

ABSTRACT

PARSONS, DARREN MICHAEL. Indirect effects of recreational fishing on spiny lobster (*Panulirus argus*) behavior, mortality and population dynamics. (Under the direction of David B. Eggleston.)

The most obvious impact of a fishery is the large amount of biomass removed. Fishing also impacts and disturbs animals that are not caught, but interact with fishing gears. These indirect effects of fishing often go unnoticed but may be an important component of the overall ecosystem modification for which fisheries are responsible.

In this study, we quantified indirect effects within the Caribbean spiny lobsters (*Panulirus argus*) fishery in the Florida Keys, USA, including mechanisms that resulted in behavioral modification and lobster mortality, and potential population and economic consequences of these indirect effects. The spiny lobster fishery in the Florida Keys has intense recreational sport-diver effort during a 2d mini-season in which 80-90% of legal lobsters are removed from some areas, and an over capitalized commercial trap fishery where >900,000 lobster traps are deployed annually.

In field surveys we observed a 27% increase in the density of injured lobsters on patch reef habitats from before to after the 2 d mini-season, but not in other habitat types. In laboratory Y-maze shelter choice experiments, we observed that un-injured lobsters were less likely to shelter with injured lobsters than with un-injured lobsters. Using disturbance experiments conducted in the field we observed that disturbing and injuring lobsters on a coral patch-head caused individuals to emigrate from that patch-head before the mini-season, but had no effect on lobster density on patch heads after the mini-season.

When lobsters were tethered in the field, mortality was higher when injured than uninjured. Similarly, lobsters that were exposed to triggerfish predators (*Balistes capriscus*) in a large seawater arena had a higher probability of mortality after being disturbed and injured.

The behavioral response of lobsters exposed to human disturbance and the predation threat presented by triggerfish were compared in the same seawater arena mentioned above. Both human disturbance and the presence of triggerfish decreased lobster fidelity to individual shelters. Overall shelter use and lobster gregariousness increased when triggerfish were present, but not as a function of human disturbance. Lobsters may not always respond to human disturbance and natural predators with similar behaviors.

We used an individual-based population model to quantify potential population and economic impacts of injuries lobsters receive from sport-divers in the Florida Keys. Model results suggest that the severity of population and economic impacts are dependent on the frequency of lobster injuries throughout the Florida Keys fishery. For example, areas associated with high densities of injured lobsters may have a $\geq 50\%$ reduction in the abundance of adult lobsters and associated recreational and commercial harvests. In areas where the density of injured lobsters was ~ 20 times lower, the impact of injuries on the adult lobster population and commercial landings was only 5 and 8%, respectively. Despite the seemingly smaller impact in areas with lower densities of injured lobsters, injuries may still be responsible for a 900 t reduction in the adult stock biomass and a 160 t, or \$1.6 million reduction in annual commercial landings when scaled to the entire spiny lobster fishery in the Florida Keys.

Sub-lethal interactions with fishing gears can lead to altered behavioral responses by injured animals, altered interactions with other members of the community, and ultimately, increased mortality. These potentially cumulative mortalities have potential population and economic consequences. The occurrence of unobserved mortalities resulting from fishing activities is probably not restricted to the spiny lobster fishery in the Florida Keys. More likely, similar undesirable and costly consequences of unobserved mortalities occur in fisheries throughout the world. To avoid these costs, it would be prudent to account for unobserved mortalities in all fisheries.

**INDIRECT EFFECTS OF RECREATIONAL FISHING ON SPINY LOBSTER
(*PANULIRUS ARGUS*) BEHAVIOR, MORTALITY AND POPULATION
DYNAMICS**

by

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BIOGRAPHY

Darren was born to Michael and Heather Parsons in Palmerston North, New Zealand, December 24th 1978. Due to his father's employment his family, which included his sister Louise, moved between many different cities in the North and South Islands of New Zealand but eventually settled on the North Shore of Auckland where they currently reside. Although Darren disliked the Auckland rugby team he eventually grew to love the recreational potential offered by Auckland's two harbours and many islands. Living less than 200 metres from the beach, Darren could be found on the shore investigating rock pools, harassing fishermen and watching bikinis. Eventually, Auckland also lost the Ranfurly Shield to Waikato.

Darren began his tertiary education at Auckland University where he thrived in an environment that encouraged rote learning. Through the consumption of beer subsidised by Auckland University Darren developed obnoxious behaviours, but also established a large social cohort. At the completion of his Bachelors degree he began Masters research at the University's marine laboratory in Leigh. Using acoustic tracking equipment to monitor snapper movements during the day and spending his free time attempting to catch snapper with rod and reel, Darren enjoyed this time immensely.

At the completion of his Masters degree Darren decided a change was due and followed his sister's tracks to the USA to earn a PhD. Being extremely opinionated, Darren was initially skeptical about American sensibilities; that conflict remains today. After an initial period of doubt he decided upon a dissertation topic, the spiny lobster of the Florida Keys. His girlfriend and another Kiwi moved to the area; this combined with frequent travel to different parts of the North American continent to visit family or just

see the sights made his time enjoyable. Also at this time his dissertation began to progress at breakneck pace, most probably due to the expert supervision of Dr. David Eggleston. Research in the Florida Keys was extremely stimulating and Darren will miss the warm tropical waters upon his return to New Zealand. On the precipice of completion Darren is excited to return home. Hopefully he has managed to learn some science, appreciate different perspectives, but remain true to his ideals.

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CHAPTER 1

INDIRECT EFFECTS OF RECREATIONAL FISHING ON SPINY LOBSTER BEHAVIOR (*PANULIRUS ARGUS*)

ABSTRACT: Sub-lethal disturbance may lead to behavioral modifications that have detrimental consequences for the individual. Sub-lethal disturbance is an indirect effect of fishing that has seldom been examined. In summer 2003, we conducted surveys of Caribbean spiny lobster (*Panulirus argus*) in the Florida Keys, (USA) before and after a 2-d mini-season exclusively for recreational sport-divers, to assess the frequency of injured lobster. We also conducted: (1) a tethering experiment to assess the influence of disturbance and injury on predation-induced mortality, and (2) Y-maze laboratory experiments to assess the effect of injury and disturbance on the choice of shelter by conspecifics. Injury surveys revealed an immediate increase (to 27.16%) in the percentage of injured lobsters from before to after the mini-season within patch reef habitats, but only a small increase (to 3.78%) in injured lobsters amongst patch head habitats. Tethering trials revealed that injured lobsters were more likely to succumb to predation than uninjured controls, while the shelter choice experiments demonstrated that the usual ability to attract conspecifics was altered by injury. Considering the ability of this fishery to unintentionally injure > 25% of the lobster population in patch reef habitats in just 2 d, the potential consequences to spiny lobster populations must be determined.

INTRODUCTION

When an animal encounters a threat of predation it must make a choice between maintaining 'normal' activity patterns or changing activity to reduce the probability of predation. Both decisions have potentially detrimental consequences (Abrams 1993). Deciding to maintain 'normal' activity could be a fatal choice with immediate effects, whereas a more conservative decision would reduce predation risk, but could indirectly and negatively affect a host of functions including activity patterns, vigilance, sheltering behavior, social interactions, time spent feeding, growth and reproductive potential (see review by Lima 1998). These behavioral decisions are not without potentially long-term consequences for the individual, population or community.

Like natural predation events, marine fisheries can expose target species to direct effects through the removal of biomass, and indirect effects when surviving animals modify some aspect of their biology. The direct impact of biomass extraction is generally the focus of fisheries management; however, its indirect impacts and disturbances are largely ignored. Some indirect impacts of fishing that have been addressed include the capture of non-target species (Davis 2002), habitat destruction caused by contact fishing gears (Thrush et al. 2001), and trophic cascades resulting from reduced abundance of target species (Babcock et al. 1999). Few studies, however, have addressed the potential for fishing practices to indirectly modify and disturb animal behavior. We do know that: (1) fish subjected to capture and release exhibit reduced growth and elevated mortality (Warner 1978, Loftus et al. 1988, Diggles & Ernst 1997), (2) fish that escape through trawl nets have altered behaviors that may increase their risk

of predation (Ryer et al. 2004), and (3) discarded bycatch from dredge fisheries can lead to behavioral modification of scavengers (Veale et al. 2000). What is lacking and needed is quantification of human disturbance events, the resulting behavioral modifications by target species, and, if altered behaviors lead to increased mortality, the mechanisms underlying elevated mortality and consequences of such delayed mortality for the population.

Recreational spiny lobster fisheries provide a unique opportunity to quantify the effects of human disturbance on animal behavior and mortality because of the intense, pulsed nature of this human disturbance in time (Eggleston et al. 2003), and because sport-divers visually locate and attack lobsters in their dens. Human disturbance of lobsters can result from either (1) an unsuccessful attack, or (2) a successful capture followed by release of a sub-legal lobster.

The Caribbean spiny lobster (*Panulirus argus*) supports important recreational and commercial fisheries throughout its range (Lipcius & Eggleston 2000). *P. argus* is highly gregarious, aggregating in crevices and beneath sponges during the day (Herrnkind et al. 1975, Eggleston & Lipcius 1992, Eggleston & Dahlgren 2001), and forages on gastropods, chitons and bivalves in nearby seagrass beds and hard bottom habitats at night (Cox et al. 1997). Ontogenetic habitat shifts occur when juveniles move from inshore macro-algal settlement habitats to back-reef crevice habitats, and finally to offshore reefs as adults (Davis & Dodrill 1989). When spiny lobsters return to their dens from nocturnal foraging, or exhibit larger scale ontogenetic habitat shifts, they are guided by olfactory cues from conspecifics, resulting in the aggregation of individuals in shelters (Ratchford & Eggleston 1998, 2000; Childress & Herrnkind 2001). Commercial

fishermen of the Florida Keys exploit the gregarious nature of spiny lobsters by baiting traps with live juveniles (Hunt et al. 1986), whereas recreational sport-divers exploit the gregarious nature of lobsters by targeting dens with high densities of lobsters, and coercing them into hand-nets with ‘tickle sticks’ (Eggleston et al. 2003). Divers disturb other lobsters within a den as they attempt to coerce the target individual out. In addition, sub-legal lobsters that are captured, measured, and released also are disturbed and may be injured. The recreational fishery not only extracts 22% of the total lobster harvest in the Florida Keys each year (Hunt 2000), but also likely exerts major indirect effects through disturbance and sublethal injury.

Approximately 50% of sub-legal and legal sized spiny lobsters in Biscayne Bay, Florida, USA had injuries after the 1977 regular fishing season (compared to 31% injury immediately before that season opened in 1976; Davis 1981). These injuries reduced growth rates and increased the probability of death of sub-legal lobsters before they recruited to the fishery (Davis 1981). Since Davis’ (1981) study in the late 1970’s, the intensity of the recreational fishery in the Florida Keys has increased greatly. Fishing intensity is highest during a 2 d mini-season exclusively for recreational sport-divers, which opens one week prior to the opening of the regular lobster fishing season for commercial and recreational fishers during August to March (Eggleston & Dahlgren 2001, Eggleston et al. 2003). For example, lobster abundance from before to after the 2-d mini-season decreased by 55% in 1987 (Blonder et al. 1992), but decreased by 80-90% after the 2000 and 2002 mini-seasons (Eggleston & Dahlgren 2001, Eggleston et al. 2003). It seems reasonable to assume that the incidence of injury and disturbance to lobsters has increased accordingly, but this is untested.

In this study, we documented the frequency of injured lobsters immediately before and after the 2 d mini-season for recreational sport-divers in the Florida Keys. We also investigated 2 potential consequences of disturbance and injury: (1) delayed predation-induced mortality, and (2) effects on gregarious sheltering behavior.

MATERIALS AND METHODS

Study sites. Lobster surveys and experiments were conducted within the Great White Heron National Wildlife Refuge on the NW side of the lower Florida Keys, Florida (Fig. 1). Within this region we surveyed 2 types of coral reef habitat: (1) continuous coral reefs and ledges, herein referred to as ‘patch reefs’, and (2) discrete aggregations of boulder coral located within shallow seagrass beds, herein referred to as ‘patch heads’ (see Eggleston et al. 2003 for a description of coral patch reef and head habitats in this region). Patch reefs formed a nearly continuous line running NE to SW and parallel to the lower Florida Keys (Fig. 1). Patch heads were located within discrete basins such as Waltz Key Basin and Turkey Basin, along the edge of Cudjoe Channel, and the area surrounding Little Crane Key (Fig. 1).

Sublethal injury to lobsters. SCUBA divers quantified the proportion and distribution of injured lobsters 4 to 6 d before and after the 2 d mini-season for sport-divers during July and August 2003. Injuries were defined as absence of $>1/2$ of an antenna, legs, or evident damage (i.e. crushed exoskeleton) to the abdomen, cephalothorax, or supraorbital horns (Davis 1981). The size of injured lobsters was estimated visually without capture, using a 50 cm length of PVC pipe marked with 1 cm increments. All divers conducting these surveys had previously practiced estimating the

size of plastic lobster models while diving, until estimates of Carapace Length (CL) were accurate within 1 cm. When a lobster was partially obscured within a crevice, a tickle stick was used to gently coerce the lobster into view so its size could be estimated.

Survey sites on patch reefs were chosen by superimposing a 1 km × 1 km grid over the continuous patch reef between Snipe Point and the Content Keys (Fig. 1). From this grid, six cells were randomly selected. At each patch reef cell location, the research boat was anchored as close as possible to the middle of the grid cell using a differential GPS, whereupon 2 divers would survey areas that were in opposite directions from the boat. Each diver swam in the same direction before and after the 2-d sport-diver fishing season. Divers used a 50 cm length of PVC pipe to estimate the width of the area searched, swimming along a nearly straight line away from the boat for 10 min, then surfacing and visually estimating the distance traveled from the boat. Distances estimated in this manner are not significantly different from distances measured with a boat using differential GPS (Eggleston et al. 2003). In the current study, the average area searched for a given 10 min survey before the mini-season was greater (380 m²) than the average survey distance after the mini-season (285 m²), but not significantly so (paired t-test; $df = 11$, $t = 1.96$, $p\text{-value} > 0.07$) and lobster abundance was standardized to density (number m⁻²), therefore the proportion of injured lobsters was compared between pre- and post-mini-season.

Patch heads surveyed in this study were chosen from those measured in 2001 and 2002 for overall lobster loss during the mini-season (Eggleston et al. 2003). Divers surveyed patch heads as described above, but searched the entire patch rather than using a transect approach (Eggleston et al. 2003). A total of 16 patch head clusters were

surveyed from a total of 4 separate locations: (1) Waltz Key Basin, (2) Turkey Basin, (3) Cudjoe Channel and (4) Little Crane Key (Fig.1). The area of each patch head was calculated by the formula πr^2 after measuring the radius of the coral patch head with a ruler. The response variable measured for coral patch heads was the proportion of injured lobsters within each survey site.

Effects of sublethal injury and disturbance on predation-induced mortality.

Tethering experiments assessed the relative effects of disturbance and sub-lethal injury on predation-induced mortality of lobsters in the field. We hypothesized that injured lobsters would suffer higher predation-induced mortality than control lobsters because leaking body fluids would attract predators and potentially repel conspecifics (Ratchford 1999), thereby reducing the benefits of group defense (Herrnkind et al. 2001). Each tether was 60 cm of 18 kg test monofilament line anchored to the substratum by a metal stake adjacent to a natural coral crevice. The other end of the tether was attached to a lobster by a cable-tie harness, which was secured around the cephalothorax between the second and third walking legs and fastened to the carapace using cyanoacrylate glue (Eggleston et al. 1990, Lipcius et al. 1998). The tether was long enough for the lobster to retreat into its shelter, but not so long that the lobster would become entangled. The minimum legal size of spiny lobsters that can be harvested in Florida is 76 mm CL, so we chose spiny lobsters with an average CL of 74 mm to mimic sub-legal lobsters that are often captured, measured and released by sport-divers. At each of the 4 patch head locations 3 lobsters were tethered to their own individual patch heads. Each lobster at a given location was randomly assigned to one of three treatments: (1) disturbed, where a

lobster was prodded with a tickle stick for 1 minute each day, (2) injured, where a lobster was initially injured by removing 1 antenna and the back 2 walking legs on one side of the cephalothorax, and (3) control, with no disturbance or injury.

If daily observations revealed that a given lobster was alive, the experiment was continued. If the lobster was absent and the tethering harness intact, the response was recorded as an escape. If part of the carapace remained attached to the tether or if the mono-filament had been snapped, then the response was recorded as a predation event. Daily observations continued for 5d unless the lobster had escaped or died. After 5 d, it was assumed that starvation might confound results. When an experiment at a patch head was discontinued for one of the above reasons another lobster would be tethered to the same patch head the next day and a treatment would be applied at random. In this way 4 replicates were conducted within Cudjoe Channel, 3 at Turkey Basin, 2 around Little Crane Key and 1 at Waltz Key Basin, for a total of 10 replicates for each treatment over a 17 d period. To avoid human interference these experiments were conducted when the fishery was closed. The response variable used was the probability of an individual within a treatment group surviving the full duration of the experiment (5 d). This was estimated with a survival function derived from the Kaplan-Meier procedure (Kaplan & Meier 1958). Standard errors for this survival probability were calculated as described by Pollock et al. (1989). These survival probabilities were then compared between treatments using a 1-tailed normal distribution Z-test.

The second response variable observed in this experiment was the number of conspecifics co-occupying the patch head den with each tethered lobster. This number was recorded daily and adjusted to represent a percentage of the number of lobsters

within that den when the experiment was initiated. We hypothesized that the average number of lobsters co-occupying a den with disturbed and injured lobsters would be significantly lower than the number of conspecifics occupying a den with control lobsters because the injured and disturbed lobsters would release body fluids or possibly stress hormones that could negate the effect of their natural attraction odor (Ratchford & Eggleston 1998, Ratchford 1999). The daily percent initial occupancy by conspecifics was averaged for the duration of each tethering trial and analysed with a 1-way ANOVA, with experimental treatment (injured, disturbed, and control) as the class variable. The assumptions of ANOVA were met for these data (normality: Kolmogorov-Smirnov test, $p > 0.15$, and homogeneity of variance: Levene's test, $p > 0.07$).

