The Refuge Effect of Unpublished Artificial Reefs Deployed on the Northwest Florida Shelf (FWC-06120): 2005-08 Modeling Report

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INTRODUCTION

Artificial reefs have been constructed of a variety of materials in marine, estuarine, and freshwater habitats around the world for myriad purposes (Seaman and Sprague 1991). Among the more commonly stated goals of artificial reef programs are 1) mitigating losses of structurally complex or hardbottom habitat; 2) enhancing production of reef-dependent invertebrate or fish species; 3) aggregating individuals to increase fishing efficiency; and, 4) providing divers with increased opportunity to view reef-associated organisms (Seaman 2000; Baine 2001; Okechi and Polovina 1995). While resource managers often cite more than one goal for a given artificial reef program, recreational and commercial fishermen generally are among the most vocal proponents of artificial reefs because increased catch rates often follow reef creation (Bohnsack 1989; Lindberg 1997; Grossman et al. 1997; Bortone 1998). This increase in catch rates has been the subject of an ongoing debate among fishery biologists and managers as to whether artificial reefs are more likely to enhance production of reef fishes or attract fishes from surrounding areas, thus making them more vulnerable to fishing mortality (i.e., the attraction versus production debate) (Bohnsack 1989; Lindberg 1997; Pickering and Whitmarsh 1997). This issue is especially important in the northern Gulf of Mexico (GOM) where many large reef fishes (e.g., snappers and groupers) targeted at artificial reefs are estimated to be fully exploited or overfished (NOAA 2007; Patterson and Cowan 2003). Therefore, concern exists that the creation of artificial reefs actually may exacerbate unsustainable levels of fishing mortality if artificial reefs function more as reef fish attractants than as production enhancers (Polovina and Saki 1989; Polovina 1991; Grossman et al. 1997; Pitcher and Seaman 2000).

Artificial reefs began to be used widely as management tools in the United States (US) during the 1970s and 1980s (Bohnsack and Sutherland 1985; Bohnsack 1989; Lindberg 1997; Seaman and Jensen 2000), although some states have had active programs for many decades (Stone 1986; Minton and Heath 1998). Lindberg (1997) suggested fishermen and managers assumed artificial reefs deployed in these early programs increased production of fish stocks due to the simple fact that high fish densities and high catch rates were observed at artificial reefs, sometimes where little or no reef fish catch previously was taken. Lindberg (1997) also opined that anglers readily accepted the assumption that artificial reefs increased fish production because it was compatible with their conservation ethic. Bohnsack and Sutherland (1985) were among the first scientists to question whether artificial reefs generally increased fish production or merely aggregated fishes from surrounding natural hardbottom habitats. They suggested a greater understanding was needed of how artificial reefs effect fish populations and marine ecosystems prior to their mass deployment. Nearly 25 years later, scientists still comment that research on the ecological function of artificial reefs lags far behind the engineering and deployment of reefs (Pickering and Whitmarsh 1997; Lindberg et al. 2006; Miller 2002).

Managers and scientists in the state of Florida have long been leaders in both the development and study of artificial reefs. Florida has the most extensive natural reef habitat in the continental US and, therefore, the greatest diversity and abundance of reef fishes (Hoese and Moore 1998). Florida also has the most comprehensive artificial reef program in the nation, and much of what is known about the ecological function of artificial reefs has resulted from studies conducted on the Florida shelf. However, we still lack fundamental knowledge of how artificial reefs function ecologically (Miller 2002; Lindberg et al. 2006). In the Florida Artificial Reef Strategic Plan (ARSP), the Florida Fish and Wildlife Conservation Commission (FWC)

emphasized the need to increase the knowledge base of artificial reef ecology in order to achieve the guiding purpose:

"To optimize the biological and economic benefits of artificial reefs in Florida to ensure that the marine environment, human health and marine organisms are protected, restored, enhanced or sustained..." (FWC 2003).

Following the spirit of the ARSP, the FWC deployed over 500 unpublished artificial reef sites in four Large Area Artificial Reef Sites (LAARS) in the northwest GOM in 2003 (Fig. 1). Reef locations were not reported to the public in hopes that they would serve as no-harvest refugia for reef fishes. Unreported reef sites also provide sites for scientific study of artificial reef ecological function in the absence of direct fishing pressure. To that end, personnel from the Fisheries Laboratory at the University of West Florida began studying a subset (n = 27) of reef sites in the Escambia East (EE) LAARS in fall 2004 to examine the ecology and community dynamics of so-called refugia reefs. This has been accomplished via a remotely operated vehicle-based video sampling protocol in which study sites were visited quarterly to examine reef fish communities. Additionally, fishes captured at a subset of experimental reefs (n = 9) from winter 2005 through fall 2007 were tagged with internal anchor tags to estimate their site fidelity to and dispersion from study reefs. Tagging data also have been used to evaluate the assumption that unpublished reef sites have not been located and targeted by fishermen.

The goal of the first two years of the study was to establish baseline community structure estimates via video sampling of reef fishes (Patterson and Dance 2005; Patterson et al. 2006, in press). In spring 2007, coordinates of a subset (n = 9) of study reefs were advertised to the public to examine the effect of fishing on reef fish communities in study years three and four (Patterson et al. 2008). The principle objective of the work presented here was to examine the ecological and fishery functions of these experimental (i.e., reported to the public) versus control artificial reef study sites. This was accomplished through statistical analysis and modeling of reef fish community data. Analysis focused on differences between control (n = 9) and experimental sites before and after coordinates of experimental sites were reported to the public in spring 2007. Results have important implications for artificial reef management in Florida, as well as fisheries management for reef fish resources throughout the northern GOM.

METHODS

Site Selection:

Deployment locations of reef sites within the EE-LAARS were provided by Mr. Keith Mille of the FWC, Division of Marine Fisheries Management in fall 2004 at the outset of the study. Reefs were of three designs (Table 1) and 3 reefs of each design were randomly selected from each of three depth strata (shallow stratum <31 m, mid-depth stratum = 31 - 35 m, and deep stratum >35 m; Table 2). One reef of each type within each depth stratum was randomly assigned to one of three treatment groups: control, tagging, and experimental. Control group reefs were video-sampled with the ROV methodology detailed below, while tagging sites were video-sampled as well as visited quarterly to capture and tag reef fishes present on those sites. In spring 2007, coordinates of the experimental reefs were advertised to the public by FWC in order to examine potential fishing effects on reef fish communities.

Video Sampling:

Video sampling was conducted during 2004-2007 onboard the chartered *F/V Dorado*, which is owned and operated by Captain Jeff Thierry. Thereafter, video sampling was conducted onboard the chartered *F/V Riptide*, which is owned and operated by Captain Seth Wilson. Video sampling was performed with a VideoRay Pro III Remotely Operated Vehicle (ROV), which is is a micro-class ROV with dimensions of 30.5 x 22.5 x 21 cm and a mass of merely 3.8 kg. The ROV was piloted at the surface by either Mr. Mike Dance (MAD) or Mr. Dustin Addis (JTA) and controlled by an integrated control box via the ROV's tether to the surface. Realtime ROV movement was observed on a high resolution monitor with a live feed from the ROV's 570-line resolution video camera. The camera is capable of 160° vertical tilt, a wide-focus range, and a wide viewing angle (105°). Lighting, when needed, was provided by twin 20-watt high efficiency halogen lights mounted on the ROV. Video output from the ROV was recorded on digital video tape with a Sony GVD1000 digital VCR.

Video sampling of reef fish communities occurred at study sites from fall 2004 through summer 2008, although no sampling was conducted in winter 2008. Video sampling with the ROV involved modifying the established Bohnsack and Bannerot (1986) diver-based stationary count method (see Patterson et al. in press for details). In our method, the ROV first was positioned 1 m above the seafloor and approximately 5.5 m away from a given reef. The ROV slowly was pivoted 360° and then moved to the opposite side of the reef. Once there, it was positioned 1 m above the seafloor and 5.5 m away from the reef and pivoted 360°. The ROV then was flown to 1 m directly above the reef and pivoted 360° to video fishes in the water column above the reef. Next, the ROV was flown to \sim 10 m above the reef and pivoted 360°. Once all sampling segments were completed, the ROV was flown back down to the reef and positioned such that fishes inside the reef structure were captured on video. Individual modules were sampled separately for fish haven and reef ball sites whose modules were >8 m apart on the seafloor (B1, B3, B4, B7, B9, B11, B16, C14, and C36) (Patterson and Dance 2005).

The entire video sampling procedure was accomplished in <10 minutes. Following video sampling, the ROV was positioned among the fish community in an attempt to increase the sample size of fish struck with the ROV's red laser scale; distance between the scale's red lasers is fixed at 100 mm. Lastly, a Sea Bird 19*plus* conductivity, temperature, depth (CTD) instrument equipped with a dissolved oxygen sensor was lowered to the seafloor to measure water parameters at a subset of reef sites immediately after video sampling.

Video Analysis

Analysis of video samples was performed in the Fisheries Laboratory at UWF with a Sony DVCAM DSR-11 digital VCR and a Sony LMD-170 high resolution LCD monitor. For a given video sample, fishes were identified to the lowest taxon possible (96.2% to species) and enumerated for the five separate video sampling segments: 1st 360° spin 1 m above seafloor, 2nd spin 1 m above seafloor on the opposite side of the reef as the 1st spin, the spin 1 m above the reef, the spin 10 m above the reef, and inside the reef. To avoid double counting individuals, fish observed during the 1st and 2nd spins were counted as part of the respective spin's sampling segment only if they occurred on the ROV side of a plane running through the reef and perpendicular to the ROV's heading when the ROV was pointed directly toward the center of the reef, and fishes in the water column on the third spin were only counted at and above the depth of the ROV. Fish numbers were summed across all five sampling segments for a total count. Fish counts at fish haven and reef ball reefs whose modules were sampled separately were averaged

between modules in an attempt to standardize counts on a per unit area basis (i.e., fish per 1.77 x 10^2 m^2).

Fork length (FL) was estimated for all fishes struck by the laser scale during video sampling. This was accomplished by multiplying the length of a given fish measured in a video frame by the known distance between lasers (100 mm), and then dividing that product by the distance measured between lasers in the frame. For example, if a red snapper measured 38 mm in a video frame and the distance between the laser points measured 12 mm, the fish would be estimated to be 317 mm {[(38 mm*100 mm)/12mm)] = 317 mm}. Fork length was converted to total length (TL) for most species with regression equations computed from tagging data (see below); otherwise, equations from the literature were used.

Accurate fish counts and unbiased estimates of species-specific length distributions were key to analyses presented below. Therefore, care was taken to test assumptions about methods employed such that accuracy and precision were ensured (Dance 2007; Patterson et al. in press). Quality control of fish count estimates was accomplished by having a second reader (WFP or DTA) read 10% of video samples analyzed by the primary reader (MAD or DTA), and then comparing average percent error (APE) in community structure estimates between readers. Patterson et al. (in press) reported that reader comparisons demonstrated high agreement in the present study, as the linear correlation between readers was high (Pearson's r = 0.997, p < 0.001) and the APE between reader counts was 7.4%. They also pointed out that 61% of species had counts of <5 individuals in initial reads and APE can be inflated when even minor differences exist in counts of uncommon species.

