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FUNCTIONAL RESPONSE OF SPORT DIVERS TO LOBSTERS WITH APPLICATION TO FISHERIES MANAGEMENT

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Abstract. Fishery managers must understand the dynamics of fishers and their prey to successfully predict the outcome of management actions. We measured the impact of a two-day exclusively recreational fishery on Caribbean spiny lobster in the Florida Keys, USA, over large spatial scales (>100 km) and multiple years and used a theoretical, predator–prey functional response approach to identify whether or not sport diver catch rates were density-independent (type I) or density-dependent (type II or III functional response), and if catch rates were saturated (i.e., reached an asymptote) at relatively high lobster densities. We then describe how this predator–prey framework can be applied to fisheries management for spiny lobster and other species. In the lower Keys, divers exhibited a type-I functional response, whereby they removed a constant and relatively high proportion of lobsters (0.74–0.84) across all pre-fishing-season lobster densities. Diver fishing effort increased in a linear manner with lobster prey densities, as would be expected with a type-I functional response, and was an order of magnitude lower in the upper Keys than lower Keys. There were numerous instances in the upper Keys where the density of lobsters actually increased from before to after the fishing season, suggesting some type of "spill-in effect" from surrounding diver-disturbed areas. With the exception of isolated reefs in the upper Keys, the proportion of lobsters removed by divers was density independent (type-I functional response) and never reached saturation at natural lobster densities. Thus, recreational divers have a relatively simple predatory response to spiny lobster, whereby catch rates increase linearly with lobster density such that catch is a reliable indicator of abundance. Although diver predation is extremely high (~80%), diver predation pressure is not expected to increase proportionally with a decline in lobster density (i.e., a depensatory response), which could exacerbate local extinction. Furthermore, management actions that reduce diver effort should have a concomitant and desired reduction in catch. The recreational diver–lobster predator–prey construct in this study provides a useful predictive framework to apply to both recreational and commercial fisheries, and on which to build as management actions are implemented.

Key words: Biscayne National Park; Caribbean spiny lobster; density independence; fishery management; Florida Keys, USA; functional response; overfishing; predator–prey theory; recreational fishing impacts; scuba divers.

INTRODUCTION

There are few, if any, recreational fisheries in the world where 80–90% of the local target population can be extracted in just two days and where participants may be injured or even die: the sport-diver mini-season for Caribbean spiny lobster (*Panulirus argus*) in southeast Florida and the Florida Keys, USA is one such example (Eggleston et al. 2003). Each year, more than 50 000 people don scuba and snorkeling gear to catch Caribbean spiny lobster in Florida during a special two-day sport season that opens in July just prior to the opening of the regular lobster season in early August for both recreational and commercial fishers (Sharp et al. 2005). The spiny lobster fishing season is closed during the peak spawning period between April and July. In an attempt to relieve the increasing conflict between commercial and recreational lobster fishermen, the Florida legislature in 1975 enacted a bill that established a special two-day recreational season on spiny lobsters that was scheduled one week prior to the opening of the commercial fishing season (Labisky et al. 1980). During several weeks preceeding the mini-season each year, boaters can be seen towing divers in shallow water searching for aggregations of lobsters and marking the locations of lobsters with GPS units (D. B. Eggleston, *personal observation*). On the opening day of the mini-season a parade of boats leave shore-based boat ramps,

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docks, and marinas and anchor at lobstering sites before dawn; fishing effort reaches a peak by early morning as divers try to obtain their bag limit (six lobsters per person per day in the Florida Keys and in Biscayne National Park; 12 lobsters elsewhere in the state). Of concern to fishery managers is the apparently increasing use of recreational and commercial diving to harvest lobsters. Increasing use of diving makes management difficult since the primary way of managing the fishery is through trap effort (J. Hunt, *personal communication*). Moreover, recent data indicate that 25% of the annual recreational fishing effort for spiny lobster can be expended during the two-day mini-season in Florida (Leeworthy 2002) and that recreational sport divers account for 22% of the total annual harvest of spiny lobster (Hunt 2000). Thus, sport divers are key predators of legal-sized spiny lobster in southeastern Florida, and improved understanding of their predatory behavior should enhance management of the spiny lobster recreational fishery. The overall goals of this study were to (1) measure the impact of the recreational two-day fishing season on the population of Caribbean spiny lobster in Biscayne National Park in the upper Florida Keys and in three distinct habitat types in the lower Florida Keys, (2) apply predator–prey theory to understand the behavioral response of divers to varying lobster densities, and thereby (3) predict the effects of management on lobster population dynamics and catch.

Recreational fishermen are opportunistic and often use sophisticated equipment and up-to-date information to respond to changes in distribution and abundance patterns of their quarry in a manner similar to natural predator–prey systems (Carpenter et al. 1994, Johnson and Carpenter 1994, Post et al. 2002). Although recreational fishers often lack economic incentives to overexploit populations (Post et al. 2002), they can produce strong direct and indirect effects in aquatic ecosystems (Magnuson 1991, Kitchell 1992, Kitchell and Carpenter 1993, Post et al. 2002, Coleman et al. 2004). Recreational fishers have caused severe declines in marine fish such as red drum (*Sciaenops ocellatus*) (Vaughan and Carmichael 2000) and intense reductions in local populations of abalone (*Haliotis* sp.) in central California, USA (Haaker et al. 1996) and Caribbean spiny lobster (*Panulirus argus*) in the Florida Keys, USA (Eggleston and Dahlgren 2001, Eggleston et al. 2003). In view of the sometimes strong effects of recreational fishing on fishery populations, and the inability of "passive regulations" such as bag limits to ensure equitable allocation to participants and sustainability of the target species, there is a growing call for more "active regulations" such as lottery-access systems to better manage total effort in recreational fisheries, similar to "limited entry" used in large commercial fisheries (Post et al. 2002, Walters and Martell 2004). To prevent overharvest and associated ecological impacts by recreational fisheries, as well as successfully predict the outcome of more active management actions, fishery scientists and managers must understand the dynamics of recreational fishermen–prey interactions, such as the functional relationship between fishing effort, prey capture, and prey density.

Spiny lobster biology and fishery

The Caribbean spiny lobster supports important commercial fisheries throughout most of its range from Bermuda to Brazil. Caribbean spiny lobster enter shallow, nearshore waters as post-larvae from the open ocean and reach a legally harvestable size of 76 mm carapace length (CL) approximately two years after settlement (Forcucci et al. 1994, Butler and Herrnkind 1997). Caribbean spiny lobsters are highly gregarious, aggregating in crevices and beneath sponges during the day (Eggleston and Lipcius 1992, Eggleston and Dahlgren 2001) and foraging on gastropods, chitons, and bivalves in nearby sea grass beds and hardbottom habitats at night (Cox et al. 1997). Although there is a general ontogenetic migration of lobsters from inshore nursery habitats to offshore reefs as lobsters mature (Davis and Dodrill 1989), the fishery targets lobsters across a continuum of inshore and offshore areas. The commercial fishery in Florida, USA targets the gregarious behavior of spiny lobsters by using traps baited with sub-legal-sized lobsters as attractants (Hunt et al. 1986) and recreational divers exploit the gregarious nature of lobsters by typically using a "tickle stick" to coerce lobsters from their daytime dens into a handheld fishing net. During the late 1970s and 1980s, the trap fishery in Florida increased sharply without a concomitant increase in landings (Hunt 2000). The size structure of the trappable population has also shifted toward an increasing proportion of smaller lobsters (Lyons et al. 1981). The spiny lobster fishery in Florida became overcapitalized (Lyons 1986), and a trap reduction program was implemented in August 1993 to reduce excess effort in the Keys spiny lobster fishery. In recent years, efforts have been made to stabilize increasing (relative to trap) landings by commercial divers. Recreational regulations have remained relatively constant. A recent stock assessment determined that the fishery was not subject to overfishing but was unable to determine whether the stock was overfished because of the contribution of larvae from outside of U.S. waters (SEDAR 2005). Nevertheless, relatively poor landings in recent years have raised concerns over the sustainability of the fishery at current harvest levels.

