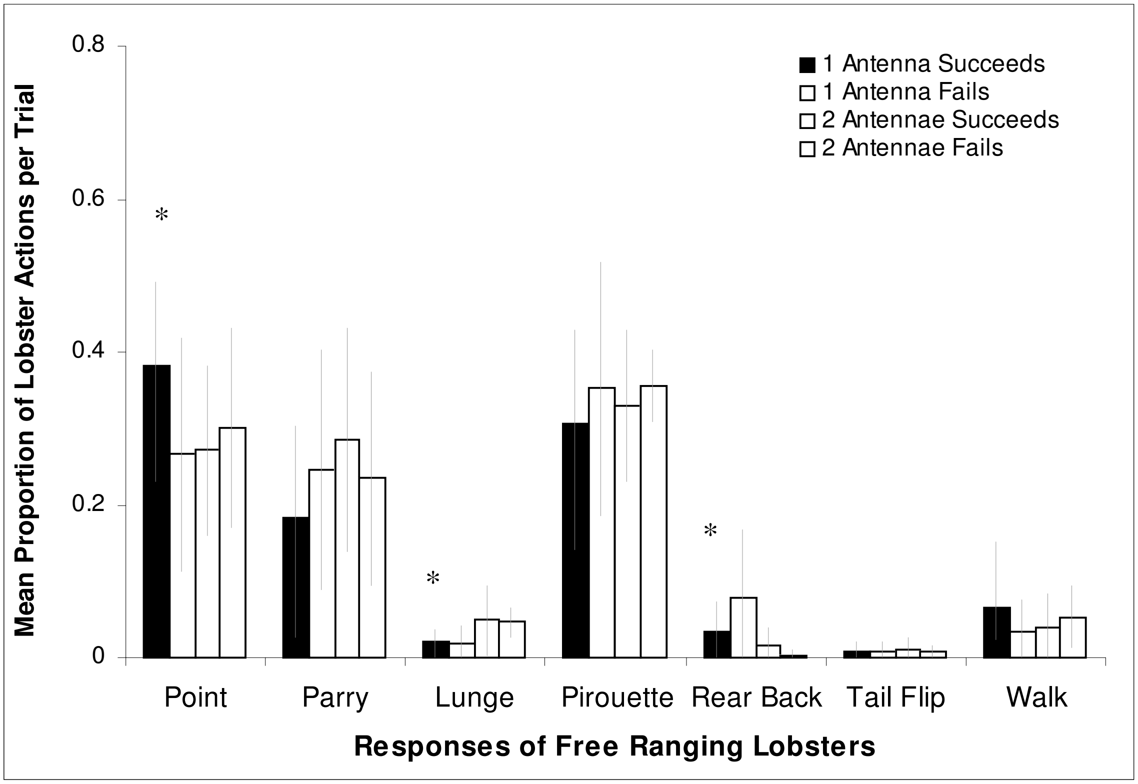

Figure 5e. While a lobster responded to fish Circling with a Pirouette, it could simultaneously Point or Parry. Lunging was performed more by lobsters with both antennae. Rearing Back was seen to increase when lobsters with only 1 antenna were failing. Succeed: n= 10 (1 antenna) and 15 (2 antennae). Fail: n= 10 (1 antenna) and 5 (2 antennae). Error bars show standard deviation. S*p < 0.05.

Direction of Circling by fish according to lobster antennae number.

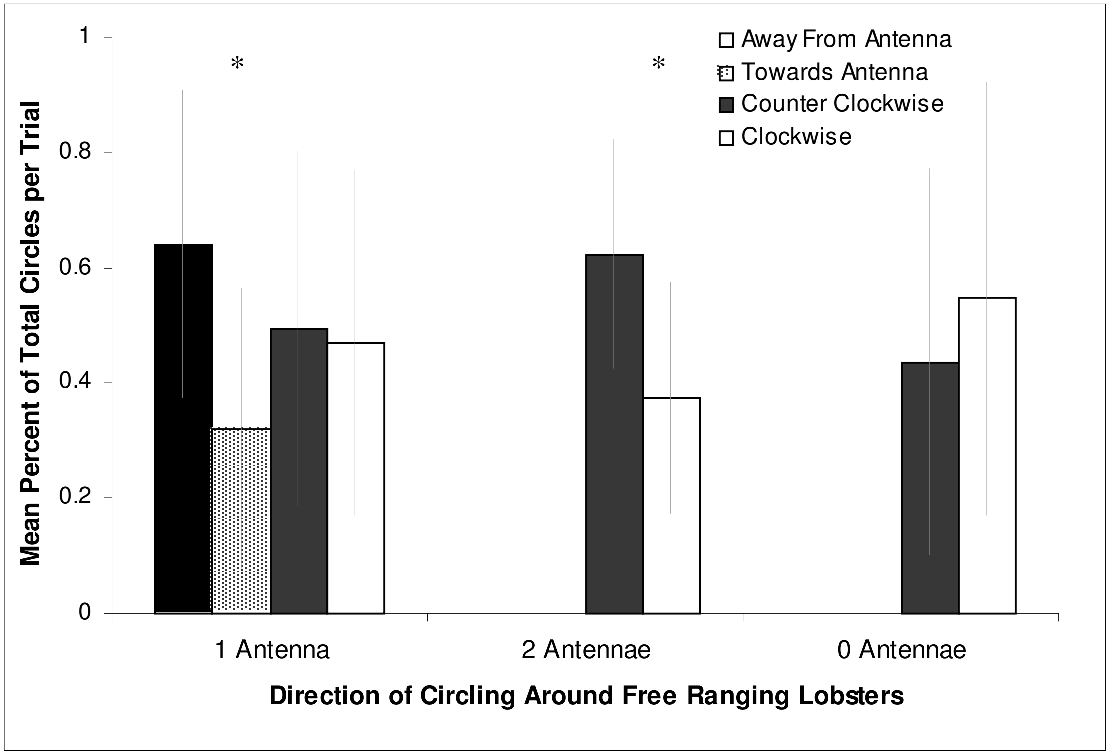

Figure 6. Fish were more likely to swim away from the remaining antenna of a 1 antenna lobster. Bias was seen for Circling Counterclockwise around lobsters with both antennae. The fish had no preference for circling direction around lobsters without antennae. N= 20. Error bars show standard deviation. *$p < 0.05$.

Table 6. For tethered lobster trails, overall fish and 0 antennae lobster action differences when compared to 2 antennae and 1 antenna lobsters.

Analysis by One-Way ANOVA. df = 2,43.

0 Antennae Lobsters, Tethered

Source	F	p <	fish (f)/lobster (l)
Attack	5.52	0.0073	(f)
Bite Attempt	6.77	0.0028	(f)
Bite	18.41	0.0001	(f)
Tail Flip	26.19	0.0001	(l)

Tethered Lobsters

Injury and Mortality

Tethered MA lobsters lost more antenna length (21%) than the Intact lobsters (12 %) although most Intact (68 %) and MA (53%) lobsters suffered no antennal injury. Mortality between Intact (47%) and MA (69%) lobsters did not differ statistically. However all NA lobsters were killed (Figure 7). Trial lengths for MA and Intact lobsters were similar and did not depend on whether the fish succeeded in killing a lobster or eventually stopped interacting with it, allowing the lobster to survive. The time until unsuccessful lobsters were defeated was not statistically different for Intact (mean, 8 min.) and MA (mean, 5.5 min.) but least for NA lobsters, which were killed quickly (mean, <3 min.) (Figure 8).

Tethered lobster injuries and survival according to antennae number.