Effects of disturbance and injury on sheltering behavior. To assess how disturbance and injury modified normal sheltering behavior of *P. argus*, a Y-maze tank system was constructed (Fig. 2). We built 3 identical 235-l Y-maze, flow-through seawater tanks (1.9 m × 0.61 m × 0.28 m) to allow 3 trials to be conducted simultaneously. Seawater was pumped into a 190-l header tank, which fed six 38-l header tanks via adjustable valves. Seawater drained from pairs of these 38-l header tanks into both sides of each Y-maze tank, after free falling ~10 cm to ensure no audible cues were transmitted directly from the header tank to the Y-maze (Ratchford & Eggleston 1998). The only shelters available within the Y-maze tank were two concrete blocks placed on either side of the corners nearest the header tanks (Fig. 2). Seawater flowed through the Y-maze tanks, out a drainpipe, and then exited into a nearby canal. Water flow into each arm of the Y-maze was set to ~1.5 l¹min (Ratchford & Eggleston 1998). To check the directionality of flow

in the Y-maze, fluorescein dye was added to 1 header tank and flow observed. In all cases, the dye would flow into the start area, and not the other arm of the Y-maze, before flowing out through the drainpipe (Fig. 2).

Experimental trials were initiated in the evening (~20:00 h) from July 29 to August 14, 2003. A trial began by randomly choosing one of the paired 38 l header tanks to contain a lobster (hereafter referred to as the ‘treatment lobster’). Another lobster (the ‘experimental lobster’) was then placed in the start area of each Y-maze tank (Fig. 2). Lobsters with an average CL of 75 mm were used in this experiment because they represented a sub-legal size that was expected to be most frequently handled and released by sport-divers, and were a close match to the average lobster size used in the field tethering experiment. The Y-maze was then left undisturbed with water constantly flowing until 04:30 h, after which one of each of the 3 treatments (disturbed, injured, and control) was randomly assigned to 1 lobster in each of the header tanks. The disturbed treatment was conducted by prodding the lobster with a tickle stick for ~ 1 min; the injured treatment was conducted by breaking 1 antenna and the last 2 walking legs on one side of the lobster, and the control lobster was left undisturbed. This procedure was conducted under red light to ensure that all other lobsters remained undisturbed (Cummins et al. 1984).

The next morning before 08:00 h, the shelter chosen by the experimental lobster in response to presence of the conspecific in the header tank was recorded. For each trial, the response was defined as either positive (experimental lobster was sheltering in the concrete block downstream of the occupied header tank) or negative (experimental lobster was sheltering downstream of the unoccupied header tank). If the experimental

lobster was not located within either concrete block shelter, then that individual trial was omitted from the results. A total of 11 disturbed, 13 injured and 10 control trials were successfully conducted. Data were analysed by comparing the observed proportion of positive shelter choices for each treatment to the proportion expected by a random choice (0.5). Differences between observed and expected shelter choices were assessed using 1-tailed binomial tests (Zar 1984). In addition, 1-tailed binomial unconditional p-values were calculated using two individual Fisher's exact tests to allow for comparison to the control treatment (Berger 1996). Where multiple comparisons were made, Type I error was controlled for by Bonferroni correction.

RESULTS

Sublethal injuries to lobsters

During July 2003, both coral patch reef and patch head habitats contained an extremely low percentage of injured lobsters per m² before the 2 d recreational mini-season (0 and 0.15 %, respectively). After the mini-season the percentage of injured lobsters had increased to 27.16% on patch reefs and 3.77% on patch heads.

Effects of sublethal injury and disturbance on predation-induced mortality

The mean percent survival (Kaplan-Meier statistic) of tethered lobsters in coral patch heads prior to the mini-season declined with increasing intensity of the experimental treatment (Fig. 3). The only statistically significant difference in percent survival, however, was between injured and control lobsters (1-tailed Z test_($\alpha = 0.05$); $Z_{\text{obs}} = 1.80$, $Z_{\text{crit}} = 1.65$). The percent survival of disturbed lobsters was not significantly

different than survival of injured (1-tailed Z test $_{(\alpha = 0.05)}$; $Z_{\text{obs}} = 0.97$, $Z_{\text{crit}} = 1.65$) or control (1-tailed Z test $_{(\alpha = 0.05)}$; $Z_{\text{obs}} = 0.35$, $Z_{\text{crit}} = 1.65$) lobsters.

While applying the daily disturbance and injury treatments to the tethered lobsters, the number of co-resident *P. argus* was recorded to determine any potential avoidance behavior by or decreased attraction of untethered conspecifics residing within those coral patch heads. There was a decrease in the daily proportion of lobsters co-resident with control and injured lobsters, but not with disturbed lobsters (Fig. 4). Significantly more co-resident lobsters remained with disturbed than injured lobsters (1-way ANOVA; $df = 2$, $F = 3.87$, $p < 0.04$). However, neither the injured or disturbed treatments were significantly different from the control (Tukey's multiple comparison).

Effects of disturbance and injury on sheltering behavior

The strength of attraction of *P. argus* to conspecific odors decreased as the intensity of the treatment increased (Fig. 5). For example, lobsters chose the shelter receiving water from an undisturbed conspecific 80% of the time, which was significantly greater than random (binomial test; $n = 10$, $p = 0.04$). The percent of lobsters attracted to conspecifics was not different than random in the disturbed (55%: binomial test; $n = 11$, $p = 0.23$) and injured (38%: binomial test; $n = 13$, $p = 0.16$) treatments. The percent of lobsters attracted to control lobsters was significantly higher than the percent of lobsters attracted to injured lobsters at the 0.05 level of significance and provided some evidence of a significant difference at the 0.025 level, after accounting for multiple comparisons (Fisher's exact test; unconditional p-value = 0.03).

The control vs. disturbed (p-value = 0.13) comparison revealed no significant difference in the percentage of lobsters attracted (Fig. 5).

DISCUSSION

This study illustrates that sub-lethal disturbances by recreational sport-divers can increase the frequency of injured lobsters, alter shelter choice behavior, and increase predation-induced mortality of injured lobsters. Examples of behavioral disturbance in the marine environment are rare, although tourism activities like dolphin-watching are known to alter marine mammal behavior (Constantine et al. 2004). The current study is one of the first examples (as far as we are aware) to demonstrate that recreational fishing disturbance may increase mortality of the target species through a modification of prey behavior. In commercial fisheries, behavioral impairment caused by escape through trawl cod-ends may elevate mortality of juvenile walleye pollock (*Theragra chalcogramma*) exposed to lingcod predators (*Ophiodon elongatus*) (Ryer 2002). In terrestrial systems, redistribution and increased nocturnal activity of white-tailed deer (*Odocoileus virginianus*) exposed to hunters has been hypothesized to increase predation by Florida panthers (*Felis concolor coryi*) (Kilgo et al. 1998). The current study has shown that sub-lethal disturbances can have detrimental consequences for individuals, and we recommend quantification of similar disturbance events in other fisheries.

Sublethal injuries to lobsters

The percentage of injured lobsters increased from 0 to 27% in coral patch reefs during the sport-diver mini-season. While previous studies have indicated a high percentage of injury resulting from the cumulative and often long-term effects of recreational and commercial fishing (an increase from 31 to 50% over a 7 month fishing season: Davis 1981), the current study illustrates that a substantial increase in the frequency of injury can occur over only 2 d. The majority of the injured lobsters observed appeared to have ‘fresh’ injuries (i.e. translucent flesh present at the site of limb breakage), suggesting that the mini-season was responsible for new injuries. Since injuries to fishery target species can reduce survival (Ryer et al. 2004), the frequency at which they occur and the subsequent increase in mortality rate should be incorporated into population and fishery stock assessment models. Conversely, on coral patch heads we did not observe a large increase in the percentage of injured lobsters from pre- to post mini-season. This was opposite to the pattern of injury frequency we expected, given that sport-diver fishing effort can be 10-fold greater on coral patch heads than coral patch reefs (Eggleston et al. 2003).

It is unclear why the percentage of injured lobsters was low in coral patch head habitats compared to coral patch reefs. Physical differences between patch heads and patch reefs may result in easier capture of lobsters at patch heads, thereby reducing the chance of injuring lobsters. For example, patch heads are generally surrounded by sand and seagrass. Lobsters that escape an initial capture attempt by divers will typically tail-flip into another den in the same patch head, or onto the surrounding sand and seagrass. Once a lobster is in the seagrass it is easily captured by placing a hand-net behind it and

coercing it into the net with a tickle stick (D.M. Parsons pers. obs.). Thus, the attack success by divers on patch heads may be higher than on patch reefs, resulting in fewer remaining injured lobsters. Another explanation might involve the dispersal of injured lobsters away from disturbed dens and towards alternative, potentially sub-optimal shelters. These hypotheses remain to be tested.

Effects of sublethal injury and disturbance on predation-induced mortality

The increased mortality of injured lobsters in the tethering study, and the elevated frequency of injury after the mini-season, suggest that lobster injury increases overall mortality rates on lobsters. While estimates of mortality may be inflated due to experimental artefacts common to all tethering experiments (Peterson & Black 1994), it is the relative differences between treatments that are of interest here. We did not observe any differences in artefacts between treatments, such as a higher probability of lobsters tangling in the tether for some treatments.

The higher predation rate on injured versus control lobsters in the field could be due to 3 non-mutually exclusive mechanisms. (1) When an injury occurs flesh is exposed, releasing a mixture of organic compounds. These compounds include amino acids, which are known chemical attractants of foraging predators (Zimmer et al. 1999). Therefore, predators with a good olfactory sense, such as sharks (Hamlett 1999), could follow this odor trail and more easily locate their prey. (2) The defensive capacity of a lobster may be reduced by injury. If legs are removed it may restrict a lobster's mobility and therefore ability to escape. Removal of the antenna, which are used to whip potential predators (Herrnkind et al. 2001), may limit a lobster's ability to successfully fend off

attackers. (3) Injured lobsters may lose the benefits of group defense (Herrnkind et al. 2001) when co-resident lobsters abandon the den. This third mechanism was probably not important in determining patterns of predator-induced mortality in this study since co-resident lobsters abandoned dens containing tethered lobsters that were exposed to both control and injury treatments. At time-scales greater than the duration of this study, an additional mechanism for higher mortality of injured lobster would be increased energetic costs associated with injury (Juanes & Smith 1995). Increased energetic demand may cause an animal to take greater risks to obtain food and reduce its ability to escape predators (Sinclair & Arcese 1995), further elevating predation.

Effects of disturbance and injury on sheltering behavior

The results from our Y-maze experiments indicated that lobsters are attracted to dens containing conspecifics, as has been previously observed (Ratchford & Eggleston 1998). This strong tendency for lobsters to seek shelter containing the odor of conspecifics appeared to be reduced when the treatment lobster was injured. Moreover, reduced attractiveness by conspecifics towards injured lobsters could alter the ecological relationship between gregariousness, predation risk, and shelter choice observed in *P. argus* (Eggleston & Lipcius 1992), and reduced social interaction could lessen the benefits of group defense (Herrnkind et al. 2001).

Lobsters find suitable shelter faster when there are conspecifics within a shelter than when they are absent (Childress & Herrnkind 2001). Therefore, when high numbers of injured lobsters exist in a den, the cues lobsters use to find dens may be reduced. This reduction in the “guide effect” (Childress & Herrnkind 2001) may alter local patterns of

habitat use, even for lobsters that are not disturbed or injured. For example, undisturbed lobsters may be stranded in soft sediment habitats in the absence of correct cues from uninjured lobsters (Childress & Herrnkind 2001). Such individuals, lacking suitable daytime shelter may be exposed to a relatively high risk of predation mortality. There are 2 mechanisms that could account for the reduced attraction behavior observed in our Y-maze choice experiments: production of the normal attractive odor (Ratchford & Eggleston 1998) may be reduced or abolished when lobsters are disturbed or injured, or disturbance and injury may initiate the release of a disturbance odor. Results of a similar experiment also indicated that disturbance may promote the release of an odor that alters the sheltering behavior of conspecifics (Ratchford 1999). If such a disturbance odor exists, it could serve as a pheromone that is unintentionally released under stressful conditions. It would provide no benefit to the message sender, but broadcast information about predation risk (Chivers & Smith 1998). Since the disturbed and injured treatments in the current study did not produce significant avoidance, it is likely that if a disturbance odor exists, it does not operate to the exclusion of the attraction odor. This would indicate that either the production of the attraction odor was reduced or terminated, or that the attraction and disturbance odors were competing with one another.

Final remarks

Reduced growth rates of sub-legal lobsters caused by injury may prolong the time they spend in smaller size classes, resulting in an additional 22% of sub-legal lobsters succumbing to natural predation before they enter the fishery (Davis 1981). Our study suggests that injured lobsters will also be exposed to a higher daily rate of predation,

which could further decrease the proportion of individuals eventually recruiting to the fishery. Spiny lobsters also appear to alter their sheltering behavior in the presence of injured conspecifics, which may have an effect on survival. The population-level and fishery implications of these indirect disturbances remain unknown, but some level of unobserved mortality likely exists. Detrimental effects of human disturbance have been demonstrated at the population-level amongst various terrestrial species (e.g. mule deer: Yarmology et al. 1988, caribou: Harrington & Veitch 1992, pink footed geese: Madsen 1994), but less frequently in marine fisheries where the indirect effects of human disturbance and the direct effects of fishing itself may be difficult to separate. Matthews (2001), however, estimated that exposure and confinement of juvenile *P. argus* used as attractants in traps reduces recruitment to the fishery by 0.646 million individuals annually. If the population-level consequences of the human disturbance events described in the current study can also be quantified, management attempts to reduce the frequency of avoidable injuries to sub-legal lobsters and/or account for this unobserved mortality may prove beneficial.

With respect to the potential impact of indirect effects in other recreational lobster fisheries, recreational catch data are rare and there have been no investigations, that we are aware of, addressing the indirect effects of recreational fishermen. In South Africa, Western Australia and New Zealand, annual recreational catches of spiny lobsters are ~, 379, 630 and 300 t respectively (Cockcroft & Mackenzie 1997, Melville-Smith et al. 2001, K.J. Sullivan unpubl. data). This represents 25, 4.8 and ~10% of the total annual landings in the respective countries. In contrast, the Floridian recreational fishery lands 225 t in the first 2 d, and accounts for ~ 40% of the total annual landings (Sharp et al.

2005). In all but one of these fisheries, there have been recent increases in the percentage of the total catch taken by recreational fishermen: an increase of ~10% between 1993-2001 in Florida (Sharp et al. 2005), ~18% between 1991-1995 in South Africa (Cockcroft & Mackenzie 1997), and ~3% between 1986-1998 in Western Australia (Melville-Smith et al. 2001). Whether the increasing proportion of landings being taken by the recreational fishery will correspondingly increase the frequency of injured lobsters is unclear. Regardless of the percentage of catch obtained by recreational fishermen, spiny lobster fisheries throughout the world may have large unobserved mortalities associated with commercial diving and trapping. Commercial fishers in the Florida Keys also have a high potential to contribute indirect effects to the lobster population because sub-legal lobsters are used as attractants and traps are set for long periods (up to a month) without escape gaps (Matthews 2001). In other countries traps usually have escape gaps and soak for ~ one day (Phillips et al. 1994, D.M. Parsons pers. obs.). The differences in fishing methods suggest that indirect effects are probably most prevalent in the Floridian fishery, but may still be of concern to other spiny lobster fisheries. The frequency of indirect impacts on a given fishery will depend on the relative proportion of different capture methods within a fishery, and the potential for sub-lethal injuries posed by each method. While indirect impacts should be assessed in all fisheries, of particular interest is how the magnitude of indirect impacts will change as some fisheries become dominated by recreational effort (Coleman et al. 2004).

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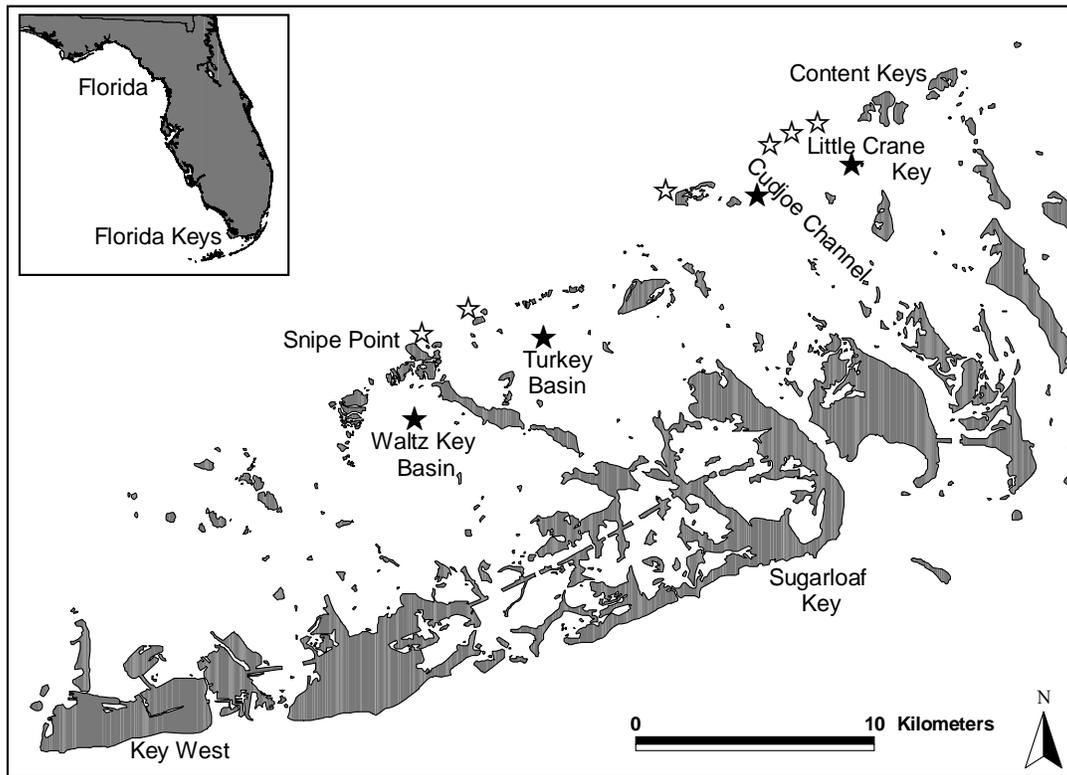


Fig. 1: Map of Florida, USA (inset) and the Florida Keys. Open stars represent patch reef study sites and filled stars represent patch head study sites.

