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Potential population and economic consequences of sublethal injuries in the spiny lobster fishery of the Florida Keys

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Abstract. Animals that interact with but are not retained by fishing gears may later die. The population and economic consequences of these sublethal fishery interactions are seldom known but may be significant. In the present study, a population model was used 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 are known to reduce growth and elevate mortality. Simulation modelling results indicated that injuries may reduce adult lobster abundance and associated landings by $\geq$50% in areas with high recreational fishing effort. When simulated injuries were $\sim$20 times lower (representing areas with lower fishing effort), these injuries were only responsible for a 5 and 8% reduction in the adult lobster population and commercial landings respectively. Important parameters within the model (growth, time in stage and mortality of injured lobsters) were altered by $\pm$10% to assess model sensitivity. Final results changed $<$10% (with the exception of one 15% change), suggesting that model output was relatively insensitive to variation in key parameters. When the impact of sublethal injuries was applied to the entire spiny lobster fishery in the Florida Keys, adult stock biomass and annual commercial landings were reduced by 900 and 160 t (US$1.6 million) respectively. These results suggest that sublethal fishery interactions can lead to high population and economic losses, and highlight the need to incorporate sublethal injuries into stock assessments and economic models.

Additional keywords: Caribbean spiny lobster, Florida Keys, individual based model, *Panulirus argus*, recreational fishing, sublethal injury.

Introduction

All fishing gear has the potential to interact with, but not successfully capture, some portion of the targeted stock. After capture, some animals may also be intentionally released owing to their quality or size. These fishery interactions have the potential to contribute to a largely unobserved additional mortality. Unobserved mortality is associated with nearly every fishing method. For example, fish that escape through trawl nets often succumb to predation (Ryer *et al.* 2004). Some invertebrate dredge fisheries have high post-release predation mortality associated with dredge discards (Bergmann and Moore 2001). 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). Unobserved mortality is also associated with many of the spiny lobster fisheries around the world. For example, in South Africa and South Australia, significant proportions of the annual lobster landings are lost through octopus predation within traps (Brock and Ward 2004; Groeneveld *et al.* 2006). In the north-western Hawaiian Islands, 25% of lobsters discarded from commercial traps later die from handling effects (DiNardo *et al.* 2002). In the Brazilian *Panulirus* fishery, the predominant fishing gear (gill nets) indiscriminately kills berried females and sublegal lobsters (Phillips and Melville-Smith 2006). Despite this growing body of evidence demonstrating unobserved mortality, sublethal fishery interactions are rarely incorporated into fishery models; however, Matthews (2001) did show that large numbers (0.646 million annually) of juvenile spiny lobsters die in commercial lobster traps.

Aside from the largely 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 coercing them out of a crevice and into a hand net. However, some of these lobsters escape during this process, often with injuries. Undersized lobsters ($<$76 mm carapace length, CL) may also be injured when they are mistaken for a legal lobster, captured and then released. Recreational fishing for spiny lobsters in the Florida Keys is among the most intense recreational fisheries in the world (Eggleston *et al.* 2003). Fishing effort peaks during a two-day mini-season that is

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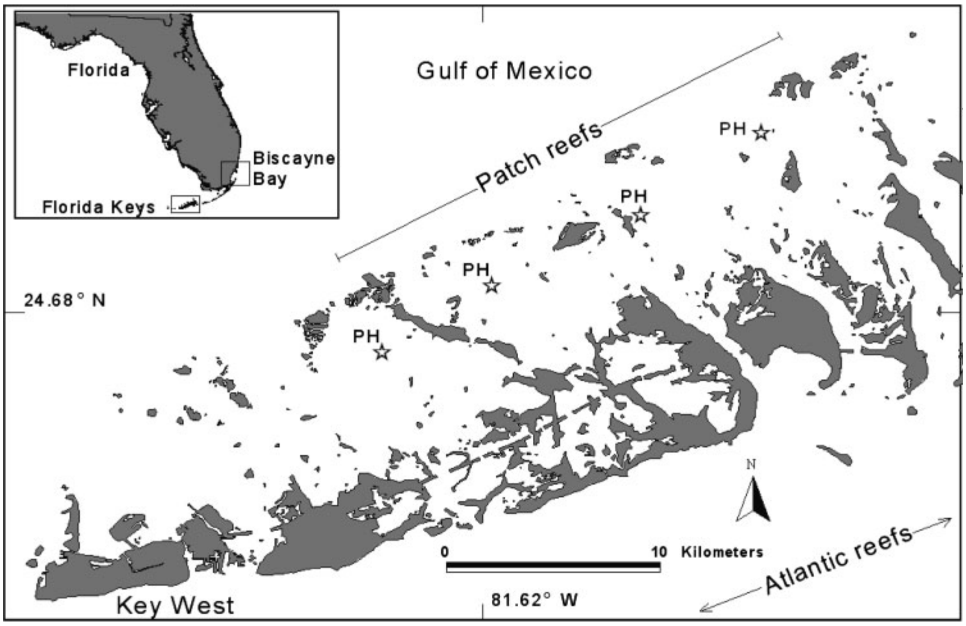