Testing of the laser scale was conducted in UWF's swimming pool to examine the effect of distance from the ROV and the angular difference from perpendicular that lasers struck fish models on the estimate of fish size (Dance 2007; Patterson et al. in press). For models of gag, red snapper, and vermilion snapper, the percent error in fish size estimates was <5% if the angle from perpendicular was $<20^{\circ}$. Therefore, by not estimating fish length *in situ* for individuals deviating more than approximately 15° from perpendicular to the ROV's heading, minimal bias in length estimates was ensured, and the degree of bias that likely existed in fish size estimates could be simulated and accounted for (see below).

Community Structure Analysis:

Taxa-specific fish counts were converted to density estimates (numbers per area sampled) by dividing counts by the area of the sampling cylinder $(1.77 \times 10^2 \text{ m}^2)$. As stated above, computing fish density for fish haven and reef ball sites with modules that had to be sampled separately first involved averaging taxa-specific counts between modules. Taxa-specific biomass per area then was computed by converting length distributions estimated from laser scale data to fish mass distributions and then expanding by fish density estimates. Bias in fish length estimates first was simulated based on results from the pool experiment in which model fish length was estimated for different angles from perpendicular and distances from the ROV (Dance 2007; Patterson et al. in press). For conditions observed *in situ*, the mean bias of underestimating fish length was estimates to be 3% with a standard deviation of 0.6 (Dance 2007). Therefore, length estimates of all fish struck by lasers throughout the study were increased between 0.28 and 4.48% based on a random probability and normally distributed bias with mean equal to 3% and standard deviation equal to 0.6%. After correcting for measurement bias, fish length was converted to fish mass based on mass-length relationships reported in the literature. For taxa that were too small to be scaled with lasers, biomass estimates were computed by multiplying the

total number of fish observed by 80% of the maximum individual mass for a given taxon. Unknown small fishes were assigned a mass of 1 g, which corresponds to the approximate mean mass at settlement for the predominant reef fishes observed in the study. Overall, taxa for which mass was assigned using either of these two conservative methods accounted for only 3.9% of the total fish biomass estimated on reef sites.

Differences in community structure among sampling quarters, reef types, and depth strata were tested with analysis of similarity (ANOSIM) in the Primer software package with fish density (fish $100m^{-2}$) as the dependent variable (Clarke 1993; Clarke and Gorley 2001). Fish density was square-root transformed and then a Bray-Curtis similarity matrix was computed for taxa-specific density data, which consisted of all of the individual similarity coefficients computed between sites. Individual ANOSIM models then were computed for sampling quarter, reef type, and depth. The experiment-wise error rate was set *a priori* to 0.05 for all ANOSIM models; however, since three separate analyses were conducted, α was split three ways such that $\alpha = 0.0167$ for each analysis. Diversity indices, including number of fish taxa observed, Shannon-Weiner (H') diversity index, and Pielou's evenness (J'), also were computed in Primer to examine shifts in community structure among sampling quarters.

Reef Fish Tagging:

Sampling trips to tag fish at nine of our sites were conducted onboard either the F/V *Dorado* or the F/V *Riptide* after video sampling was completed in each quarter from fall 2004 through fall 2007 (Fig. 1, Table 2). At a given site, four fishermen fished with two-hook (3/0 J hooks) bottom rigs baited with squid and cut mackerel and one fisherman fished in the water column over the reef with a whole mackerel scad on a sow rig. Sow rigs were made by snelling two 5/0 J hooks to the end of a 1.5 m leader with a spacing of about 10 cm apart. Effort was further standardized by fishing for 30 min at each site. Fish were brought to the surface at a rate of ~1 m sec⁻¹. Fish were removed from hooks and placed in a 475-l cooler with flowing seawater prior to tagging. Fish were measured to the nearest mm fork length (FL) or total length (TL), tagged with Floy[®] 95M internal anchor tags, and returned overboard. Tags were marked with the word "REWARD", a number identifying the fish, and a toll free telephone number to report tag recoveries. The tagging study was widely advertised among recreational and commercial fishing groups to encourage reporting of tag recoveries. Fishermen who reported tags received a \$5 reward per tag and were entered into \$500 annual drawings of all tag returners.

Distance moved by recovered tagged fish was computed as the straight line distance between tagging and reported recapture location when sufficient information was provided by fishermen of the latter (e.g., GPS or Loran C coordinates or reef name). Unbiased estimates of mean distance moved and dispersion rate (distance moved/time free) for red snapper, gray triggerfish, and groupers (red grouper, gag, and scamp) were computed with the delta method (Aitchison 1955; Pennington 1993).

Burnham's (1993) joint encounter mark recapture model was employed to estimate site fidelity to study reefs. The joint encounter model is a Cormack-Jolly-Seber type model that models data from live recaptures and dead recoveries to estimate several parameters: survival (S), probability of recapture (p), reporting rate of tagged fish recaptured by fisherman (r), and site fidelity (f; denoted as F in Burnham's notation but given f here so as not to confuse with instantaneous fishing mortality, F) (White and Burnham 1999). Joint encounter models were computed with the program MARK (White et al. 2006). Fully-reduced models were computed for red snapper, gray triggerfish, and groupers, meaning that the estimated parameters (S, p, r, f)

were held constant across all tagging events (i.e., sampling quarters). A bootstrapped goodness of fit test was computed for each model to test for overdispersion of the data, therefore significant lack of fit of a given model.

Fishing Experiment:

Coordinates of a subset of our study reefs (sites: A35, A53, A56, B4, B7, B16, C14, C25, and C36) were advertised to the fishing public in May 2007 via a press release from FWC's Artificial Reef Program. Coordinates of these experimental sites subsequently were posted on FWC's online database for public artificial reef sites off Escambia County. The purpose of releasing the coordinates of these sites was to examine the effect of fishing on the fish community at study sites. Routine ROV-based video sampling continued in spring, summer and fall 2007, as well as during spring and summer 2008 (Table 3). The effect of the fishing experiment on reef fish community structure was evaluated with two-factor crossed ANOSIM models that tested the effect of sample timing and treatment group on fish density and biomass.

Catch curve analysis was employed to model instantaneous annual disappearance rates (D) of red snapper and gray triggerfish from study sites before (fall 2005 through winter 2007) and after (spring 2007 through summer 2008) coordinates of reported sites were released to the public. The "before" group was restricted to sampling quarters 5-10 (fall 2005 through winter 2007) because sample sizes of laser scaled fish were much smaller prior to fall 2005. Furthermore, the time period of "before" samples was then equal to the time period of "after" samples by restricting the before time period to quarters 5-10. Only data from red snapper and gray triggerfish were modeled with catch curves because they were the only species for which sufficient data existed. Among the other important fishery species, sample sizes either were evaluated to be too small, as in the case of gray and vermillion snappers and gag, scamp, and red grouper, or only a severely truncated size, therefore age, distribution existed, as with greater amberjack.

Age distributions of red snapper and gray triggerfish were estimated from length distributions and size-at-age data. The source of red snapper size-at-age data was otolith-based aging analysis presented in Patterson et al. (2001a) and Snyder et al. (2007), while gray triggerfish size-at-age estimates were derived from annuli counts from sectioned dorsal spines that were reported by Ingram (2001). Red snapper size-at-age data were used to create an agelength key (ALK) for that species with the method of Ricker (1975). While only a portion of the data that went into the red snapper ALK was collected contemporaneously with video sampling, the combined studies contained a large percentage fishery-independent samples (23%; n = 408 of 1,803) of sub-legal fish, and ALKs have been shown to be superior to age slicing when data exist to compute them (Goodyear 1997). Ages were estimated probabilistically for laser scaled samples based on their bias-corrected TL estimate, a randomly drawn probability between 0 and 1 using the RAND function in Microsoft Excel, and the probability of age-at-length distribution for corresponding 20 mm length bins in the ALK. Once age was assigned to red snapper, sampling quarter- and reef site-specific age distribution estimates were expanded by the total number of fish observed at a given site during a given sampling event. When length distributions did not exist for given reef site/sampling quarter combinations (10.8%), age distributions were assigned to those sites based on a average of numbers at age for the other two reef replicates of a given reef type within a given treatment group during that quarter.

Gray triggerfish age at size was estimated by deterministic age slicing by solving Ingram's (2001) von Bertanffy growth function (VBGF) for age:

Age =
$$-\frac{\ln(1-\frac{L}{598})}{0.200} - 1.373$$
 equation 1

where:
$$L =$$
fork length in mm.

Ingram's (2001) VBGF ($R^2 = 0.99$) was based on age estimates derived from 1,690 sectioned first dorsal spines of gray triggerfish sampled in the north central GOM from July 1996 through October 2000. In the current study, no fish greater than the length asymptote (598 mm) of Ingram's (2001) function were observed. Therefore, age could be estimated for all samples with the age slicing approach described.

Estimated numbers at age were ln-transformed and plotted versus age for both red snapper and gray triggerfish for 1) all study sites prior to advertising coordinates of experimental sites to the public, 2) control sites after advertising experimental sites, and 3) experimental sites after advertising their coordinates. Catch curves were computed by fitting linear regressions to the fully recruited ages with the equation:

$$ln(number at age) = a - D(age)$$
equation 2
where:
$$a = y \text{ intercept}$$
and
$$D = instantaneous disappearance rate y^{-1}.$$

The parameter, D, is modeled in the same context as presented by Patterson and Cowan (2003), in that the decline in numbers at age is not only due to total instantaneous mortality, Z, which is typically modeled with an exponential decay function:

$$N_t = N_0 e^{-Zt}$$
 equation 3

where: N_t = number alive at time t N_0 = number alive at time zero age = time in years and Z = instantaneous total mortality rate y⁻¹.

Instead, D is equal to Z plus net instantaneous emigration (E') away from sites. Estimates of annual site fidelity derived from tagging data could be used to estimate emigration rates away from tagging sites. However, if fish were moving among reefs within the EE LAARS, then estimating movement away from study sites (i.e., instantaneous emigration, E) alone would not fully address net emigration, given that instantaneous immigration rate (I) must also be estimated to compute net emigration.

Instantaneous total mortality, Z, also can be partitioned into its sub-components: instantaneous natural mortality (M) and instantaneous fishing mortality (F). Estimates of M for

red snapper and gray triggerfish, reported by Porch (2007) and Ingram (2001), respectively, were derived with the method of Hoenig (1983) based on maximum longevity observed for these species in the northern GOM. In the most recent stock assessment for GOM red snapper, M was estimated to be 0.1 for fish ages 2+ (Porch 2007), while Ingram (2001) estimated M for gray triggerfish in the north central GOM to be 0.49 y⁻¹ based on Hoenig's (1983) method and a maximum observed longevity of 9 years.