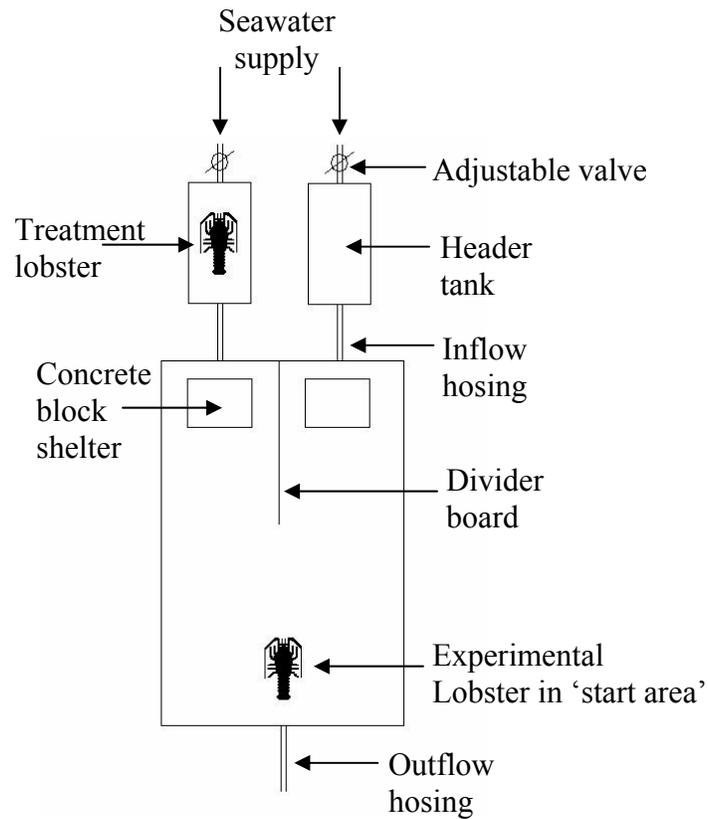


Fig. 2: Schematic diagram of the experimental Y-maze arena used to examine sheltering behaviour of *P. argus* in response to injury and disturbance. The treatment (control, disturbance, or injury) was applied to the lobster in header tank and shelter occupancy of the experimental lobster was recorded in the concrete block shelters.

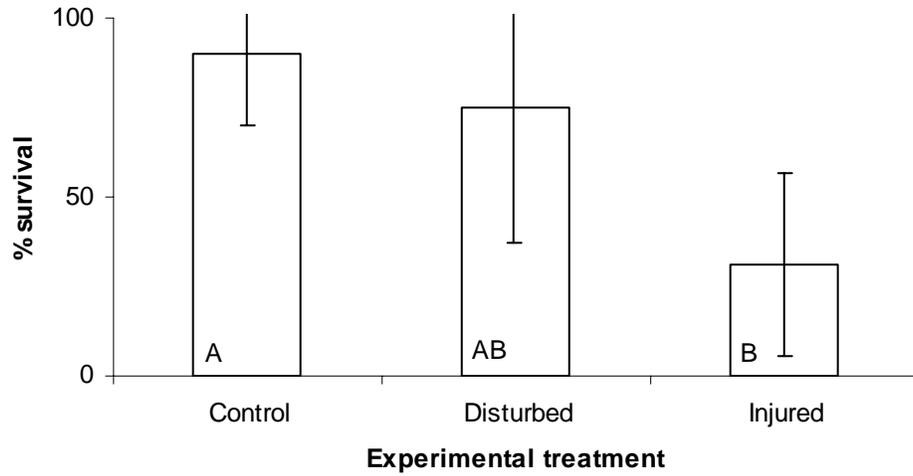


Fig. 3: Percent survival of *P. argus* tethered to coral patch heads as a function of disturbance (prodding with a tickle stick daily) or injury (loss of antenna and two walking legs). Error bars \pm SE; $n = 10$ for each treatment. Treatments with matching letters denote no significant difference upon pairwise comparison. See text for results of statistical tests.

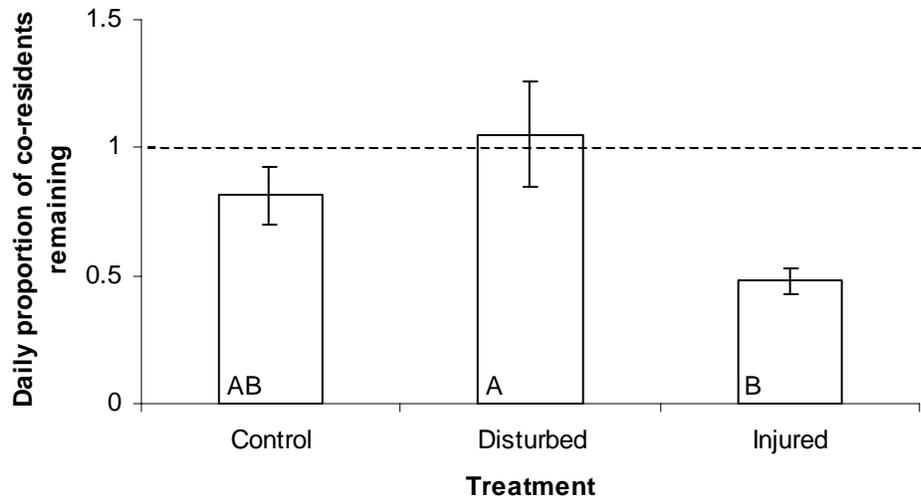


Fig. 4: Average daily proportion of the original number of co-resident lobsters remaining in coral patch heads during tethering experiments. This number was determined by counting the initial number of co-resident lobster within the same coral patch head as the tethered lobster. Each day as the treatment was applied to the tethered lobster, the number of co-resident lobsters was recounted, and is represented on this graph as the average daily proportion of the original. The dashed line, marked at 1, represents the null hypothesis of no change in the number of co-resident lobsters over time. Error bars \pm SE. Treatments with matching letters denote no significant difference upon pairwise comparison.

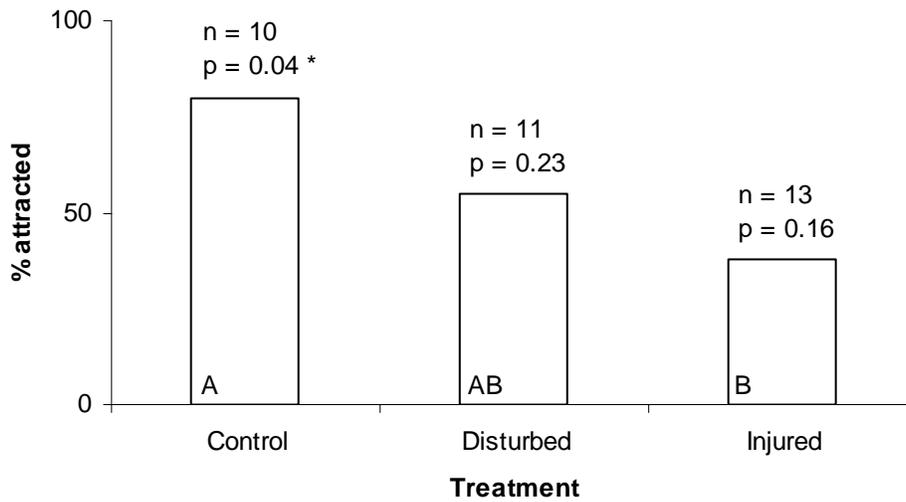


Fig. 5: Results of Y-maze laboratory experiment testing the effects of disturbance and injury on the attractiveness of experimental lobsters to conspecifics. P-values were based on a one-tailed binomial test (Zar 1984), where the null probability of choosing a shelter having the conspecific odor was 0.5. * indicates significance at $\alpha = 0.05$. Treatments without matching letters denote a borderline significant difference, at $\alpha = 0.025$, upon pairwise comparison using multiple Fishers exact tests.

CHAPTER 2

HUMAN AND NATURAL PREDATORS COMBINE TO ALTER BEHAVIOR AND REDUCE SURVIVAL OF CARIBBEAN SPINY LOBSTER

ABSTRACT

Fishing disturbance can have indirect negative effects on animal behavior and survival, but receives little attention compared to measures of direct fisheries extraction. We quantified changes in the density of Caribbean spiny lobster *Panulirus argus* when exposed to experimental human disturbance and injury typical of sport-diver harvest attempts in the field. A complementary study in a large seawater arena quantified lobster sheltering behavior and survival when exposed to the single and combined effects of human disturbance and natural predators (triggerfish, *Balistes capriscus*). Human disturbance and injury of lobsters in the field caused lobsters to emigrate from shelters that had typically been occupied over successive days. Similarly, both the presence of triggerfish predators and human disturbance promoted decreased fidelity of lobsters to individual shelters in the arena. Overall shelter use and gregariousness increased in the presence of natural triggerfish predators but not as a function of human disturbance. Decreased shelter use and gregariousness by lobsters when exposed to human disturbance may have contributed to their decreased survival when exposed simultaneously to triggerfish. These results highlight how human disturbance and injury of lobsters can alter their behavior and reduce subsequent survival in the presence of their natural

predators, and illustrate the need to incorporate the negative effects of sport-divers into models that estimate population demographic rates.

INTRODUCTION

One of the most conspicuous human perturbations within marine ecosystems is the large-scale extraction of biomass through marine fisheries. There are less obvious disturbances that receive less attention, however, including by-catch (Davis, 2002), habitat damage (Thrush et al., 2001), altered trophic cascades (Babcock et al., 1999) and unobserved mortality (Matthews, 2001). These less conspicuous disturbances can increase mortality rates and may be detrimental to marine populations and communities. For example, not all individuals that interact with fishing gears are harvested. Individuals that do not meet harvest restrictions on minimum size must be released (Veale et al., 2000), some individuals may escape (Ryer et al., 2004), and recreational fishermen may catch and release certain species (Diggles and Ernst, 1997). In each of these scenarios animals may be injured and their behavior altered in ways that increase their probability of mortality.

The fishery for the Caribbean spiny lobster, *Panulirus argus* Latreille, 1804, in the Florida Keys (USA) is an ideal model system to study non-extractive disturbances and unobserved mortality in the marine environment. These disturbances can largely be attributed to the commercial and recreational fisheries. The commercial trap fishery is extremely intense and exploits the gregarious nature of spiny lobsters by baiting traps with sub-legal (<76 mm Carapace Length (CL)) lobsters. These 'bait' individuals are

exposed to the air and may be injured in the baiting process (Hunt et al., 1986). Lobster traps, which lack escape gaps, may also go unchecked for up to one month, in which case the lobsters in them often starve to death (Matthews, 2001). As a consequence of these activities, many individual lobsters (~0.646 million annually) are lost from the fishery without contributing to the catch (Matthews, 2001). The recreational fishery also has a high potential to negatively affect lobster populations. Approximately 25% of the annual recreational fishing effort in the Florida Keys is expended during the two day, exclusively recreational mini-season (Sharp et al., 2005), which takes place one week before commercial fishermen are allowed access to the fishery and after a four month closure to all forms of lobster fishing. During these two days ~50,000 people attempt to catch lobsters with hand nets and tickle sticks whilst SCUBA diving or snorkeling. Up to 255 t of lobsters are landed during these two days (Sharp et al., 2005), which can account for 80-90% of the legal-sized lobsters on reefs in some areas at this time (Eggleston et al., 2003). During this intense fishing season many sub-legal lobsters are caught and measured before release, and a large proportion of the legal lobsters that avoid capture may have done so after handling and escape from sport-divers. Recently, we observed a 27% increase in the density of injured lobsters at some locations from before to after the two day mini-season (Parsons and Eggleston, 2005). The consequences of these injuries and disturbances include reduced growth (Davis, 1981), reduced potential to attract conspecifics, and higher mortality from predators (Parsons and Eggleston, 2005).

In this study, we quantified and compared the effect of disturbance by sport-divers and natural predators (Frid and Dill, 2002; Beale and Monaghan, 2004) on behavior and survival of Caribbean spiny lobster in the Florida Keys (USA). The results

indicate that human disturbance and natural predators are not equivalent threats, that the frequency and specific type of threat are important determinants of a lobsters' behavioral response to disturbance, that human disturbance has the capacity to modify lobster behavior, and that human disturbance in combination with natural predators can increase mortality of spiny lobsters.

METHODS

Effects of disturbance and injury on lobster site fidelity: field experiments

Disturbance experiments were conducted at three locations within the Great White Heron National Wildlife Refuge, which is located along the Gulf of Mexico side of the lower Florida Keys: Cudjoe Channel, Turkey Basin and Little Crane Key (Fig.1). Three individual coral patch heads harboring multiple lobsters (>3) were selected for experiments within each location. The lobsters in each patch head were counted and their size (Carapace Length, or CL) estimated to the nearest cm using a ruler attached perpendicular to a 50 cm PVC-pipe (e.g. Eggleston and Dahlgren, 2001). To avoid any individual patch head effects, one of three treatments was randomly applied to individual patch heads at a given location: (1) 'disturbance + injury', in which two lobsters were caught and an antenna and two legs broken while the remaining lobsters were harassed with a tickle stick for ~ one minute; (2) 'disturbance', as above but without injuring any lobster; and (3) 'control', in which lobsters were counted and sized by visual estimation without injury or disturbance. The treatment was usually applied between 1500-1700 on

day one, and the number and size of the lobsters at each patch head recorded the following morning between 0800-1000 h. These experiments were repeated twice before the two day mini-season and twice after the mini-season during July-August 2004 for a total of 6 replicates for each treatment both before and after the mini-season. Individual patch heads were allowed ≥ 6 d without disturbance from previous experiments or the two day mini-season before the experiments were repeated. We hypothesized that disturbance and injury of lobsters residing within coral patch heads would cause the abundance of lobsters to decrease. Although this hypothesis is intuitive and is supported by anecdotal observations by lobster divers, it has, to our knowledge, never been tested.

The response variable was termed 'site fidelity' and defined as the number of lobsters inhabiting a patch head after experimental disturbance/the number of lobsters inhabiting a patch head before experimental disturbance. While the term 'site fidelity' implies that the location of individual lobsters was monitored before and after the treatment, we were not able to identify individual lobsters in this study. Lobsters are likely to return to the same shelter after foraging in the evening, however (Herrnkind et al. 1975), suggesting that 'site fidelity' may still be an appropriate term. A two-factor ANOVA, with treatment and time as factors, would have been the most elegant design. Unfortunately the increase in variance around the treatment means from before to after the mini-season violated an assumption of this test, reducing its power to detect differences that preliminary analysis revealed to be biologically realistic. Therefore, data from before and after the mini-season were analyzed as two separate one-factor ANOVAs with treatment ('disturbance'; 'disturbance + injury'; and 'control') as the

factor. No departures from the ANOVA assumptions of normality or heterogeneity of variance were observed in this analysis.

Effects of disturbance, injury and predators on lobster sheltering behavior and mortality:

Arena experiments

Manipulative experiments were conducted in a concrete seawater pond, hereafter referred to as an “arena”, at the Keys Marine Laboratory, Long Key, Florida, USA (Fig. 2). The arena was roughly elliptical in shape ($40 \times 20 \times 0.75$ m deep) with a concrete island in the center, and a flow-through seawater system with an inflow pipe and drain at each end. To form two independent experimental arenas of similar dimensions the arena was divided by barriers constructed with double layers of black plastic sheeting, PVC pipe and concrete cinder blocks (Fig. 2). Two lobster shelters, consisting of a plywood (30×56 cm) roof raised off the floor by two clay bricks ($10.1 \times 6.8 \times 20.3$ cm), were placed in each arena. During experimental trials, lobsters resided in both shelters within each arena, as well as other refuges such as corners of the tank where outflow pipes were located. Large crevices and overhangs that could have prevented access by triggerfish predators (see below) and thereby served as lobster refuges were blocked by plastic mesh or black plastic sheeting.

Lobsters were caught by divers using SCUBA or snorkel in the areas surrounding Long Key. Only uninjured, juvenile lobsters with a hardened carapace between 66 and 79 mm CL were used in experiments. This size range encompassed those lobsters most likely to be captured, measured and released underwater by sport divers. While in

captivity, lobsters were housed in flow-through seawater tanks at natural photoperiod, temperature and salinity and fed a diet of squid (*Loligo sp.*). Before being used in an experiment, each lobster was measured to the nearest mm (CL), sexed, re-inspected for injuries, and tagged with a unique individual combination of colored cable-ties around the base of its antennae. After experiments all surviving lobsters were returned to the sea.

Grey triggerfish *Balistes caprisiscus*, which are known predators of palinurid lobsters (Vose and Nelson, 1994) were used as the natural predator disturbance factor in these experiments. Alternative predators, such as large snappers (Lutjanids) and nurse sharks *Ginglymostoma cirratum*, were considered as potential predators, but were not used because snappers do not exhibit consistent predatory attacks on lobsters while in captivity (D.B. Eggleston pers. obs.) and the nurse sharks would be impractically large (> 1.5 m). Triggerfish, in contrast, consistently attack lobsters in captivity and were easily collected by hook and line from abundant populations in the northern Gulf of Mexico (near Tallahassee, Florida). From there they were trucked in a tank to the Keys Marine Laboratory, where they were held in a flow-through seawater pond. Triggerfish from the northern Gulf of Mexico may not have previously encountered lobsters. Therefore, to equalize their experience with lobsters and to reduce the capacity for learned behaviors to alter predation efficiency (Bouwma and Herrnkind, unpub. data), triggerfish were exposed to live lobsters on numerous occasions before experiments commenced. The only supplemental food provided to triggerfish during the experimental period (see below) was live lobsters, to ensure that triggerfish would not wait out experiments for an easier source of food. Six triggerfish (37-40 cm fork length) were used in these

experiments, each identified by a unique combination of fluorescent elastomer tags placed in transparent parts of their dorsal and caudal fins. The food intake of each triggerfish was monitored to ensure that a given triggerfish chosen for an experiment had not been fed for two to three days while also attempting to evenly distribute individual triggerfish across both the treatments where they were needed.