Fig. 1. The lower Florida Keys, USA, with Florida and Biscayne Bay inset, showing the locations of patch-reef habitats, patch heads (PH), and Atlantic reefs where lobster populations were simulated in this study.

exclusively for sport-divers and occurs in the last week of July before the fishery opens to commercial and recreational fishers at the beginning of August. The fishery is closed for ~4 months from April to July to allow lobsters to mate and spawn. During the two-day sport-diver mini-season, a total of 80 to 90% of legal-sized lobsters can be extracted (Eggleston *et al.* 2003), and up to 27% of the remaining population of legal and sublegal lobsters may become visibly injured (Parsons and Eggleston 2005). These injuries are detrimental to lobsters, reducing their growth (Davis 1981) and elevating their mortality (Parsons and Eggleston 2005). The population and economic consequences of lobster injuries are unknown, but considering that 50 000 sport-divers harvest lobsters during the two-day mini-season in the Florida Keys (Sharp *et al.* 2005), and that >900 000 lobster traps without escape gaps are deployed by commercial fishermen each year (Hunt 2000), it is important to estimate the potential population and economic consequences of sublethal injuries in this fishery. Fortunately, many demographic and fisheries aspects of the Caribbean spiny lobster are well known, which facilitates parameterising population models.

Modelling studies have great potential to assess the potential population and economic consequences of by-catch and unobserved mortality (Crowder and Murawski 1998; Kellison and Eggleston 2004). In the present study, we used a spatially explicit, individually based population model to estimate population and economic consequences of unobserved mortality in the Florida Keys lobster fishery. 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 specific questions to be addressed (Judson 1994). In the present 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 used to predict potential population and economic consequences of sport-diver-inflicted injuries on spiny lobsters inhabiting the Florida Keys. Specifically, we hypothesised that injuries lobsters received from sport divers would reduce predicted adult lobster populations and predicted recreational and commercial landings.

Materials and methods

General modelling approach

A computer simulation model was constructed to calculate lobster population abundance and fishery landings under two injury scenarios in which (1) injured lobsters with higher individual mortalities and lower growth rates were included and (2) 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 lobster growth and injury status, natural mortality, fishing mortality and movement behaviour were reassessed for each lobster (see Fig. 2 for a schematic description of these factors). Each model simulation was run for a 5-year period, after which the abundance of adult lobsters and recreational and commercial landings were compared between simulations with and without lobster injury.