RESULTS

Sampling and Community Structure Analysis

From fall 2004 through summer 2008, 134,698 individual fish belonging to 99 taxa were counted at study reefs (Table 3; see Appendix Tables 1 and 2 for 2008 data). The ten taxa that had the highest estimated densities among study reefs were red snapper (25.6% of all individuals observed), mackerel scad (15.4%), tomtate (10.0%), round sardinella (6.6%), vermilion snapper (5.3%), blue runner (4.4%), pinfish (4.4%), greater amberjack (3.4%), gray triggerfish (3.4%), and slippery dick (3.3%) (Table 4, Figure 2A). Snappers clearly have consistently been the most abundant family at our study sites, with red snapper having the highest abundance of any single species in all four years of the study.

Examination of percent biomass estimates reveals a different picture of the community structure at artificial reef study sites. The ten taxa that had the highest estimated biomass among study reefs were red snapper (42.8% of total estimated biomass), greater amberjack (6.8%), gray triggerfish (6.1%), gag (5.2%), vermilion snapper (5.1%), gray snapper (4.2%), mackerel scad (3.9%), blue runner (3.7%), tomtate (3.2%), and red grouper (3.1%) (Table 4, Figure 2B). Therefore, two things are apparent when examining overall taxa-specific biomass versus density estimates. First, red snapper was even more dominant on study sites as a percentage of biomass versus density. Second, relatively large invertivores and piscivores, such as gray triggerfish, greater amberjack, groupers, and snappers, made up a much larger percentage of total biomass than they did overall fish density, while small planktivores, such as mackerel scad, blue runner, and round sardinella ranked much lower as a percentage of biomass than density. That latter difference becomes even more evident when percent density and biomass are compared among trophic position groupings (Fig. 3).

There were significant differences in fish community structure among sampling quarters (ANOSIM, p < 0.001 for all; Figs. 4&5). Mid-depth stratum sites and fish haven reefs tended to have the highest diversity of taxa, but the number of taxa observed increased among all reef types and depth strata throughout the study. Fish density also increased from fall 2004 through summer 2008, but mean biomass estimates hovered around 50 kg 100m⁻² per reef site throughout the study. Dance (2007) documented one reason for an increase in overall fish density but not biomass was that large groupers declined precipitously from high densities in fall 2004 (mean = 10.2 fish 100m⁻²) to low levels by fall 2005 (mean = 1.2 fish 100m⁻²). He hypothesized that groupers recruited to study sites in summer and fall 2004 following tropical weather in summer 2004, and attributed the subsequent decline to groupers eventually dispersing among other available habitat. Another reason for the increase in taxonomic diversity and fish numbers, without a concurrent increase in biomass, was the increase in the fouling community over time and the subsequent recruitment of small, reef-associated fishes, such as blennies, cardinalfishes, damselfishes, butterflyfishes, and frogfishes (Patterson et al. 2008).

Estimation of Laser-scaled Fish Length

Length was estimated for 6,977 fishes with the laser scale, with red snapper (n = 3,455; 49.5%), greater amberjack (n = 871; 12.5%), gray triggerfish (n = 630; 9.0%), tomtate (n = 470; 6.7%) and gray snapper (n = 344; 4.9%) being the most frequently measured (Table 5). Among the important fishery species, most fish observed at study reefs were small, young individuals estimated to be much shorter than estimated species-specific L_{∞} (the length asymptote from a computed VBGF) and much younger than maximum longevity estimates (Table 5). A large gray snapper observed in June 2006 was larger than estimated L_{∞} for that species, and the mean size of vermilion snapper actually was above its estimated L_{∞} . However, size at age is highly variable for vermilion snapper, thus age cannot be predicted reliably from size for that species (Allman et al. 2005).

Size distributions of the most important fishery species observed at study reefs reveals information about species-specific size, therefore age, classes that recruited to study reefs, which adds a greater dimension to study data than fish density or biomass estimates alone (Fig. 6). For example, it is apparent from red snapper size frequency plots, and based on size-at-age data for the species (Patterson et al. 2001a), that while some fish recruited to study reefs as 1 year olds, red snapper really did not recruit in large numbers until reaching age two (i.e., modal length \approx 300 mm). Also apparent is the fact that regardless of the timing of sampling (i.e., before or after reporting experimental site coordinates to the public in spring 2007) or the treatment group, relatively few red snapper were estimated to have total lengths above the recreational size limit of 406 mm TL (Fig. 6A-D). In fact, only 8.4% and 22.0% of fish scaled with lasers at control sites had TL greater than 406 mm before and after spring 2007, respectively (Fig. 6A&B), while those percentages were 8.4% and 12.8% for experimental reefs before and after reporting their coordinates to the public (Fig. 6C&D). A very different pattern was apparent in gray triggerfish size estimates in that 36.3% and 60.3% of fish at control reefs were estimated to have FL greater than the recreational size limit of 305 mm before and after spring 2007, respectively (Fig. 6E&F), while experimental sites had percentages of 30.0% and 48.1% above the size limit before and after spring 2007 (Fig. 6 G&H).

Greater amberjack had the most truncated size distribution among important fishery species (Fig. 6I-L). Their modal length of 300 mm, and the limited variability around that mode, indicate that basically only two year-old greater amberjack appeared at study reefs (Thompson et al. 1999), and no greater amberjack even remotely close to the recreational size limit of 737 mm were observed. Grouper size frequencies, on the other hand, had broad size distributions, but that resulted partly because gag, scamp, and red grouper were plotted jointly (Fig. 6M-P). Among those three species, 54.4% and 31.4% of fish scaled with lasers at control sites had TL greater than their recreational size limits before and after spring 2007, respectively (Fig. 6M&N), while experimental reefs had percentages of 39.5% and 30.0% before and after spring 2007 (Fig. 6O&P). However, many fewer groupers were scaled with lasers later in the study (Fig. 6N&P), which is consistent with their density and biomass trends.

A larger percentage of gray snapper observed at control reefs was above their recreational size limit (305 mm TL) before (76.1%) coordinates of experimental reefs were reported than after (29.6%; Fig. 6Q&R), but experimental sites actually had a higher percentage of fish above the size limit after spring 2007 (55.9%) than did control sites (Fig. 6T). However, total sample size (n = 203) was somewhat limited for gray snapper. The same could be said of vermilion snapper (total n = 112), but interesting trends still exist in their estimated size distributions (Fig.

6U-X). A high percentage of vermilion snapper was estimated to be above its recreational size limit (254 mm TL) regardless of whether fish were laser-scaled at control reefs before (45.5%) or after (69.7%) spring 2007, or at experimental sites before (61.5%) or after (81.8%) spring 2007. Data for both groups seem to indicate recruitment of smaller fish to reef sites occurred early in the study, and then a lack of fish less than 200 mm TL existed later in the study.

Reef Fish Tagging

A total of 3,115 reef fish was tagged at study reefs (Table 5). An additional 545 fish were caught at tagging sites but not tagged, typically due to be being too small to handle the internal anchor tags. Red snapper were tagged most frequently and constituted a disproportionately high percentage of the total number of tagged fish (68.8% of tagged fish versus 31.1% of fish observed on study sites from 2004-2007). Red porgy and gray triggerfish were the next most frequently tagged species, and their numbers tagged also were high relative to their abundance observed in ROV video (red porgy = 13.5% of fish tagged versus 1.2% of fish observed and gray triggerfish = 9.1% of fish tagged versus 4.0% of fish observed). This demonstrates that catch per unit of effort during tagging is a poor reflection of reef fish community structure. However, comparison of length frequencies for red snapper derived from tagging and laser data suggests fishing gear was not overly selective for a given size range of fish (Fig. 7). Modes of red snapper TL appeared similar between laser and tagging data, although a Kolmogorov-Smirnov test for equal distributions indicated laser and tagging length distributions were significantly different (K-S, p < 0.001). The key difference between the two distributions was the presence of fish greater than 500 mm in the laser data that apparently were not vulnerable to the fishing gear used to capture fish for tagging. Fish smaller than 200 mm also were somewhat more prevalent in the laser than hook-and-line data.

Eighty-six tagged fish were recaptured on subsequent tagging trips, and 225 recaptures were reported by fishermen (Table 5). No tagged fish was recaptured on tagging trips at a site other than where it was tagged, although what appeared to be tagged fish were observed on two occasions during ROV sampling at non-tagging sites. Multiple recaptures were reported by fishermen as being caught within the Escambia East LAARS, but extensive fish movement also was estimated for several reported tag recoveries (Figs. 8&9). Several fish moved tens of km, with three red snapper being recaptured on the Florida Middle Grounds south of Cape San Blas. The farthest movement of any fish in the study was 319.9 km for a red snapper free for 792 days, while the longest time free was for a red snapper that was recaptured 11.7 km to the northeast of its tagging site 807 days after being tagged. Much more limited movement was observed in fishes other than red snapper, although one gag free for 806 days moved 258.6 km and was recaptured just west of the mouth of the Mississippi River (Fig. 8B). Six tagged gray triggerfish were free for longer than a year. Three of those fish were recaptured at their tagging sites, while the one free the longest (616 days) was recaptured 60.8 km to the east southeast of its tagging site.

Overall, red snapper displayed the greatest movement among tagged fishes (Fig. 8). Their mean distance moved (\pm standard deviation (SD)) was 25.2 (\pm 4.2) km (Fig. 9A). Gray triggerfish displayed the highest site fidelity (54.5% of recaptures made at tagging sites) and lowest dispersion [mean distance (\pm SD) = 7.8 (\pm 1.7) km] among tagged fishes (Fig. 23B). Collectively, groupers (red grouper, gag, and scamp) displayed site fidelity (31.0% of recaptures made at tagging sites) and movement [mean distance (SD) = 14.5 (7.5) km] intermediate to red snapper and gray triggerfish. The high SD of grouper distance moved resulted from the one gag that

moved west of the mouth of the Mississippi River (Fig. 8C). Overall, red snapper displayed the highest mean dispersion rate (\pm SD) of 96.2 (\pm 21.2) m d⁻¹, while gray triggerfish and grouper dispersion rates were 47.8 (\pm 16.5) and 88.6 (\pm 38.3) m d⁻¹, respectively.

Burnham (1993) joint encounter models computed for gray triggerfish and groupers suffered from significant lack of fit (χ^2 ; p < 0.001); therefore, model results are only available for red snapper (Addis 2008). Parameter estimates (±SE) for red snapper were a survival rate (S) of 67.4% (±7.20), a probability of recapture (p) of 2.3% (±0.62), a 14.4% (±2.66) reporting rate (r), and annual site fidelity (*f*) of 10.8% y⁻¹ (±5.20). Addis (2008) reported that when a second joint encounter model was computed for red snapper in which data from the first tagging event (winter 2005) were omitted from the model, results were S = 67.2 ± 8.45%, p = 1.4 ± 0.42%, r = 13.1 ± 2.85%, and *f* = 21.3 ± 10.41%.