Experiments were initiated by releasing eight individually tagged lobsters into each experimental arena at 0900 hours. Lobsters were then allowed ~11 hours to acclimate to the arena before observations were made or treatments applied. At 1800 hours the position of each lobster, the number of co-residents (defined as other lobsters that were less than two body lengths away), and its exposure status (sheltering or exposed; an exposed lobster was defined as any lobster that was not residing under an object that would obstruct a predator's access to some part of the dorsal carapace) were recorded by snorkeling. Some lobsters would respond by facing the snorkeler as he passed. This disturbance was short lived and consistent across all treatments, making any estimates of treatment effect conservative. Two treatments (see below) were haphazardly applied to a given arena in a crossed design while attempting to balance the number of replicates across factors, time, and the two arenas. The two treatments were: (1) 'human disturbance + injury', in which two lobsters were captured and an antenna and the back two walking legs broken, and all other lobsters harassed with a tickle stick for ~ one minute or until the lobster tail flipped away, and (2) 'fish disturbance', where two triggerfish were placed in a arena. Final observations of individual lobster position, co-residency, exposure status, injuries and mortality were made the following day at 0700 hours. Lobsters, triggerfish and broken body parts were then removed from the arenas

before another experiment was initiated with eight new lobsters. Between experiments, the arenas were skimmed with a surface net to remove debris and, less frequently, algal growth removed from the substratum with a suction pump. Eleven replicates of each of the four combinations of the two treatments were conducted during June-August 2004. We hypothesized that the presence of either ‘human disturbance + injury’, or ‘fish disturbance’ would cause lobsters to increase aggregation, decrease fidelity to the shelter where they were disturbed, and spend less time in the open during daylight hours. When both of the above treatments were applied together we hypothesized that increased predation on lobsters would occur.

Response variables and statistical analyses of arena data:

Aggregation. The level of aggregation of lobsters in the arena (i.e. aggregation index) was calculated by dividing the number of lobsters that co-resided with at least one other lobster by the total number of sites occupied by co-resident groups and solitary lobsters. Lobsters were defined as co-residing if they were less than two body lengths away. The change in aggregation index from before to after the application of a treatment was the response variable.

Shelter fidelity. Lobsters that were found in the same shelter within the arena both before and after the application of a treatment were called ‘residents’. Lobsters that were not observed in a shelter before the application of a treatment were disregarded in this analysis because they had not selected a shelter, hence they could not exhibit fidelity to it.

The proportion of lobsters residing in the same shelter before and after the application of a given treatment was the response variable.

Exposure status. Exposure status was defined as either (1) ‘sheltering’ (a lobster that resided under an object that would restrict the access of a predator to part or all of the dorsal carapace), or (2) ‘exposed’ (a lobster with no structure protecting any part of its dorsal carapace). The response variable was the difference in the proportion of lobsters in the open from before to after a treatment application.

The three response variables (aggregation, shelter fidelity and exposure status) were analyzed with separate two factor ANOVA models with ‘human disturbance + injury’ (present, absent), and ‘fish disturbance’ (present, absent) as factors. The ANOVA assumptions of normality and heterogeneity of variance were assessed with Kolmogorov-Smirnov and Levene’s tests, respectively. One of the variables, shelter fidelity, did not meet the assumption of normality even after arcsine transformation; however, the lack of gross departures from normality evident on the QQ plot of the transformed data and the robustness of a balanced ANOVA to departures from normality (Underwood, 1981) suggested that it would still be acceptable to proceed with a two factor ANOVA of the transformed data. These results agreed with those of non-parametric analyses for this variable (not reported), further increasing our confidence that any observed effect was real.

Predation. The probability of a triggerfish eating a lobster was compared for trials in which lobsters received the ‘human disturbance + injury’ treatment vs those in which fish predators were the only treatment. Probability of mortality was calculated in each situation by dividing the number of trials where a mortality occurred (there was never

more than one predation event/trial) by the total number of trials in that treatment category. Data were analyzed with a one-tailed Fisher's exact test because we anticipated that the injured lobsters in the 'human disturbance + injury' treatment would be more vulnerable to triggerfish predation.

RESULTS

Effects of disturbance and injury on lobster site fidelity: field experiments

Before the sport-diver mini-season of July 2004, when lobster densities were 10-fold higher in coral patch heads than after the mini-season (D. Eggleston unpubl. data), lobster site fidelity (i.e. the number of lobsters inhabiting a patch head after experimental disturbance/the number of lobsters inhabiting a shelter before experimental disturbance) decreased as the intensity of experimental disturbance increased (Fig. 3a; one-way ANOVA: $df = 2$, $F = 7.90$, $p < 0.005$). The decline in site fidelity was significantly different between the control and the 'disturbance + injury' treatment (Tukey's multiple comparison, Fig. 3a). For example, the 'disturbance + injury' treatment reduced lobster density by 5 lobsters m^{-2} whereas the control treatment increased lobster density by 0.34 lobsters m^{-2} . After the mini-season, when the density of lobsters in coral patch heads was relatively low, the level of experimental disturbance had no effect on site fidelity (Fig. 3b; one-way ANOVA: $df = 2$, $F = 0.09$, $p > 0.92$).

Effects of disturbance, injury and predators on lobster sheltering behavior and mortality: arena experiments

Aggregation. Lobster aggregation in the arena increased significantly in the presence of predators (two-way ANOVA: $df = 1$, $F = 34.4$, $p < 0.0001$), whereas there was a non-significant change in aggregation when lobsters were disturbed and injured by humans (two-way ANOVA: $df = 1$, $F = 3.52$, $p > 0.06$) (Fig. 4). There were no significant interaction effects ($p > 0.6$).

Shelter fidelity. Lobster shelter fidelity was significantly lower in the presence of either ‘human disturbance + injury’, or triggerfish (two-way ANOVA; both p -values < 0.01); however, a significant ‘human disturbance + injury’ \times ‘fish disturbance’ interaction precluded conclusions across main effects (Fig. 5). The significant interaction effect ($df = 1$, $F = 6.08$, $p = 0.018$) was due to the significantly higher lobster shelter fidelity (Tukey’s multiple comparison) in the absence of both human disturbance and triggerfish than in other treatment combinations (Fig. 5). Site fidelity did not differ between the other treatment combinations (i.e. ‘human disturbance + injury’, ‘fish disturbance’ and ‘human and fish disturbance’).

Exposure status. The number of lobsters in the open decreased significantly in the presence of triggerfish (two-way ANOVA: $df = 1$, $F = 7.36$, $p < 0.01$), whereas there was a non-significant change in the number of lobsters in the open when lobsters were disturbed and injured by humans (two-way ANOVA: $df = 1$, $F = 3.75$, $p > 0.059$) (Fig. 6). There were no significant interaction effects ($df = 1$, $F = 0.01$, $p > 0.9$).

Predation. Predation-induced mortality of spiny lobsters was significantly higher in trials in which lobsters had been exposed to human disturbance than in those without (Fig. 7a; Fishers exact test unconditional p value = 0.0335). Similarly, injured lobsters within the human disturbance trials appeared to have a higher probability of mortality due to triggerfish predators vs uninjured lobsters within the same trials (Fig. 7b). This result could not be explicitly tested, however, due to a lack of independence; one predation event would be likely to affect the probability of another predation event within the same trial.

DISCUSSION

Field and arena experiments demonstrated that human disturbance and injury typical of that observed in an intense sport-diver recreational fishery for Caribbean spiny lobster in the Florida Keys, USA can alter lobster sheltering behavior and increase predation-induced mortality. Human disturbance and injury of *P. argus* can lead to elevated predation-induced mortality in the field and alter communication and sheltering behavior in the laboratory (Parsons and Eggleston, 2005; this study). Field surveys in 2003 indicated that 27 % of lobsters remaining in coral patch reef habitats in the lower Florida Keys after the 2-d sport diver season were injured (Parsons and Eggleston, 2005). These results, in combination with the known detrimental effects injuries have on lobster growth (Davis, 1981) suggest that unintentional human disturbance may be an important component of mortality in the Florida Keys Caribbean spiny lobster fishery.

In the current study, during field experiments before the mini-season, ‘human disturbance + injury’ decreased the relative count of lobsters present on patch heads from before to after the application of the treatment. Similarly, in the arena study any form of disturbance (‘human disturbance + injury’, ‘fish disturbance’ or ‘human and fish disturbance’) decreased lobster shelter fidelity. These results are consistent with observations made by Herrnkind et al. (1975) and Davis (1977), who found *P. argus* to increase movement in response to disturbance in the form of experimental artifacts and recreational sport-divers, respectively. Lobsters presumably decrease shelter fidelity to remove themselves from the site of a perceived threat. This behavior may assist lobsters in avoiding resident predators and reduce the potential for predators to habituate to prey locality. Conversely, the same behavior may also expose lobsters to a higher predation threat as they spend more time in the open looking for new shelter after a disturbance (Childress and Herrnkind, 2001). Other studies have suggested that animals have a greater tendency to remain in disturbed sites when high population densities increase the level of competition for resources at alternative sites (Gill and Sutherland, 2000). The opposite may occur for spiny lobsters, for which conspecifics are a potential resource that offers group defense (Mintz et al., 1994; Herrnkind et al., 2001) and facilitates locating shelter (Ratchford and Eggleston, 1998; Childress and Herrnkind, 2001). This interpretation is consistent with results of our field experiment, in which lobsters demonstrated a lower tendency to move away from disturbed field sites when population densities were low after the mini-season.

As expected, lobsters increased aggregation and were more likely to reside in shelters instead of being in the open after being exposed to fish predators in the arena.

This response likely benefits lobsters by increasing the probability that would-be predators are deterred by physical structure and group defense (Eggleston et al., 1990; Herrnkind et al., 2001). Unexpectedly, however, lobsters demonstrated a non-significant change in aggregation and use of shelters after exposure to ‘human disturbance + injury’. The constant presence of triggerfish predators during each arena trial, compared to the single ‘human disturbance + injury’ treatment 13 hours before the final observation, may explain the latter’s lack of effect in aggregation. If the effects of ‘human disturbance + injury’ on lobster gregariousness are short-lived, we should not expect a response identical to that induced by constantly present triggerfish. Lobsters that are not threatened by natural predators decrease their use of shelters during the day (Glaholt, 1990) and may use more spacious shelters (Eggleston and Lipcius, 1992), or decrease aggregation to avoid aggressive encounters with conspecifics (Berrill, 1975). Similar responses may have occurred in the current study.

The final consequence of ‘human disturbance + injury’ was elevated mortality when natural predators were present. The decreased shelter fidelity, aggregation and use of shelters that were observed in the presence of ‘human disturbance + injury’ probably contributed to this higher predation rate. There was also a good indication that, during the predation events we observed in the arena, triggerfish were either selectively choosing or were just more successful at preying on the injured lobsters. Other studies have suggested that triggerfish preferentially attack lobsters with missing appendages (A. Parsons, Florida State University, unpub. data). These results suggest the presence of a synergistic interaction between human disturbance and natural predators that elevates mortality of lobsters. Certain small reef fish species suffer similar synergistic predation

effects due to the interaction of two natural predator suites (pelagic and benthic predators) (Hixon and Carr, 1997).

The risk-disturbance hypothesis (Frid and Dill, 2002) proposes that the decision by a prey species, whether to flee or stay and risk mortality, is similar when animals are exposed to natural predators or to human disturbance. Our results suggest that different threats evoke different responses from the prey species. For example, the ‘human disturbance + injury’ that lobsters experienced was a single short event just prior to sunset. Exposure to triggerfish, a diurnal predator, resulted in potentially prolonged predation disturbances before sunset and after sunrise. We might have seen a stronger response by lobsters to human harassment in the arena experiment had the disturbance been more frequent or intense, as may occur during the two day mini-season (Eggleston et al., 2003). The specific circumstances of disturbance, whether natural or human induced, as well as the frequency of disturbance, must be considered when assessing the behavioral response of a disturbed animal. Other studies have shown varied responses to different disturbance scenarios within the same species (Rees et al., 2005).

When compared to the direct removal of biomass through predation and human fisheries extraction, the population consequences of sublethal disturbance may seem inconsequential. The seemingly less important cost of intimidation that animals experience when exposed to predators, however, may account for the majority of overall predator effects (Preisser et al., 2005), and previously unobserved mortality and non-extractive effects of human activities are now being regularly documented in marine systems. For example, catch and release fisheries reduce growth and increase mortality of the target species (Diggles and Ernst, 1997). Fish that escape through trawl cod ends

often succumb to predation (Ryer et al., 2004). The majority of animals caught in some dredge fisheries are discarded (Bergmann and Moore, 2001), often with injuries (Bergmann et al., 2001), potentially aggregating predators (Veale et al., 2000) and becoming exposed to higher rates of mortality because of these factors (Bergmann and Moore, 2001). Depending on trap soak time, lobsters confined in traps without release gaps can starve to death before the traps are hauled (Matthews, 2001), and even non-extractive SCUBA diving can cause damage to coral reefs (Barker and Roberts, 2004). Currently, no population estimate of the impact of disturbance and injury by humans exists for the Caribbean spiny lobster fishery in Florida, USA. Lobster mortality due to initially sublethal disturbance may be substantial and it would be prudent to account for it. One approach would be to model a population of lobsters and incorporate estimates of the percentage of lobsters injured throughout the fishing season and account for the higher mortality (Parsons and Eggleston, 2005) and reduced growth (Davis, 1981) that these lobsters are likely to experience.

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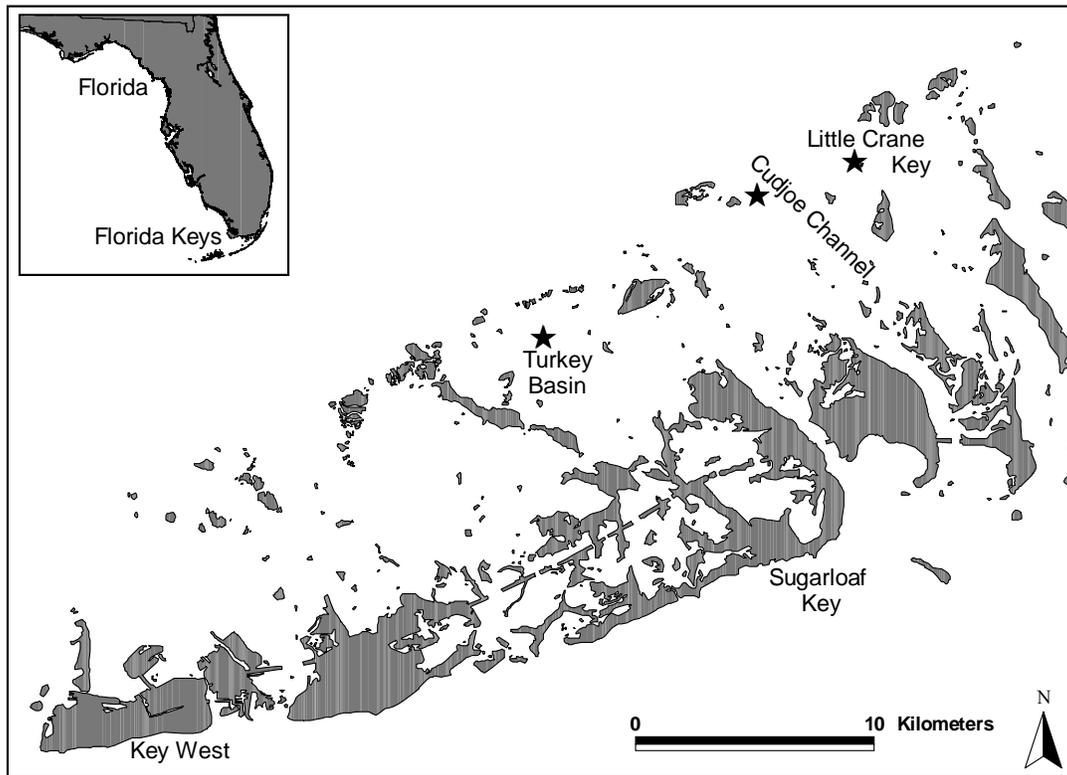


Fig. 1: Map showing Florida (inset) and locations where field experiments were conducted (stars).