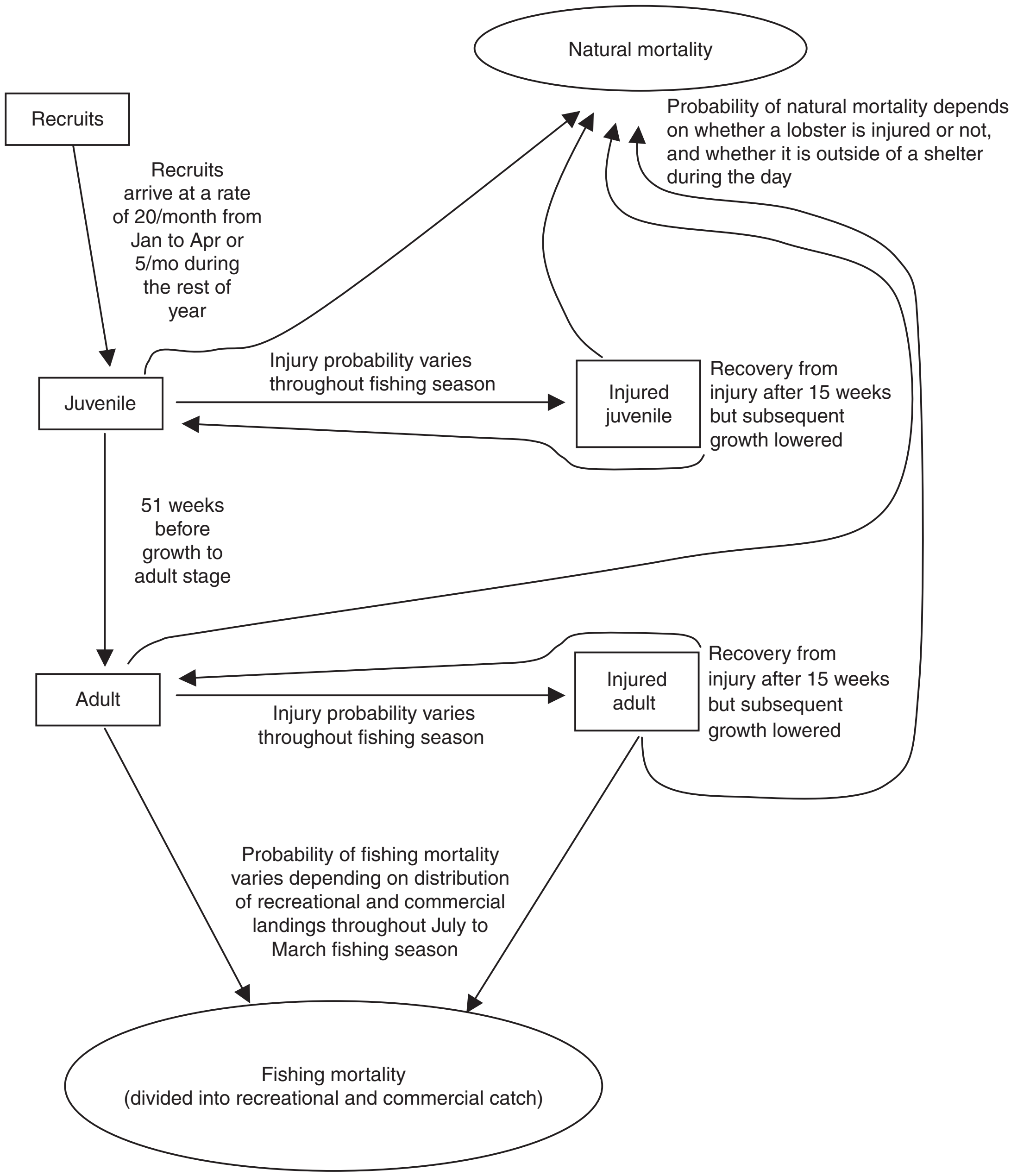

Fig. 2. Schematic diagram showing the factors that affect individual lobster demographics and abundance within computer model simulations. For simplicity, lobster movements are excluded from this diagram but are described in the text. Individual lobsters occupy four possible stages (juvenile, injured juvenile, adult and injured adult); however, 'no injury' simulations exclude all injured stage classes. Arrows denote transition between stages or a particular fate of an individual lobster.

Specific description of model

Physical environment and initial population

The spatial environment of the model-simulated patch-reef habitats is 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 1 m relief (Eggleston *et al.* 2003). The simulation of a 1-ha reef consisted of 10 000 × 1 m^2 individual habitat cells. Each 1 m^2 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 the patch-reef habitat, so we chose a value (0.008 shelters m^{-2}) that agreed with our observations of shelter density in this habitat and that fell within the range of known shelter densities for similar habitats that lobsters 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 such as sand, seagrass and hard-bottom. This environment was initially populated with 152 adult (>76-mm CL) and 75 juvenile lobsters (50–76-mm CL), representing average pre-mini-season lobster abundances (mid-July) based on densities (number m^{-2}) observed over a 4-year period in this habitat (D. B. Eggleston, G. W. Bell, E. G. Johnson and G. T. Kellison, unpublished data).

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 sublethal affects of the fishery (i.e. they could be captured and used as bait in commercial traps, as well as accidentally captured and released by recreational sport-divers). Lobsters smaller than 50-mm CL have little interaction with the fishery (Dolan and Butler 2006) and were omitted from the model. 'Adults' (>76-mm CL) were exposed to harvest and sublethal impacts of the fishery. When selected for injury (see below), both juveniles and adults could transition into 'injured juvenile' and 'injured adult' stages, which incorporated reduced growth, elevated mortality and altered social behaviour 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 before the two-day sport diver mini-season in mid-July (D. Eggleston, unpublished data).

Recruitment

On average, 120 new 50-mm CL juvenile lobsters recruited to the model's spatial domain annually. This recruitment 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 over time. Rather, arrival of new recruits to the model domain peaked in spring (on average, two lobsters every 3 days from January to April), whereas recruitment during the remainder of the year was lower (on average, one 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).

Time-step and data output

To account for individual lobster behaviours that may have been affected by fishery-induced injury (i.e. social interactions and the acquisition of shelter; Parsons and Eggleston 2006), lobster movements, growth and mortality were calculated on a 1-min 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 2006). The remaining 5 years of the simulation study allowed adult lobster abundance and associated harvests to be compared among different injury treatments and multiple fishing seasons.

Movement

Lobsters in the model occupied shelters during the day, and left these shelters at 1800 hours to begin nocturnal foraging. The rate of movement during these night-time excursions was 1 m per minute (Herrnkind *et al.* 1975), with a random alteration to lobster heading (±15°) at each time-step. This random movement was maintained until 0300 hours (Herrnkind *et al.* 1975), after which 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 behaviour is similar to the social interactions of lobsters observed at this time of day (Herrnkind *et al.* 1975; Ratchford and Eggleston 2000). 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 behaviours took effect at a radius of 5 m. While the scale over which lobster-attraction odours operates is unknown, laboratory (Ratchford and Eggleston 1998, 2000) and field trials (Nevitt *et al.* 2000) have indicated that it is at least several meters. Attraction behaviours were further modified in the model by the presence of injured lobsters, which did not have the ability to attract conspecific individuals (Parsons and Eggleston 2005) but were attracted to uninjured conspecific individuals.

After 0600 hours, all lobsters stopped moving wherever they were located, and remained there until 1800 hours. 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 (D. Eggleston, unpublished data). 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 simulated shelters during the daytime.

While lobsters can move over areas larger than our 1-ha domain, their night-time movements generally do not take them more than 300 m from their previous daytime shelter, and they usually return to the same or a nearby shelter within a 100-m 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 modelled environment re-entered on the opposite side.