Application of predator–prey theory

The field of fisheries management diverged from its academic parent discipline of ecology in the late 1950s and 1960s with the development of quantitative fisheries models (Ricker 1954, Beverton and Holt 1957). During that time, the field of ecology matured from an observational science to an experimental, process-based science (Connell 1972), while quantitative fisheries science began to incorporate life history traits and be supplemented with ecosystem-based models that rely heavily on food-web modeling (Walters and Martell 2004, Winemiller 2005). The discipline of fisheries management could benefit enormously through improved application of ecological experimentation, in particular mechanistic understanding of forging theory (Hassell 1978, Peterson 1990). For example, if human predators extract a disproportionate proportion of a target fishery at low prey abundances, then effort management in such a fishery should be more risk averse than if humans extracted prey in a linear manner with their abundance.

Interactions between fishermen, their prey, and management actions can be complex. The functional response, which is the relationship between the consumption rate of a predator and the density of its prey, provides a powerful theoretical framework to predict the outcome of fishery management actions on the dynamic relationship between recreational fishers and their prey (Hilborn and Walters 1992, Carpenter et al. 1994, Johnson and Carpenter 1994, Post et al. 2002). Functional responses are generally thought to have three basic forms, although this traditional typology may be inadequate under some natural situations (Abrams 1982). The simplest form is a predator whose pattern of searching is random and whose rate of searching remains constant at all prey densities, leading to a type-I functional response where $N_\mathrm{e} = N_t\{1 - \exp(-a' \times T)\}$. In this case, the number of prey encountered (N_e) is equal to the product of the prey density (N_t) and the exponent of the product of the instantaneous attack rate (a') and period of observation (T). In a type-I functional response, the linear increase in consumption rates with prey density abruptly reaches an asymptote where the predator becomes saturated; the relationship between proportional mortality and prey density is density independent (Holling 1966). Non-saturating functional responses have been reported for zooplankton (Huntley [1981] and references therein) and are considered a form of type-I functional response. The implication of an unsaturated type-I functional response to fisheries management is that a reduction in harvest levels, such as reductions in the length of the fishing season or in catch limits, would lead to a linear reduction in catch. The application of a type-I functional response to fisheries management and potential caveats is further expanded in the discussion section of this paper.

A hyperbolic, type-II functional response rises at a continuously decreasing rate to an upper asymptote and is inversely density dependent (Hassell 1978). A type-III functional response is sigmoid, demonstrating density-dependent acceleration in feeding rates at low to moderate prey densities. The key difference between type-II and type-III responses is that in a type-II functional response, proportional mortality rates increase with decreasing prey density (i.e., depensatory mortality), which is destabilizing to predator–prey dynamics and could lead to localized extinction of a prey species. Conversely, in a type-III response, proportional mortality rates decrease with decreasing prey density (i.e., compensatory mortality), which is stabilizing to predator–prey dynamics (Hassell 1978, Lipcius and Hines 1986, Murdoch and Bence 1987, Eggleston et al. 1992, Seitz et al. 2001 and references therein). A type-I functional response could be considered partially stabilizing to predator–prey dynamics relative to a type-II response.

In this paper, we apply the functional response framework to recreational divers harvesting Caribbean spiny lobster in the Florida Keys, USA during a two-day, exclusively recreational fishing season. Our approach used scuba diver surveys of lobster distribution and abundance patterns before and after the two-day fishing season, coupled with counts of recreational diver effort at each sampling location. Linear and nonlinear regression models and ANOVA were then used to assess the form (i.e., type I, II, III) of diver–lobster functional responses. An important application from our work is that management actions that reduce diver effort should result in a proportional decrease in lobster catch rates due to the non-saturating, linear nature of diver functional responses.

METHODS

Study sites

The functional response of sport divers to Caribbean spiny lobster was measured in two regional locations in southeastern Florida, USA: (1) the lower Florida Keys portion of the Florida Keys National Marine Sanctuary, and (2) the upper Florida Keys in Biscayne National Park (Fig. 1). In the lower Florida Keys, surveys were conducted in three habitat types: (1) continuous coral reefs and ledges (hereafter referred to as patch reefs) and (2) patch head coral reefs (hereafter referred to as patch heads), both of which were located in the back-reef environment on the Gulf of Mexico side of the lower Keys, as well as (3) offshore coral reefs located in the Atlantic Ocean (Fig. 1). Marine habitats within the back reef include mangrove, sea-grass beds, channels, macroalgal beds, sand flats, and coral reefs. Patch reef habitats consist of a thin veneer of sand overlying low-relief rock and exposed rock containing gorgonians, patch coral heads, sponges, and ledges of 0.5–1 m relief. Patch heads consist of discrete aggregations of dome-shaped and circular corals such as *Siderastrea siderea*, *Colpophyllia natans*, and *Montastraea annularis*, which are located in shallow sea grass beds some distance from the shoreline. Patch heads generally range from 1 to 3 m in diameter. Atlantic reefs were part of the Florida Reef Tract, the third largest bank-barrier reef in the world, and consisted primarily of low- to moderate-relief hardbottom (1–2 m) reef structure such as corals and octocorals, and spur-and-groove formations that were typically 3–10 m deep.

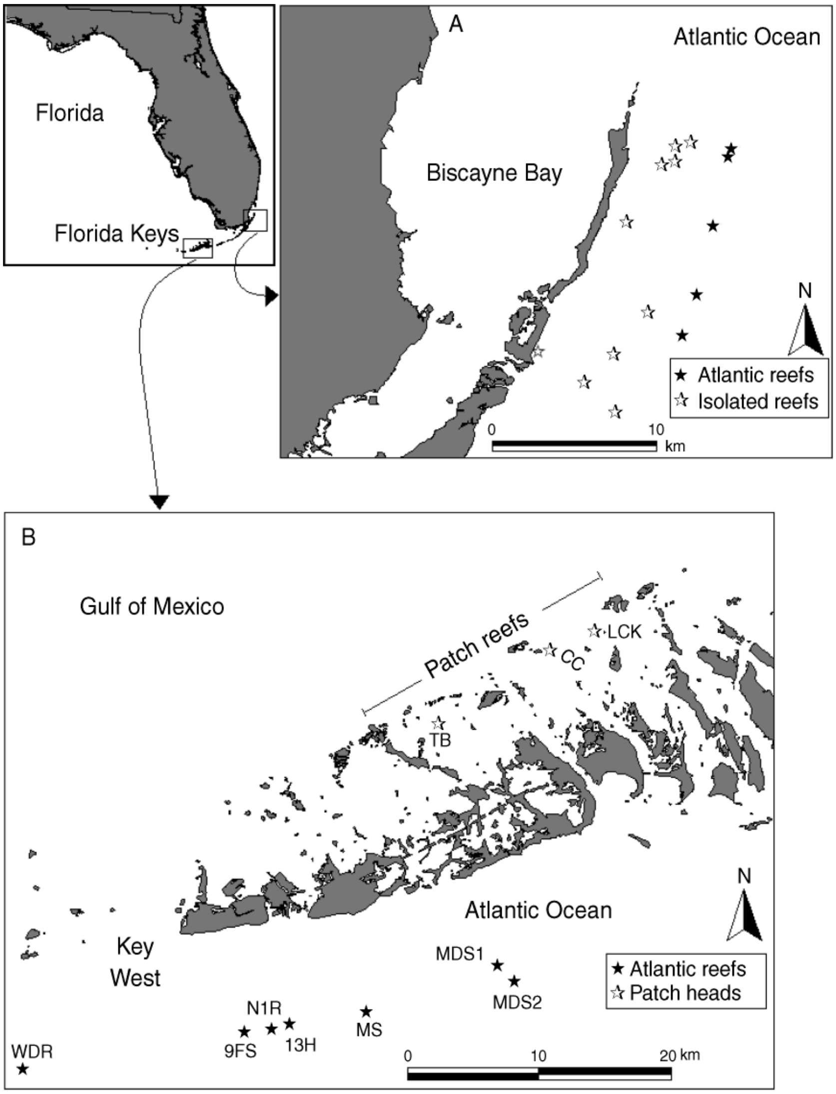

FIG. 1. Map of sampling sites within two regions of southeastern Florida, USA: (A) Biscayne Bay in the upper Florida Keys and (B) the lower Florida Keys portion of the Florida Keys National Marine Sanctuary. Descriptions of the different reef types (Atlantic reefs [solid stars] and isolated reefs [open stars] are given in *Methods: Study sites*. From left to right for patch coral heads in the lower Keys, abbreviations are TB = Turkey Basin, CC = Cudjoe Channel, and LCK = Little Crane Key. For Atlantic Reefs in the lower Keys, abbreviations are WDR = Western Dry Rocks, 9FS = Nine Foot Stake, N1R = Number 1 Marker Reef, 13H = 13 Foot Hump, MS = Middle Sambos, and MDS1 and MDS2 = Maryland Shoal 1 and 2, respectively. All sites are open to lobster fishing.