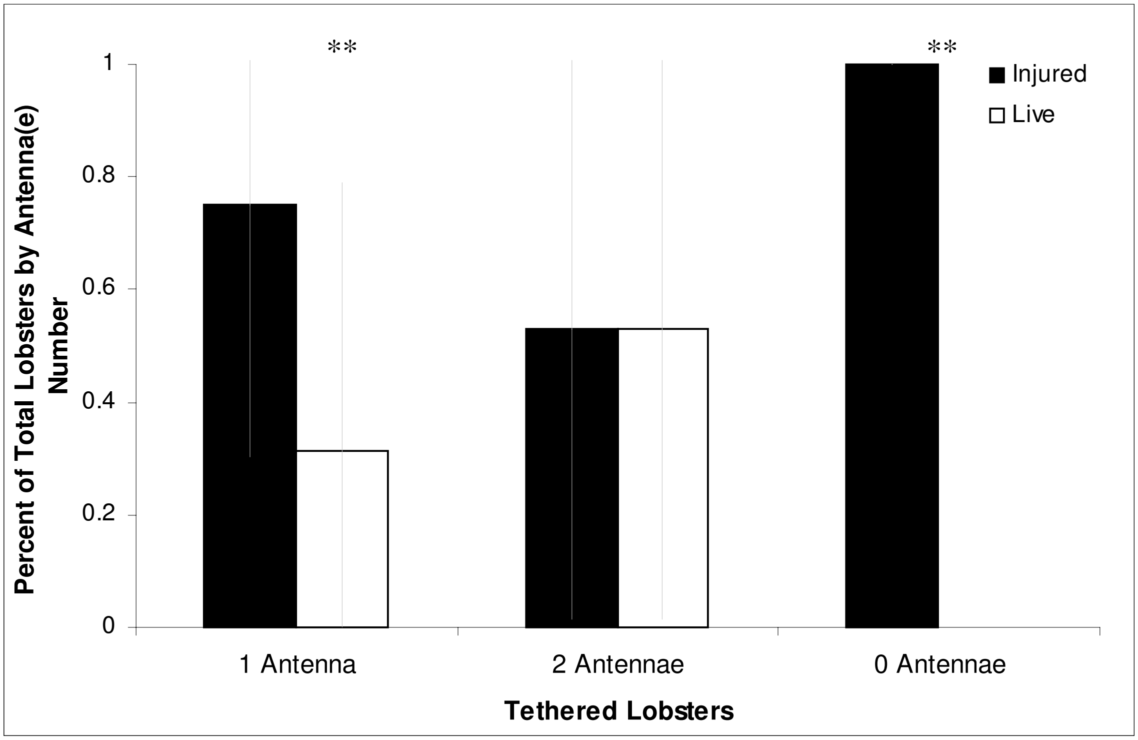

Figure 7. Lobsters without antennae only differ from lobsters with 2 antennae for injuries obtained. Without antennae, survival was low. Lobsters with one or both antennae did not differ significantly in survival. n= 16 (1 antenna), 17 (2 antennae), and 13 (0 antennae). Injuries are both lethal and nonlethal. Error bars show standard deviation. *p < 0.05.

Average trial length for tethered lobsters.

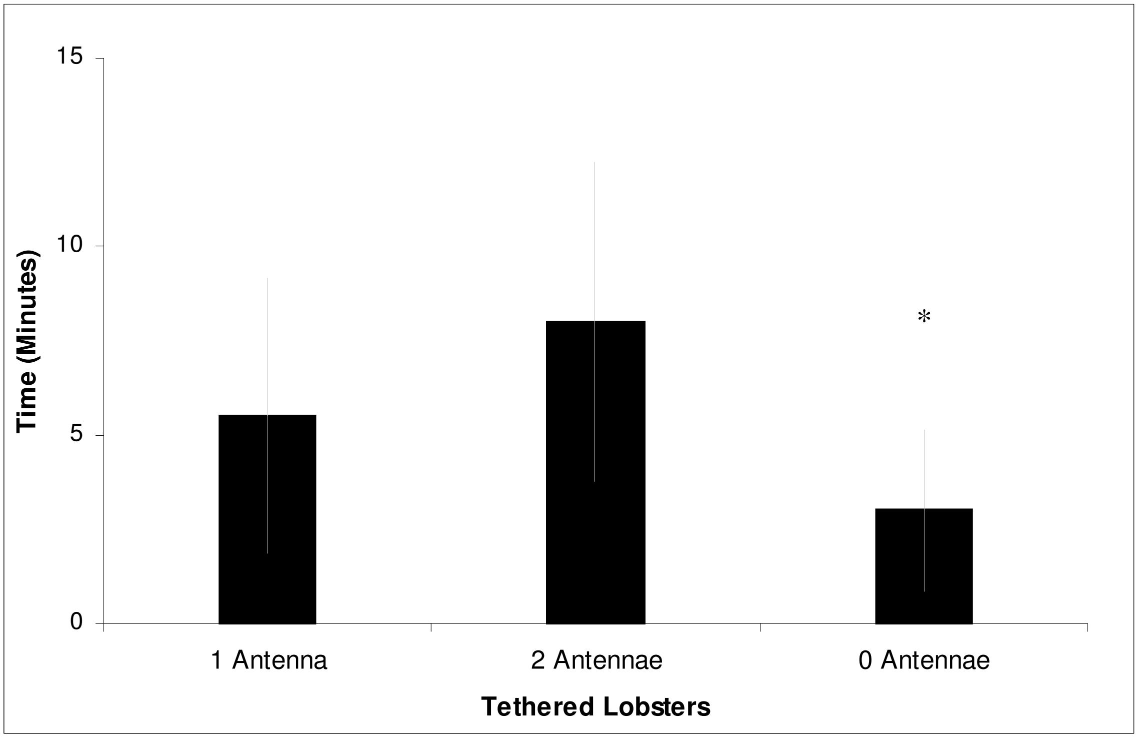

Figure 8. Trails were shortest for lobsters missing an antennae. Though not different from 1 antenna, lobsters with both antennae showed a trend for having the longest trial time of all. n= 16 (1 antenna), 17 (2 antennae), and 13 (0 antennae). Error bars show standard deviation. *$p < 0.05$.

Fish Actions

Overall, the actions of the fish against MA and Intact lobsters were similar. By comparison, NA lobsters received comparatively more Bites and Bite Attempts but fewer Attacks (Table 6; Figure 9). Fish that were successful at defeating a MA lobster Approached less often but exhibited more Attacks, Bite Attempts, and Bites as compared to unsuccessful fish (Table 7a; Figure 9). Fish that defeated Intact lobsters landed more Bites than unsuccessful fish (table 7b; Figure 9). Fish behaviors were similar whether or not they were successful against either Intact or MA lobsters.

Lobster Actions

Intact and MA lobsters overall responded similarly to fish actions. NA lobsters, which could not Point or Parry, Lunged as often as MA and Intact individuals and Tail Flipped more than either (Table 7c; Figure 9).

Failing MA lobsters tended to Point less but Parry and Tail Flip more than their successfully defending counterparts (Figure 10a). Intact lobsters that eventually lost a bout Reared Back and Tail Flipped more frequently than those that effectively defended (Table 7b; Figure 10b). Failing MA lobsters tended to Tail Flip more frequently than failing Intact lobsters, otherwise the actions were statistically similar between the two groups (Figures 11a,b).

Tethered Lobsters compared to Free Ranging Lobsters

Antennal loss was the same between Tethered and Free Ranging MA and Intact lobsters. Although the Free Ranging trials were longer than Tethered trials ($p < 0.0001$) (Figure 12), differences in mortality and injury rate were not statistically different (Figure 13).

Intact Tethered and Free Ranging lobsters exhibited similar responses to triggerfish (Figure 14a). The most apparent difference was with Tethered MA lobsters, which triggerfish Bit more than free-ranging cohorts (1-Way ANOVA: $df = 1, 34$, $F= 12.91$, $p < 0.001$) and which exhibited more Rearing Back (1-Way ANOVA: $df = 1,34$, $F= 5.36$, $p < 0.03$) (Figure 14b). The fish Attacked Free Ranging NA lobsters more (1-Way ANOVA: $df = 1, 31$, $F= 5.39$, $p < 0.03$) than Tethered NA individuals but Bit Tethered NA lobsters most (1-Way ANOVA: $df = 1, 31$, $F= 11.53$, $p < 0.002$). Correspondingly, Tethered NA lobsters lunged more often than Free Ranging cohorts (1-Way ANOVA: $df = 1, 31$, $F= 10.17$, $p < 0.003$) (Figure 14c).

Table 7. Tethered lobster survival comparisons.

a) Comparison of 1 antenna lobster differences in their success or failure to survive a trial. **b)** Comparison of 2 antennae lobster differences in their success or failure to survive a trial. **c)** 1 antenna lobsters that failed to survive are compared to 2 antenna lobsters that failed. Only one difference occurred. No difference was seen between successful 2 antennae and 1 antenna lobsters. All tests used One-Way ANOVA. df = 1,18.

a) 1 Antenna, Tethered Lobster Success vs. Failure to Survive

Source	F	p <	fish (f)/lobster (l)
Approach	9.33	0.0086	(f)
Attack	5.58	0.030	(f)
Bite Attempt	12.58	0.0032	(f)
Bite	12.90	0.003	(f)
Point	9.48	0.0082	(l)
Parry	7.78	0.015	(l)
Tail Flip	22.52	0.0003	(l)

b) 2 Antennae, Tethered Lobster Success vs. Failure to Survive

Source	F	p <	fish (f)/lobster (l)
Bite	12.19	0.033	(f)
Tail Flip	5.28	0.037	(l)
Rear Back	6.83	0.020	(l)

c) 2 Antennae vs. 1 Antenna, Tethered Lobster Failure to Survive

Source	F	p <	fish (f)/lobster (l)
Tail Flip	9.09	0.010	(l)

Overall actions of fish and tethered lobsters based on antennae number.