Fishing Experiment

Timing of sampling (i.e., before versus after spring 2007) and reef treatment group both significantly affected reef fish community structure (ANOSIM; p < 0.001). Key differences between control and experimental sites were large increases in the percent density and percent biomass estimates of planktivores at experimental sites, along with concurrent decreases in invertivore/piscivores and piscivores, after advertising the coordinates of experimental sites to the public (Table 7, Fig. 10). The percent difference in mean planktivore biomass after versus before spring 2007 was actually greater at control sites; however, the absolute increase in mean planktivore biomass was twice as great at experimental (8.6 kg 100m⁻² after, 4.4 kg 100m⁻² before) versus control sites (3.0 kg 100m⁻² after, 0.9 kg 100m⁻² before). The observed increase in planktivore biomass was due mostly to mackerel scad and round sardinella, which made up 64.2% and 22.9%, respectively, of planktivore biomass at study sites. These, small, schooling pelagic planktivores only were observed in 12.5% of video samples, but occurred in large numbers when they were present (see Appendix Tables 1&2).

The biomass of fishes that have a hybrid planktivore/invertivore feeding ecology increased at both control and experimental sites, but the percentage increase in biomass was much greater at control sites (Table 7, Fig. 10B). That increase was due mostly to vermilion snapper biomass increasing more substantially at control versus experimental sites (Table 12, Fig. 11C), which in turn was to due to increases in both vermilion snapper density (Fig. 11A) as well as mean length (Fig. 11B) at control sites. Among all study sites, vermilion snapper represented, on average, 57.9% of the planktivore/invertivore biomass, while blue runner represented 42.0%. Increases in blue runner explained some of the increase in planktivore/invertivore biomass observed at experimental sites.

Invertivore biomass increased at both control and experimental sites after spring 2007, but it increased to a much greater extent at control sites (Table 7, Fig. 10B). That difference was due mostly to an increase in size of gray triggerfish at control sites (Fig. 11B) and a decrease in density of gray triggerfish at experimental sites (Fig. 11A). The net increase in invertivore biomass at experimental sites was due to an increase in tomtate, which represented 21.8% of total observed invertivore biomass versus 29.7% for gray triggerfish.

The biomass of fishes with a hybrid invertivore/piscivore feeding ecology was dominated by red snapper, which constituted 82.0% of invertivore/piscivore biomass (Fig. 11B and Fig. 11C). Red snapper density actually decreased at both control and experimental sites after spring 2007 (Table 8, Fig. 11A); however, the larger size of red snapper present at control sites translated to an increase in biomass (Fig. 11B&C). The decline in invertivore/piscivores at reported sites also was affected by a decline in gray snapper density and biomass (Fig. 11A&C), as gray snapper constituted 8.1% of invertivore/piscivore biomass estimated at study reefs.

Piscivore biomass was dominated by greater amberjack (37.8%), and gag and scamp (jointly 35.2%). Overall, piscivore biomass increased 61.6% at control sites and decreased 45.7% on experimental sites after spring 2007 (Table 7). Part of the increase at control sites is attributable to an increase in the size and density of greater amberjack present (Fig. 11A&B). It may appear that the decline in grouper biomass at control sites would have more than offset any gains in greater amberjack biomass. However, a large portion of the decline in grouper biomass at both control and experimental sites was due to declines in red grouper, which has an invertivore/piscivore feeding ecology. Increases in the biomass of other *Seriola* sp. and barracuda also balanced declines in gag and scamp biomass.

Estimating Instantaneous Decline Rates

The estimated red snapper age distribution from all study sites prior to spring 2007 indicates that most red snapper recruited to study reefs as two year-olds, although some fish were estimated to have recruited to reefs as young as age 1 (Fig. 12A). That same trend is evident in gray triggerfish numbers at age estimates as well (Fig. 12B); however, a larger percentage of gray triggerfish were estimated to be 1 year-olds when they recruited to study reefs. Estimated age distributions for both species indicate a rapid disappearance from study sites with increasing fish age. Catch curves fitted to ln-transformed numbers at estimated age for the fully-recruited ages confirm that qualitative assessment, as estimated D was 1.00 y⁻¹ for red snapper and 0.52 y⁻¹ for gray triggerfish prior to spring 2007 (Fig. 12 C&D). Given an M estimate of 0.49 y⁻¹ for gray triggerfish, nearly all of the decline at age estimated for gray triggerfish at study sites prior to reporting experimental site coordinates to the public can be attributed to natural mortality alone (i.e., D – M = 0.03 y⁻¹). However, a much different picture emerges for red snapper disappearance at age, given an estimated M of 0.10 y⁻¹ and a D of 1.00 y⁻¹ (i.e., D – M = 0.90 y⁻¹).

Catch curve models computed for control and experimental sites with data collected after coordinates of experimental reefs were advertised to the public indicate higher Ds for both species on experimental reefs (Fig. 13). In applying the following formula:

$$\delta = 1 - e^{(D_e - D_c)} \qquad \text{equation 5}$$

where: δ = percent difference in annual disappearance rate D_e = instantaneous disappearance rate for experimental reefs (y⁻¹) and D_e = instantaneous disappearance rate for control reefs (y⁻¹),

the percent difference in annual disappearance rate (versus instantaneous disappearance rate) was estimated to be 20.5% for red snapper and 17.3% for gray triggerfish. Lastly, by simulating predicted numbers at age for different levels of D, or for different levels of M and F while assuming zero net emigration, study results can be compared to other reported estimates of these instantaneous rates (Fig. 14).

DISCUSSION

The most general statement that can be made about study results is that advertising coordinates of experimental reef sites to the public had a significant effect on reef fish communities. However, analysis of trends in community structure across all four years of the study indicated that reef type, sampling depth, and sampling quarter also significantly affected community structure. Therefore, isolating the experimental effect of advertising reef coordinates to the public was somewhat problematic due to the variance contributed by these other factors. Still, effects from advertising experimental reefs' coordinates, which presumably facilitated direct fishing on those reefs, were apparent on reef fish community structure. Furthermore, the difference in rates of disappearance-at-age for red snapper and gray triggerfish at experimental versus control reefs provides direct evidence that fishing mortality affected the size distribution and biomass of those fishes at experimental versus control sites.

Key to interpreting fish community data generated during this study, as well as to drawing conclusions from analytical or modeling results, is the assumption that sampling methods employed were unbiased. Therefore, steps were taken to test assumptions about method accuracy and to evaluate precision of the methods employed to estimate fish density and size distribution. High between reader agreement in estimates of fish community structure indicate those estimates were reasonably precise, as the tolerance set a priori was an APE of <10%between readers. However, high reader agreement does not address whether fish counts were accurate. As with all visual sampling techniques, the issue of double-counting individual fish was a concern. Another concern was the potential for fish avoidance of the ROV. From observations of fish behavior in situ, we feel neither double-counting nor avoidance were significant sources of error in the current study. The sampling method developed for the ROV ensured that video samples, and especially the various component spins of a sample, were conducted quickly, and almost none of the fish species typically encountered appeared to be agitated by the presence of the ROV during routine sampling. A noted exception to the latter statement was gag, which often either sought shelter within a given module or moved to the perimeter of the sampling cylinder, where they were still counted (Dance 2007).

Fish communities at artificial reefs on the shallow (<40 m) shelf of the northern GOM typically have been sampled with scuba divers (e.g., Bohnsack et al. 1994; Bortone et al. 1997; Turpin and Bortone 2004; Lindberg et al. 2006), while ROV-based methods have been employed for examining fish community structure on deeper reef sites (e.g., Quanttrani et al. 2004; Bryan et al. 2006; Church et al. 2007). Although reefs in the current study were at depths that could have been sampled with divers, our ROV-based method offered some benefits over utilizing divers. Multiple (up to 15) ROV dives could be accomplished on a given day, which would have been possible only with several teams of divers. Furthermore, safety is always a concern with divers, while sampling with the ROV elevated that issue. We also could quickly (in <1 minute) pull the ROV out of the water if we perceived that any nearby vessel was approaching too closely. Lastly, Stanley and Wilson (1995) reported that using divers to groundtruth the composition of fish communities perceived with hydroacoustics at petroleum platforms was problematic due to fish avoiding divers when they swam survey transects. No such avoidance was observed when transects were flown with an ROV instead of divers.

Another benefit of the ROV-based sampling protocol used in the current study was being able to estimate fish size with the laser scale attached to the ROV. Obviously, the utility of fish length estimates would be questionable if they were highly biased (Pilgrim et al. 2000). Dance (2007) reported results from pool experiments indicated bias was minor if the distance between a fish and the ROV was <5 m and the angular deviance from perpendicular that the laser scale struck the fish was $<20^{\circ}$. Therefore, measurement bias was greatly reduced by not attempting to estimate size from fish that were struck by the lasers at angles $>15^{\circ}$ from perpendicular. While that threshold angle may be difficult to estimate precisely on video, we attempted to err on the side of caution when estimating laser angles. Therefore, we are confident that measurement bias was effectively minimized throughout the study. Furthermore, bias that likely did exist was accounted for by simulating it and correcting for it in species-specific length distributions.

Community Structure Effects

The purpose of advertising the locations of experimental sites was to evaluate the effect of fishing on reef fish community structure. However, two assumptions had to be met in order for the inference to be made that changes in community structure were in fact caused by fishing mortality. The first assumption was that recreational, and perhaps commercial, fisherman actually targeted experimental sites after their coordinates were advertised. While we did not attempt to estimate fishing effort at experimental sites, the appearance of obvious amounts of fishing line and tackle fouling experimental sites after spring 2007 indicates it is safe to assume that shifts in their community structure were due to fishing mortality. Furthermore, Turpin and Bortone (2004) and Lindberg and Lofton (1998) also reported shifts in community structure and declines in the density of large, exploited fishes after reporting unknown reef coordinates to the fishing public.

The second assumption related to interpreting the effect of advertising the locations of experimental reefs as a fishing effect is that fishing did not occur at any unreported sites, including experimental reefs prior to spring 2007. Addis et al. (2008) reported that no tagged fish were reported by fishermen as being recaptured at sites that matched the coordinates of any of the 27 study reefs, and that trend continued through the fourth year of the study. Furthermore, no fishing activity was directly observed at study sites during quarterly sampling, although what appeared to be monofilament was observed at site A36, which is not a tagging site, in spring 2006. There also was a fishing rod repeatedly observed on site B16 after summer 2005 that may have been lost overboard by a fisherman fishing at that site. However, the rod appeared after the active hurricane season of summer 2005 when much other debris was observed next to modules at other reef sites during the same time period. Therefore, although it cannot be completely ruled out that fishing occurred at control reef sites, or fishing sites before spring 2007, there was no direct evidence of fishing having occurred at them.

In the end, changes in community structure at experimental versus control sites after spring 2007 are consistent with the *a priori* expectation that large, fishery species would be removed with fishing effort being directed at study sites (Polovina 1994; Lindberg and Lofton 1998; Turpin and Bortone 2002). Interestingly, the decline in piscivores and invertivore/ piscivores at experimental reefs coincided with an increase in small planktivores. The most abundant planktivores, mackerel scad and round sardinella, observed at reef sites were transient pelagic fishes that appeared infrequently but in large schools when they were present. After spring 2007, their schools were observed more frequently at experimental reefs when the biomass of potential predators had decreased.