Located in southeastern Florida, Biscayne National Park (BNP) encompasses an area of 700 km^2, of which 95% is marine. BNP's boundaries extend from the western mainland shoreline adjacent to the city of Miami, east to the 18.3 m depth contour. The park includes mangrove forest and hardwood hammock along the mainland shoreline, as well as more than 40 undeveloped Keys and a portion of the Florida Reef Tract. The bay portion of BNP, which is closed to lobster harvest, provides extensive juvenile lobster habitat in the form of sea grass beds, hardbottom communities, and solution holes. Oceanside waters include ~32 km of fore-reef and reef-crest habitats, and more than 2000 patch reefs consisting of mixtures of hard and soft corals. These waters provide extensive subadult and adult lobster habitat and are open to commercial and recreational lobster harvest. Lobster and sport diver surveys were conducted in two habitat types: (1) offshore coral reefs located in the Atlantic Ocean, which were similar to those of the lower Keys but slightly deeper (10–15 m) and (2) isolated reefs of moderate to high relief (2–4 m) and roughly circular shape (diameters ranging from ~10 to 100 m) in depths of 2.5–7 m. Isolated reefs were located west of Atlantic reefs in the back-reef area of BNP and often surrounded by sea grass and generally consisted of hardbottom or carbonate platform, corals, octocorals, and macroalgae (Fig. 1).

Lobster surveys

All visual surveys for lobsters were conducted by scuba divers during the day (09:00–16:00 hours) when water visibility exceeded 6 m. Spiny lobster carapace length (CL) in centimeters was estimated by comparing a lobster to a ruler attached perpendicularly to the far end of a 70-cm rod held out from a diver in the lower Keys and with an incrementally marked 1-m piece of PVC in BNP. These devices helped avoid underwater magnification problems in estimating lobster sizes and were also used in estimating the width of an area searched during lobster surveys in offshore coral reefs. Lobster CL was estimated to the nearest 1 cm. For consistency, a core group of experienced ecologists conducted the visual surveys in all years.

To sample lobsters in patch reefs on the Gulf of Mexico side of the lower Keys, we superimposed a grid system containing cells measuring 2 × 2 km over a 20-km length of continuous-patch reefs and ledges (Fig. 1) and then randomly chose five of 10 cells to survey lobster. At each patch reef location, the research boat was anchored as close as possible to the middle of a grid cell using a differential GPS, and three to four divers surveyed areas by traveling at compass headings 90° from each other to ensure that each survey was independent. Each diver swam in the same direction before and after the sport diver fishing season, so that observations could be paired for subsequent statistical analyses (*Methods: Statistical analyses*). Divers searched along a nearly straight line away from the boat for 10 min, after which they surfaced and visually estimated the distance traveled from the boat. Area searched averaged 369 ± 50.1 m^2 (mean ± SE, $n = 39$ areas). In a related study, we assessed the accuracy of visual estimates of distance traveled and area searched during 10-min surveys and found that although divers tended to overestimate the distance traveled by an average of 4.5 m, estimates were not significantly different from known distances as measured with a differential GPS on a research boat (Eggleston et al. 2004). The response variable for patch reefs was the density of spiny lobster (number of lobsters/m^2).

We used a directed approach to survey lobsters in patch heads in the lower Keys rather than randomly choosing patch head locations due to the clumped and somewhat limited nature of their distribution. In this case, we used a combination of nautical charts, local lobster fishing guides, and our own reconnaissance to identify major clusters of patch heads in shallow back-reef areas. We identified three locations with patch heads in the lower Keys (TB = Turkey Basin, CC = Cudjoe Channel, LCK = Little Crane Key; Fig. 1), each harboring an average of five to six distinct patch heads that were visible from the boat and located in shallow water (2 m). Divers surveyed patch heads for lobsters as described above for patch reefs; however, the entire patch head was surveyed rather than using a transect approach. The mean area searched for each patch head was 7.33 ± 2.43 m^2 (mean ± SE, $n = 14$ areas). Initially, to express lobster density as a function of patch head volume, we estimated the volume of each patch head by measuring (in cm) the radius (r) and height of each head with a ruler and multiplying height by πr^2. Subsequent statistical analyses indicated no significant relationship between the volume of a patch head and number of lobsters (linear least-squares regression: $F = 0.02$, df $= 1, 28$, $P = 0.88$). Therefore, we used the density of spiny lobster (number/m^2) as a response variable for patch heads to allow comparisons with patch reefs and Atlantic Reefs. Each patch head was relocated after the mini-season using differential GPS coordinates. The impact and functional response of sport divers to lobsters on patch reefs and heads was quantified in the lower Keys during July–August 2002–2005 (4 years × 3 patch head locations + 1 additional patch head location sampled in 2002 only).

For the BNP surveys, ~30 potential isolated reef sites (those containing typical lobster habitat and likely to be utilized by lobsters) in the back-reef and ~10 predominantly spur-and-groove Atlantic reef sites were identified from field surveys and from discussions with area resource managers. A random subset of 7–11 isolated reef sites and five Atlantic reef sites was then chosen for surveys in each year, such that the chosen sites resulted in spatial coverage along both north–south and east–west axes within the BNP reef system (Fig. 1). Lobster surveys consisted of whole-reef surveys (for smaller isolated reefs) or replicate ($n = 4$) transects (100 m long, 2 m wide). For whole-reef surveys, the area searched was calculated by marking the perimeter of the reef with a differential GPS, importing the reef perimeter into ArcView (ESRI, Redlands, California, USA), and using the ArcView software to calculate total reef area. The impact and functional response of sport divers to lobsters on isolated patch reefs and Atlantic reefs in BNP was quantified during July–August 2003–2005.

As with BNP, inferences concerning lobster density in Atlantic Reefs of the lower Keys were restricted to the spur-and-groove fore-reef habitat, which typically contains the highest densities of lobsters within this reef type (Cox and Hunt 2005). To sample lobsters in the lower Keys, we superimposed a grid system containing cells measuring 2 × 2 km over the reef, and then randomly chose one cell to sample. At each offshore reef location, the research boat was anchored as close as possible to the middle of a grid cell using a differential GPS and three to four divers surveyed areas by swimming at compass headings 30° apart radiating from offshore to inshore, typically along grooves of the fore-reef. Each diver swam along the same tract before and after the fishing season, so that observations could be paired for subsequent statistical analyses (*Methods: Statistical analyses*). Surveys consisted of ~10-min timed searches for spiny lobsters. Time was kept only when divers were over suitable lobster habitat. When it was necessary to traverse a large area of sand or sea grass, the clock was turned off. Divers searched for lobsters for ~10 minutes, during which time they recorded lobster density and size. After the timed survey was complete, divers surfaced, and visually estimated the distance traveled from the boat as previously described for the patch reef surveys. Area searched by an individual diver averaged 253 ± 27.9 m^2 (mean ± SE, $n = 56$). The impact and functional response of sport divers to lobsters on the fore-reef of coral reefs in the Atlantic Ocean in the lower Keys was quantified during July–August 2004–2005.

Recreational diver surveys

To quantify the functional relationship between fishing effort (divers/m^2) and prey density (lobsters/m^2), we counted the number of dive boats anchored at each of our lobster survey locations and estimated the number of divers per boat during both days of the two-day mini-season in all years (lower Keys) and in 2005 (BNP). Two methods were used: (1) on-water counts of recreational dive boats anchored at each of our lobster survey sites on each day of the mini-season in the lower Keys, except for offshore sites (e.g., Eggleston and Dahlgren 2001, Eggleston et al. 2003), and (2) supplementary aerial counts of recreational dive boats or use of aerial photography conducted with fixed-wing aircraft at all sites in 2005. On-water counts in the lower Florida Keys were conducted on both days of the mini-season over four years (2002–2005) by counting the number of boats and divers per boat in a 100 m radius surrounding each patch reef site and the number of boats and divers per boat at each patch head location. The 100 m radius was chosen to match the approximate area searched by our divers during preseason lobster surveys. Locations of lobster sampling sites and the 100 m radius were determined with a differential GPS. The order in which sites were checked varied each day.