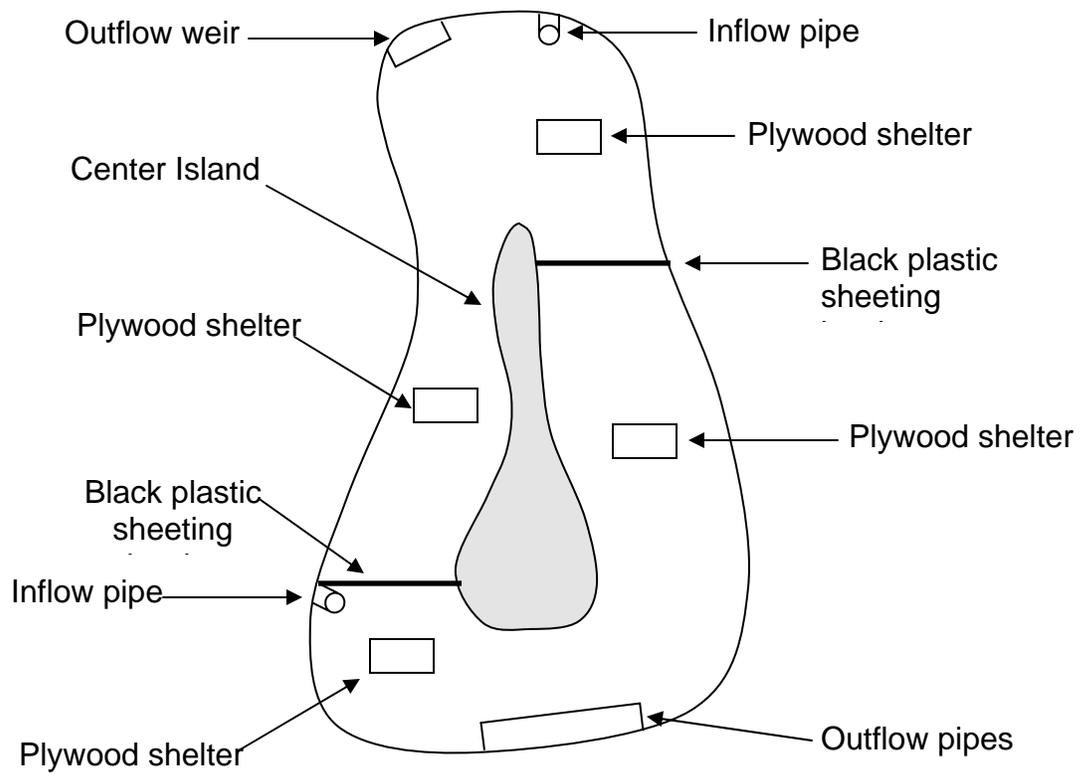


Fig. 2: Diagram of the concrete experimental arena where lobster sheltering experiments were conducted. Approximate dimensions were $40 \times 20 \times 0.75$ m deep.

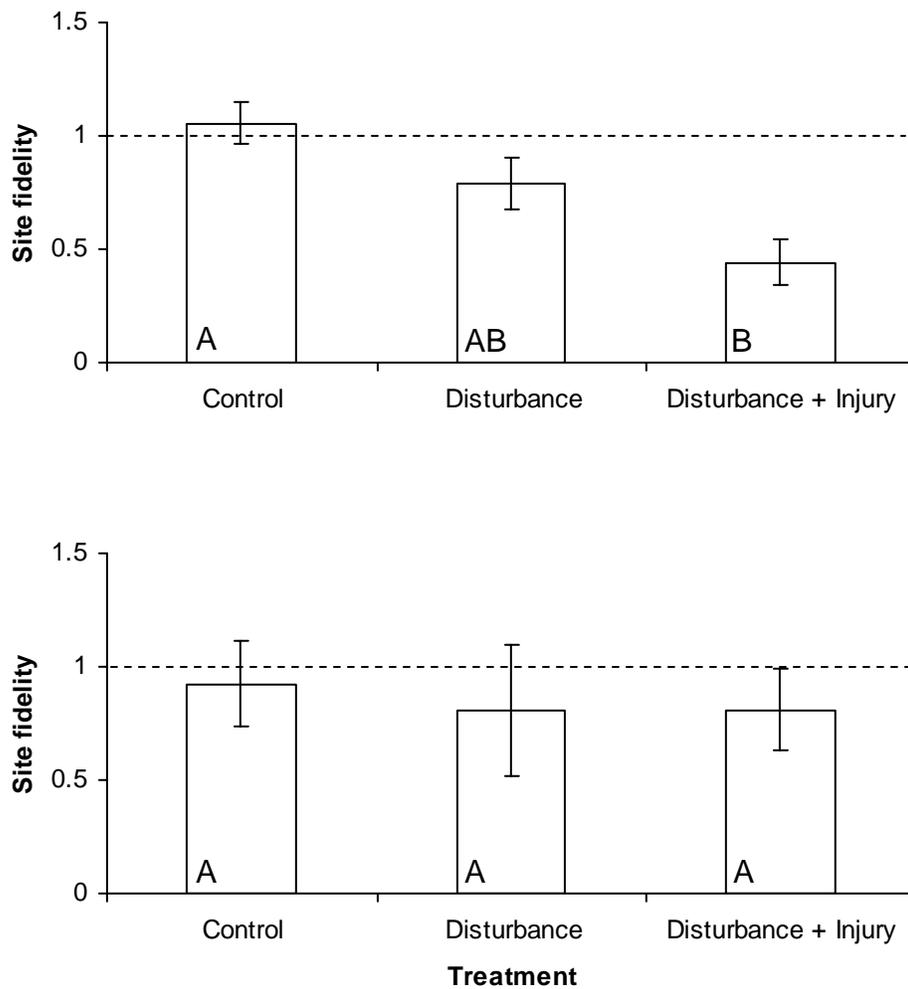


Fig. 3: Mean lobster site fidelity (\pm SE) as a function of the treatments: ‘human disturbance’, ‘human disturbance + injury’, and no disturbance (‘control’). Lobster site fidelity is defined as the number of lobsters inhabiting a patch head after experimental disturbance/the number of lobsters inhabiting a patch head before experimental disturbance. The dashed line, marked at 1, represents the null hypothesis of no change in lobster site fidelity. Experiments were conducted on patch heads in the field both before (a) and after (b) the mini-season for recreational lobster sport-divers. $n = 6$ for all

treatments. Treatments with matching letters denote no significant difference upon multiple comparison.

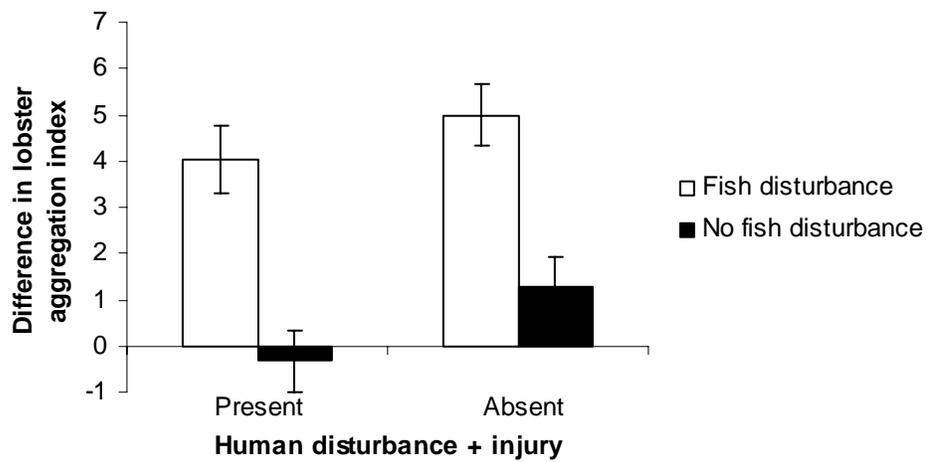


Fig. 4: Mean difference in the aggregation of lobsters (\pm SE) during the arena experiment as a function of the factors ‘human disturbance + injury’, and ‘fish disturbance’. The lobster aggregation index was calculated by dividing the number of lobsters that co-resided with at least one other lobster by the number of different locations occupied by individual or groups of co-resident lobsters. $n = 11$ for all treatments.



Fig. 5: Mean shelter fidelity of lobsters (\pm SE) during the arena experiment as a function of the factors ‘human disturbance + injury’, and ‘fish disturbance’. The proportion of resident lobsters is defined as the number of lobsters that were observed in the same shelter both before and after the application of the treatment divided by the total number of lobsters that occupied shelters before the treatment was applied. Lobsters that were not observed in a shelter before the application of the treatment were disregarded in this analysis. $n = 11$ for all treatments.

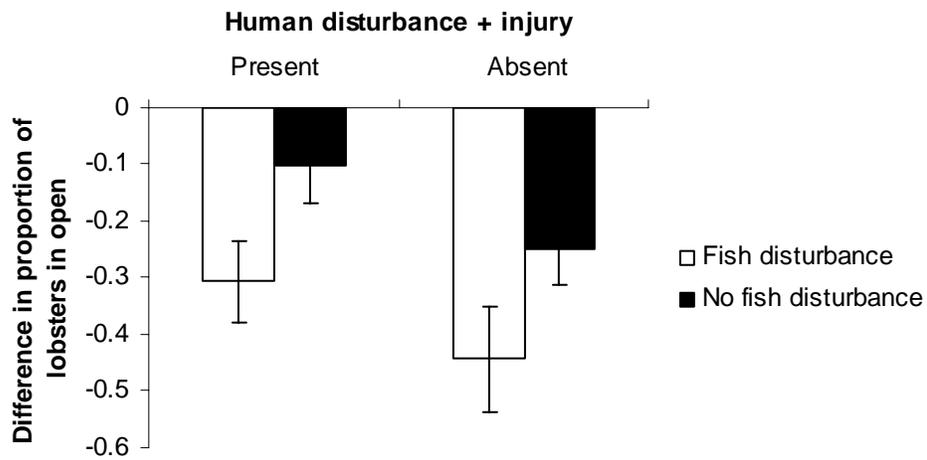


Fig. 6: Mean decline in the proportion of lobsters residing in the open (\pm SE) during the arena experiment as a function of the factors ‘human disturbance + injury’, and ‘fish disturbance’. The differences in the proportion of lobsters observed in the open was defined as the proportion of lobster in the open before the application of the treatment subtracted from the proportion of lobsters in the open after the application of the treatment. $n = 11$ for all treatments.

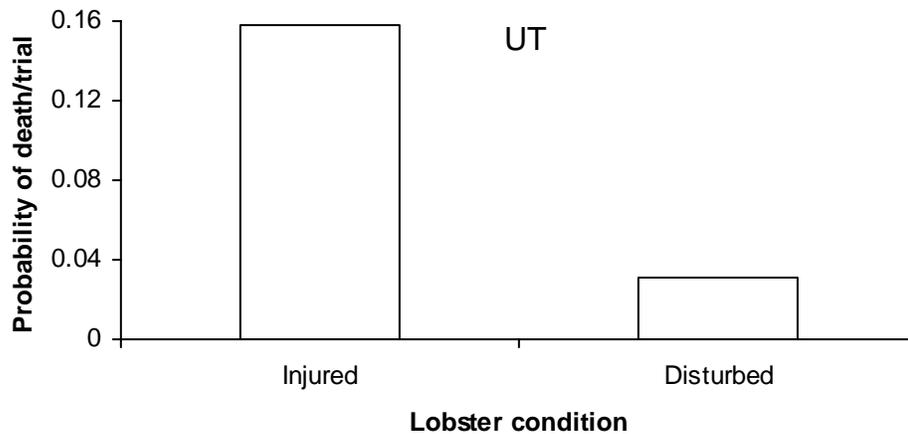
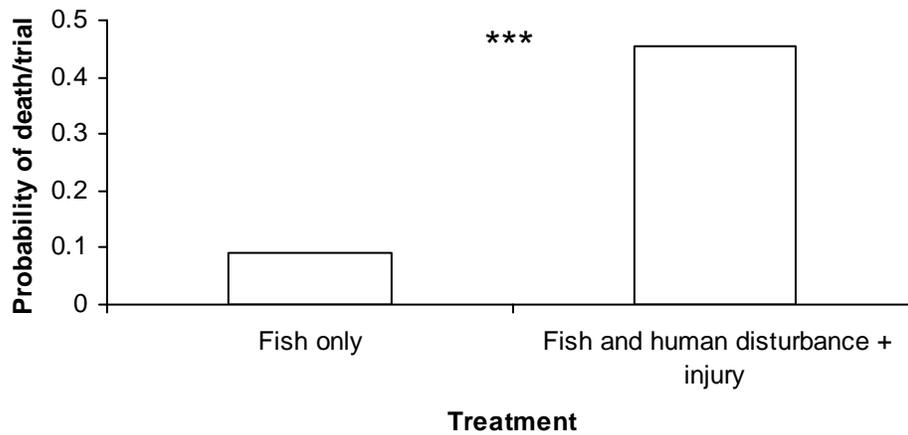


Fig. 7: The influence of experimental treatment (a) and lobster condition (b) on the probability of death/trial for lobsters exposed to triggerfish *Balistes capriscus* predators in or not in combination with human disturbance + injury. ‘***’ denotes a significant difference at the 0.05 level whereas ‘UT’ denotes that data were un-testable due to a lack of independence.

CHAPTER 3

POTENTIAL POPULATION AND ECONOMIC CONSEQUENCES OF SUB-LETHAL INJURIES IN THE SPINY LOBSTER FISHERY OF THE FLORIDA KEYS

ABSTRACT

Unobserved mortality resulting from an animals interaction with fishing gear, may form a significant portion of total fishing mortality in many populations of fish. Demonstrations of its occurrence within a fishery are few; ones quantifying its effect on populations and fishery landings are even rarer. In this study, we used an individually based population simulation model to quantify potential population and economic consequences of injuries that Caribbean spiny lobsters, *Panulirus argus*, sustain from fishing activities in the Florida Keys, USA. Injuries generated by the fishery can reduce growth and elevate mortality. Modeling results suggest that these effects may reduce adult lobster abundance and associated landings by $\geq 50\%$ in areas with high recreational fishing effort. In areas where recreational fishing effort for spiny lobster is ~ 20 times lower than patch reef areas in the lower Florida Keys, and the density of injured lobsters similarly lower, the impact of injuries on the adult lobster population and commercial landings were reduced by only 5 and 8%, respectively, compared to simulations with ‘no injury’. When important parameters within the model such as the growth rate of injured lobsters, the time lobsters remained in the injured stage, and the mortality of injured lobsters were altered by $\pm 10\%$ of the mean, the final results changed $< 10\%$ (except one

instance where a 15% change in recreational harvest was observed). This sensitivity analysis suggests that the results were relatively insensitive to variation in key parameters. Fishery-induced injuries may reduce adult stock biomass by 900 t and annual commercial landings by 160 t, or \$1.6 million revenue, if applied to the scale of the entire spiny lobster fishery in the Florida Keys. Educating sport-divers to restrict capture attempts to lobsters they are certain meet minimum size requirements may be a relatively easy first attempt at reducing the impact of lobster injuries in the fishery. Unobserved fishery-induced mortality probably is not restricted to a few fisheries such as the spiny lobster fishery in the Florida Keys; its undesirable and costly consequences may occur in fisheries throughout the world. To avoid these costs it would be prudent that unobserved mortalities be accounted for in all fisheries.

INTRODUCTION

All fishing gears have the potential to interact with, but not successfully capture, some portion of the targeted stock. Furthermore, even after capture, some animals may be intentionally released due to their quality or size. Depending on the severity of this interaction (i.e. how much physical damage, physiological stress or behavioral disturbance has occurred), some of these animals may die later, and contribute a largely unobserved additional mortality associated with the fishery. Examples of this unobserved mortality are now associated with nearly every method of fishing. For example, fish that escape through trawl cod ends often succumb to predation (Ryer et al. 2004). The majority of animals caught in some dredge fisheries are discarded (Bergmann and Moore

2001), often with injuries (Bergmann et al. 2001), potentially aggregating predators (Veale et al. 2000) and leading to higher rates of mortality because of these factors (Bergmann and Moore 2001). Depending on trap soak time, lobsters confined in traps without release gaps can starve to death before the traps are hauled (Matthews 2001), and recreational sport-divers unintentionally injure some Caribbean spiny lobster (*Panulirus argus*), elevating their mortality rate (Parsons and Eggleston 2005). Despite this growing pool of evidence suggesting substantial indirect effects and unobserved mortalities, the population impact of a fishery is usually calculated as the number of animals that the fishery extracts. Less often, 'bycatch', animals that are unintentionally caught by fishing gears and usually discarded dead, may be incorporated into population models. For example, there are indications that the steady decline in landings of finfish species that are often incidentally taken by shrimp trawls (e.g. summer flounder and weakfish), can be largely attributed to bycatch, which often outweighs the intended catch 4:1 (Murray et al. 1992). Quantifying the population effect of unobserved mortality, when there is an additional uncertainty as to how many individuals the fishery is actually killing, can be even more problematic than incorporating bycatch. Matthews (2001), however, did show that large numbers (0.646 million annually) of juvenile spiny lobsters (*P. argus*) die in lobster traps before these traps are hauled.

Aside from the large unobserved mortality associated with the commercial trap fishery for spiny lobsters in the Florida Keys, USA, recreational sport-divers also unintentionally injure and kill spiny lobsters. Sport-divers attempt to catch spiny lobsters by using a tickle stick to coerce them out of a crevice and into a hand net. Some of these lobsters, however, escape during this process, often with injuries. Undersized lobsters

(<76 mm CL) also may be injured when they are mistaken for a legal lobsters, captured and then released. Some of the most intense recreational fishing effort in the world occurs in the recreational fishery for spiny lobsters in the Florida Keys (Eggleston et al. 2003). This fishing effort peaks during the 2 d mini-season that is exclusively for sport-divers and occurs in the last week of July before the regular season for commercial and recreational fishers opens at the beginning of August. During these 2 d 80-90% of the legal sized lobsters present at that time are removed (Eggleston et al. 2003) and up to 27% of the remaining population of legal and sublegal lobsters may become visibly injured from interaction with sport-divers (Parsons and Eggleston 2005). These injuries are known to be detrimental to lobsters, reducing their growth (Davis 1981), altering their social behavior and interacting with potential predators (Parsons and Eggleston in press), and elevating their mortality (Parsons and Eggleston 2005). The population and economic consequences of these lobster injuries are unknown. Considering that 50,000 sport-divers harvest lobsters during the 2 d mini-season in the Florida keys each year (Sharp et al. 2005), that many other divers do so during the regular fishing season, and that > 900,000 lobster traps without escape gaps are deployed by commercial fishermen each year (Hunt 2000), it is important to estimate potential population and economic consequences of sub-lethal injuries in the spiny lobster fishery in the Florida Keys. Fortunately, many demographic and fisheries aspects of the Caribbean spiny lobster in the Florida Keys are well known, which facilitates parameterizing population models.