Clearly, the decline in invertivore/piscivores at experimental sites was due to the decrease in red snapper density and biomass. While other targeted species, such as gray snapper, also declined at experimental sites, red snapper was so numerically dominant, as well as by biomass, that it clearly drove the overall declines in invertivore/piscivores at experimental sites, as well as the increases at control sites. Red snapper density actually declined at control sites after spring 2007, but biomass increased due to the increase in size of fish present. Still, the mean size of red snapper on control remained much lower than the recreational size limit for the species.

The difference in piscivore biomass at control versus experimental sites after spring 2007 was attributed to an increase in greater amberjack, as well as other *Seriola* sp. and barracuda, biomass at control sites, while a decline occurred at all experimental reefs. The curious aspect of that trend is the fact that all greater amberjack observed at study reefs were estimated to be much shorter than the legal size limit for the species. Therefore, if fishing mortality affected greater amberjack density, it was likely due to a bycatch effect. However, the difference in amberjack biomass at control versus experimental sites was due more to an increase in size of fish at control sites than a decrease in density at experimental reefs.

Grouper biomass decreased at study reefs irrespective of treatment group. The largest contributor to that decline was red grouper, but scamp and gag biomass declined as well. Dance (2007) reported that grouper density declined by an order of magnitude in the first year of the study. He hypothesized that tropical weather in summer 2005 may have concentrated groupers that are more commonly found to the east and farther offshore than our study sites, and that declines in grouper density after the start of the study were likely due to fish dispersing among other available habitats. Bell and Hall (1994) reported the same phenomenon for groupers that were found at higher densities on shallow artificial reefs off South Carolina following the passage of Hurricane Hugo in 1989. In the time period following storms, densities of several reef fishes also have been shown to dissipate either due to movement or fishing mortality (Bell and Hall 1994; Patterson et al. 2001b; Turpin and Bortone 2002). The high return rates for tagged grouper in the current study, as well as their mostly limited movement and short time free, may suggest that groupers were heavily targeted by recreational or commercial fisherman after leaving study sites and visiting nearby publically-known reef sites. It is possible that groupers were caught directly at study reefs, but again, the preponderance of evidence does not support that conclusion. It should be reiterated that no recapture coordinates were reported for groupers that matched study reef locations despite several sets of GPS coordinates provided of other reefs with the EE-LAARS.

Middle trophic level fishes displayed mixed results with respect to the advertising of experimental sites' locations. Planktivore/invertivore biomass increased at both study reefs and experimental sites. However, the increase was greater at study reefs and taxa driving increases were different between the two treatment groups. Blue runner, a relatively small, schooling pelagic fish drove the increase at experimental sites, while increases in vermilion snapper biomass was more substantial at control reefs. Invertivore biomass similarly increased at both experimental and control sites, but again the increase was greater at control sites and due to changes in biomass of different fishes than at experimental reefs. Gray triggerfish size and biomass increased at control sites and decreased at experimental reefs, while tomtate, a small benthic invertivore not targeted by fishermen, drove the substantial increase in fish density but only modest increase in biomass at experimental reefs. Therefore, while increases in numbers and biomass of planktivore/invertivores and invertivores was observed at both control and experimental sites, increases at control sites were due to increases in fishery important species, while increases in non-targeted species basically offset losses of fishery species at experimental sites.

Disappearance Rates

The most compelling evidence of a fishing effect at experimental reefs after spring 2007 was the substantial increase in D estimates for red snapper and gray triggerfish after coordinates were advertised to the public. In the case of gray triggerfish, M (0.49 y⁻¹) alone accounted for nearly all the D (0.52 y⁻¹) estimated on study sites prior to advertising experimental reefs' coordinates. The source of the remaining decline may have been due to emigration of fish away from study sites. Although site fidelity could not be estimated directly for gray triggerfish in the current study, Ingram (2001) estimated annual site fidelity of gray triggerfish tagged over artificial reefs off Alabama was as high as 87% y⁻¹. Qualitatively, gray triggerfish demonstrated much higher site fidelity to reef sites in the current study than did other species. Therefore, limited movement away from study sites may easily account for the remaining source of the decline in fish numbers at age beyond M alone.

A much different picture emerges from the red snapper age distribution data. Natural mortality, M, was estimated to be 0.1 y^{-1} for fish ages 2+ during the last stock assessment for red snapper (Porch 2007), yet here D was estimated to be 1.00 y^{-1} among all study sites prior to spring 2007. Potential explanations for such a large discrepancy between D and M for red snapper are that M was vastly underestimated; there was some source of F at or away from reef sites that is not being accounted for; or, there was high E' away from study sites. Szedlmayer (2007) estimated M to be 0.34 y^{-1} for red snapper off Alabama that were of similar age range as fish in the current study, but he did not provide sufficient detail in his manuscript about assumptions made with fish tagging data from which he estimated Z and M. Furthermore, life history considerations would suggest that red snapper could only live to be teenagers if M was as high as 0.34 y^{-1} (Hoenig 1983; Hewitt and Hoenig 2005). Patterson et al. (2001a) reported a maximum age of 34 years for red snapper they sampled off Alabama, while Szedlmayer and Shipp (1994) reported several fish in their 40s. In fact, Wilson and Nieland (2001) reported a 59 year-old fish that was sampled off Louisiana, while Mitchell et al. (2004) reported several 40 year-old fish and one 53 year-old from the western GOM. Therefore, it just does not seem possible that M could be anywhere near 0.34 y^{-1} for adult red snapper.

We have stated repeatedly in this report and elsewhere that while we have no direct evidence that fishing occurred at unreported reef sites in this study, we simply cannot rule out the possibility that it did. If fishing had occurred directly on unreported study sites, and to an extent that could explain the vast difference between red snapper D and M estimates for the time period prior to spring 2007, it would seem likely that reef sites would have been fouled as heavily with fishing line and tackle early in the study as observed at experimental reefs after spring 2007. It seems evident that an increase in F of a similar magnitude occurred for red snapper and gray triggerfish at experimental reefs after spring 2007 (see below). Therefore, it would appear odd that fishing effects would only have been apparent for red snapper, and for no other species, prior to spring 2007 if fishing effort had been directed at unreported study sites. Perhaps declines in grouper density throughout the study is additional evidence of F having occurred at unreported reefs, but explanations offered above seem more plausible in explaining grouper density and biomass trends over time. Furthermore, grouper size actually increased at control reefs after spring 2007, while decreasing at experimental reefs.

If fishing mortality occurring at control or otherwise unreported reef sites before spring 2007 did explain much of the difference between D and M estimates, then that would imply that building artificial reefs but not reporting their coordinates to the public did not effectively create no-harvest refugia for reef fishes, or at least for red snapper. Furthermore, it would imply that F

was likely higher from fall 2005 to spring 2007, than the apical F (0.6 y⁻¹) estimated for the recreational fishery in the eastern GOM in the last red snapper assessment (Porch 2007). As stated above, it seems unlikely that such high levels of F, had they occurred at unreported sites, could have gone undetected by either direct observation or fishing gear fouling reef sites. What seems more plausible is that red snapper, which displayed very low site fidelity to study reefs, moved among unreported and nearby publically-known reef sites where they were exposed to considerable fishing pressure. Given the low site fidelity and extensive movement estimated for the species, it seems likely that any estimate of F computed from study data really should be considered a regional and not a study reef-specific estimate.

Another potential explanation for the large difference between D and M estimates for red snapper is that E' was substantial and that recruitment to offshore natural hardbottom, or otherwise lightly fished reefs, explained some proportion of the decline at age seen at study reefs. Red snapper site fidelity was estimated to be very low in this study. In fact, it was much lower than previous estimates of between 25% and 50% y^{-1} (Patterson and Cowan 2003; Schroepfer and Szedlmayer 2006; Strelcheck et al. 2007). What is not known, however, is what percentage of fish movement away from tagging sites was to offshore reefs. Clearly, recapture locations indicate most tagged red snapper actually were caught by fisherman farther inshore than the tagging sites. However, recreational effort is higher inshore than offshore, thus the distribution of recapture locations may be more a function of effort distribution than fish movement.

Gallaway et al. (2009) cited the age distribution of red snapper captured with longline gear during scientific surveys in the western GOM as evidence that a large percentage of the rapid disappearance (D = 0.54 y^{-1}) of red snapper from petroleum platforms there was due to recruitment to natural habitats away from platforms (Gitschlag et al. 2004; Mitchell et al. 2004). In fact, if one were to fit a linear regression to the ln-transformed numbers at age data reported by Mitchell et al. (2004) from longline survey catches in the western GOM, the positive slope of the line for ages 3-8 is actually 0.54 y⁻¹. Gallaway et al. (2009) did not estimate the rate of recruitment to natural habitats explicitly as this example, but they did imply what the example demonstrates. The issue, however, is that by simply examining catch at age data without accounting for the increase with age in vulnerability (probability of being caught) to the gear, this back-of-the-envelope estimate, whether implicit or explicit, is flawed due to overestimating the increase in fish numbers at age in the population versus the catch. The terminal tackle on longlines deployed by Mitchell et al. (2004) was 15-0 circle hooks, which small, young fish would have difficulty taking. In fact, Porch (2007) reported that 3 year-old red snapper had a vulnerability of less than 10% for commercial longline gear in the western GOM, and that vulnerability increased almost linearly from age 3 until age 8, when it was nearly 100%. Correcting for this change in vulnerability with age actually yields a slope of 0.08 y⁻¹ for the recruitment to offshore habitats function implied by Gallaway et al. (2009).

It seems unlikely that the difference between D (1.00 y^{-1}) and M (0.1 y^{-1}) estimates for red snapper prior to spring 2007 was due to by F alone. As stated above, however, we are not presently able to estimate the rate of recruitment of fish to offshore habitats, which then precludes our ability to discount the percentage of D that would be attributed to F. What is interesting is that Mitchell et al. (2004) reported standardized catch rates of large, old fish with longline gear were 14.4 times higher in the western (off western LA and TX) than in the eastern (off MS, AL, and northwest FL) GOM. Furthermore, the median age of fish (n = 232) captured in the western GOM was 12 years, while only 6 years (n = 12) in the eastern GOM (Mitchell et al. 2004). Therefore, Mitchell's (2004) fishery-independent samples indicate that many fewer older red snapper exist on, or perhaps are surviving to recruit to, offshore natural habitats in the eastern GOM than in the western GOM. That inference is supported by estimates of fishery-specific apical F estimates in the eastern versus western GOM (Porch 2007), as well as by estimates that the genetic effective population size is 10 times greater in the western versus eastern GOM (Gold and Saillant 2007).

It seems apparent that δ estimates from experimental reefs for both gray triggerfish and red snapper were due to an increase in F directly at those sites. In the recreational fishery, gray triggerfish and red snapper tend to be targeted with similar tackle. Therefore, near equal estimates of δ for the two species corroborate that fishing effort was similar for both at experimental reefs after advertising their coordinates to the public. For gray triggerfish, which demonstrate very high site fidelity to reef sites (Ingram 2001; Ingram and Patterson 1999), it seems reasonable to infer that F was effectively zero at study sites prior to spring 2007, as well as at control sites after spring 2007. However, it also seems reasonable to infer that the difference between D (0.73 y⁻¹) and M (0.49 y⁻¹) at experimental reefs after spring 2007 was due almost entirely to fishing mortality at those sites, which would yield an F of approximately 0.24 y⁻¹. If D approximately equaled Z for gray triggerfish, then estimates of D, hence Z, were within the range of previous estimates in the region. Ingram (2001) estimated Z to be 0.82 y⁻¹ on artificial reefs off Alabama, while Hood and Johnson (1997) estimated Z to be 0.67 y⁻¹ off Panama City.