Boat counts in the lower Keys were supplemented in 2005 by aerial surveys of patch reef, patch head and offshore coral reef areas. These aerial surveys were conducted with a single engine Cessna Cardinal fixed-wing aircraft flying at an altitude of ~560 m using a floor-mounted camera. Date, time, and GPS coordinates were provided for each digital photograph. Boat counts in BNP were conducted during 2005 with a Cessna 182 aircraft flying at an altitude of ~150 m. During each flight, observers recorded vessel data using a mobile GIS system linked to a differential GPS unit mounted to the airplane. For both aerial surveys, we used GIS ArcView software to identify the center coordinates of a given lobster survey site and then counted the number of boats within a 100 m radius as previously described. Vessel activity (e.g., underway, anchored, fishing, diving/snorkeling) was recorded for each vessel. Vessels that were underway, fishing (angling), or obviously associated with a non-lobster activity were excluded from this analysis. The order in which we checked sites for dive boats varied from day to day.

Based on on-water counts, the mean number of divers observed per boat in the lower Florida Keys was 4.15 ± 1.21 divers (mean ± SE, $n = 561$ boats) during 2002–2005. During creel surveys at boat launching ramps in BNP during 2005, the mean number of divers per boat was 3.60 ± 0.91 ($n = 243$ boats). Therefore, for statistical analyses of the relationship between diver effort and lobster density, we used a mean of four divers per boat.

Statistical analyses

The overall impact of sport divers on spiny lobster within a given location (e.g., patch reefs, patch heads, Atlantic Reefs, BNP Atlantic Reefs, BNP isolated reefs) was identified with separate one-factor, repeated-measures ANOVA models with the density of legal-sized spiny lobsters (>7.6 cm CL; number of lobsters/m^2) as the response variable, year as a factor, and time (pre- vs. post-fishing season) as the repeated measure. Location was not included as a second factor in the ANOVA model because of the large differences in survey area between patch heads (mean = 7.3 m^2) and reefs (mean = 370 m^2), an order of magnitude higher density of lobsters in patch heads than reefs, and the unequal numbers of years sampled between regions (lower Keys = 4 years; BNP = 3 years). Densities were $\log(x + 1)$-transformed when necessary to meet assumptions of normality and homogeneity of variance. We then examined the relationship between fishing effort (divers/m^2) and the density of lobsters (number of lobsters/m^2) 1–2 days prior to the fishing season with both linear and nonlinear regression models.

Our goal concerning the functional response of recreational divers to spiny lobsters was to determine if removal rates (fishing mortality rates) were density independent or dependent, and if density dependent, whether the functional response was potentially stabilizing (type III) or destabilizing (type II) to lobster population dynamics. We used two approaches to determine the most appropriate mechanistic functional response model: (1) ANOVA of proportional mortality as a function of lobster density to identify the form of the response (type I, II, or III) and then (2) fitting a mechanistic functional response model to the lobster removal data. In our previous analysis of the functional response of sport divers to spiny lobster in two habitat types (lower Keys patch reefs and heads) in one year (2002), we used Akaike's Information Criterion, AIC (Akaike 1973), to evaluate maximum likelihood results from fitting mechanistic functional response models to the lobster removal data (Eggleston et al. 2003). For example, the functional response model generating the lowest AIC value dictated which mechanistic functional response model (type I, II, or III) was used to describe the best estimates of attack rate (a') and handling time (T_h) (Holling 1966). The application of AIC was not

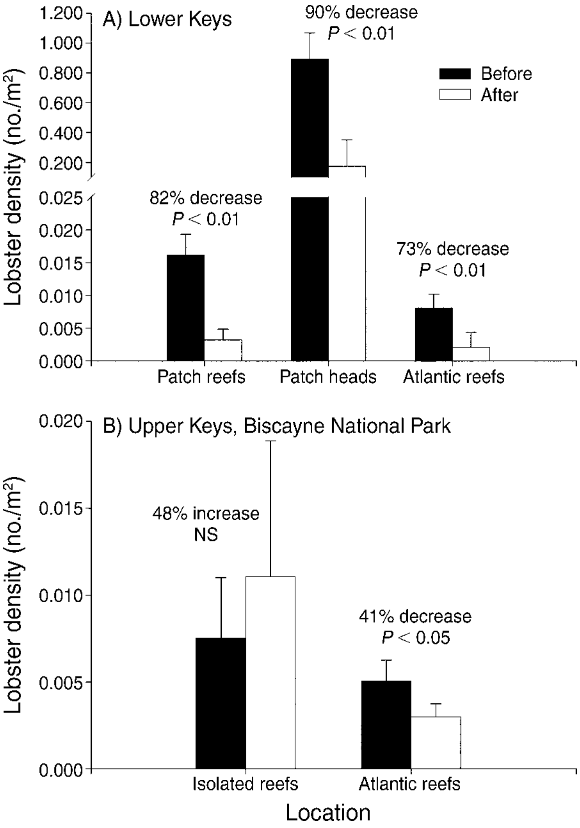

FIG. 2. Density (mean + SE) of spiny lobsters >7 cm in carapace length (CL) as a function of before (black bars) vs. after (white bars) a two-day recreational sport diver fishing season and as a function of habitat types in the (A) lower Keys, which contained patch reefs, patch heads, and Atlantic reefs, and (B) the upper Keys in Biscayne National Park, which contained isolated patch reefs and offshore Atlantic reefs. Sample sizes and the results of statistical tests are given in *Results: Location-specific sport diver impacts on lobsters.*

necessary in the present study because the relationship between proportional lobster mortality and pre-fishing-season lobster density was clearly density independent in all cases (see *Results*), thereby indicating a type-I functional response model be used to fit the data.

In the traditional Holling (1965) formulation of functional response curves, the equations are essentially built on simple, individual-based models incorporating search time, handling time, attack rates, capture success, and consumption rates. Thus, a' and T_h have a specific interpretation. When using alternative variables (i.e., density removed) instead of the traditional number eaten·predator^{-1}·d^{-1} to measure predation, a' and T_h lose their classical connotation and become parameters x and y. In this study, we quantified the aggregate functional response of sport divers, similar to studies assessing the functional response of specific predator guilds (e.g., Seitz et al. 2001), rather than individual sport divers.

RESULTS

Location-specific sport diver impact on lobsters

The sport diver mini-season had a striking negative impact on the density of legal-sized lobsters in the lower Florida Keys, with a somewhat weak and very surprising positive impact in the upper Keys. In the lower Florida Keys, there was an 82% decline in the mean density of legal-sized spiny lobsters during the two-day mini-season on patch reefs, a 90% decline at patch heads, and a 73% decline on Atlantic Reefs (Fig. 2A). The mean density of legal-sized spiny lobsters at patch reefs, patch heads, and Atlantic reefs in the lower Keys varied significantly with time (pre- vs. post-fishing season) but not by year (repeated measures ANOVA; time, all $P < 0.01$; year, all $P > 0.47$). There was no significant time by year interaction effect for any location in the lower Keys (all $P > 0.36$). The significant time effect was due to significantly lower lobster densities after the two-day fishing season than before (Fig. 2A).

In Biscayne National Park in the upper Florida Keys, there was a 41% decline in the mean density of legal-sized spiny lobsters during the two-day mini-season on Atlantic Reefs, and a 48% increase on isolated patch reefs (Fig. 2B). The mean density of legal-sized spiny lobsters at Atlantic reefs in the upper Keys varied significantly with time (pre- vs. post-fishing season) but not by year (repeated-measures ANOVA; time, $P < 0.05$; year, $P > 0.67$). In contrast, the mean density of spiny lobsters at isolated patch reefs in the upper Keys did not vary significantly with time or year (repeated-measures ANOVA; both $P > 0.29$). There was no significant time by year interaction effect for both locations in the upper Keys (all $P > 0.74$). The significant time effect for Atlantic reefs was due to significantly lower lobster densities after the two-day fishing season than before (Fig. 2B).