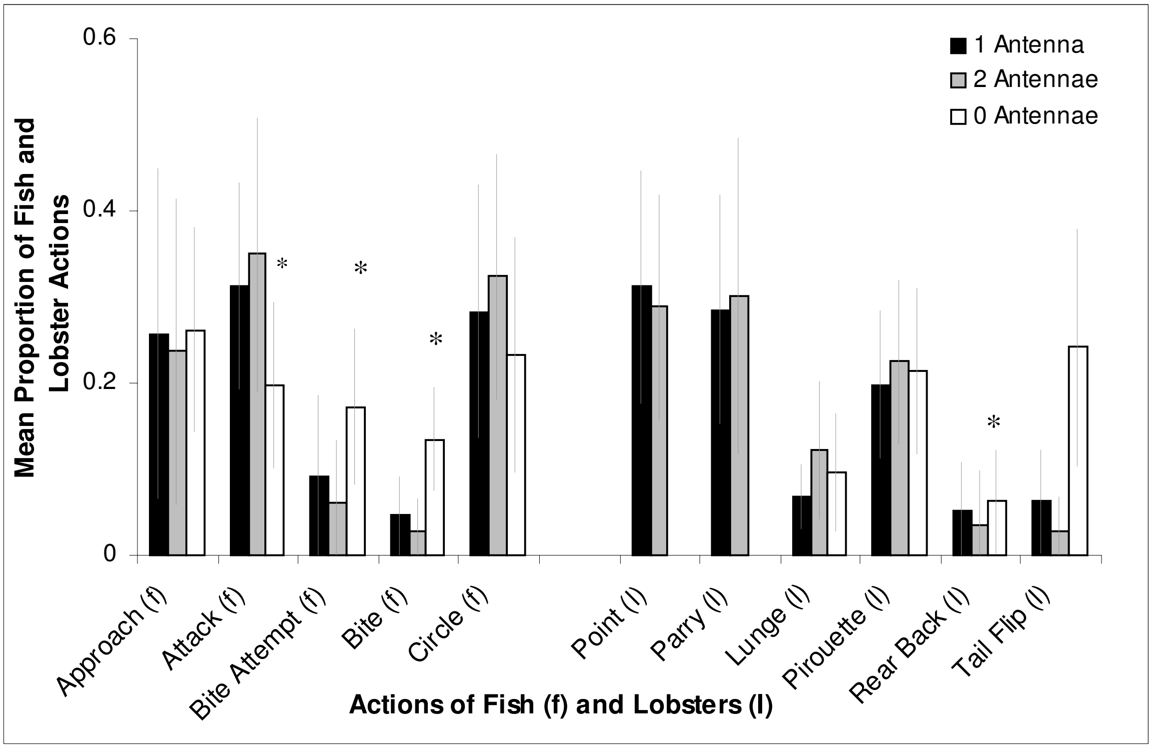

Figure 9. During tethered trials, differences in action frequencies are only seen for lobsters without antennae and their fish. Lobsters with any antennae and their fish behaved similarly. N= 16 (1 antenna), 17 (2 antennae), and 13 (0 antennae). Error bars show standard deviation. *$p < 0.05$.

Comparison of trials based on tethered lobster survival success with one antenna.

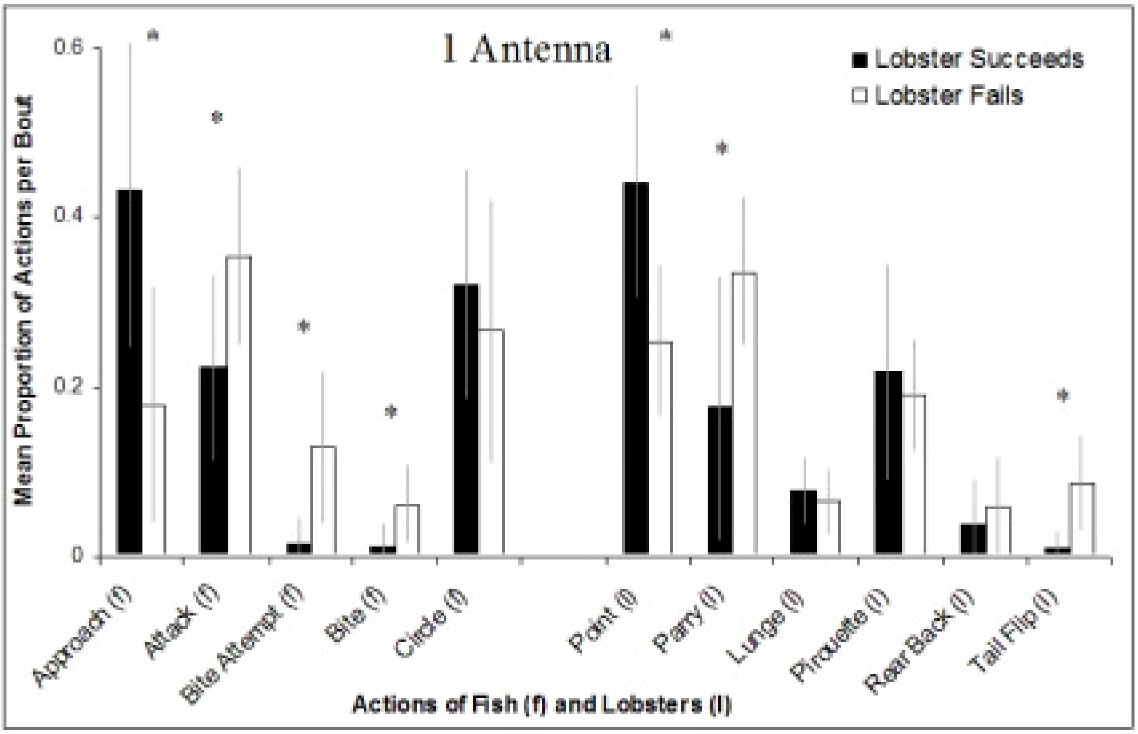

Figure 10a. Successful lobsters were better able to keep the fish out of antenna range. n= 5 (succeeds) and 11 (fails). Error bars show standard deviation. *$p < 0.05$.

Comparison of trials based on tethered lobster survival success with two antennae.

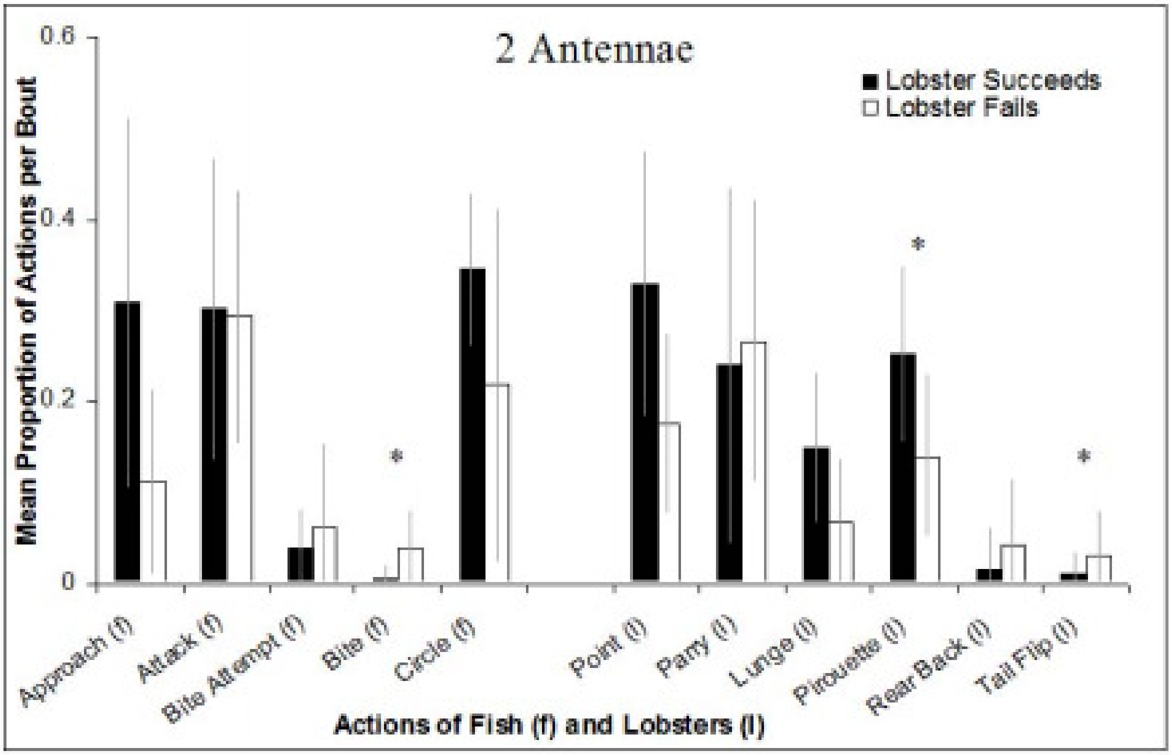

Figure 10b. Successful lobsters were more responsive to the fish. n= 9 (succeeds) and 8 (fails). Error bars show standard deviation. *$p < 0.05$.

Comparison of successful tethered lobsters with one and two antennae.