Implications for Management

Results of this study have several implications for management of reef fish resources in the northern GOM, and especially for the role artificial reefs may currently play in reef fish fisheries. Foremost, results suggest that building artificial reefs but not advertising their coordinates is not likely to provide no-harvest refugia for fishes, such as red snapper, that display low site fidelity and are likely to move between fished and unfished habitats. Even if artificial reefs were deployed within marine protected areas (MPAs), the area protected would have to be on the scale of 100s, if not 1,000s, of km² to see an enhancement effect for fish that typically move significant distances (Ingram and Patterson 1999). For species that demonstrate low site fidelity and limited movement, even small protected areas might be beneficial. However, almost none of the important fishery species that were observed at artificial reefs in the present study would fit that latter description, with gray triggerfish and, perhaps, vermilion snapper, being exceptions (Ingram and Patterson 1999).

Study results suggest that the idea proposed by Bortone (2007) that perhaps artificial reefs could be protected for some period of time and then, basically, mined, would not appear to be a conservative approach to managing reef fish resources in the northern GOM, in that unreported reef sites do not appear to function as effective no-harvest refugia when reef fishes that move only short distances (<5 km) encounter heavily fished habitats, and MPAs would not be expected to be effective in accumulating SSB unless areas protected were expansive. Under Bortone's rotational harvest model, certain reefs would be protected from fishing for several years and then only fished rotationally such that biomass could accumulate until harvested again. Fish such as red snapper, greater amberjack, and the various grouper species observed at reefs in the current study simply display too much movement for biomass to accumulate within protected areas without being exposed to F outside the boundaries of protection. Furthermore, the ultimate goal of fisheries management should be to set target, as opposed to threshold, yields such that

spawning stock biomass (SSB) is sufficiently high to ensure that future yields can be extracted with a low probability of either growth or recruitment overfishing occurring. It seems impractical that SSB of long-lived species, such as snappers and groupers, could even achieve a sustainable SSB level if their biomass was mined every few years.

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TABLES

Table 1. Dimensions of three artificial reef types deployed by the FWC in the Escambia East LAARS prior to start of this study. Type-A refers to Pyramid reefs, type-B refers to Fish Haven reefs, and type-C refers Reef Ball reefs.

Reef Parameters	A: Pyramid	B: Fish Haven	C: Reef Ball
Modules per site	1	2	2
Module height m	3.05	1.83	1.45
Module base m	3.05	3.05	1.83
Module volume m ³	4.09	4.90	2.84

Table 2. Depths of study artificial reef sites at which video sampling took place from fall 2004 through fall 2007. Asterisks indicate tagging sites; crosses indicate sites released to the public in spring 2007. Site A34 was replaced by A19 as a tagging site after spring of 2005 because of apparent high release mortality due to depth.

Site	Station Depth m	Site	Station Depth m	Site	Station Depth m
A53 ⁺	27.0	$\mathrm{B7}^+$	29.0	C36 ⁺	27.0
A12*	28.5	B2*	30.5	C39	29.0
A56 ⁺	29.0	$\mathrm{B4}^+$	31.0	C32*	29.5
A20*	33.0	B8*	32.5	C14 ⁺	32.0
A19*	34.0	B11	33.5	C15*	32.0
A36	36.5	B16 ⁺	34.5	C22	33.5
A35 ⁺	37.5	В3	35.0	C21*	34.0
A31	38.5	B1	35.5	C12	35.0
A34*	41.0	B9*	37.5	C25 ⁺	37.0

Reef	Spring 2008	Summer 2008	Reef	Spring 2008	Summer 2008	Reef	Spring 2008	Summer 2008
A12	5/22/08	8/17/08	B1	5/22/08	8/17/08	C12	5/28/08	8/17/08
A19	5/22/08	8/17/08	B2	5/22/08	8/17/08	C14	5/22/08	8/17/08
A20	5/28/08	8/17/08	B3	5/22/08	8/17/08	C15	5/22/08	8/17/08
A31	5/28/08	8/21/08	B4	5/22/08	8/17/08	C21	5/28/08	8/21/08
A34	5/28/08	8/21/08	B7	5/28/08	8/28/08	C22	5/28/08	8/21/08
A35	5/28/08	8/21/08	B8	6/12/08	8/28/08	C25	5/28/08	8/21/08
A36	5/28/08	8/28/08	B9	5/28/08	8/21/08	C32	5/28/08	8/28/08
A53	6/12/08	8/28/08	B11	5/28/08	8/21/08	C36	6/12/08	8/28/08
A56	5/22/08	8/19/08	B16	5/28/08	8/28/08	C39	5/22/08	8/17/08

Table 3. Dates video sampling was conducted at study reefs in 2008.

Table 4. Reef fish taxa observed at artificial reef study sites during 2004-2008. Residency: R = reef resident, RA = seasonally reef-associated neritic pelagic species, S = demersal or benthic shelf species, and T = transient. Trophic position: H = herbivore, P = planktivore, I = invertivore, F = piscivore. Life stage: J = juvenile and A = adult. Reef limited: O = obligate reef resident likely to demonstrate habitat-limited populations and G = fishes for which reefs may function to increase growth or decrease natural mortality. Multiple letters for trophic position indicate feeding on more than one trophic level. Multiple letters for life stage indicate more than one life stage present on study sites. Percent number is the taxa-specific percentage of total individuals observed among all sampling events. Percent biomass is the taxa-specific percentage of total biomass estimated among all sampling events.

			Trophic	Life	Reef	Percent	Percent
Taxon	Common Name	Residency	Position	Stage	Limited	Density	Biomass
Acanthurus chirurgus	doctorfish	R	Н	A	G	< 0.01	< 0.01
Aluterus heudeloti	dotterel filefish	R	Ι	А	G	< 0.01	< 0.01
Aluterus monoceros	unicorn filefish	R	Ι	А	G	0.06	0.17
Aluterus schoepfi	orange filefish	R	Ι	А	G	0.03	0.06
Aluterus scriptus	scrawled filefish	R	Ι	А	G	< 0.01	< 0.01
Anisotremus virginicus	porkfish	R	Ι	А	0	< 0.01	< 0.01
Antennarius sp.	frogfish	R	IF	А	0	< 0.01	< 0.01
Apogon psuedomaculatus	twospot cardinalfish	R	Р	J,A	0	1.64	0.06
Apogon sp.	cardinalfish	R	Р	J	0	0.69	< 0.01
Balistes capriscus	gray triggerfish	R	Ι	А	G	3.35	6.14
Balistes vetula	queen triggerfish	R	Ι	А	G	< 0.01	< 0.01
Balistidae	triggerfish	R	Ι	А	G	< 0.01	< 0.01
Blennidae	blenny	R	PI	J,A	0	0.01	< 0.01
Calamus leucosteus	whitebone porgy	S	Ι	A	G	< 0.01	< 0.01
Calamus nodosus	knobbed porgy	S	Ι	А	G	< 0.01	< 0.01
Calamus proridens	littlehead porgy	S	Ι	А	G	< 0.01	< 0.01
Calamus sp.	porgy	S	Ι	А	G	0.01	0.02
Canthigaster rostrata	Caribbean sharpnose puffer	R	Ι	А	G	0.12	0.02
Caranx bartholomaei	vellow jack	Т	F	А	G	0.01	0.02
Caranx crysos	blue runner	Т	PI	А	G	4.38	3.72
Caranx ruber	bar jack	Т	IF	А	G	0.03	0.02
Carcharhinus limbatus	blacktip shark	Т	F	А	G	0.01	0.52
Carcharhinus plumbeus	sandbar shark	Т	F	А	G	0.01	1.29
Carcharhinus sp.	requiem shark	Т	F	А	G	< 0.01	0.20
Centropristis ocyurus	bank seabass	S	Ι	А	G	1.08	0.87
Chaetodipterus faber	Atlantic spadefish	R	Ι	А	G	0.94	0.36
Chaetodon ocellatus	spotfin butterflyfish	R	Ι	А	0	0.02	< 0.01
Chaetodon sedentarius	reef butterflyfish	R	Ι	А	0	< 0.01	< 0.01
Chilomycterus atinga	spotted burrfish	R	Ι	А	0	< 0.01	0.02
Chilomycterus schoepfi	striped burrfish	R	Ι	А	G	< 0.01	< 0.01
Chromis enchrysura	yellowtail reeffish	R	Р	J,A	0	< 0.01	0.04
Chromis sp.	damselfish	R	Р	J,A	0	0.53	< 0.01
Dasyatis americana	southern stingray	S	IF	А	G	< 0.01	0.01
Decapterus macarellus	mackerel scad	Т	Р	А	G	15.35	3.86
Diplectrum formosum	sandperch	S	IF	А	G	0.11	0.07
Echeneis naucrates	remora	Т	IF	А	G	0.02	0.04
Elagatis bipinnulata	rainbow runner	Т	IF	А	G	< 0.01	0.01
Epinephelus cruentatus	graysby	R	IF	А	G	< 0.01	< 0.01
Epinephelus drummondhayi	speckled hind	R	IF	J	G	< 0.01	< 0.01
Epinephelus morio	red grouper	R	IF	А	G	0.41	3.09
Epinephelus nigritus	Warsaw grouper	R	IF	J	G	0.15	0.03
Epinephelus niveatus	snowy grouper	R	IF	J	G	0.01	0.01
Equetus acuminatus	high-hat	R	Ι	А	0	< 0.01	< 0.01
Equetus lanceolatus	jackknife fish	R	Ι	А	0	0.20	0.13

Table 4. Continued.