Relationship between diver fishing effort and lobster density

There was a positive increase in fishing effort with legal lobster density in both patch reefs of the lower Florida Keys and Atlantic reefs in the upper Keys (Fig. 3); however, the trend was only significant on day 1 for patch reefs in the lower Keys (Fig. 3A; linear regression, $P < 0.04$). On-water and aerial surveys indicated that boats were nearly always anchored at patch head sites in the lower Keys; however, there was no relationship between lobster density within a coral head and diver pressure, probably because a single boat with four divers can easily extract all legal lobsters within a single patch coral head during a single visit, with that same head being visited 20 times or more after lobsters are initially extracted (Eggleston et al. 2003). Although dive boats were anchored within the vicinity of our lobster survey sites on Atlantic reefs in the lower Keys during aerial surveys in 2005, there was no relationship between the

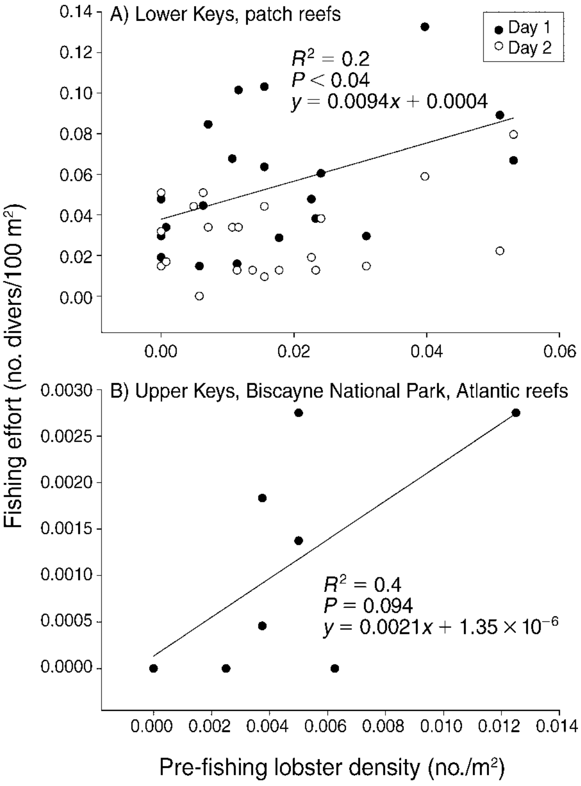

FIG. 3. The relationship between sport diver fishing effort over 5-min observation periods (divers·[100 $m^2]^{-1}$·[5 $min]^{-1}$) and the pre-fishing season density of spiny lobsters at the same site as observed over a four-year period using (A) on-water counts on patch coral reefs in the lower Keys and (B) aerial surveys during the afternoon of day 1 of the mini-season in 2005 in the upper Keys. The data points in (A) represent surveys of five patch-reef locations per year for four years. The relationship between diver effort and lobster density in the lower Keys was statistically significant on day 1 of the mini-season but not on day 2. Although there was a positive relationship between diver effort and lobster density in the upper Keys, the trend was not statistically significant.

density of divers and pre-fishing season lobster densities. During aerial surveys of isolated patch reefs in the BNP 2005, very few boats were observed at any of our lobster survey sites.

Recreational diver functional responses

Patch reefs, lower Keys.—The relationship between the proportion of spiny lobster removed from continuous-patch reefs in the lower Keys during the mini-season and pre-fishing density was not significant (ANOVA, $F = 0.58$, df = 1, 9, $P = 0.46$) and therefore density independent (Fig. 4A), which is indicative of the initial increasing portion of a type-I functional response (Hassell 1978). The relationship between pre-fishing density and the number of lobsters removed from patch reefs was modeled effectively with a mechanistic type-I functional response model ($R^2 = 0.95$, $P < 0.0001$; Fig. 4B). The functional response model provided estimates of the components of diver predation, attack rates (a'), and lobster handling time (T_h), for comparisons of exploitation rates between habitats (e.g., patch reefs vs. heads vs. Atlantic reefs) and between lobsters and other recreational fisheries with intense exploitation. By fitting a mechanistic type-I functional response model to the relationship between the number of lobsters removed by divers and lobster density (Fig. 4B), we estimated that the attack rate in patch reefs was 0.021 lobsters·m^{-2}·h^{-1}. Given that lobsters are generally not harvested by divers at night, the true estimates of a' are probably twice that of model estimates, which are based on a 48-h diver "foraging" period, and are likely closer to 0.04 than 0.02 lobsters·m^{-2}·h^{-1}. At a harvest rate of 0.04 lobsters·m^{-2}·h^{-1}, for example, the patch reef with

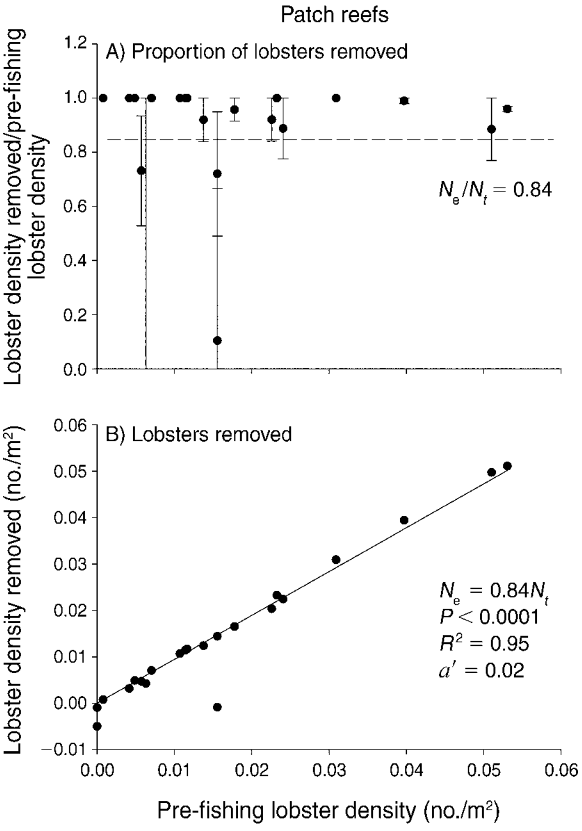

FIG. 4. Functional response of recreational divers to spiny lobsters (>7 cm CL) in patch reefs in the lower Keys: the relationships between (A) the proportion (mean ± SE) of lobster density removed (N_e/N_t) and pre-fishing density (N_t) and (B) the mean density of lobsters removed (N_e) and pre-fishing density (N_t). Parameter a is the instantaneous attack rate by a predator. A density-independent relationship (A) between N_e/N_t and N_t indicates a type-I functional response and justifies fitting a mechanistic type-I functional response model to (B) the relationship between N_e and N_t. The dashed line in panel (A) is the mean proportion of lobster density removed; $n = 20$ (5 patch reef sites per year × 4 years; some data points are hidden by others). Certain data points in (A) have 0 variance. See *Results: Recreational diver functional responses: Patch reefs, lower Keys* for additional discussion of results of statistical analyses and justification for the type-I functional response model.

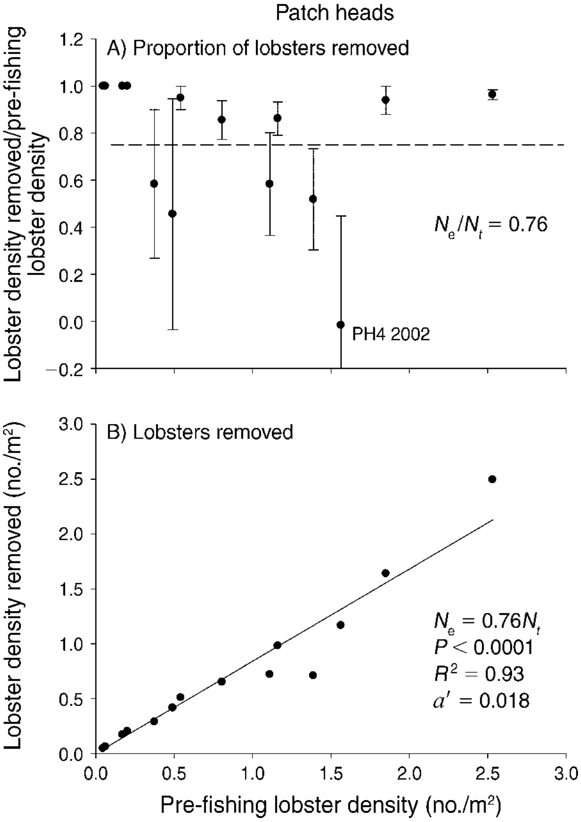

FIG. 5. Functional response of recreational divers to spiny lobsters (>7 cm CL) in patch coral heads in the lower Keys: the relationships between (A) the proportion (mean ± SE) of lobster density removed (N_e/N_t) and pre-fishing density (N_t) and (B) the mean density of lobsters removed (N_e) and pre-fishing density (N_t). A density-independent relationship (A) between N_e/N_t and N_t indicates a type-I functional response and justifies fitting a mechanistic type-I functional response model to (B) the relationship between N_e and N_t. The dashed line in panel (A) is the mean proportion of lobster density removed. Sample size is $n = 13$ ([3 patch head locations × 4 years] + 1 additional patch head location sampled in 2002 only [PH4 2002]). Certain data points in (A) have 0 variance. See *Results: Recreational diver functional responses: Patch heads, lower Keys* for additional discussion of results of statistical analyses and justification for the type-I functional response model.

the highest density would, theoretically, be harvested completely in one hour. This intense harvest rate is probably realistic, especially in habitats where divers were anchored at dawn over areas of high lobster aggregations as identified during pre-fishing season reconnaissance, and where these boats apparently reached their limit in less than one hour after entering the water as evidenced by their return to shore (D. B. Eggleston, *personal observation*). Thus, within the range of natural densities of lobsters measured on continuous-patch coral reefs over a four-year period, recreational divers display a type-I functional response and remove a very high and constant proportion (0.82) of lobsters.