Modeling studies have great potential to assess potential population and economic consequences (Crowder and Murawski 1998, Kellison and Eggleston 2004) of bycatch and unobserved mortality. In this study, we used a spatially explicit, individually-based

population simulation model. Individual based models are powerful ecological tools that predict the dynamics of whole ecosystems by monitoring the unique, complex interactions of individuals (Judson 1994). These models are based on biologically meaningful information, allowing very specific questions can be addressed (Judson 1994). In the current study the individual agents in the model were lobsters, and the environment they occupied was a representation of the patch reef habitat of the lower Florida Keys. Estimates of the percentage of lobsters injured by sport-divers (Parsons and Eggleston 2005) and individual consequences of these injuries (Davis 1981, Parsons and Eggleston 2005) were incorporated to predict potential population and economic (i.e. reduced fishery landings) consequences of sport-diver inflicted injuries on spiny lobsters inhabiting the Florida Keys, USA. Specifically, we hypothesized that injuries lobsters received from fishing activities would reduce predicted adult lobster populations and reduce predicted recreational and commercial landings. Furthermore, we hypothesized that even if the number of lobsters injured by fishing activities was reduced, the consequences would still be reduced predicted adult populations and landings.

METHODS

General modeling approach

A computer simulation model was constructed to calculate lobster population abundance and fishery landings under two injury scenarios: (1) where injured lobsters with higher individual mortalities and lower growth rates were included, and (2) where injured lobsters were ignored. The model domain represented patch reef habitats of the

lower Florida Keys (Fig. 1). Individual lobsters populated this environment, moving between shelters, that they occupied during the day and the surrounding areas in which they foraged at night, and transitioning between four different stage classes depending on their age and injury status. Model iterations were conducted on a minute by minute basis; after each minute time step, individual growth and injury status, natural mortality, fishing mortality, and movement behavior were reassessed for each lobster (see Fig. 2 for a schematic description of these factors). Each model simulation was run for a 5-yr period, after which the abundance of adult lobsters and recreational and commercial landings were compared between simulations with and without lobster injury.

Specific description of model

(1) Physical environment and initial population

The spatial environment of the model simulated patch reef habitats on the Gulf of Mexico side of the lower Florida Keys (Fig. 1). The patch reef habitat consists of a thin veneer of sand overlying low-relief rock and exposed rock with gorgonians, coral patch heads, sponges, and ledges of 0.5 to 1m relief (Eggleston et al. 2003). The simulation, of a 1-ha reef consisted of 10,000 1m² individual habitat cells. Each 1m² cell was either a shelter or a non-shelter. Shelters were distributed as isolated patches, clusters and linear arrays, similar to the small and large patch heads, sponges, solution holes and crevices observed during lobster and habitat surveys in this patch reef habitat (Eggleston et al. 2003). The density of shelters has not been described for this patch reef habitat, so we chose a value (0.008 shelters m⁻²) that agreed with our previous observations and fell within the range of known shelter densities for similar habitats that lobsters also use (e.g. ~0.03 sponges m⁻² in channel habitats of the Marquesas Islands: Eggleston and Dahlgren

2001, and 0.004 sponges m^{-2} in channel habitats of the Florida Keys: Eggleston et al. 2004). The non-shelter cells represented habitats like sand, seagrass and hard-bottom. This environment was initially populated with 152 adult (> 76 mm CL) and 75 juvenile lobsters, representing average pre-mini-season abundances (mid-July) based on lobster densities (number $\cdot m^{-2}$) observed over a 4 year period in this habitat (D. Eggleston unpub. data.).

(2) Life Stages

Lobsters within the model were assigned to different life stages based on their size and injury status. “Juveniles” (50-76 mm CL) were vulnerable to the sub-lethal affects of the fishery (i.e. they could be captured and used as bait in commercial traps and accidentally captured and released by recreational sport-divers). Lobsters smaller than 50 mm CL have little interaction with the fishery (Dolan and Butler in press) and were omitted from the model. “Adults” (> 76 mm CL) were exposed to harvest and sub-lethal impacts of the fishery. Both juveniles and adults could move into “injured juvenile” and “injured adult” stages, which incorporated reduced growth, elevated mortality and altered social behavior specific to that stage (Davis 1981, Parsons and Eggleston 2005). Juvenile lobsters could also transition to the adult stage, according to their age and growth rate (see below). The initial population of lobsters consisted only of juvenile and adult stages because field surveys indicated that injured lobsters were rare (0-3%) in the patch reef habitat prior to the fishing season in mid-July (D. Eggleston unpub. data.).

(3) Recruitment

On average, 120 new 50mm CL juvenile lobsters recruited to the model domain annually. This estimate was based on lobster growth and immigration data, which

contributed ~120 new juvenile lobsters (15-45 mm CL) to 1 ha of Florida Keys back-reef habitat each year (Herrnkind and Butler 1994). The recruitment of these new lobsters was not evenly distributed through time. Rather, arrival of new recruits to the model domain peaked in spring (on average 2 lobsters every three days from January to April), whereas recruitment during the remainder of the year was lower (on average 1 lobster every 6 days from May to December). This temporal dichotomy in the addition of juveniles to the model domain was based on the spring peak of settling by spiny lobster post-larvae in the Florida Keys (Acosta et al. 1997), and on the ~1 year that it takes a newly settled spiny lobster to grow to 50 mm CL (see SEDAR (2005) for a summary of growth studies).

(4) Time step and data output

To account for individual lobster behaviors that may have been affected by fishery-induced injury (i.e. social interactions and the acquisition of shelter), lobster movements, growth and mortality were calculated on a 1 minute time step. Data output from the model occurred once a day and included the population size of each stage class (adults, injured adults, juveniles, injured juveniles), and the number of lobsters removed by recreational and commercial harvest (see below). Each model simulation was run over a period of 6 years. Results during the initial year of model simulation were discarded because they would have been strongly affected by initial conditions and would not accurately reflect steady-state conditions (Dolan and Butler in press). The remaining 5 years of the simulation allowed adult abundance and associated harvests to be compared between different injury treatments and across multiple fishing seasons.

(5) Movement

Lobsters in the model occupied shelters during the day, which they would leave at 6pm to begin nocturnal foraging. The rate of movement during these night-time excursions was 1m per minute (Herrnkind et al. 1975), with a random alteration to lobster heading ($\pm 15^\circ$) at each time-step. This random movement was maintained until 3am (Herrnkind et al. 1975), after 3 am their movements became affected by shelters and other lobsters. If they passed over a shelter they would stop. If they were not yet in a shelter they became attracted to other nearby lobsters that were not in shelters, usually resulting in queues of lobsters moving through the model domain. This behavior is similar to the social interactions of lobsters observed at this time of day (Herrnkind et al. 1975). Lobsters passing near another lobster within a shelter moved towards that shelter and stopped when they reached it. Thus, sheltered lobsters attracted unsheltered lobsters in a manner similar to the ‘guide effect’ (Childress and Herrnkind 2001). Both of these attraction behaviors took effect at a radius of 5m. While the scale over which lobster attraction odors operates is unknown, laboratory (Ratchford and Eggleston 1998, 2000) and field trials (Nevitt et al. 2000) have indicated it is a few meters. These attraction behaviors were further modified by the presence of injured lobsters, which did not have the ability to attract conspecifics (Parsons and Eggleston 2005) at any distance, but were attracted to uninjured conspecifics.

After 6am, all lobsters stopped moving wherever they were located, and remained there until 6pm. While Herrnkind et al. (1975) rarely observed lobsters that failed to find a shelter, lobsters were sometimes observed in suboptimal shelters such as depressions in the substratum or seagrass beds during our field surveys in the lower Florida Keys

(Eggleston et al. 2004). Furthermore, Herrnkind et al. (1975) noticed that lobsters released away from the reef during the day would move to the reef edge and reside in a small depression until the evening. Preliminary simulations using the model revealed that lobsters were rarely forced to reside away from shelter during the daytime.

While lobsters can move over larger areas than our 1-ha domain, their nighttime movements generally do not take them more than 300m from their previous days shelter, and they usually return to the same or a nearby shelter within a 100m radius (Herrnkind et al. 1975), therefore any further incorporation of den fidelity was not considered. There was no reason to assume that emigration from the model domain would not be equal to immigration into the same area, so the model was given ‘torus’ boundaries; any lobster that moved out of one side of the modeled environment re-entered on the opposite side.

(6) Growth

The age of each individual lobster was initially defined and increased at minutely increments thereafter. New juveniles entering the model domain were given an age of 0 yr and were required to reach an age of 0.9808 yr before transitioning to the adult stage. This represented the 51 weeks it takes a 50 mm CL lobster to grow to 76 mm CL at a rate of 0.51 mm/week (Davis 1981). The individual ages of the initial population of juvenile lobsters, however, was randomly distributed between 0 yr and 0.9808 yr to avoid all the initial juveniles transitioning to the adult stage at the same time. If a juvenile became injured, it would transition to the injured juvenile stage. It remained in this injured stage for 15 weeks, the average inter-molt period for an injured lobster (Davis 1981). After previously injured juveniles returned to the normal juvenile stage, their growth rate was decreased to 0.33 mm/week (Davis 1981). Therefore, the time it took a previously

injured lobster to reach 76 mm CL depended on its size when it received its injury. For example, a lobster injured at 50 mm CL would take an extra 33 weeks to reach 76 mm CL, while a lobster injured at 65 mm CL would take an extra 13 weeks to reach the same size. As with juveniles, injured adults remained in their injured stage for 15 weeks. Adult growth was not considered by the model because there was no stage for adults to grow into.

(7) Mortality

The base probability of natural mortality for juveniles and adults was 0.0006 chance of dieing/day (Muller et al. 2000). Natural mortality was raised, however, for certain situations: (1) raised for lobsters residing in the open during the day (0.0014 chance of dieing/day; Mintz et al. 1994) and (2) raised for injured lobsters (0.006 chance of dieing/day; Parsons and Eggleston 2005). Injured lobsters retained this elevated natural mortality probability until they reentered a un-injured stage by molting (15 weeks). While it is not known if injured lobsters experience elevated mortality for the entire time they possess injuries, we observed a consistent distribution of elevated mortality over a 5 day period when injured lobsters were tethered to coral patch heads (Parsons and Eggleston unpub. data).

The probability that a lobster within the model would experience fishing mortality each year was based on the annual fisheries extraction probability (0.4773 chance of dieing/yr: SEDAR 2005). This total fishing extraction probability was divided among the recreational and commercial fishing sectors and distributed throughout the year based on the monthly distribution of lobster landings between these sectors (R.G. Muller unpub. data., Sharp et al. 2005). For example, on average, the commercial fishery landed 718

tons of lobsters in the Florida Keys in August. This represents ~25% of the total annual recreational and commercial landings (2893 t) in the Florida Keys, hence 25% of the annual fishing mortality. Commercial fishing mortality in August was therefore parameterized as an extraction rate of 0.0038/day. Similarly, monthly recreational and commercial landings were also used to partition the remaining 75% of annual fishing mortality over the remainder of the fishing season. Based on landings data (R.G. Muller unpub. data., Sharp et al. 2005), however, recreational harvest during the 2 day sport-diver mini-season accounted for only ~3.5% of total annual commercial and recreational landings. This percentage of total annual landings would not account for the 80-90% extraction rate observed in the patch reef habitat (Eggleston et al. 2003) that this model was attempting to simulate. To find a compromise between the observed extraction rate and the percentage of total landings accounted for by the mini-season, the recreational extraction rate during the mini-season was incrementally raised, while holding the total extraction rate constant and ensuring that the annual pattern of recreational and commercial landings did not become visibly distorted. The probability of recreational fishing mortality during the mini-season was eventually set at 0.023/day, which represented ~10% of annual commercial and recreational landings. In this scheme, probabilities of mortality from the recreational fishery were 0.023/day during the mini-season, 0.0021/day in August, and 4.8^{-5} /day from September to March. Similarly, probabilities of mortality from the commercial fishery were: August 0.0038/day, September 0.0027/day, October 0.0022/day, November 0.0015/day, December 0.0009/day, January 0.0007/day, February 0.0004/day, March 0.0004/day.

(8) Injury

On average, the percentage of injured spiny lobsters residing on patch reefs increased from 0-24% during the 2d sport-diver mini-season ($n = 3$ years, D. Parsons and D. Eggleston unpub. data.), so we used a probability of 0.128/day that a lobster would be injured during the mini-season. The probability that a lobster would be injured during the remainder of the fishing season (August–March) was set by adjusting the above injury rate proportional to the average daily recreational fishing effort during that part of the year. For example, the daily recreational fishing effort during August was ~19.5% of that during the mini-season (Sharp et al. 2005), so the probability of injury was adjusted to ~0.025/day. From September to March, recreational effort was ~0.83% of that during the mini-season, so the probability of injury was adjusted to ~0.0011/day.

There are no estimates of the percentage of lobsters injured by the commercial fishery; however, there are estimates for the percentage of sub-legal lobsters that are found injured in traps and the percentage of lobsters that escape. For example, there is a 0.005 probability that a juvenile lobster will go into a trap on any given day (Lyons and Hunt 1992). Of all the juvenile lobsters in traps, 11.5% have injuries (Lyons et al. 1981) and there is a 1% chance that a juvenile will escape from a trap each day (Lyons and Kennedy 1981). Combining these probabilities produces a 0.0000058 probability that a juvenile lobster would be injured each day by the trap fishery. Initial computer simulation trials indicated that this probability of injury produced an extremely small number of injured lobsters, which is in accord with the observation that most juvenile lobsters captured by commercial gear are never intentionally released (Hunt 2000), and the percentage of injured lobsters in the population does not vary throughout the

commercial fishing season (Lyons et al. 1981). Despite this low percentage, the probability a lobster would be injured by commercial fishing gear was incorporated into the model to simulate all possible sub-lethal effects of the fishery.

Simulations

Lobster population size and fishery landings with and without injury: The simulation program was written in Netlogo software and run on a Pentium 4 (3.0Ghz) microcomputer. Initial simulations were conducted under two scenarios, 'injury' vs. 'no injury'. Ten replicate simulations were conducted for each of these scenarios and three response variables were extracted from them for each year of the simulation: (1) the number of adult lobsters present in the model simulation each year just prior to the mini-season in July (adult abundance at this time should be at a peak because no simulated fishery extraction had occurred for the previous ~ 4 months), (2) annual recreational harvest, and (3) annual commercial harvest. We hypothesized that all three response variables (abundance of adult lobsters, recreational, and commercial landings) would be reduced when injury was incorporated into model simulations and that this effect would be consistent across time.

Reduced probability of injury: Reducing the probability of a lobster becoming injured during the fishing season is a potential management approach to reducing the overall impact of injuries on lobster populations and associated harvests. Some areas of the Florida Keys are also known to have lower sport-diver effort than others, and the probability of a lobster becoming injured in these areas is also likely to be less. Therefore, we conducted simulations with reduced probabilities of injury and compared

them to the ‘no injury’ and ‘injury (patch reef)’ simulations described in the previous section. These scenarios were (1) ‘No injury’, as before, but in which lobster injuries were excluded from the model. (2) ‘Low injury’, in which the probability of a lobster being injured during the mini-season was reduced by 96%, to 0.005/day, during the two day mini-season. This reduction was based on sport-diver density being $24 \times$ greater in the patch reefs of the lower Florida Keys, compared to areas of the upper Keys like Biscayne Bay, Florida (2.5^{-5} divers m^{-2} : T. Kellison and D. Eggleston, unpub. data). (3) ‘Medium injury’, where the probability of a lobster being injured during the mini-season was reduced by 60%, to a 0.048/day probability of injury during the two day mini-season. This was the average probability of injury during the mini-season for the patch reef, patch head, Atlantic reef and Biscayne Bay habitats (D. Eggleston and D. Parsons unpub. data). (4) ‘High (patch reef) injury’, as before, but with the probability of a lobster being injured during the two day mini-season was 0.128/day. We hypothesized that reducing the probability of injury in the ‘low injury’ and ‘medium injury’ simulations would reduce the abundance of adult lobsters, and recreational and commercial landings as compared to the ‘high (patch reef) injury’ simulations, but the abundance of adult lobsters, and recreational and commercial landings would still be less compared to the ‘no injury’ simulations

Sensitivity analysis: The sensitivity of model results to variation in certain parameters was assessed by increasing and decreasing some parameters by 10% and observing the percentage change for each response variable (adult abundance, recreational harvest, and commercial harvest) compared to simulations without altered parameters. These comparisons were made using the ‘medium’ probability of injury, and all response

variables were averaged over five years of model output. The parameters that were altered were: (1) the growth rate of injured lobsters, (2) the time an injured lobster remained in an injured stage class, and (3) the probability of mortality for injured lobsters. Three replicate simulations were conducted for each parameter alteration.

RESULTS

Lobster population size and fishery landings with and without injury

Model simulations estimating juvenile and adult lobster abundance, without incorporating injury, produced a seasonal pattern of adult abundance with an overall increasing trend across years (Fig. 3a). The juvenile population displayed a similar seasonal pattern in abundance, but the oscillations were of smaller amplitude and abundance did not appear to increase across years (Fig. 3a). Abundance of adults was higher than juveniles (Fig. 3a) because juveniles eventually grew into and accumulated in the adult stage. This pattern reflected the higher adult abundances observed in this habitat prior to the mini-season (Eggleston et al. 2003). Estimates of monthly recreational harvest from this population of lobsters were high in July and August, with few lobsters caught thereafter, while commercial harvest estimates were high in August and declined every month until the end of the regular fishing season in March (Fig. 3b). Both the seasonal pattern of adult abundance and the estimates of recreational and commercial harvest closely matched observed seasonal patterns of recreational and commercial landings, (R. Muller, FWC, unpub. data., Eggleston et al. 2003, Sharp et al. 2005), suggesting the model was producing realistic population and harvest estimates.