			Trophic	Life	Reef	Percent	Percent
Taxon	Common Name	Residency	Position	Stage	limited	Number	Biomass
Equetus iwamotoi	blackbar drum	R	Ι	А	G	0.01	< 0.01
Equetus sp.	reef drum	R	Ι	А	R	< 0.01	< 0.01
Equetus umbrosus	cubbyu	R	Ι	А	G	< 0.01	< 0.01
Fistularia tabacaria	cornetfish	R	F	А	G	< 0.01	0.02
Ginglymostoma cirratum	nurse shark	S	IF	А	G	0.01	0.90
Gymnothorax moringa	spotted morray	R	F	А	G	< 0.01	< 0.03
Haemulon aurolineatum	tomtate	R	Ι	A	G	10.04	3.18
Halichoeres bivittatus	slippery dick	R	Ι	A	0	3.28	0.50
Halichoeres sp.	wrasse	R	Ι	J	0	< 0.01	< 0.01
Hemicaranx amblyrhynchus	bluntnose jack	Т	IF	A	G	0.06	0.04
Hemipteronotus novacula	pearly razorfish	R	I	A	G	0.01	< 0.01
Holacanthus bermudensis	blue angelfish	R	I	A	G	0.07	0.14
Holacanthus ciliaris	queen anglefish	R	I	A	G	< 0.01	< 0.01
Hyperoglyphe perciformis	barrelfish	Т	PI	A	G	< 0.01	< 0.01
Hypleurochilus bermudensis	barred blenny	R	I	A	0	< 0.01	< 0.01
Hypoplectrus sp.	hamlet	R	IF	A	G	< 0.01	< 0.01
Kyphosus sectator	Bermuda chub	R	HI	A	G	< 0.01	< 0.01
Lactophrys quadricornis	scrawled cowfish	R	I	A	G	< 0.01	< 0.01
Lactophrys trigonus	buffalo trunkfish	R	I	A	G	< 0.01	< 0.01
Lagadon rhomboides	pinfish	Т	I	A	G	4.36	1.59
Lutjanus campechanus	red snapper	R	IF	A	G	25.60	42.79
Lutjanus griseus	gray snapper	R	IF	A	G	2.20	4.24
Lutjanus synagris	lane snapper	R	IF	A	G	1.08	0.92
Monacanthus hispidus	planehead filefish	R	Ι	A	G	< 0.01	0.02
Monacanthus setifer	pygmy filefish	R	PI	A	G	< 0.01	< 0.01
Mycteroperca microlepis	gag	R	F	A	G	0.77	5.19
Mycteroperca phenax	scamp	R	F	A	G	0.53	1.15
Opsanus pardus	leopard toadfish	R	I	A	G	< 0.01	< 0.01
Pagrus pagrus	red porgy	R	I	A	G	1.18	0.92
Pareques umbrosus	cubbyu	R	I	A	0	0.07	0.02
Parblennius marmoreus	seaweed blenny	R	I	A	0	1.39	0.04
Paralichthys albigutta	gulf flounder	S	IF	A	G	< 0.01	0.01
Paranthias furcifer	creolefish	R	PI	A	G	< 0.01	< 0.01
Pomacanthus paru	French anglefish	R	I	A	G	< 0.01	< 0.01
Pomacentrus variabilis	cocoa damselfish	R	I	J,A	0	0.08	< 0.01
Priacanthus arenatus	Atlantic bigeye	R	PI	A	0	< 0.01	< 0.01
Rachycentron canadum	cobia	Т	F	A	G	< 0.01	0.16
Rhomboplites aurorubens	vermilion snapper	R	PI	J,A	G	5.28	5.14
Rypticus maculatus	whitespotted soapfish	R	Ι	A	G	0.54	0.18
Sardinella aurita	round sardinella	Т	P	A	G	6.61	2.02
Sciaenops ocellatus	red drum	Т	IF	A	G	< 0.01	0.03
Scomberomorus cavalla	king mackerel	Т	F -	A	G	0.15	0.86
Seriola dumerili	greater amberjack	RA	F -	A	G	3.43	6.83
Seriola fasciata	lesser amberjack	RA	F	A	G	0.06	0.18
Seriola rivoliana	almaco jack	RA	F	A	G	0.69	1.16
Seriola zonata	banded rudderfish	RA	F	A	G	0.10	0.52
Serranus phoebe	tatler	R	l	A	0	< 0.01	< 0.01
Serranus subligarius	belted sandfish	S	I	A	G	< 0.01	< 0.01
Sphyraena barracuda	greater barracuda	RA	F	A	G	< 0.01	0.11
Stegastes leucostictus	beaugregory	R	P -	J,A	0	< 0.01	< 0.01
Stegastes sp.	damselfish	R	Р	J,A	0	< 0.01	< 0.01
Stegastes variabilis	cocoa damselfish	R	Р	J,A	0	0.02	< 0.01
Stenotomus caprinus	longspine porgy	S ~	1	A	G	< 0.01	< 0.01
Synodus foetens	inshore lizardfish	S	IF	A	G	< 0.01	< 0.01
Trachinocephalus myops	snakefish	S	IF	A	G	< 0.01	< 0.01
Unknown small fishes						3.09	0.01

age could not be estimated for those species with age slicing. SD = standard deviation. All length units are mm. Scamp estimates of Balistes capriscus, and greater amberjack, Seriola dumerili, for which fork length is reported. Maximum estimated age from the growth functions was employed to estimate age. Maximum size for gray and vermilion snappers were above L_{∞} ; therefore, maximum Table 5. List of predominant fishery species measured with the laser scale during remotely operated vehicle sampling of artificial reef sites off Pensacola, Florida between spring 2005 and summer 2008. Lengths are total length for all species except gray triggerfish, current study was estimated with an age length key for red snapper, otherwise deterministic age slicing from reported von Bertalanffy $L_{\ensuremath{\varpi}}$ and maximum age are from the Atlantic.

Species	Laser Scale Sample Size	Max Estimated Length	Mean Estimated Length (±SD)	Max Estimated Age	Estimated L_{∞} for Species in GOM	Max Age Observed in GOM	Source of L_{∞} and Max Age Estimates
Red Snapper	3,454	854	339.4 (±84.7)	15	983	59	Patterson et al. (2001a); Wilson and Nieland (2004)
Gray Triggerfish	630	569	302.7 (±70.8)	6	583	6	Ingram 2001
Greater Amberjack	870	635	338.7 (±51.2)	3	1,389	15	Thompson et al. (1999)
Gray Snapper	344	764	354.2 (±94.5)	na	656	28	Fischer et al. (2005)
Vermilion Snapper	162	439	268.6 (±47.7)	na	271	14	Allman (2007)
Scamp	136	494	361.42 (±44.9)	4	897	21	Harris et al. (2005)
Red Grouper	86	797	547.2 (±111.3)	16	848	27	Lombardi-Carlson et al. (2008)
Gag	34	757	527.7 (±118.5)	9	1,190	32	Hood and Schlieder (1992)

)))	, ,	5	×)		
Species	Common name	Number tagged	Mean length at tagging (SD)	Reported by fishermen (% of total tagged)	Recaptures at study sites (% total recaptures)	Mean days free among all recaptures (SD)
Lutjanus campechanus	red snapper	2,114	358.8 (55.8)	165 (7.8%)	44 (21.1%)	312.6 (218.6)
Pagrus pagrus	red porgy	422	300.1 (26.3)	12 (2.8%)	2 (14.3%)	80.6 (135.5)
Balistes capriscus	grey triggerfish	267	343.6 (50.6)	25 (9.4%)	30 (54.5%)	195.0 (137.9)
Mycteroperca microlepis	gag grouper	96	518.3 (83.2)	13 (13.5%)	5 (27.8%)	191.6 (205.4)
Rhomboplites aurorubens	vermilion snapper	84	327.1 (34.4)	2 (2.4%)	1 (33.3%)	309.7 (233.0)
Seriola rivoliana	almaco jack	32	356.8 (41.6)	0	0	na
Epinephelus morio	red grouper	31	521.0 (90.4)	2 (6.5%)	4 (66.7%)	92.7 (66.0)
Mycteroperca phenax	scamp	21	408.8 (58.5)	5 (23.8%)	0	273.2 (251.0)
Seriola dumerili	greater amberjack	21	413.6 (65.9)	0	0	na
Lutjanus synagris	lane snapper	10	326.5 (67.2)	1 (10.0%)	0	na
Total		3,098		225 (7.3%)	86 (27.7%)	248.8 (168.9)

Table 6. List of predominant reef fish species tagged (n = 3,098 of 3,115 fish tagged) at artificial reef study sites in the Escambia East LAARS between November 2004 and December 2007, and recaptured through December 2008. Lengths are total length for all species except gray triggerfish, almaco jack, and amberjack, for which fork length is reported. SD = standard deviation.

Table 7. Trophic level-specific percent change in estimated fish density (individuals 100m⁻²) and biomass (kg 100m⁻²) for fishes observed at study reefs before and after spring 2007 when coordinates of experimental sites were advertised to the public.

Trophic Level	Treatment	Percent Density Difference	Percent Biomass Difference
Planktivores	Control	178.7	226.0
Planktivores	Experimental	110.2	95.3
Plank/Invertivores	Control	139.1	420.3
Plank/Invertivores	Experimental	202.1	329.2
Invertivores	Control	237.7	55.7
Invertivores	Experimental	130.8	15.5
Invert/Piscivores	Control	-11.8	13.1
Invert/Piscivores	Experimental	-21.7	-12.1
Piscivores	Control	1.4	61.6
Piscivores	Experimental	-32.2	-45.7

Table 8. Taxa-specific percent change in estimated fish density (individuals $100m^{-2}$) and biomass (kg $100m^{-2}$) for selected fishery species observed at study reefs before and after spring 2007 when coordinates of experimental sites were advertised to the public.

Reef Fish Taxon	Treatment	Percent Density Difference	Percent Biomass Difference
Red Snapper	Control	-16.9	18.6
Red Snapper	Experimental	-34.1	-12.0
Gray Triggerfish	Control	2.2	33.0
Gray Triggerfish	Experimental	-28.1	-31.2
Groupers	Control	-78.7	-74.9
Groupers	Experimental	-89.4	-93.0
Greater Amberjack	Control	8.9	52.5
Greater Amberjack	Experimental	-8.1	-15.1
Vermilion Snapper	Control	87.2	184.9
Vermilion Snapper	Experimental	134.7	104.6
Gray Snapper	Control	-10.5	-11.6
Gray Snapper	Experimental	-36.1	-32.5

Figures

Figure 1. A) Location of the Escambia East Large Artificial Reef Site in the northern Gulf of Mexico; Pensacola, Florida is indicated with a star. B) Map of the relative location of study sites within the EE-LAARS. A = pyramid reefs, B = fish haven reefs, and C= reef ball reefs. Green symbols = shallow stratum (<31 m) reefs. Blue symbols = mid-depth (31-35 m) reefs. Red symbols = deep (>35 m) stratum reefs. Control sites: A31, A34, A36, B1, B3, B11, C12, C22, C39. Tagging sties: A12, A19, A20, B2, B8, B9, C15, C21, and C32. Sites reported to the public: A35, A53, A56, B4, B7, B16, C14, C25, and C36.





Figure 2. Taxa-specific percent number (A) and biomass (B) observed among all sample events at artificial reef study sites (n = 27) off northwest Florida for the 25 most abundant fish taxa. Taxa in panel A: Lc = *Lutjanus campechanus*, Dm = *Decapterus macarellus*, Ha = *Haemulon aurolineatum*, Sa = *Sardinella aurita*, Ra = *Rhomboplites aurorubens*, Cc = *Caranx crysos*, Hb = *Halichoeres bivittatus*, Lr = *Lagadon rhomboides*, Sd = *Seriola dumerili*, Bc = *Balistes capriscus*, USF = unknown small fishes, Lg = *Lutjanus griseus*, Ap = *Apogon psuedomaculatus*, Pm = *Parblennius marmoreus*, Pp = *Pagrus pagrus*, Co = *Centropristis ocyurus*, Ls = *Lutjanus synagris*, Cf = *Chaetodipterus faber*, Mm = *Mycteroperca microlepis*, AS = *Apogon sp.*, Sr = *Seriola rivoliana*, Rm = *Rypticus maculatus*, CS = *Chromis sp.*, Mp = *Mycteroperca phenax*, and Em = *Epinephelus morio*. Taxa unique to panel B: Gc = *Ginglymostoma cirratum*, Sc = *Scomberomorus cavalla*, Sz = *Seriola zonata*, Cl = *Carcharhinus limbatus*, and CS = Carcharinus sp. Legend applies to both panels.