Table 1. Daily probabilities of mortality from recreational and commercial fishing extraction (per individual lobster) throughout the recreational and commercial fishing seasons

	Mini-season	August	September	October	November	December	January	February	March
Recreational extraction	0.023	0.0021	~0.000049	~0.000049	~0.000049	~0.000049	~0.000049	~0.000049	~0.000049
Commercial extraction	0	0.0038	0.0027	0.0022	0.0015	0.0009	0.0007	0.0004	0.0004

Growth

The age of each individual lobster was initially defined, and increased at minute increments thereafter. New juveniles entering the model domain were given an age of 0 years and were required to reach an age of 0.9808 years before transitioning to the adult stage. This period 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^{-1} (Davis 1981). However, the individual ages of the initial population of juvenile lobsters was randomly distributed between 0 and 0.9808 years 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, which is 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^{-1} (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 lobster growth was not considered by the model because there was no stage for adults to grow into.

Mortality

The base probability of natural mortality for juvenile and adult spiny lobsters was a 0.0006 chance of death each day (Muller *et al.* 2000). However, natural mortality was raised for certain situations: (1) lobsters residing in the open during the day (0.0014 chance of death each day; Mintz *et al.* 1994) and (2) injured lobsters (0.006 chance of death each day; Parsons and Eggleston 2005). Injured lobsters retained this elevated natural mortality probability until they re-entered an 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 (D. Parsons and D. Eggleston, unpublished 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 extraction per year; SEDAR 2005). This total fishing extraction probability was divided between the recreational and commercial fishing sectors and distributed throughout the year based on the monthly distribution of lobster landings of these sectors (R. Muller, unpublished data; Sharp *et al.* 2005). For example, on average, the commercial fishery landed 718 t of spiny 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 chance of extraction per 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 spiny lobster landings data (R. Muller, unpublished data; Sharp *et al.* 2005), 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 to 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 chance of extraction per day, which represented ~10% of annual commercial and recreational landings. In this scheme, probabilities of mortality from the recreational and commercial fisheries can be found in Table 1.

Injury

On average, the percentage of injured spiny lobsters residing on patch reefs increased from 0 to 24% during the 2-day sport-diver mini-season ($n = 3$ years, D. Parsons and D. Eggleston, unpublished data), so we used an injury probability of 0.128 day^{-1} 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 to 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^{-1}. 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^{-1}.

There are no estimates of the percentage of lobsters injured by the commercial fishery. There are, however, estimates of the percentage of sublegal lobsters 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 that 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 that a lobster would be injured by commercial fishing gear was incorporated into the model to simulate all possible sublethal effects of the fishery.

Simulations

Lobster population size and fishery landings with and without injury

The computer simulation program was written in Netlogo software (Wilensky 1999) and run on a Pentium 4 (3.0 Ghz) microcomputer. Initial simulations were conducted under two scenarios, 'injury' *v.* '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 before 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 hypothesised 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 negative effect would be consistent over 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 be subjected to 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 four simulations with reduced probabilities of injury and compared them with the 'no injury' and 'injury (patch-reef)' simulations described in the previous section. (1) 'No injury': as before, lobster injuries were excluded from the model. (2) 'Low injury': the probability of a lobster being injured during the mini-season was reduced by 96%, to a 0.005 chance of injury each 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 with areas of the upper Florida Keys such as Biscayne Bay, Florida (2.5^{-5} sport-divers m^{-2}; T. Kellison and D. Eggleston, unpublished data). (3) 'Medium injury': the probability of a lobster being injured during the mini-season was reduced by 60%, to a 0.048 chance of injury each day during the two-day mini-season. This 'medium injury' was the average probability of injury during the two-day mini-season for all habitats (i.e. patch-reef, patch-head, Atlantic reef and Biscayne Bay habitats (D. Eggleston and D. Parsons, unpublished data). (4) 'High (patch-reef) injury': as before, but where the probability of a lobster being injured during the two-day mini-season was 0.128 each day. We hypothesised that reducing the probability of injury in the 'low injury' and 'medium injury' simulations would reduce the effect that injury had on the abundance of adult lobsters, as well as on recreational and commercial landings, compared with the 'high (patch-reef) injury' simulations, but that the abundance of adult lobsters and recreational and commercial landings would still be less comparable with 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 with 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 altered parameters 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 that estimated lobster abundance without incorporating injury produced a seasonal pattern of adult abundance with an overall increasing trend over time (Fig. 3*a*). The juvenile population displayed a similar seasonal pattern in abundance, but the oscillations were of smaller amplitude and abundance and did not appear to increase over time (Fig. 3*a*). Abundance of adults was higher than juveniles (Fig. 3*a*) because juveniles eventually grew into and accumulated in the adult stage. This pattern reflected the higher adult abundances observed in this habitat before the two-day mini-season in late July of each year (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. 3*b*). 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, unpublished data; Eggleston *et al.* 2003; Sharp *et al.* 2005), suggesting that the model was producing realistic population and harvest estimates.