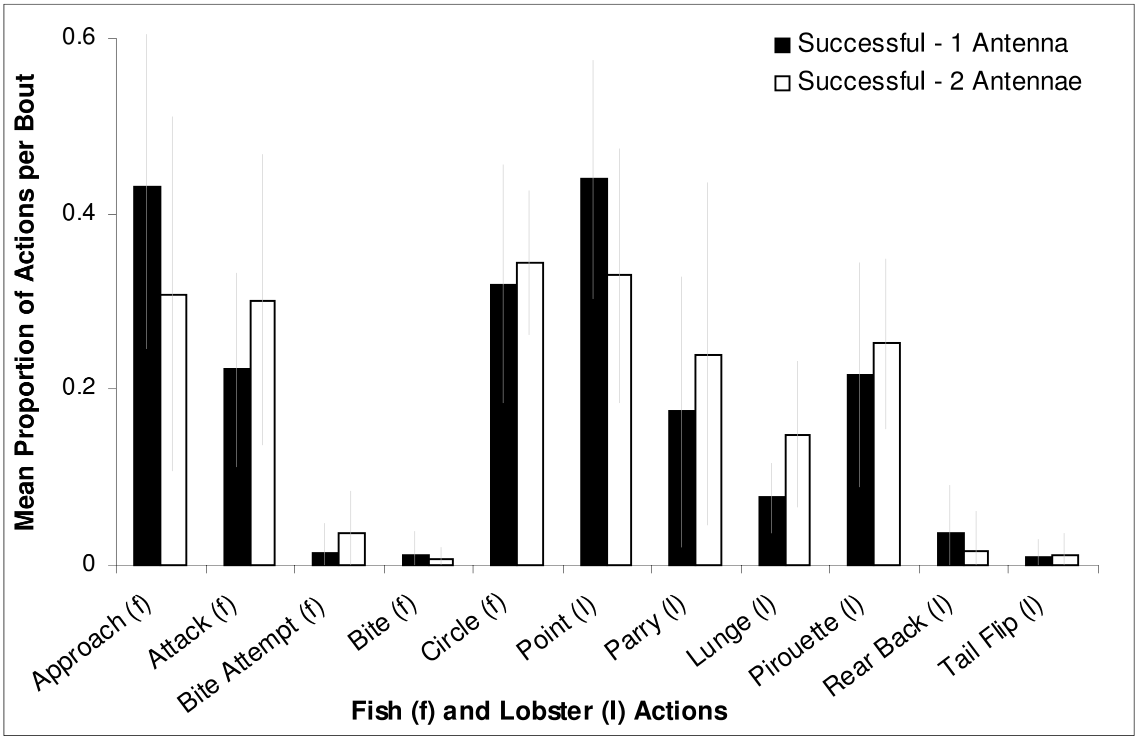

Figure 11a. No difference was found in the overall actions of lobsters that survived a trial if they had one or both antennae. n = 5 (1 antenna) and 9 (2 antennae). Error bars show standard deviation. *$p < 0.05$.

Comparison of failed tethered lobsters with one and two antennae.

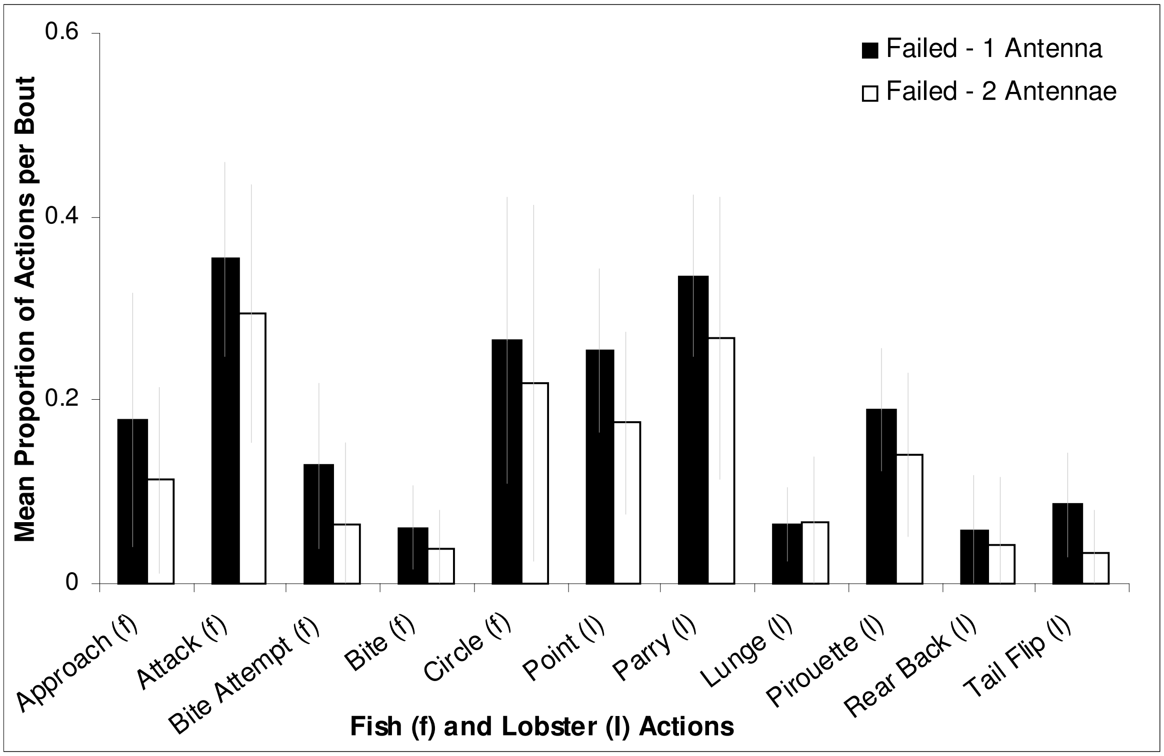

Figure 11b. No difference was found in the overall actions of lobsters that failed to survive a trial if they had one or both antennae. n= 11 (1 antenna) and 10 (2 antennae). Error bars show standard deviation. *$p < 0.05$.

Average trial time for free-ranging and tethered lobsters.

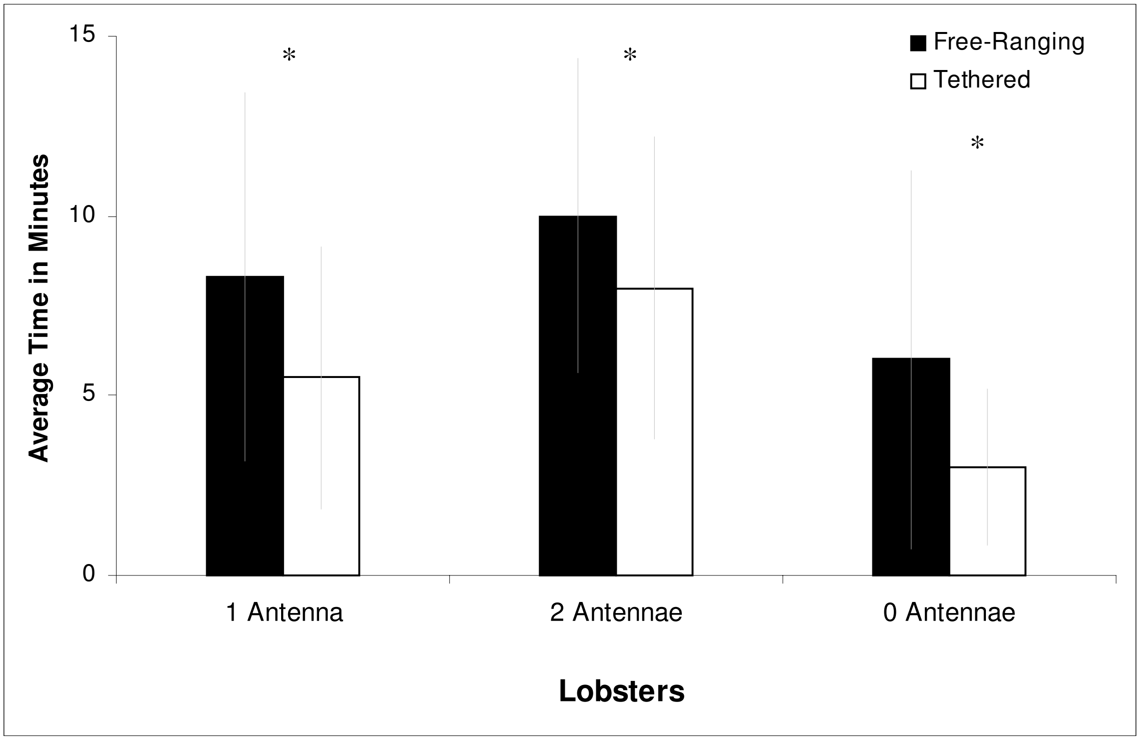

Figure 12. Though different, the trends for free-ranging and tethered lobsters are similar. Free Ranging n= 20 each. Tethered n= 16 (1 antenna), 17 (2 antennae), and 13 (0 antennae). Error bars show standard deviation. *$p < 0.05$.