Patch heads, lower Keys.—The relationship between the proportion of lobsters removed at patch heads and pre-fishing density was also non-significant and density independent (ANOVA, $F = 0.83$, df = 1, 13, $P = 0.38$; Fig. 5A). A type-I functional response model described 93% of the variation in the density of lobsters extracted by divers ($R^2 = 0.93$, $P < 0.0001$; Fig. 5B) and estimated that attack rates were 0.018 lobsters·m^{-2}·h^{-1}. Given that divers only harvest lobsters during the day, as just discussed, a' was probably closer to 0.04 than 0.018 lobsters·m^{-2}·h^{-1}. Thus, similar to the pattern observed for divers hunting lobsters on coral patch reefs, divers exhibit a type-I functional response to varying lobster densities in patch coral heads in the lower Keys, and removed a constant and relatively high proportion of lobsters (0.9) regardless of lobster density (Fig. 5).

Atlantic reefs, lower Keys.—The relationship between the proportion of lobsters removed from Atlantic reefs in the lower Keys and pre-fishing density was also nonsignificant and density independent (ANOVA, $F = 0.24$, df = 1, 10, $P = 0.64$; Fig. 6A). A type-I functional response model explained 85% of the variation in lobster extraction by divers ($R^2 = 0.85$, $P < 0.001$; Fig. 6B) and estimated attack rates were 0.019 lobsters·m^{-2}·h^{-1}, which, as previously discussed, was more likely closer to 0.04 than 0.019 lobsters·m^{-2}·h^{-1}. Thus, similar to the pattern observed for coral patch reefs and heads, divers exhibit a type-I functional response to varying lobster densities in Atlantic offshore reefs in the lower Keys and removed a constant and relatively high proportion of lobsters (0.73).

Atlantic reefs, upper Keys: BNP.—The relationship between the proportion of lobsters removed from Atlantic reefs in the upper Keys in Biscayne National Park and pre-fishing density was also nonsignificant and density independent (ANOVA, $F = 0.01$, df = 1, 17, $P = 0.97$; Fig. 7A). The lobster density removed by divers was highly variable across preseason lobster densities and, in nearly half the cases, there was an increase in lobster density from before to after the mini-season, as evidenced by negative values (Fig. 7A; preseason lobster density minus postseason density/preseason lobster density). A type-I functional response model explained 58% of the variation in lobster extraction by divers ($R^2 = 0.58$, $P < 0.0001$; Fig. 7B), and was highly significant regardless of whether or not the data point for the highest lobster density removed was present in the model (Fig. 7B). Estimated attack rates were 0.013 lobsters·m^{-2}·h^{-1}, which, as previously discussed, was more likely closer to 0.03 than 0.013 lobsters·m^{-2}·h^{-1}. Thus, similar to the pattern observed for coral patch reefs, heads, and Atlantic reefs in the lower Keys, divers exhibit a type-I functional response to varying lobster densities in Atlantic offshore reefs in the upper Keys, but the proportion removed (0.21; Fig. 7A) and attack rates ($a' = 0.013$) were lower than for Atlantic reefs in the lower Keys (compare Figs. 6 and 7).

Isolated reefs, upper Keys: BNP.—The relationship between the proportion of lobsters removed from isolated reefs in the upper Keys in Biscayne National

Park and pre-fishing density was also nonsignificant and density independent (ANOVA, $F = 1.88$, df = 1, 11, $P = 0.20$), which is suggestive of a type-I functional response. A functional response model, however, was unable to adequately fit the observed relationship between lobster density removed as a function of preseason lobster density because there was essentially no extraction of lobsters by divers at the survey sites. Similar to the pattern observed for Atlantic reefs in the upper Keys, there were five data points where lobsters densities actually increased from pre- to post-fishing season, rather than decreased as expected. Thus, in the shallow back-reef habitat of Biscayne National Park where there are thousands of isolated patch coral heads, divers do not appear to exhibit a predatory functional response to spiny lobsters.

Discussion

What is desperately needed but rarely attempted is a theory to predict behavioral responses of fishers to management actions (Clark 1985, Post et al. 2002, Walters and Martell 2004). Recreational fishers are generally considered more complex in their motivations and behavior than commercial fishers or the type of predators traditionally represented in predator–prey models (Carpenter et al. 1994, Johnson and Carpenter 1994, Post et al. 2002). Our study indicates the opposite; exploitation rates (μ) of spiny lobster and fishing effort (f) generally varied linearly with lobster density, such that catchability (q), although extremely high (~80% in two days), was constant across lobster density (N). Conservation of exploited species requires knowledge of the relationship between exploitation rate or fishing mortality, fishing effort, catchability of the exploitable segment of the population, and population size. For example, the growing call for active management of total effort in recreational fisheries (Post et al. 2002, Coleman et al. 2004, Walters and Martell 2004) requires knowledge of whether catchability is density dependent (i.e., compensatory [Neave 1953]) or inversely density dependent (i.e., depensatory [Neave 1953]). If q is inversely density dependent, then even a constant, regulated effort can result in a depensatory increase in μ or instantaneous fishing mortality rate (F) during a decline in stock size, which potentially leads to recruitment overfishing, population collapse, or inefficient exploitation (Crecco and Overholtz 1990, Post et al. 2002). In this study, recreational sport divers generally exhibited a simple, type-I functional response to varying densities of spiny lobster. A type-I functional response suggests that efforts to manage total fishing effort can be less risk averse than if divers exhibited a depensatory, type-II functional response, but should be more risk averse than if divers exhibited a type III, compensatory functional response (see *Discussion: Application of predator–prey theory*).

The intense removal rates of spiny lobsters by recreational divers measured in this study are among the highest reported rates for marine recreational fishers in the world. For example, fishing effort by recreational divers, as measured by the number of boats observed along the continuous reef tract in the back-reef of the lower Florida Keys, can be ~900-fold higher during the two-day mini-season than during the "regular" lobster fishing season (Eggleston et al. 2003). In this study, the two-day recreational mini-season reduced lobster (>7 cm CL) density by a mean of 82% across a broad range of habitat types in the lower Keys in just two days, with exploitation rates of ~0.03–0.04 lobsters·m^{-2}·h^{-1} in these habitats. We measured similar rates of exploitation in the nearby Key West National Wildlife Refuge (KWNWR) during 2000, where lobster densities decreased by 80% in two days (Eggleston and Dahlgren

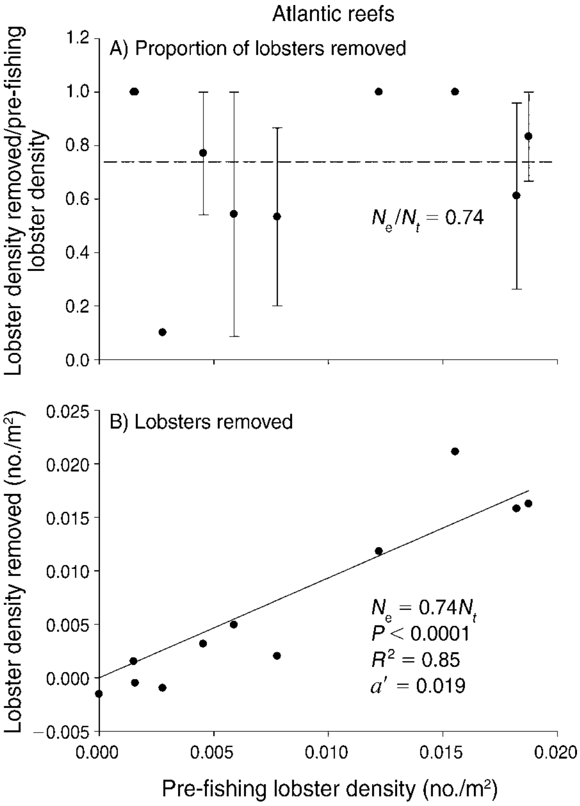

FIG. 6. Functional response of recreational divers to spiny lobsters (>7 cm CL) in offshore Atlantic reefs in the lower Keys: the relationships between (A) the proportion (mean ± SE) of lobster density removed (N_e/N_t) and pre-fishing density (N_t) and (B) the mean density of lobsters removed (N_e) and pre-fishing density (N_t). A density-independent relationship (A) between N_e/N_t and N_t indicates a type-I functional response and justifies fitting a mechanistic type-I functional response model to (B) the relationship between N_e and N_t. The dashed line in panel (A) is the mean proportion of lobster density removed. Sample size is $n = 12$ (6 reef locations × 2 years [2004–2005]). Certain data points in (A) have 0 variance, and certain data points in (A) and (B) are masked by others. See *Results: Recreational diver functional responses: Atlantic reefs, lower Keys* for additional discussion of results of statistical analyses and justification for the type-I functional response model.