When injury was incorporated into model simulations, adult and juvenile lobster abundances varied seasonally, with juvenile abundances higher than adults, in direct contrast to the pattern observed without injury (compare Figs 3*a* and 4*a*). Moreover, seasonal variation in lobster abundance was more pronounced (Figs 3*a* and 4*a*). When accounting for injury, adult abundance similarly did not increase over the multiple years of the simulation as it did when injury was absent (Figs 3*a* and 4*a*). The seasonal pattern of recreational and commercial landings

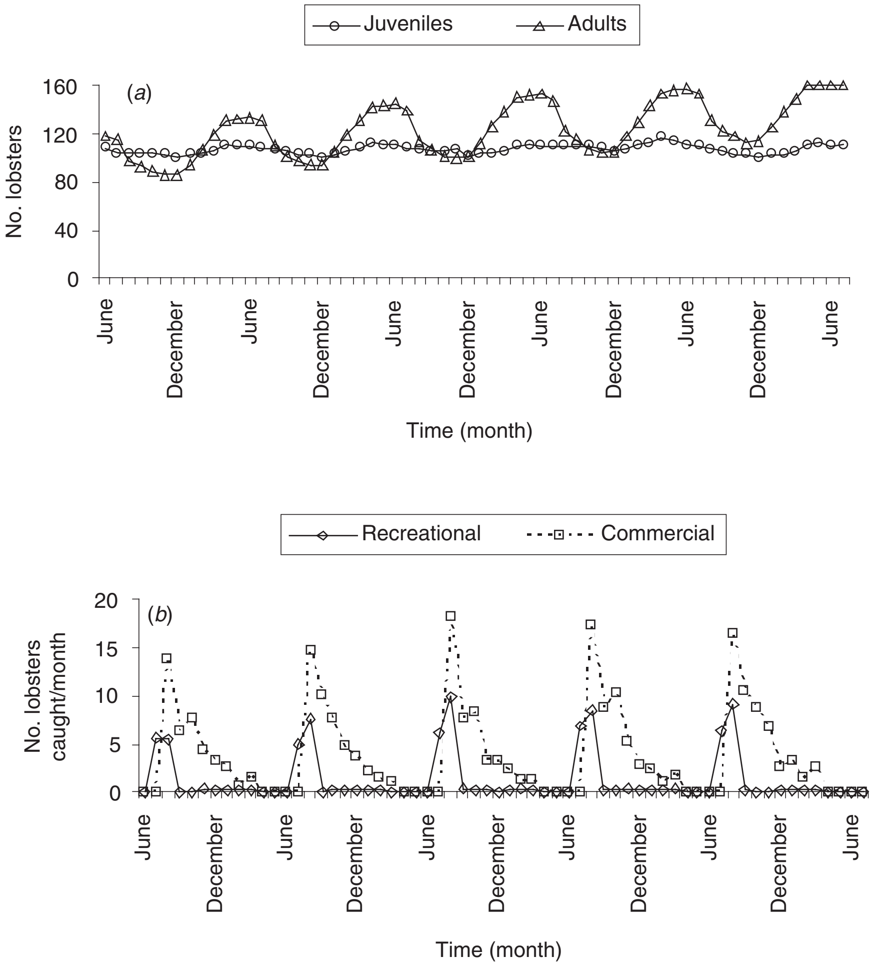

Fig. 3. (*a*) Mean adult and juvenile spiny lobster abundance and (*b*) monthly recreational and commercial harvest over 5 years of model simulation without the incorporation of injury. Values represent the mean of 10 replicate simulations.

appeared similar, but the overall catch was lower (Fig. 4*b*). When the results of the injury simulations were broken down to illustrate all stages that contributed to the population (i.e. so that injured stages could also be observed), seasonal patterns of injured juveniles and adults were evident (Fig. 5), with highest abundances of injured lobsters present in July and August and decreasing to very few or no injured lobsters by November. The periods with the highest proportion of injured lobsters (July and August) occurred at the times of year when annual recreational fishing effort peaked (Eggleston and Dahlgren 2001; Eggleston *et al.* 2003; Sharp *et al.* 2005).

Model simulations that incorporated injury reduced adult abundance by ~50% compared with simulations without injury (Fig. 6*a*). The adult population in the no injury treatment also appeared to increase each year, whereas the population incorporating injury did not (Fig. 6*a*).

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

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 with the no injury simulations, whereas the low injury treatments reduced adult abundance estimates by ~5% compared with the no injury simulations (Fig. 7*a*). Adult lobster abundance increased each year for some injury treatments (e.g. no injury and low injury) and remained stable over time for other injury treatments (e.g. high (patch-reef) injury; Fig. 7*a*).

Recreational harvest

Mean recreational harvest varied according to injury treatment, even when the probability of lobsters becoming injured