Free-ranging and tethered lobster injuries and survival according to antennae number.

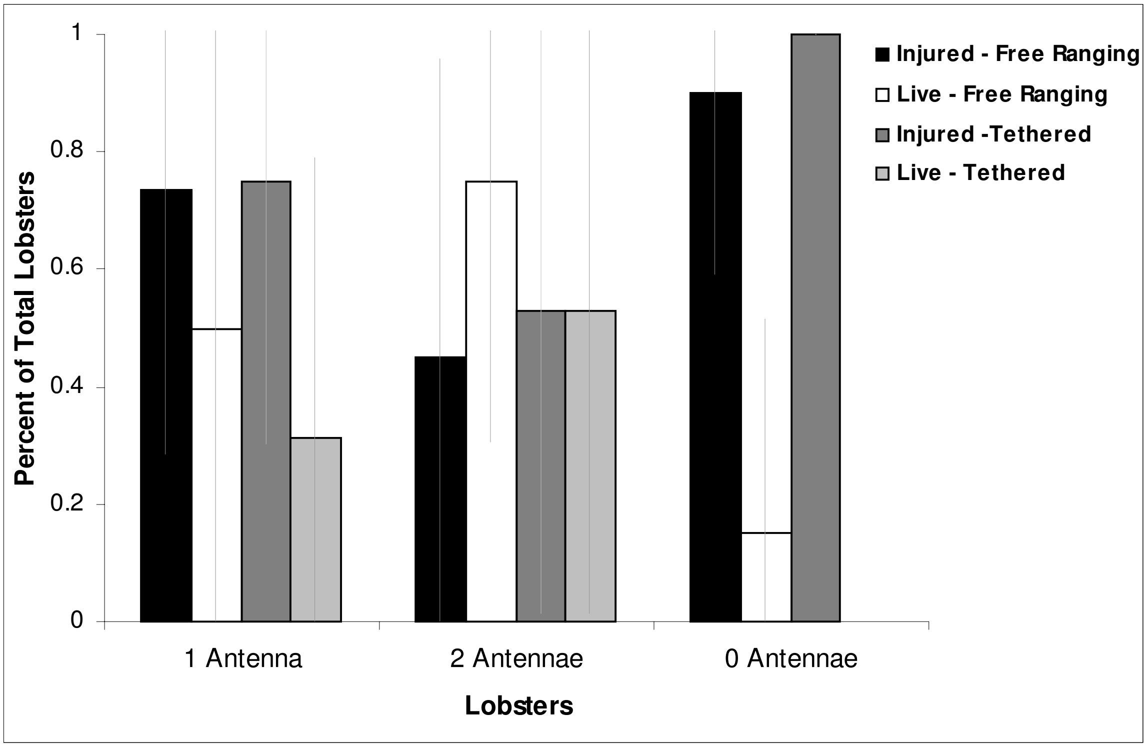

Figure 13. No differences were found between injury rate and the ability to survive according to whether the lobsters were tethered or not. Free-ranging n= 20 for each antennal class. Tethered n= 16 (1 antenna), 17 (2 antennae), and 13 (0 antennae). Injuries are both lethal and nonlethal. Error bars show standard deviation.

Overall trial comparison of tethered and free ranging lobsters with two antennae.

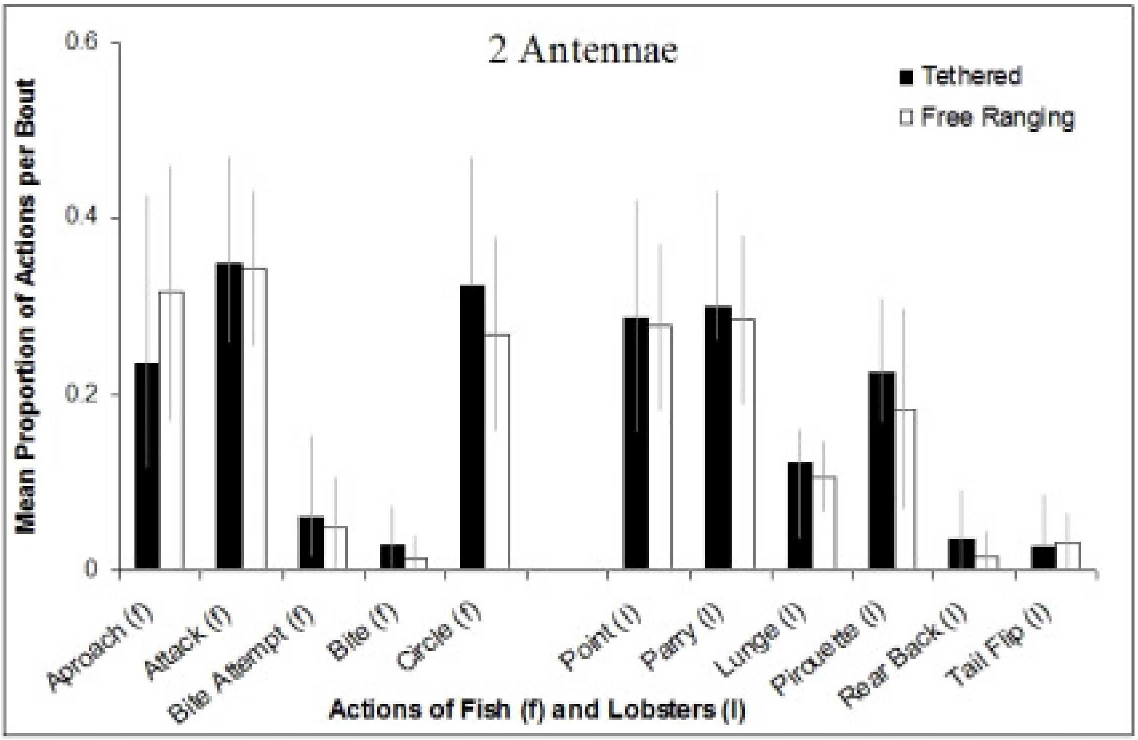

Figure 14a. No differences were found between actions of tethered and free-ranging lobsters and their fish. Tethered n = 17. Free ranging n= 20. Error bars show standard deviation.

Overall trial comparison of tethered and free ranging lobsters with one antenna.

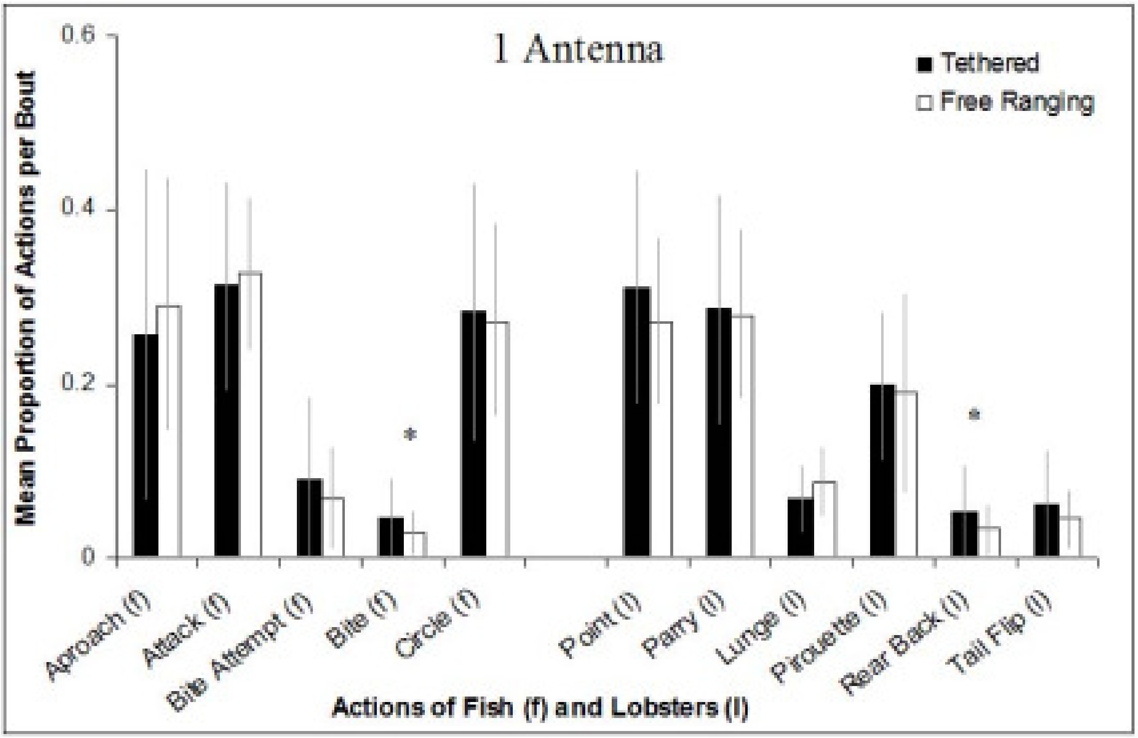

Figure 14b. Tethered lobsters were Bitten more and responded with more frequent Rear Backs. Tethered n= 16. Free Ranging n= 20. Error bars show standard deviation. *$p < 0.05$.