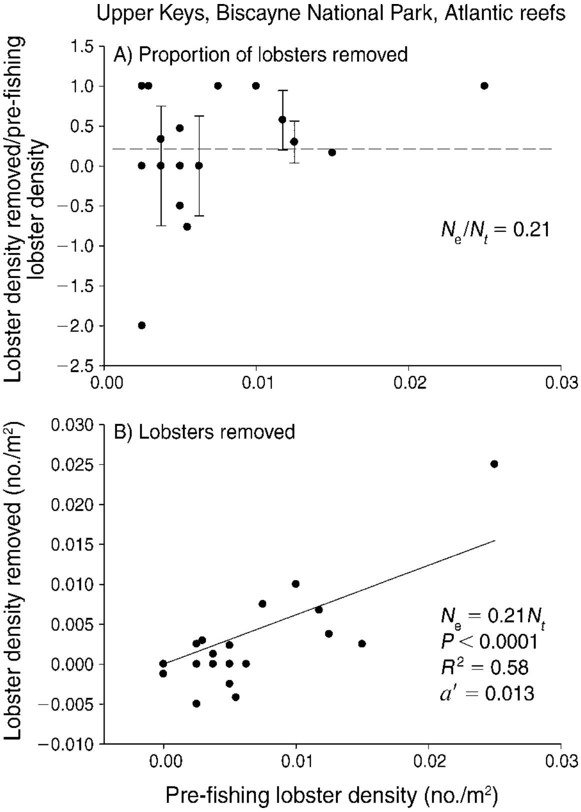

FIG. 7. Functional response of recreational divers to spiny lobsters (>7 cm CL) in offshore Atlantic reefs in the upper Keys in Biscayne National Park: the relationships between (A) the proportion (mean ± SE) of lobster density removed (N_e/N_t) and pre-fishing density (N_t) and (B) the mean density of lobsters removed (N_e) and pre-fishing density (N_t). A density-independent relationship (A) between N_e/N_t and N_t indicates a type-I functional response and justifies fitting a mechanistic type-I functional response model to (B) the relationship between N_e and N_t. Only positive values of lobsters removed were used when fitting the mechanistic functional response model in panel (B). The dashed line in panel (A) is the mean proportion of lobster density removed. Sample size is n = 20 (6–7 reef locations/year × 3 years [2003–2005]). Certain data points in (A) have 0 variance, and one data point in both panels (A) and (B) is masked by another. See *Results: Recreational diver functional responses: Upper Keys: BNP* for additional discussion of results of statistical analyses and justification for the type-I functional response model. The data for isolated reefs in Biscayne National Park are not shown because the lobster density and proportional lobster density removed from before to after the mini-season were extremely low and showed no relationship with lobster density.

2001). The percentage decline in lobster density observed in this and our previous studies (Eggleston and Dahlgren 2001, Eggleston et al. 2003) is higher than that observed for Looe Key, Florida in 1987, when abundance of spiny lobster declined by 55% immediately after the mini-season (Blonder et al. 1992). Similarly, Davis (1977) observed a 58% decline in spiny lobster abundance after the entire eight-month fishing season in the sport harvest area of Fort Jefferson National Monument, Dry Tortugas, Florida; a result that prompted the U.S. National Park Service to halt all fishing in waters of Fort Jefferson National Monument in 1974, which became Dry Tortugas National Park in 1992. The relatively high exploitation rates measured in the back-reef area of the lower Keys were somewhat surprising given that this area is located in the "backcountry" of the Florida Keys, where boat navigation is difficult due to a general lack of navigational aids across numerous shoals and because this area is further away from the large population center of Key West, where our previous study was conducted. The relatively large decline in spiny lobster abundance observed in the lower Florida Keys and off Key West (Eggleston and Dahlgren 2001) is probably due to the increasing popularity of scuba diving and lobster hunting and detailed knowledge of lobster distribution and abundance patterns due to intense mapping work conducted before the mini-season and the use of technological aids, such as GPS, which allow accurate relocation of prime lobster habitats.

One unexpected finding was that diver effort and impact on lobsters was actually lower near the city of Miami than in the lower Keys. The intense diver effort in the lower Keys may also be due to relatively high lobster densities in this region as compared to the upper Keys in Biscayne National Park. For example, the density of spiny lobster was generally twice as high in the lower than upper Keys and ranged up to two orders of magnitude higher in the lower than upper Keys (Fig. 2). Thus, although Biscayne National Park is adjacent to the large metropolis of Miami, diver fishing effort was an order of magnitude higher in the lower than upper Keys (Fig. 3), in accord with the relatively high lobster densities in this region. Moreover, divers did not even exhibit a detectable functional response to lobsters in isolated reefs in the upper Keys, probably because lobster shelters are so plentiful (thousands of isolated reefs) in Biscayne National Park, likely making diver encounter rates with lobsters extremely low. These results suggest that certain areas in the Florida Keys are ineffectively fished by sport divers during the two-day season, and should help dispel notions by taken by various commercial fishers that the catch and removal rates experienced in the back-reef environment on the Gulf of Mexico side of the lower Keys, which has been heavily fished since the 1980s (Sharp et al. 2005), can be reasonably applied across the entire spatial extent of the Florida Keys spiny lobster fishery.

Another unexpected finding was an apparent lobster "spill-in" effect to certain reefs from before to after the mini-season in Biscayne National Park. For example, in nearly half of the sites sampled in Atlantic Reefs (Fig. 7) and isolated reefs (Fig. 2B), the density of lobsters increased from before to after the mini-season. Although some of this apparent increase in density from before to after the mini-season is likely due to natural variation in lobster abundance over a week-long survey period, we did not see this "spill-in" pattern in the lower Keys, where the majority of lobster shelters were likely disturbed by this intense sport diver fishery. We hypothesize that although the density of lobsters should decline significantly in fished areas from before to after the two-day mini-season (as has been the case in this study for the lower Keys), the density of lobsters should increase in non-disturbed areas, such as isolated reefs not visited by divers in BNP or in marine reserves. The mechanisms underlying this hypothesis are that lobsters disturbed by divers in fished areas would migrate from the shelters where they were disturbed (Herrnkind et al. 1975, Parsons and Eggleston 2006) and follow queues of lobsters from non-disturbed areas back to their shelters (Herrnkind et al. 1975) or use the attractive odors of conspecific lobsters as a volume-dependent guide effect (Ratchford and Eggleston 1998, Nevitt et al. 2000, Childress and Herrnkind 2001) or both. We have evidence that spiny lobsters spill-in to marine reserves in the lower Florida Keys in a density-dependent manner (D. B. Eggleston and D. Parsons, *unpublished manuscript*), and suggest that lobster spill-in may not only operate in marine reserves, but operate in relatively undisturbed reefs that are surrounded by diver-disturbed reefs.