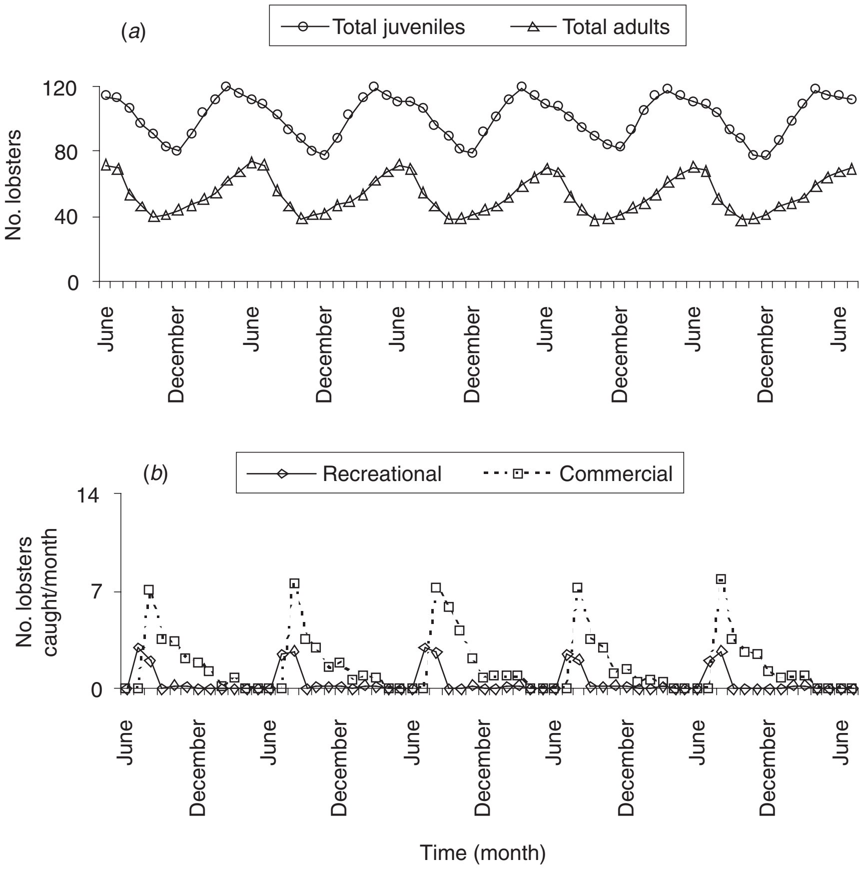

Fig. 4. (*a*) Mean adult and juvenile spiny lobster abundance and (*b*) monthly recreational and commercial harvest over 5 years of model simulation with the incorporation of injury. Values represent the mean of 10 replicate simulations.

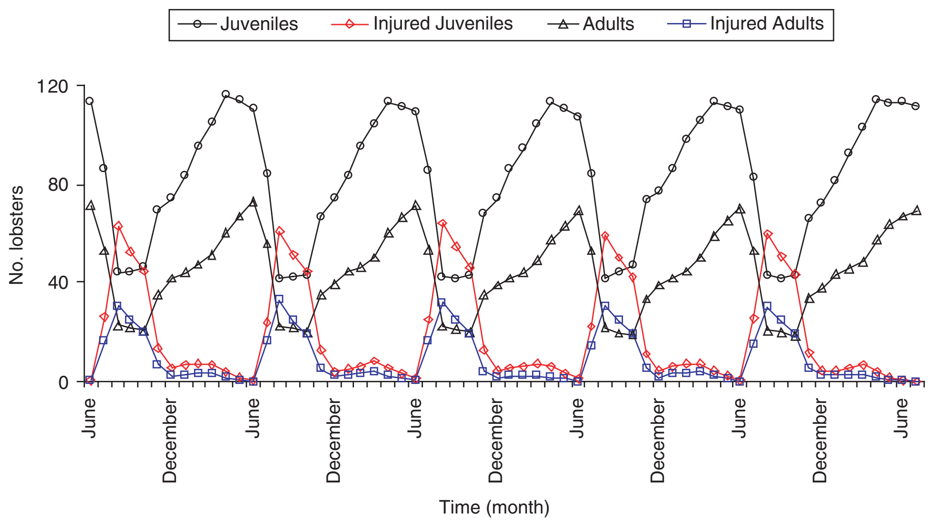

Fig. 5. Mean abundance of spiny lobsters over 5 years of model simulation with injury. Values are the same as those in Fig. 3, but separated into injured and normal stage classes. Values represent the mean of 10 replicate simulations.