Overall trial comparison of tethered and free-ranging lobsters without antennae.

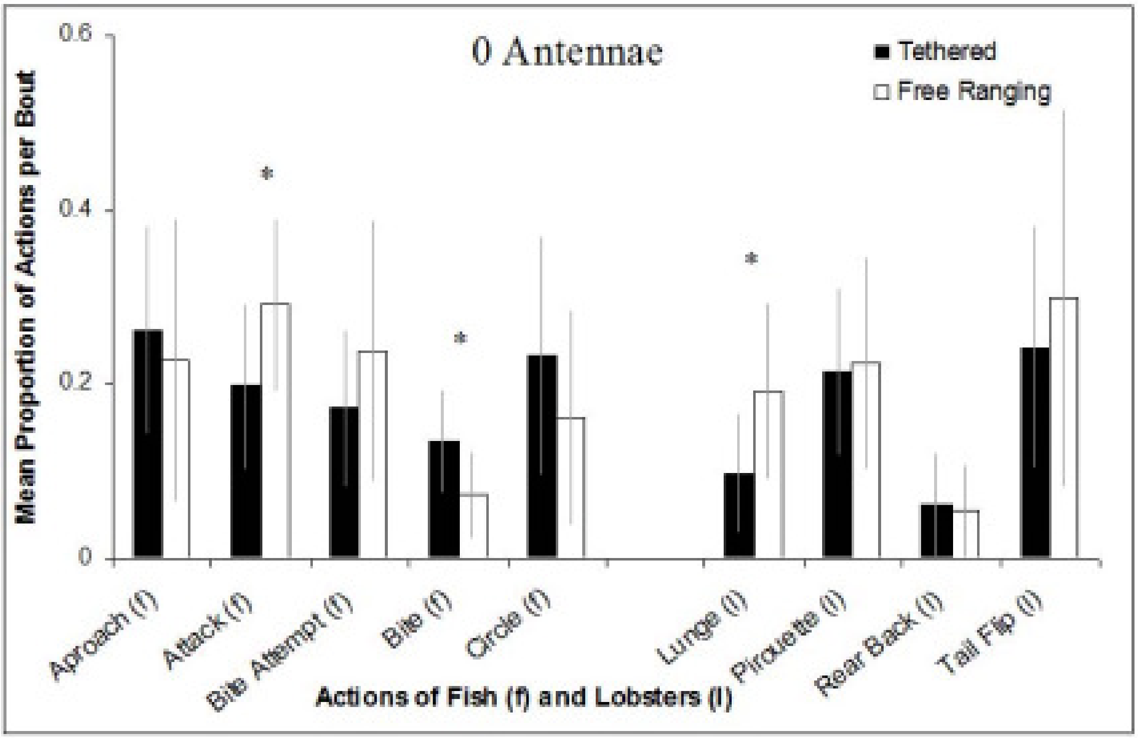

Figure 14c. Tethered lobsters were Bitten more frequently and Attacked less frequently. Free-ranging lobsters were more likely to Lunge. Tethered n= 13. Free-ranging n= 20. Error bars show standard deviation. *$p < 0.05$.

Taster's Choice- Triggerfish Preference for De-antennated Lobsters

All triggerfish initially exhibited Circling around both the MA and Intact lobsters but Circled much more (1-Way ANOVA: $df = 1, 30$, $F = 23.40$, $p < 0.0001$) around the MA individuals as predatory attacks progressed (Figure 15). Once a focal lobster was chosen, whether MA or Intact, Circling of the other individual became infrequent and brief. Likewise, the fish mostly Approached during the beginning of the trials but similarly for Intact and MA cohorts.

Biting was directed largely on the MA lobsters, resulting in more injuries (90% vs. 13%) (1-Way ANOVA: $df = 1, 55$, $F = 72.88$, $p < 0.0001$) and higher mortality compared to Intact lobsters (90% vs. 10%) (1-Way ANOVA: $df = 1, 55$, $F = 90.95$, $p < 0.0001$) (Figure 16). Whereas all of the MA lobsters were bitten, only 3 of 15 Intact lobsters were bitten. The initial Bites of the trial were nearly always on the MA lobster (13 of 15), usually after a bout of Circling. Also, the triggerfish took significantly longer (1-Way ANOVA: $df = 1, 28$, $F = 5.19$, $p < 0.031$) to land the first Bite on an Intact lobster (Figure 17). In most trials, the Intact lobster received few actions from the fish.

Triggerfish interest in lobsters according to antennae number.

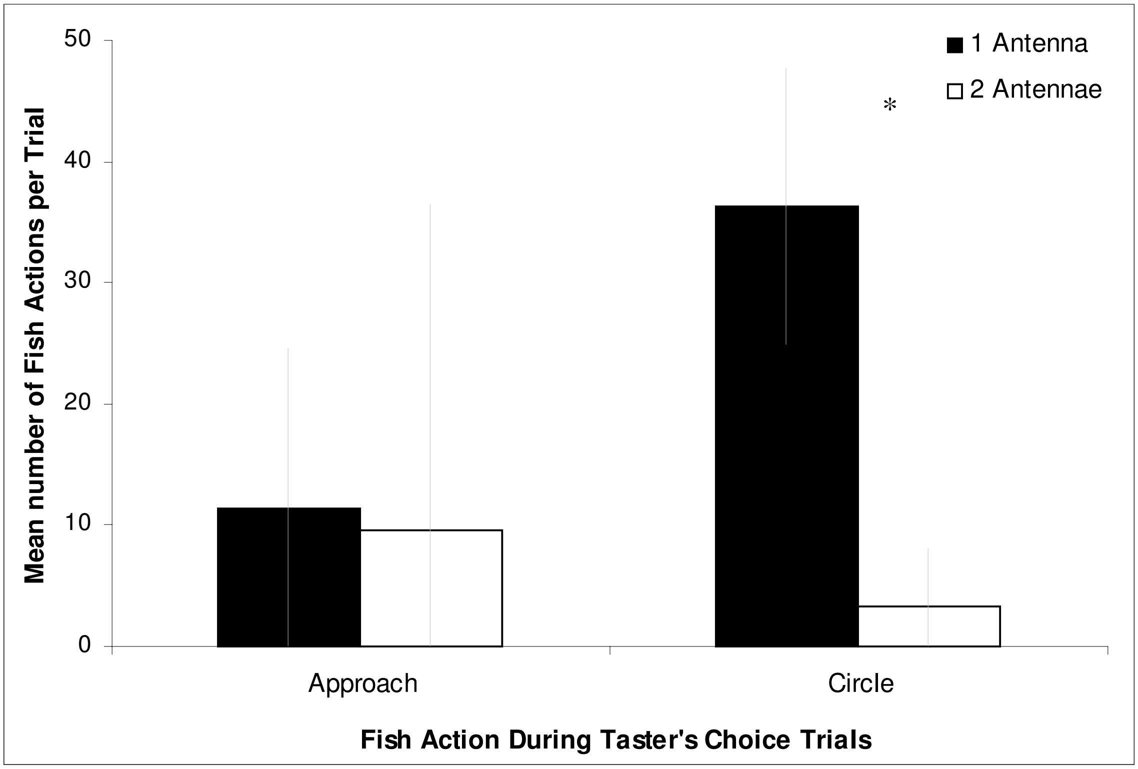

Figure 15. Visual inspection of the lobsters might have occurred during Approaching at the beginning of a trial. Once Circling started, the triggerfish Circled lobsters missing an antenna most frequently. N= 29. Error bars show standard deviation. *$p < 0.05$.

Injury and/or survival of lobsters during Taster's Choice trials according to antennae number.