When injury was incorporated into model simulations, adult and juvenile abundances varied seasonally, with juvenile abundances higher than adults, opposite the pattern observed without injury (compare Figs. 3a and 4a). Moreover, seasonal variation in abundances was more pronounced (Figs. 3a and 4a). When accounting for injury, adult abundance also did not increase across the multiple years of the simulation as it did when injury was absent (Figs. 3a and 4a). The seasonal pattern of recreational and commercial landings appeared similar, but the overall catch was lower (Fig. 4b). When the results of the injury simulations were broken down to illustrate all stages that contributed to the population (i.e. so injured stages could also be observed), seasonal patterns of injured juveniles and injured adults were evident (Fig. 5), with highest abundances of injured lobsters present in July and August and decreasing to very few to no injured lobsters by November. The periods with the highest proportion of injured lobsters (July and August) occurred at the time of year when annual recreational fishing effort peaks (Eggleston and Dahlgren 2001, Eggleston et al. 2003, Sharp et al. 2005).

Adult lobster population abundance was ~50% of the adult abundance when injury was incorporated into the model. The adult population from the no injury treatment also appeared to increase each year, whereas the population incorporating injury did not (Fig. 6a).

Model simulations that incorporated injury reduced recreational and commercial harvests (63 and 58% lower respectively) compared to simulations without injury. Both the annual recreational and commercial harvests appeared to increase each year when injury was absent, and remained stable across years when injury was present.

Reduced probability of injury

Adult abundance: Mean abundance of adult lobsters varied according to injury treatment even when the probability of lobsters becoming injured was reduced. For example, the medium injury treatment reduced adult abundance estimates by ~28% compared to the no injury simulations, whereas the low injury treatments reduced adult abundance estimates by ~5% compared to the no injury simulations (Fig. 7a). Adult lobster abundance increased each year for some injury treatments (e.g. no injury and low injury) and remained stable through time for other injury treatments (e.g. high (patch reef) injury; Fig. 7a).

Recreational harvest: Mean recreational harvest varied according to injury treatment even when the probability of lobsters becoming injured was reduced. For example, the medium injury treatment reduced recreational harvest estimates by ~36% compared to the no injury simulations, whereas the low injury treatments reduced recreational harvest estimates by only ~1% compared to the no injury simulations, which probably did not represent a meaningful difference (Fig. 7b). Recreational harvest varied through time, but with any general trend.

Commercial harvest: Mean commercial harvest varied according to injury treatment even when the probability of lobsters becoming injured was reduced. For example, the medium injury treatment reduced commercial harvest estimates by ~33% compared to the no injury simulations, whereas the low injury treatments reduced commercial harvest estimates by ~9% compared to the no injury simulations (Fig. 7c). Commercial harvest increased each year for some injury treatments (e.g. no injury) and remained stable through time for others (e.g. high (patch reef) injury; Fig. 7c).

Sensitivity analysis

The model parameters altered in the sensitivity analysis (growth rate of injured lobsters, the time lobsters remained in the injured stage and the mortality rate of injured lobsters) had little effect on adult lobster abundance, recreational harvest and commercial harvest (Table 1). In all but one instance (the estimated recreational harvest produced when the mortality of injured lobsters was reduced by 10%), the percentage change in each response variable was less than the 10 percent alteration each parameter received (Table 1). In some instances, we anticipated a specific parameter alteration would decrease the value of each response variable, but a small increase in these response variables was observed. This sensitivity analysis suggests that stochastic variation within the model had a greater effect on final results than assumptions of certain parameter values.

DISCUSSION

Estimating population and economic consequences of unobserved fishing mortality is inherently difficult because of the uncertainty associated with the number of individual animals affected by the fishery and the proportion of those individuals that subsequently die. The results of this simulation, however, clearly demonstrate that in the spiny lobster fishery in the Florida Keys, large reductions in landings and stock abundance may be attributed to this unobserved mortality under certain circumstances. While the results of modeling studies are only an estimate of the actual dynamics of a modeled system, they are useful for indicating areas of interest and concern within that

system, especially where logistics restrict actual field estimation. Furthermore, sensitivity analysis suggested that altering parameter estimates within the model was unlikely to effect the final conclusions of the model.

Calculating a fishery-scale estimate of the total loss in landings and stock abundance due to lobster injuries depends on the probability of lobster injuries occurring throughout the entire geographic range of the fishery. At the scale of the Florida Keys, the probability of a lobster being injured is variable. For example, in the patch reef areas where we have observed high recreational fishing effort and an ~24% increase in injured lobsters from before to after the mini-season, injury may reduce the abundance of adult lobsters and annual landings by $\geq 50\%$. This estimate was insensitive to variation in important model parameters such as the growth rate of injured lobsters, the time lobsters remained in the injured stage, and the mortality of injured lobsters, suggesting that injuries to lobsters should be a serious management concern for certain regions. At the other extreme, recreational fishing effort in Biscayne Bay is only ~5% that in the lower Keys (Eggleston and Kellison unpubl. data), and the prevalence of lobster injuries is likely similarly lower; there the overall impact of injuries on the abundance of adult lobsters and associated landings was only ~5 and 8%, respectively.

The overall probability and distribution of lobster injuries throughout the Florida Keys must be learned if the full impact of lobster injuries on lobster populations and associated harvests is to be estimated. Lacking such data we used the lowest probability of injury (from Biscayne Bay) to generate fishery-scale estimates of the impact of lobster injuries on adult abundance and harvests. Even with this reduced probability of injury, applying the reduced adult abundance generated from 'low injury' simulations to the

entire stock biomass suggests that adult abundance at the beginning of the fishing season in the Florida Keys may be reduced by 900 t (based on a stock estimate of 17280 t: SEDAR 2005). If we apply the reduced commercial harvest generated from ‘low injury’ simulations to commercial fishery landings of spiny lobsters from the Florida Keys, landings are reduced by 160 t or \$1.6 million revenue (based on annual landings of 1855 t or \$19.2 million: Fisheries Statistics Division, NMFS, unpub. data). This emphasizes the importance of lobster injuries even if they occur infrequently. We suggest that extensive surveys of lobster injuries be undertaken throughout the entire Florida Keys and repeated multiple times during each fishing season to fully account for their effect on the fishery.

When the indirect effects of lobster fishing described in the current study are considered in conjunction with the annual loss of ~0.646 million juvenile lobsters used as bait in commercial traps (Matthews 2001), and the overcapitalization of the trap fishery (Hunt 2000), the Florida Keys spiny lobster fishery can be considered as extremely inefficient. There are few other examples documenting the influence of unobserved mortality at the level of the population or entire fishery. High indirect mortality, however, has been demonstrated in an Australian scallop dredge fishery. In this fishery, an estimated 12-22% of the stock at the start of each fishing season is actually landed as catch (McLoughlin et al. 1991). Mortality within the stock remains high, however, even after the fishery has closed. High post-fishing mortality is caused by bacteria that initially infect scallops injured by dredge contact but eventually spread to and kill the remainder of the fished population (McLoughlin et al. 1991). While this is an extreme example of inefficiency, unobserved mortality is likely significant in many other fisheries and needs to be regarded as a management priority (Alverson and Hughes 1996).

An interesting result of the current study was that as the probability of lobster injury was reduced, annual recreational harvest became similar to that predicted under the 'no injury' simulations, whereas commercial harvest remained significantly depressed. The lack of effect of injury on recreational harvest may be because a large proportion of the annual recreational catch occurs early in the season (Sharp et al. 2005), before injuries raise mortality and decrease growth of juvenile lobsters. A large proportion of commercial landings occurs later in the fishing season, when injuries may have taken effect. Therefore, the model simulations presented in the current study suggest that recreational fishers generate most of the injuries within the lobster population, but commercial fishermen bear most of the consequences (i.e. reduced landings). Actual observations of the number of lobsters commercial trap fishermen are injuring would be required, however, to verify this statement.

Another interesting result of the current study is that lobster exploitation rates observed during the mini-season (80-90% extraction, Eggleston et al. 2003) could not be incorporated into the model without vastly distorting the known annual pattern of recreational and commercial landings (SEDAR 2005, Sharp et al. 2005). This is because annual recruitment estimates used in the current study (120 lobsters/ha/year; Herrnkind and Butler 1994) were not capable of supplementing the fishery after the initial mini-season extraction. This suggests that the current understanding of recruitment processes in the Florida Keys is not accurate or that a large portion of the lobster population avoids initial extraction during the 2 d mini-season and subsequently become exposed to fishery mortality through their own movements or the movements of fishermen. Understanding how adult lobster populations are replenished throughout the fishing season is an

important issue that should be clarified by investigating recruitment of juvenile lobsters, movements of juvenile and adult lobsters and the spatio-temporal distribution of fishing effort.

Evidence of large, unobserved mortalities would generally be regarded as a conservation issue that could potentially threaten stock biomass and have negative consequences on the ecosystem. In the case of the Florida Keys spiny lobster fishery, this is not necessarily the case. The abundance of adult lobsters there is probably heavily subsidized by upstream pan-Caribbean sources of larvae; the lack of any evidence for restricted gene flow between *P. argus* populations throughout the Caribbean supports this notion (Silberman et al. 1994). Moreover, the fishery relies heavily on new recruitment of legal sized lobsters, through molting, in each fishing season (Powers and Sutherland 1989). This suggests that most of the lobsters that die because of injuries would have been killed by the fishery even if they had not been injured. This is a unique situation implying that the only real consequences of unintentional injuries are economic (lost revenue through decreased landings) and social (how the catch is divided amongst various sectors of the fishery). These are sufficient reasons to try and reduce injuries and unobserved mortality by educating recreational sport-divers; reducing attempts to capture under-sized lobsters would be a prudent and relatively easy first attempt at reducing lobster injuries. In the majority of the world's fisheries, where recruitment is likely dependent to some extent on local stock biomass, unobserved mortality likely has major conservation consequences. Fishery, managers and scientists must attempt to account for the entire impact of fishing (Alverson and Hughes 1996), whether it is observed in

landings or not, to avoid the significant social, economic and conservation consequences that are currently being ignored.

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Table 1: The percentage change in adult abundance, recreational harvest and commercial harvest when the growth rate of injured lobsters, the time a lobster remained in the injured stage and the mortality of injured lobsters was altered by $\pm 10\%$. Values in the table represent the average percentage change over 5 years of model simulations compared to ‘medium injury’ simulations without any parameter alteration. $n = 3$ for all simulations.

Response variable	Growth rate		Time injured		Mortality of injured lobsters	
	-10%	+10%	-10%	+10%	-10%	+10%
Adult abundance	-0.2	-0.7	6.5	0.8	5.8	-5.1
Recreational harvest	-7.9	-0.8	9.7	10.4	15.3	2.0
Commercial harvest	1.9	-6.1	1.0	-6.1	5.3	-4.4

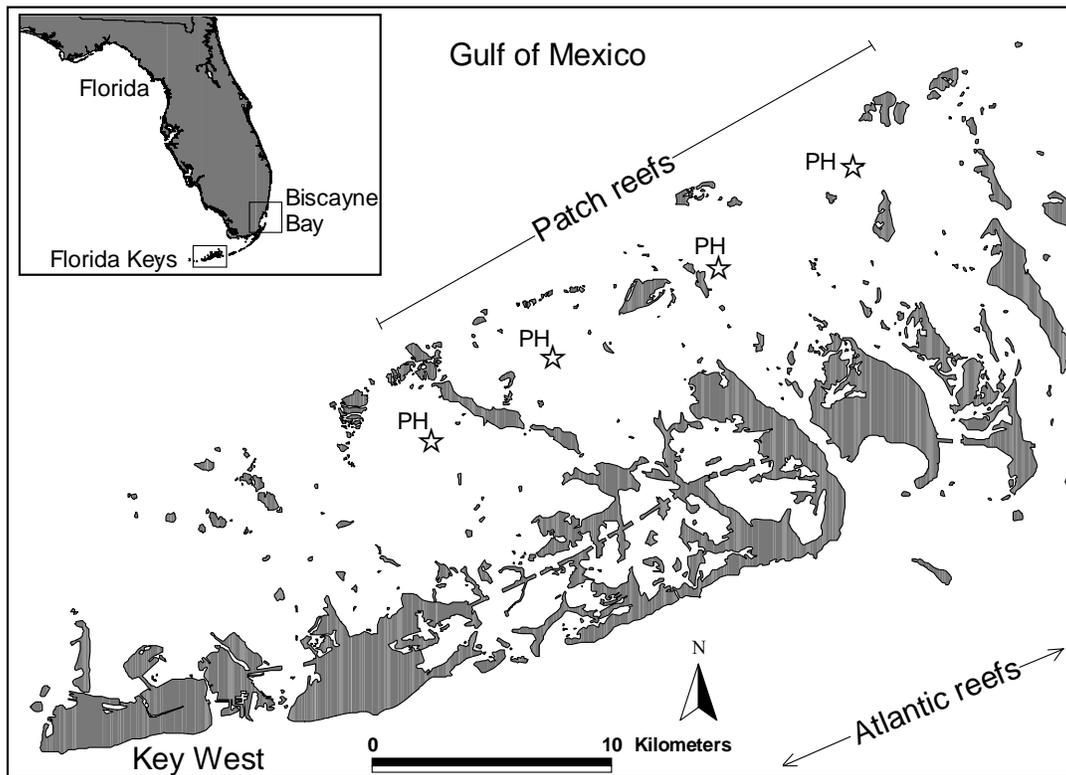


Fig. 1: Map of the lower Florida Keys, USA, with Florida and Biscayne Bay inset, showing the locations of patch reef habitats, patch heads (PH), and Atlantic reefs where lobster populations were simulated in this study.

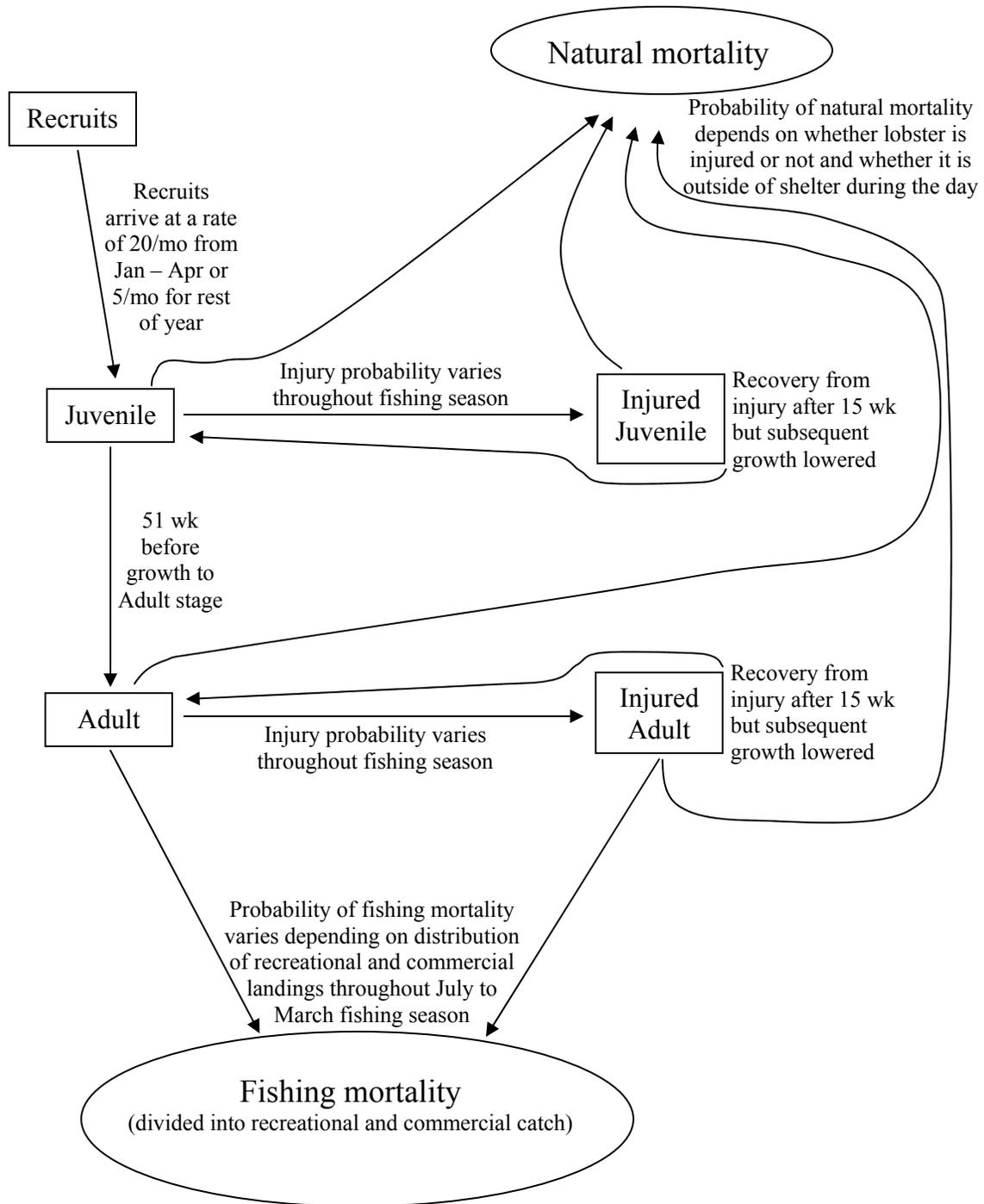


Fig. 2: Schematic diagram showing the factors that affect individual lobsters within model simulations. For simplicity lobster movements are excluded from this diagram but are described in the text. Individual lobsters occupy four possible stages (juvenile,

injured juvenile, adult and injured adult), although 'no injury' simulations exclude all injured stage classes. Arrows denote transition between stages or a particular fate of an individual lobster.