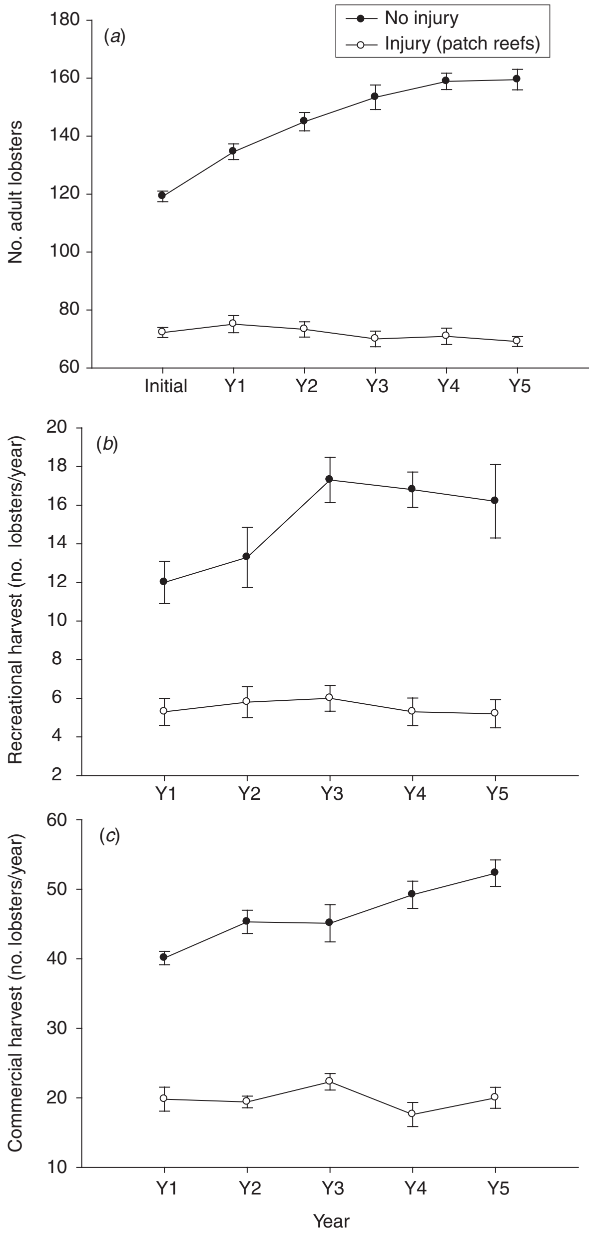

Fig. 6. (*a*) Mean abundance of adult spiny lobsters (±s.e.) before the mini-season in July, (*b*) mean annual recreational harvest (±s.e.) and (*c*) mean annual commercial harvest (±s.e.) over 5 years of model simulations. The two scenarios depicted in this figure represent simulations where lobsters 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 (D. Parsons and D. Eggleston, unpublished data). Values represent the mean of 10 replicates ± s.e.

was reduced. For example, the medium injury treatment reduced recreational harvest estimates by ~36% compared with the no injury simulations, whereas the low injury treatments reduced recreational harvest estimates by only ~1% compared with the no injury simulations, which probably did not represent a meaningful difference (Fig. 7*b*). Recreational harvest varied over time, but without any general trend.

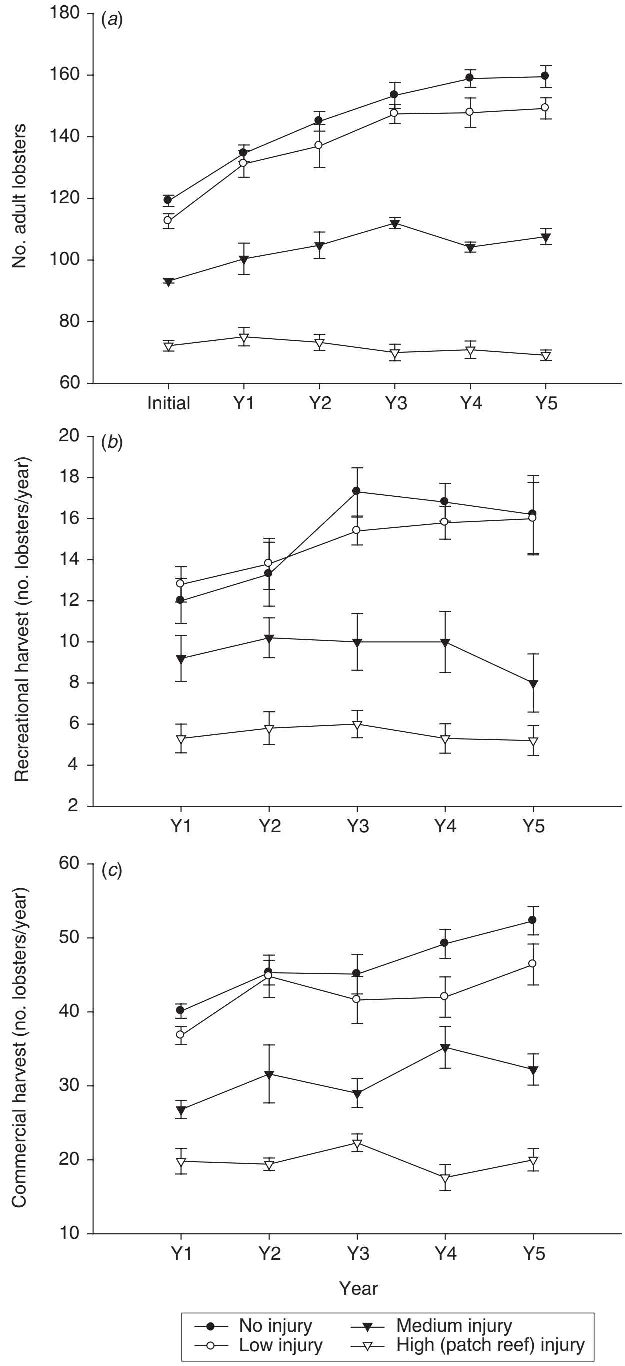

Fig. 7. (*a*) Mean abundance of adult spiny lobsters (±s.e.) before the mini-season in July, (*b*) mean annual recreational harvest (±s.e.) and (*c*) mean annual commercial harvest (±s.e.) over 5 years of model simulations. The four scenarios depicted in this figure were (1) 'no injury', in which lobsters were not exposed to injuries, (2) 'low injury', in which lobsters were exposed to a probability of injury that was set proportionally to the recreational fishing effort in Biscayne Bay, (3) 'medium injury', in which 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 (4) 'high (patch-reef) injury', in which 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 mean of 10 replicates ± s.e.