The only other recreational fishery that we are aware of with comparable exploitation rates to those of this and our previous studies (Eggleston and Dahlgren 2001, Eggleston et al. 2003) are fish in freshwater lakes and streams (Jones 1987, Johnson and Staggs 1992, Post et al. 2002). For example, individual cutthroat trout (*Salmo clarcki bouvieri*) in the Yellowstone River in Yellowstone National Park, USA, were caught and released a mean of 9.7 times during a 108-d recreational fishing season, with catch rates averaging >1 fish/h (Jones 1987). Catch rates of walleye (*Stizostedion vitreum*) in Lake Mendota, Wisconsin, USA averaged 0.061 fish/h over a three-year period (Johnson and Staggs 1992). Such high catch rates are apparently not always sustainable. For example, catch rates for several Canadian recreational fisheries have declined from 5.6 to 0.25 fish/h, despite a doubling of fishing effort, leading to collapse of many of these fisheries (Post et al. 2002). Direct comparisons of recreational catch rates between fish and spiny lobster are difficult because once captured, spiny lobster are not released, as is the case with many species of fish, and because our catch rates were in units of density (number of lobsters/m^2) or density/time (number of lobsters$\cdot$m$^{-2}\cdot$h^{-1}), whereas fish catch rates are typically reported in units of time (fish/h). Release of fish after capture coupled with stocking, especially stocked catch-and-release trout fisheries, would also help maintain high catch rates.

Application of predator–prey theory

Given such high exploitation rates of spiny lobster, how can knowledge of recreational diver functional responses be applied to management of the fishery? The most common approach to modeling predation is to assume that the consumption rate per predator is proportional to the abundance of the prey. This linear relationship between predator consumptions rates and increasing prey abundance is based on a simple random search model of predation, assuming that each time a predator detects a prey item it instantaneously captures it and begins searching again (type-I functional response). Our assumption from fitting functional response models was that the relationship between lobsters removed and lobster density was a type-I (linear) relationship. If this assumption was incorrect, then the equation $N_t(1 - \exp[-(a'/2)T] = N_t(1 - \exp[-(a[T/2])])$ is not true since a' varies with prey density in type-II and type-III functional responses. Therefore, the impact of changing a' on the number of lobsters removed will depend on prey density, while the impact of changing T is independent of density. However, this does not invalidate the analyses in this study, it simply changes the effectiveness of managing for a' and T to limit catch depending on prey density. For example, in a type-II functional response, one can reduce prey eaten (or extraction by divers) more by reducing T than a proportional reduction in a', since a' varies with prey density. Conversely, with a density-independent type-I functional response, the effect of reducing a' via catch limits or T via time limits on prey eaten (or extraction by divers) is equivalent for either parameter, which provides fishery managers with greater flexibility in managing catch and effort than if divers exhibited a nonlinear functional response to lobster density.

Given the relatively long period to fish (T) in this study (48 hours), and depending upon the values of a' and T_h, it is possible that type-I and type-II functional responses may be indistinguishable. In contrast, type-III functional responses are often distinguishable over relatively long predation periods (T). In this study, lobster extraction rates by divers over 48 hours were between 74% and 84% for the lower Florida Keys, and even lower in the upper Keys. The ideal survey design in this study would have been to measure the functional response of divers over shorter intervals during the two-day fishing season to better distinguish type-I vs. type-II; however, we could not accomplish this task because of logistical constraints of covering such a large area within each day (Fig. 1). Given that lobster extraction rates by divers, however, were well below 100% at 48 hours (40–84%), type-I and type-II functional responses should be distinguishable at low densities, with type III being the most distinguishable (Lipcius and Hines 1986). The most important implication of this sport diver–lobster data is to determine the functional relationship between prey density and removals, whether we call them type I, II, III or linear, hyperbolic, and sigmoidal does not change the main implications for fishery management.

Our data indicated that the number of lobsters removed by divers was directly proportional to lobster density and that the diver functional responses did not become saturated at natural levels of lobster density.

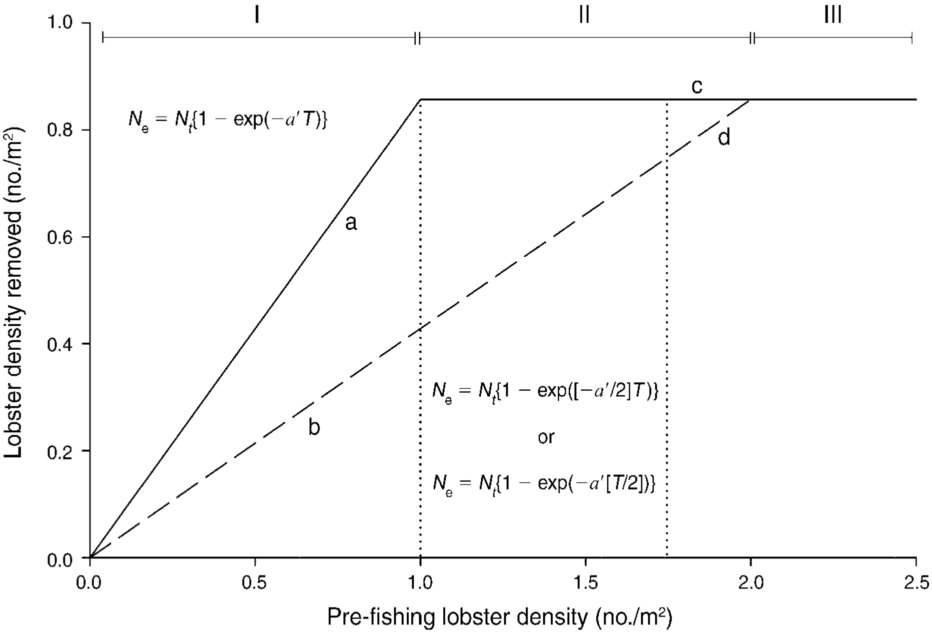

FIG. 8. Schematic of theoretical implications of type-I functional response to fisheries management actions. Shown is a linear relationship (solid line) between density removed (N_e) and prey fishery density (N_t) that reaches an upper asymptote as the fishery becomes saturated between regions I and II. Management actions that reduce the catch by reducing bag limits or fishing season by half (i.e., $a'/2$ and $T/2$, respectively) will have a proportional reduction (i.e., a/b = 1) in catch (N_e) below saturation (i.e., within region I) and a decreasing effect (i.e., c/d ≪ 1) on catch rates above saturation (i.e., within region II). If the fishery were highly saturated (region III), management actions that reduced fishing effort would have little, if any, effect. The dashed line shows the linear relationship lobster density removed by sport divers and pre-fishing season lobster densities when catch is reduced by half. The lines "a" and "b" denote differences in the increasing slope of lobster density removed by sport divers as a function of pre-fishing season lobster densities both (b) with and (a) without reductions in catch by fisheries management actions. The line "c" denotes no change in lobster densities removed as a function of pre-fishing season lobster density due to satiation of the fishery, whereas line "d" denotes lobsters removed just prior to delayed satiation by the fishery due to fishery management actions that reduce catch. The figure is adapted from Eggleston et al. (2003).

Thus, in general, recreational divers appear to follow this simple predator–prey model at the levels of lobster density measured in our study, which is consistent with our previous study of two habitat types (patch reefs and heads) over one fishing season. The application of a linear, non-saturated type-I functional response to fisheries management is that lobsters do not attain a relative refuge from divers at low lobster densities, such that removal of lobsters by divers can, and does, lead to local extinction. However, management efforts intended to reduce catch, through decreases in bag limits or the fishing season, would result in a concomitant decrease in exploitation (Fig. 8). Conversely, if lobster densities were relatively high, such that proportional densities removed by divers were above the minimum level of diver saturation (e.g., region III of Fig. 8), management efforts to reduce catch rates would have much less of a desired effect on lobster removal.

Density-independent removal of spiny lobsters by recreational divers contrasts the general pattern in fisheries where fishing mortality is inversely density dependent (i.e., depensatory mortality; Hillborn and Walters 1992). For example, a depensatory relationship between q (or in some cases f) and N has been reported for Pacific sardine *Sardinops sagax caerula* (McCall 1976), Norwegian herring *Clupea harengus* (Dragesund et al. 1980), North Sea cod *Gadus morhua* (Houghton and Flatmann 1981), lake whitefish *Coregonas clupeaformis* (Henderson et al. 1983), and Georges Bank haddock *Melanogrammus aeglefinus* (Crecco and Overholtz 1990). The simple predator–prey response by recreational divers to lobster density identified in this study should be important to fishery managers because already intense diver exploitation rates of lobsters are not expected to increase disproportionately at low population densities, which could exacerbate local extinction. The recreational diver–lobster predator–prey construct in this study provides a useful predictive framework to apply to both recreational and commercial fisheries, and on which to build as management actions are implemented.

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