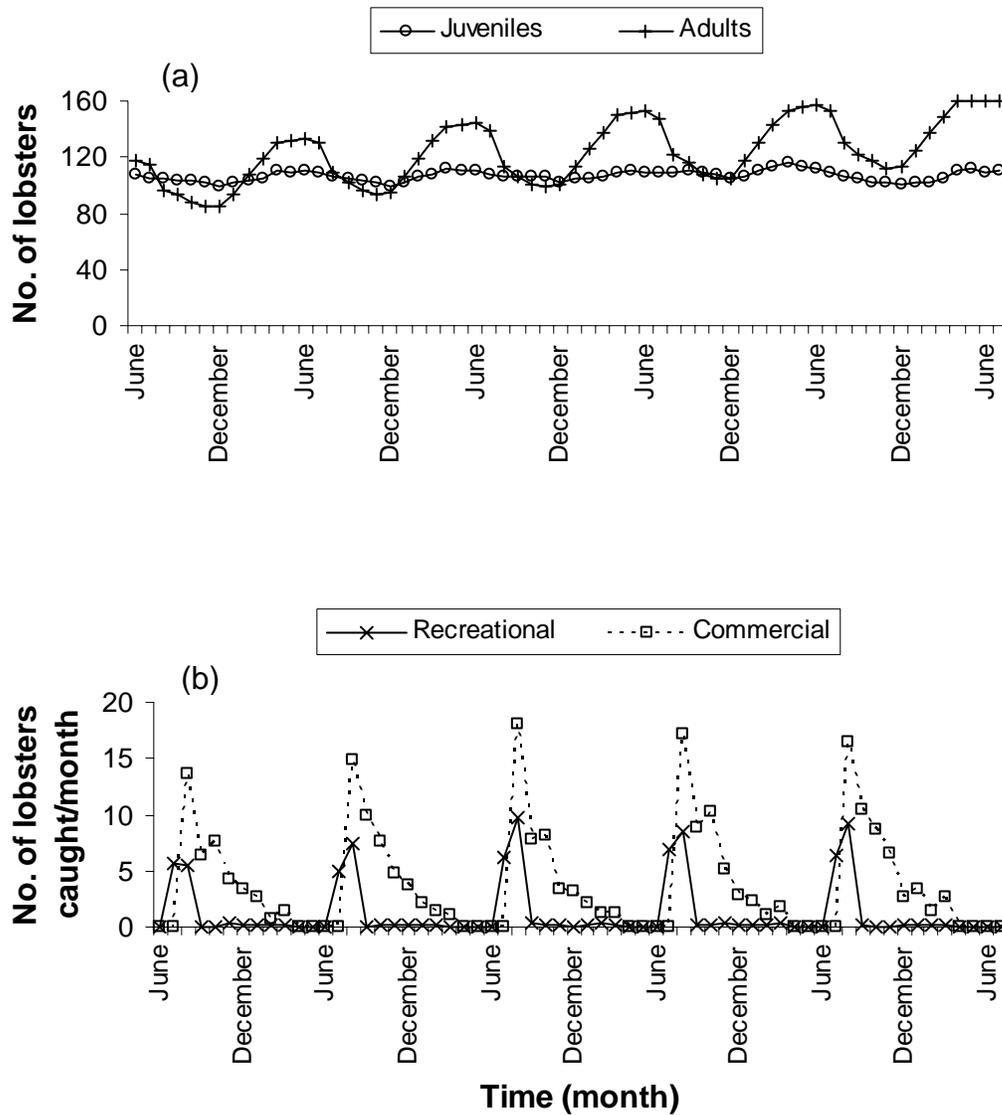


Fig. 3: Mean adult and juvenile spiny lobster abundance (a), and monthly recreational and commercial harvest (b) across five years of model simulation without the presence of injury. Values represent the average of 10 replicate simulations.

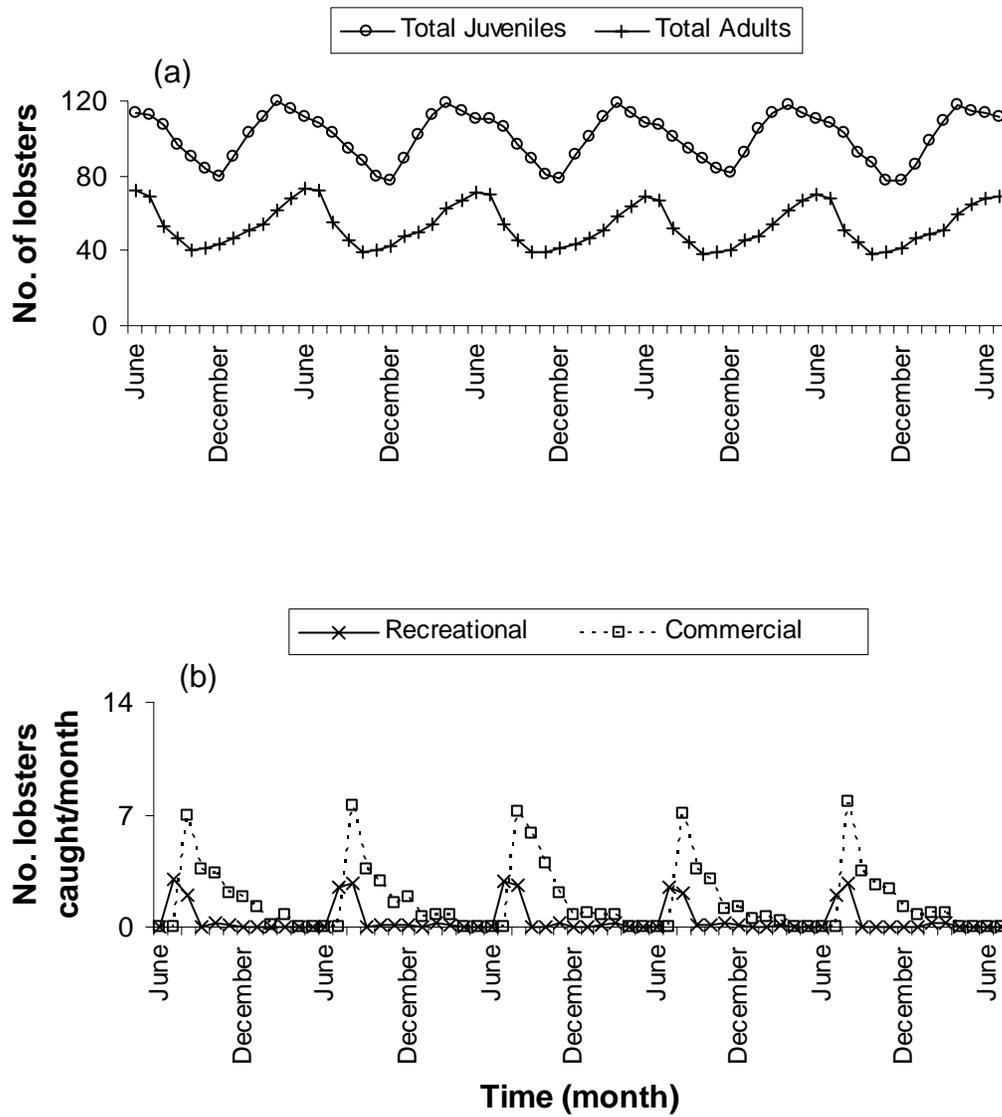


Fig. 4: Mean adult and juvenile spiny lobster abundance (a), and monthly recreational and commercial harvest (b) across five years of model simulation with the presence of injury. Values represent the average of 10 replicate simulations.

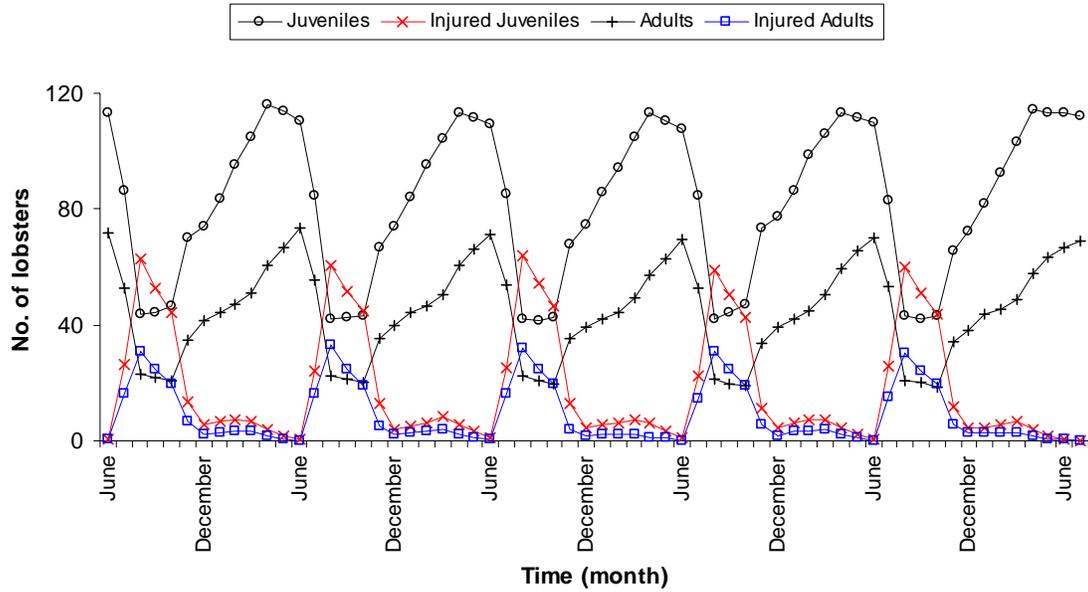


Fig. 5: Mean abundance of spiny lobsters across five years of model simulation with injury. Values are the same as those in Fig. 3, but separated into injured and normal stage classes. Values represent the average of 10 replicate simulations.

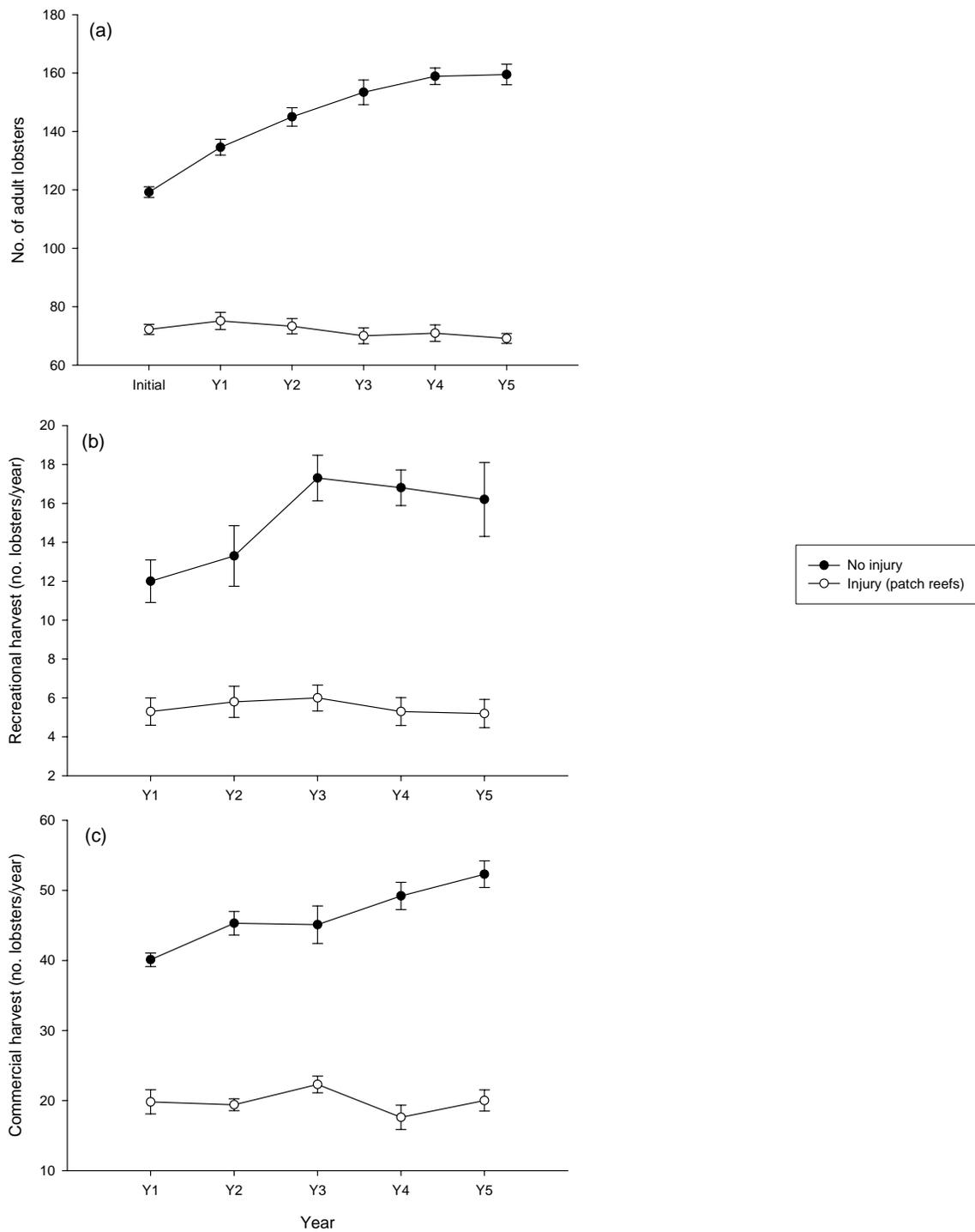


Fig. 6: Mean abundance of adult spiny lobsters (\pm SE) before the mini-season in July (a), mean annual recreational harvest (\pm SE) (b), and mean annual commercial harvest (\pm SE) (c) across five years of model simulations. The two scenarios depicted in this figure

represent simulations where lobsters were not exposed to injury, 'no injury', and simulations where lobsters were exposed to injuries, 'Injury (patch reefs)', representative of those observed in the patch reefs of the lower Florida Keys (Parsons and Eggleston unpub. data.). Values represent the average of 10 replicates \pm SE.

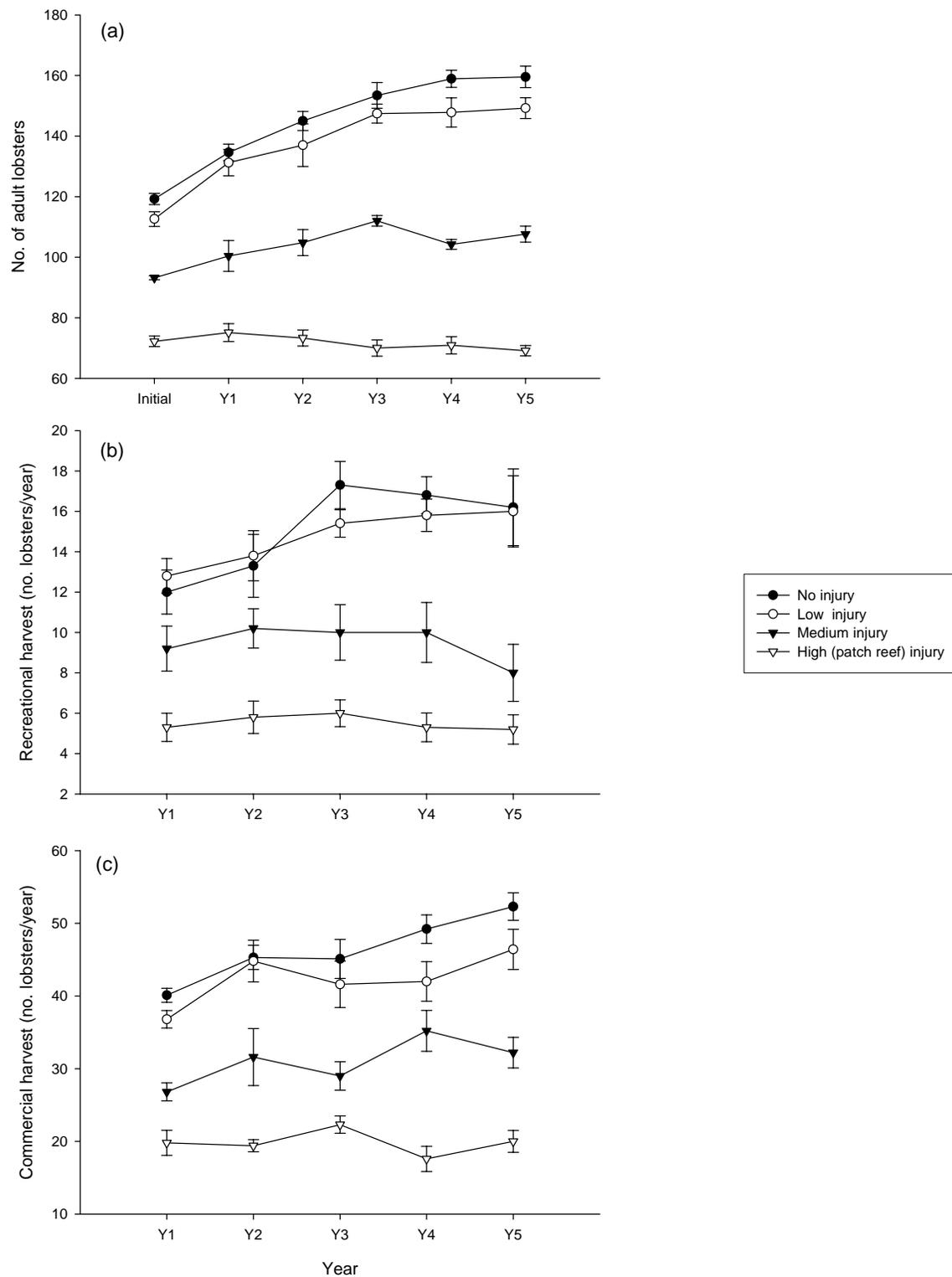


Fig. 7: Mean abundance of adult spiny lobsters (\pm SE) before the mini-season in July (a), mean annual recreational harvest (\pm SE) (b), and mean annual commercial harvest (\pm SE)

(c) across five years of model simulations. The four different scenarios depicted in this figure were: 'No injury' where lobsters were not exposed to injuries, 'Low injury' where lobsters were exposed to a probability of injury that was set proportionally to the recreational fishing effort at Biscayne Bay, 'Medium injury' where lobsters were exposed to a probability of injury based on the increase in the density of injured lobsters from before to after the mini-season at patch head and Atlantic reef sites, and 'High (patch reef) injury' where lobsters were exposed to a probability of injury based on the increase in the density of injured lobsters from before to after the mini-season at patch reef sites. Values represent the average of 10 replicates \pm SE.