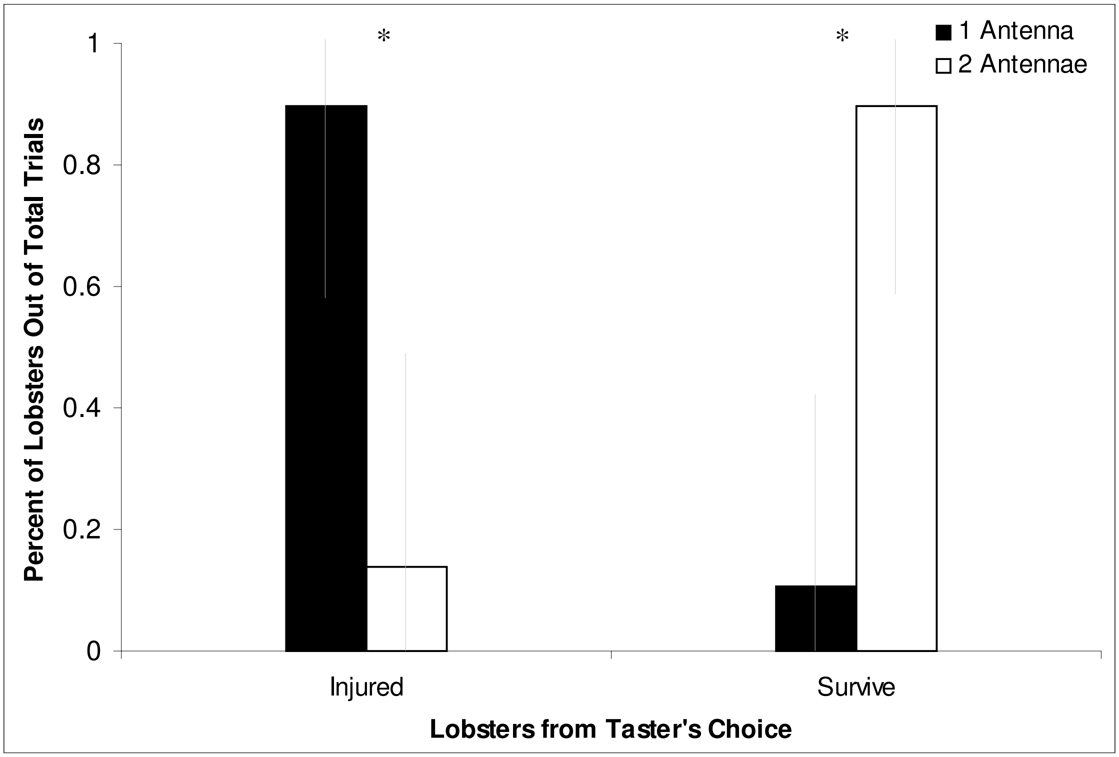

Figure 16. Injuries are both lethal and nonlethal. Lobsters missing an antenna were injured more than intact lobsters. Lobsters with both antennae were more likely to survive a trial. N= 29. Error bars show standard deviation. *$p < 0.05$.

Time until the first Bite was received during a Taster's Choice trial according to antennae number.

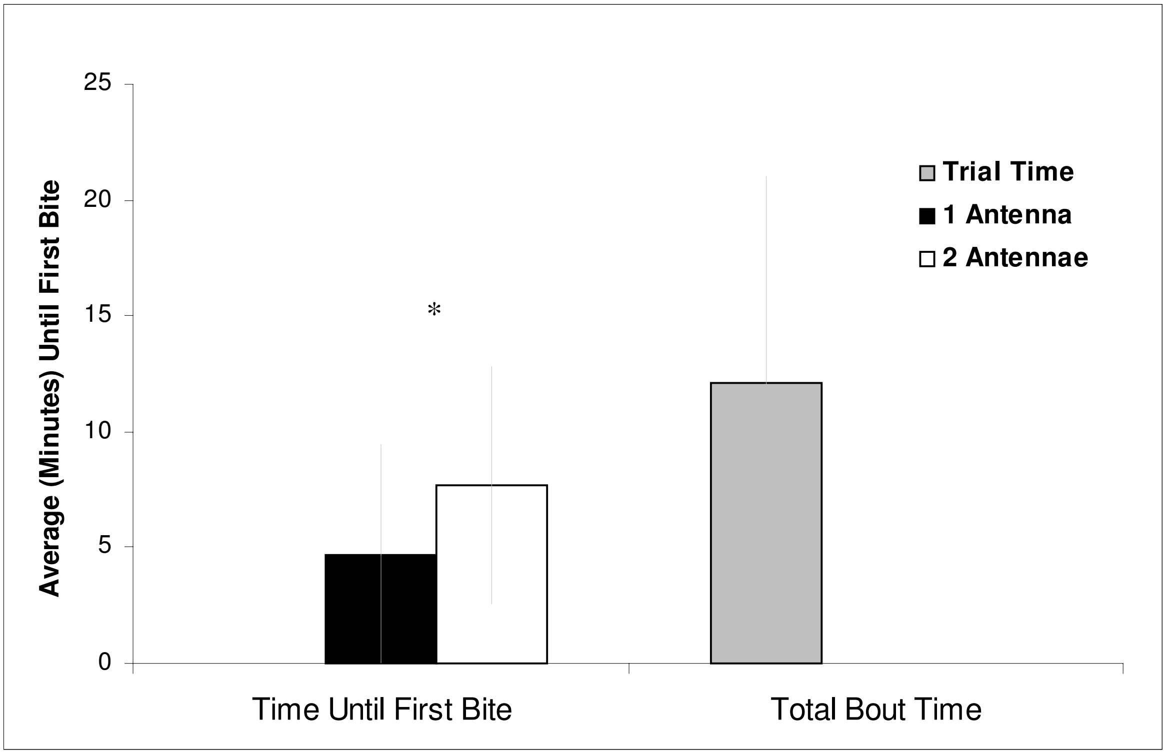

Figure 17. Lobsters missing an antenna were Bitten sooner than intact lobsters. N= 29. Error bars show standard deviation. *p < 0.05.

DISCUSSION

Effect of antenna loss.

Antennal loss heightens injury and mortality during triggerfish predatory clashes, mainly when both antennae are missing (NA lobsters), as was also reported by Barshaw et al. (2003) for *Palinurus elephas*. Triggerfish nearly always successfully killed antenna-less lobsters and did so in much less time than MA and Intact lobsters. Lunging by the former provided only very brief repulsion of an attacker. Potentially evasive actions, Tail Flipping and Walking, were ineffective in the structure-less KML arena that resembled natural open foraging and migratory substrate. In nature, these escape behaviors are probably useful only amidst abundant shelter or in a familiar area from which a lobster can return rapidly to a home den. Otherwise, a lobster without antennae needs to remain sheltered, perhaps only emerging to forage in complete darkness near a den. Testing this would be useful.

Shelter seclusion by antenna-less lobsters may function best against relatively small diurnal biting or grasping predators such as triggerfish or large portunid crabs. The den may not be a completely effective refuge against octopus that can reach into it to extract prey or large suction predators like Goliath grouper or nurse sharks. In this case, the antennae cannot be jammed against the den walls, making an antenna-less lobster easier to remove. In the open, when a triggerfish grasps an antenna and drags a lobster about, the lobster usually does not attempt to escape. Rather than immediately autotomizing that antenna and fleeing, the lobster remains still until the fish releases it (sometimes having bit off a piece of the antenna) then resumes its defensive actions. However, it seems more beneficial for a lobster within a den to give up its antenna to the fish while remaining within the protection of the cavity. This may be why so many antennae are seen littering the substrate near crevices where divers hunt lobsters (pers. obs.).

The Taster's Choice experiment showed that triggerfish quickly distinguish between Intact and MA lobsters then concentrate attack on the latter. The initial Circling and

Approaching gave the impression of inspection by the triggerfish. Close approach with scanning eye movements of an object is a characteristic behavior of triggerfish in the field as well as in captivity (WFH, unpublished observations; Barshaw et al., 2003). Very rarely triggerfish attempted to Bite an Intact lobster when faced with both options. In nature, this selectivity is likely to put greater predation pressure on a MA lobster to defend itself even if Intact lobsters are nearby. In fact, free moving MA lobsters in arena trials were bitten and killed sooner than Intact cohorts, although the variance was high (difference in percent killed was not statistically significant). However, a strong effect of reduced antennal coverage was apparent because 76% of bite injuries were on the antenna-less side. Damage to the antennae of MA lobsters also was twice that of Intact lobsters; i.e., all the antennal bites were on one antenna rather than spread between two antennae. Over a prolonged period, a MA lobster, unable to soon deter a fish, might lose its entire antennal defense. Also, under natural conditions MA lobsters may have less time than Intact cohorts to find shelter, conspecifics or a structure to aid in defense.

Because missing an antenna halves the primary defensive armament of a MA lobster, I expected that the frequencies or types of defensive actions of the lobster would need to radically change to compensate. For example, Tail Flipping sooner or for longer distances might sufficiently increase the probability of escape to offset the risk of exhaustion. Alternatively, intense initial Lunging might intimidate an ambivalent predator. However, based on all trials, Intact and MA lobsters responded similarly, while receiving similar treatment from the triggerfish, regardless of whether they eventually deterred an attacker or were killed. Unexpectedly, mortality and injury rates were also statistically similar between MA and Intact lobsters. Although the injury trend was higher for MA lobsters, the levels were far less than expected for an exposed individual missing its defensive weaponry on one side. That is, MA lobsters partly compensated for the antennal loss during retaliatory encounters with triggerfish.

Timing and consistency of defensive actions.