Table 2. The percentage change in adult abundance, recreational harvest and commercial harvest when the growth rate of injured lobsters, the time that a lobster remained injured and the mortality of injured lobsters was altered by ±10%

Values represent the average percentage change over 5 years of model simulations compared with '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

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 with the no injury simulations, whereas the low injury treatments reduced commercial harvest estimates by ~9% compared with the no injury simulations (Fig. 7*c*). Commercial harvest increased each year for some injury treatments (e.g. no injury) and remained stable over time for others (e.g. high (patch reef) injury; Fig. 7*c*).

Sensitivity analysis

The model parameters altered in the sensitivity analyses (the 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 or commercial harvest (Table 2). 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% alteration each parameter received (Table 2). 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. The sensitivity analyses suggested that stochastic variation within the model had a greater effect on final results than assumptions inherent to 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. However, the results of the present study clearly demonstrate that in the spiny lobster fishery of the Florida Keys, USA, large reductions in landings and stock abundance may be attributed to sublethal mortality associated with recreational and commercial fishers. While the results of modelling studies are only an estimate of the actual dynamics of a modelled system, they are useful for indicating areas of interest and concern within that system, especially where logistics restrict actual field estimation. Furthermore, sensitivity analyses 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 owing 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 observed high recreational fishing effort and a ~24% increase in injured lobsters from before to after the mini-season, injury may reduce the abundance of adult lobsters and annual landings by ≥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 Florida Keys (D. Eggleston and T. Kellison, unpublished data), and the prevalence of lobster injuries is likely similarly lower, such that 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 injuries on lobster populations and associated harvests is to be more precisely estimated. Lacking such spatial data, we used the lowest probability of injury (from Biscayne Bay) to generate a very conservative, fishery-scale estimate of the impact of lobster injuries on adult abundance and harvests. Even with this reduced probability of injury, adult lobster abundance at the beginning of the fishing season in the Florida Keys may be reduced by 900 t (based on a stock estimate of 17 280 t: SEDAR 2005) as a result of sublethal injuries. 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 US$1.6 million revenue (based on annual landings of 1855 t or US$19.2 million; Fisheries Statistics Division, National Marine Fisheries Service, unpublished data). This result emphasises the economic 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.

There are few other examples documenting the influence of unobserved mortality at the level of the population or entire fishery. However, high indirect mortality has been demonstrated in an Australian scallop dredge fishery. In this fishery, an estimated 12 to 22% of the stock at the start of each fishing season is actually landed as catch (McLoughlin *et al.* 1991), but mortality within the stock remains high even after the fishery has closed. High post-fishing mortality is caused by bacteria that initially infect scallops injured by dredge contact and 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 occur later in the fishing season, when injuries may have taken effect. Therefore, the model simulations presented here suggest that recreational fishers generate most of the injuries within the lobster population, but that commercial fishermen bear most of the consequences (i.e. reduced landings). However, actual observations of the number of lobsters that commercial trap fishermen are injuring would be required to verify this statement.

Another interesting result of the present study is that lobster exploitation rates observed during the two-day sport-diver mini-season (80 to 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^{-1} $year^{-1}$; 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 proportion of the lobster population avoids initial extraction during the two-day mini-season and subsequently becomes exposed to fishery mortality through their own movements or the placement of traps. 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 spatiotemporal 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. Lobster recruitment within the Florida Keys 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 moulting, in each fishing season (Powers and Sutherland 1989). This system of high recruitment and high fisheries extraction rates 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 among various sectors of the fishery). These are sufficient reasons to attempt to reduce injuries and unobserved mortality by educating recreational sport-divers. For example, reducing attempts to capture under-sized lobsters would be a prudent and relatively easy first attempt at reducing lobster injuries. Similar practices may also be effective at reducing unobserved mortality in other spiny lobster fisheries. For example, reducing trap soak time, using double chambered traps to avoid octopus predation (Brock *et al.* 2006), eliminating destructive gears such as gill-nets, making escape gaps compulsory in trap fisheries and educating fishermen on the importance of correct handling procedure for discarded lobsters (e.g. quick processing and return of lobsters to water) may have positive consequences not just for lobster fisheries but for the whole environment.

Unlike the Florida spiny lobster fishery, the majority of the world's fisheries have some dependence of recruitment on local stock biomass. In these situations, unobserved mortality likely has detrimental population and conservation consequences as well. Despite this, discard mortality is the only additional source of mortality regularly considered in fishery assessments (Alverson and Hughes 1996). There is a long list of unobserved mortalities, similar to that discussed in the present study that are rarely accounted for. These include illegal and misreported landings, delayed mortality of fish that contact fishing gears and die from stress or injuries, mortality from ghost fishing gears and predation mortality of fish that escape fishing gear (Alverson and Hughes 1996). To avoid the significant social, economic and conservation consequences of unobserved mortality, fishery managers and scientists must attempt to account for the entire impact of fishing, whether it is observed in landings or not.

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