The relatively strong defense by MA lobsters, using the same actions as Intact individuals, raises the question of how they were able to so effectively compensate. Likewise, the distribution and types of actions by successful and unsuccessful triggerfish and lobsters were similar for both Intact and MA lobsters. That is, the compensatory events were not apparent from the overall frequency of actions by either the triggerfish or lobsters. Instead, the success of an attacking action by the predator or the deterring action by the prey seemed to depend on a lobster consistently performing a common action at a critical time, especially MA lobsters. The events of the free ranging trials support this.

Fish that were deterred by a lobster made Attempted Bites more frequently than successful fish but were instantly Parried or deflected away, failing to make solid, damaging contact. In fact, more Attacks and Bite Attempts were made on Intact lobsters than MA cohorts. In either case, successful fish concentrated Biting efforts late in a trial causing severe, eventually mortal injury, but actually making comparatively fewer Bites than unsuccessful fish. However, over many encounters, a lobster using both antennae may better prevent mortal injury than one with a single antenna. On the other hand, the fish must continue to press the attack until it either lands a debilitating Bite or gives up. Successful MA and Intact lobsters Pointed more often, possibly intimidating the fish and keeping it from getting into Attack range. Unsuccessful lobsters, negligent at keeping a fish out of potential Biting range, had to Parry more or attempt escape through Tail Flipping or Walking, which happened mostly at the end of a trial. Tail Flipping tires lobsters quickly, and appears to excite the fish to press the attack, yet does not propel a lobster faster than the fish's ability to keep up. Successful Intact lobsters mostly Walked to leave the point of engagement while simultaneously defending, which cannot be done while Tail Flipping. Though not statistically significant, this trend was shown by MA lobsters as well.

The differences in behavior between MA and Intact lobsters was most clearly discerned when I examined lobster responses in reaction to individual fish actions. Although there were no overwhelming differences in tactics, certain responses to the fish apparently determined whether the lobster deterred the predator. These differences were seen mainly when the fish came within antennal range. Successfully defending lobsters strongly Parried nearly all Attacks even though fish that got within antennal range often only feinted or veered away without making a Bite Attempt even if it was not Parried. Biting received noticeably weaker Parrying effort than Attack because the antenna(e) become less effective once the fish is close to the lobster's body. Most Parrying associated with a Bite either failed to deflect the fish or happened immediately after the Bite or Bite Attempts, especially for failing MA lobsters. However, the main response by losing Intact and MA lobsters was Tail Flipping that sometimes but only very temporarily put the fish out of Attack range.

Successful MA lobsters responded more aggressively to a fish. They were more likely to Pirouette and face a fish that Approached from behind or to the side. If a fish Approached the side missing an antenna, a MA lobster leaned against the substrate to swing the remaining antenna across the midline of the body (Crossing Over) to engage the fish, effectively protecting the vulnerable flank. Interestingly, the lobsters usually initiated this action only after Bite Attempts. In a separate study, I had to sharply poke MA lobsters on the exposed side of the body to induce Cross Over. Intact lobsters seemed to be more successful at Parrying without Pirouetting, perhaps because their only exposed area was at the rear. For them, a slight turn, not counted as a Pirouette, may be enough to deter the fish. Being 'aware' of gaps in the area around the body not covered by antennae may allow the lobster to adjust its actions accordingly both when out in the open and when structures are nearby.

I documented elsewhere how lobsters with one antenna use a tank wall or other vertical surface to protect the vulnerable side (Parsons and Herrnkind, unpublished abstract). MA lobsters keep the antenna-less side next to the structure and the remaining antenna pointing toward the fish, effectively covering the opening in its defenses. In nature, a lobster could take advantage of a sea whip, large sponge, etc. to assist defense. By contrast, a lobster with both antennae backs its tucked abdomen against a structure while directing both antennae at the fish.

More than one lobster response may happen in succession to a single fish action; i.e., a lobster can perform many actions with its antenna(e) while Pirouetting as a fish Circles. Especially, they Point, Parry or Lunge depending on the distance of the fish. Lunging may be crucial for MA lobsters because successful lobsters did so most frequently. Lunging and Parrying both occasionally cause contact with the fish's eye, probably causing injury. Vision appears to be critical to feeding and social interactions of triggerfish. A Lunge involves substantial force and may be especially daunting to a fish. However, it appears to require such a high expenditure of effort that it can't be sustained repeatedly for a long bout. A MA lobster also may tire from being Circled rapidly. The fish circled the MA lobsters with a tighter radius and at a faster rate than they did against Intact lobsters.

Rearing Back may have been a last resort for a tired lobster to protect its rear without turning because it was almost only seen during the last quarter of a trial in both Intact and MA lobsters. For MA lobsters, Rearing Back leaves the side without an antenna completely open and it takes longer to swing the antenna from completely behind the lobster to the front.

In response to Rearing Back a fish rapidly changed direction, swam to the front of the lobster, and Bit an eye. Successful lobsters rarely Reared Back.

Effect of Tethering

Tethering allows defense only by antennal action and carapace Bite resistance since it prevents fleeing, even momentarily, by Tail Flipping and Walking. Yet, in time-limited trials, mortality was the same for both Free Ranging and Tethered lobsters, although antennal injuries were greater among tethered lobsters. Extended trials would likely show greater mortality of tethered lobsters. Barshaw et al. (2003) tethered large spiny lobsters, *Palinurus elepha,* in an area with Atlantic triggerfish (*Balistes carolinensis*) for 24 hours. The effectiveness of lobster antennal defense decreased with time, although little mortality was seen for the first 4 hours.

I saw few behavioral differences between tethered and free *P. argus*. Intact lobsters showed no overall behavioral difference between the two treatments. These results suggest that exposed, solitary Caribbean spiny lobsters fight triggerfish by standing their ground and interposing the antennae to deter, fend away or intimidate the attacker. This matches the few spontaneous encounters witnessed in nature (Kanciruk, 1980). This probably applies also to *Palinurus elephas* used by Barshaw et al (2003) to evaluate the relative capacity of clawed, slipper and spiny lobsters to deter Atlantic triggerfish, *Balistes carolinensis*. Tail flipping by tethered adult *P. elephas* was also infrequent while fish and lobster actions were almost identical to those reported here for sub-adult *P. argus*.

There is strong evidence in the literature that tethering makes many prey species exceedingly vulnerable to predators. Yet no previous studies directly compared the behaviors of tethered and free lobsters under identical conditions as was done here (Butler and Herrnkind, 2000). Hence, most researchers apply tethering techniques only to estimating comparative differences with other tethered individuals. For example, this technique was used to estimate survival differences of lobsters tethered in and out of shelter (Herrnkind and Butler, 1986). It was assumed that the actual mortality by predators was much higher than expected for unrestrained lobsters. Yet, tethering of *P. argus* and *P. elephas* that allows free bodily rotation and adequate space to lunge (~ one half body length) may approximate natural predator-prey interactions during the initial phases of an encounter.

SUMMARY

The antennae of *P. argus* are a very effective primary defense against gray triggerfish. Even the removal of an entire antenna reduces lobster defensive ability less than might be expected. Adjustments in the use and timing of certain actions and in body posture substantially compensate for the loss. However, neither fleeing in the open nor having an armored exoskeleton is adequate for thwarting triggerfish predation. In fact, tethered lobsters in the open defended nearly as effectively and by the same actions as free moving lobsters. These results suggest that how well an intact or MA lobster stands and fights by intimidating (Pointing), warding (Parrying) and retaliatory (Lunging) defense is essential. Nevertheless, over time, a lobster missing one antenna probably is not as effective in defense as a lobster with both antennae. In the field, selective predation and a higher injury rate probably reduces the survival of lobsters missing an antenna. In addition, a lobster may have to survive several encounters with a predator before regaining a new antenna at next molt. The energetic cost of having to regenerate the antenna, should the lobster survive the interim, may reduce growth rate and ultimately fecundity. Lobsters lose antennae or have them partially broken off by both natural events (predation) and through improper handling by humans. Human induced mortality indirectly via antennal damage deserves research because it may cause measurable decline of the valuable and heavily fished Florida spiny lobster population.

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BIOGRAPHICAL SKETCH

Amy Parsons was born September 2, 1973, in Effingham, Illinois. From the moment she was independently mobile, she was frequently found following, watching, and gifting her mother with all things non-human. Upon learning that people actually do this (sans mother) for a living, her career choice was firmly set in her mind…around kindergarten. She continued a fanatic study of animals as she grew. During the ‘90s, she escaped Illinois and moved to South Florida. It was there she had her first overwhelming view of the marine environment and tourists. Not long after, she pulled her head out of the trees and dropped her goals for ornithology, became a diver, and submerged herself into the marine world. Invertebrates (gasp!) were especially of interest. “Doc” Herrnkind at FSU transferred his enthusiasm for spiny lobsters over to her, thus causing, to the delight of the triggerfish, the carnage of multitudes of lobsters for her study of lobster/triggerfish interactions. Sadly, an additional attempt by Doc to transfer his fishing skills failed after meters of tangled line, and the use of many lures with a curious disrespect for gravity. Currently she is following another creature, somewhere (hopefully warm and with a paycheck).