Figure 3. A) Percent fish density and B) percent biomass by trophic position of fishes observed among all sample events at artificial reef study sites (n = 27) off northwest Florida. Abbreviations on the x-axis: H = herbivore, P = planktivore, PI = planktivore/invertivore, I = invertivore, IF = invertivore/piscivore, F = piscivore, and RS = red snapper.



Figure 4. Descriptive statistics of species diversity and fish density at artificial reef study sites by reef depth stratum. Panel A = total fish taxa observed. Panel B = fish density (fish $100m^{-2}$). Panel C = fish biomass (kg $100m^{-2}$). Panel D = Shannon-Weiner diversity index. Panel E = species evenness index. Mean ± SE is plotted. Legend in panel A applies to all.



Figure 5. Descriptive statistics of species diversity and fish density at artificial reef study sites by reef type. Panel A = total fish taxa observed. Panel B = fish density (fish $100m^{-2}$). Panel C = fish biomass (kg $100m^{-2}$). Panel D = Shannon-Weiner diversity index. Panel E = species evenness index. Mean ± SE is plotted. Legend in panel A applies to all.



Figure 6. Length distributions of red snapper (A-D) and gray triggerfish (E-H) estimated with a laser scale at artificial reef sites off Pensacola, Florida. Panels A-D depict red snapper total length estimates for control sites A) before and B) after and experimental sites C) before and D) after spring 2007. Panels E-H depict gray triggerfish fork length estimates for control sites before (E) and after (F) and experimental sites before (G) and after (H) spring 2007. Dashed green lines indicate minimum size for the recreational fishery.



Figure 6. continued. Length distributions of greater amberjack (I-L) and groupers (M-P) estimated with a laser scale at artificial reef sites off Pensacola, Florida. Panels I-L depict greater amberjack fork length estimates for control sites before (I) and after (J) and experimental sites before (K) and after (L) spring 2007. Panels M-P depict grouper total length estimates for control sites before (M) and after (N) and experimental sites before (\overline{O}) and after (P) spring 2007.



Figure 6. continued. Length distributions of gray (Q-T) and vermilion snappers (U-X) estimated with a laser scale at artificial reef sites before (U) and after (V) and experimental sites before (W) and after (X) spring 2007. Dashed green lines are min size for rec. fishery. experimental sites before (S) and after (T) spring 2007. Panels U-X depict vermilion snapper total length estimates for control sites off Pensacola, Florida. Panels Q-T depict gray snapper total length estimates for control sites before (Q) and after (R) and



Figure 7. Relative frequency distributions of red snapper total length estimated with the laser scale attached to the remotely operated vehicle (blue bars) versus measured directly for fish captured with hook-and-line gear during sampling for tagging (green bars). Included in the tagging data are 58 red snapper which were captured at tagging sites but not tagged due to being shorter than an a prior determined limit of 250 mm total length. Sample sizes for each data type are noted on the figure.



Figure 8. Recapture locations for tag recoveries reported by fishermen from the northern Gulf of Mexico. Black rectangles indicate the Escambia East Large Artificial Reef Site. Panel legends indicate species plotted.



Figure 9. Movement distributions for A) red snapper, B) gray triggerfish, and C) groupers tagged at artificial reef study sites (n = 9) and recaptured by UWF personnel on subsequent tagging trips (black bars) or reported by fishermen (colored bars).



Figure 10. Mean (-SE) A) fish density and B) biomass by trophic position estimated for control and experimental sites before (quarters 5-10) and after (quarters 11-16) advertising coordinates of experimental sites to the public in spring 2007. Legend applies to both panels.



Figure 11. Species-specific mean (\pm SE) fish A) density, B) length (fork length for gray triggerfish and greater amberjack; else total length), and C) biomass of significant fishery species estimated at control and experimental sites before (quarters 5-10) and after (quarters 11-16) advertising coordinates of experimental sites to the public in spring 2007. Legend applies to both panels. RS = red snapper, GT = gray triggerfish, Groupers = gag, scamp, and red grouper, AJ = greater amberjack, GS = gray snapper, and VS = vermilion snapper.



triggerfish observed at all study sites from fall 2005 through winter 2007. Plotted lines are catch curves (linear regressions) fitted to 2005 through winter 2007. Scatterplots of In(number of individuals) versus estimated age for all C) red snapper and D) gray Figure 12. Distribution of numbers at estimated age for A) red snapper and B) gray triggerfish observed at all study sites from fall fully-recruited ages; p < 0.001 for each.



Scatterplots of ln(number of individuals) versus estimated age for A) red snapper and B) gray triggerfish observed at control sites from spring 2007 through summer 2008. Scatterplots of ln(number of individuals) for C) red snapper and B) gray triggerfish observed at experimental sites from spring 2007 through summer 2008. Plotted lines are catch curves (linear regressions) fitted to fully-recruited ages; p < 0.001 for each. Figure 13.



Figure 14. A) Predicted numbers at age for a cohort of red snapper between ages 3 and 8 under three different scenarios: $M = 0.1 \text{ y}^{-1}$ and F = 0, $M = 0.34 \text{ y}^{-1}$ and F = 0, $M = 0.1 \text{ y}^{-1}$ and F = 0.6, and $D = 0.93 \text{ y}^{-1}$; population size at age 3 for each function is 3,220 fish. B) Predicted numbers at age for a cohort of gray triggerfish between ages 3 and 9 under three different scenarios: $M = 0.48 \text{ y}^{-1}$ and F = 0, $D = 0.52 \text{ y}^{-1}$, or $D = 0.72 \text{ y}^{-1}$; population size at age 3 for each function is 523 fish.



APPENDIX

Table A1. Fishes identified and enumerated over unreported artificial reefs off northwest Florida in the northern Gulf of Mexico during spring 2008. Modules at a given site were sampled separately if they were greater than 8 m apart. Abundances at those sites are reported for each module (a,b) and also summed (T) between modules.

Taxon	A12	A19	A20	A31	A34	A35	A36	A53	A56	B1a	B1b	B1T	B2	B3
Acanthurus chirurgus														
Aluterus monoceros	2													
Aluterus schoepfi														
Aluterus scriptus														
Antennarius sp.														
Apogon pseudomaculatus	32		15	35	113	115	1			15	1	16	2	
Apogon sp.	2		3	76	8	10		22		2	7	0	23	13
Balistes vetula	2		5								,	5	23	15
Balistidae														
Blennidae	3													
Calamus nodosus														
Calamus proridens														
Calamus sp.								2					2	
Caranx bartholomaei								2					2	
Caranx crysos														213
Caranx ruber														1
Carcharhinus nimbatus														
Carcharhinus sp.														
Centropristis ocyurus		19				31	68				1	1	2	
Chaetodon ocellatus														
Chaetodon sedentarius			2										2	
Chilomycterus atinga														
Childringcterus schoepti Chromis sp.														
Chromis enchrysurus			4		1			1		2	2	4	7	1
Dasyatis americana														
Diplectrum formosum						545	296		318					
Echeneis naucrates								1	1					
Elagatis bipinnulata														
Epinephelus cruentatus Epinephelus drummondhavi														
Epinephelus morio				1	2									
Epinephelus nigritus														
Epinephelus niveatus	1													
Equetus acconinatus Equetus lanceolatus		11		10						1	7	8	2	
Equetus iwamotoi														
Equetus umbrosus		1		4	1	2	2			1	1	2		2
Ginglymostoma cirratum		1		4	1	2	3			1	1	2		2
Gymnothorax moringa														
Haemulon aurolineatum	106	60				25	60	50	1 144	40	15	64	466	
Halichoeres sp.	5	4	28	112	57	23	65	10	144	49	5	5	400	28
Hemicaranx amblyrhynchus														
Hemipteronotus novacula														
Holacanthus bernudensis														
Hyperoglyphe perciformis									1					
Hypleurochilus bermudensis														
Kyphosus sectator														
Lactophrys quadricornis														
Lactophrys trigonus														
Lagodon momboldes	49	4	25	61	127	2	7	94	26	27	19	46	36	37
Lutjanus griseus			10										11	6
Lutjanus synagris														
Monacanthus hispidus Monacanthus setifer	7						2	4	6				3	
Monocanthidae sp.														
Mycteroperca microlepis														
Mycteroperca phenax			1		1	1								3
Pagrus pagrus		15	7				29	1					19	2
Parablennius marmoreus		8	23	7	3	5	10	29		12	20	32	58	6
Paralichthys albigutta Paranthias furcifer									1					
Pareques umbrosus		1		4	1	2	3			1	1	2		2
Pomacanthus paru														
Pomacentrus variabilis Priacanthus arenatus					1			8						
Rachycentron canadum														
Rhomboplites aurorubens			5			36	24	5	1				7	9
Rypticus maculatus Sardinella aurita	2	2	3	4	3	9	1		2	2	2	4	3	8
Sciaenops ocellatus														
Scomberomorus cavalla														
Seriola dumerili	1	2	15	7		1	2			1	2	3	66	68
Seriola rivoliana	5		13			<u> </u>	<u> </u>	1		2		2	1	
Seriola zonata														
Serranidae														
Serranus proebe Serranus subligarius						1								
Sphyraena barracuda														
Stegastes leucostictus														
Stegastes sp.		1												
Stenotomus caprinus														
Synodus foetens														
Unknown small fishes						680								

Table A1. continued.

Taxon	B4a	B4b	B4T	B7a	B7b	B7T	B8	B9a	B9b	B9T	B11a	B11b	B11T	B16a
Acanthurus chirurgus														
Aluterus heudeloti							-							
Aluterus monoceros Aluterus schoenfi														
Aluterus scriptus														
Anisotremus virginicus														
Antennarius sp.				40		44								
Apogon pseudomaculatus				10	31	41	42							/
Balistes capriscus	4	1	5	9	2	11	3	16	2	18	15	10	25	14
Balistes vetula														
Balistidae														
Blennidae														
Calamus nodosus														
Calamus proridens														
Calamus sp.														
Canthigaster rostrata				1		1								
Caranx crysos	822	595	1417											
Caranx ruber														
Carcharhinus limbatus														
Carcharhinus sp														
Centropristis ocvurus														
Chaetodipterus faber														
Chaetodon ocellatus	1		1					2		2		2	2	
Chaetodon sedentarius Chilomycterus atinga														
Chilomycterus schoepfi														
Chromis sp.														
Chromis enchrysurus					5	5								
Decanterus macarellus														
Diplectrum formosum														
Echeneis naucrates														
Elagatis bipinnulata	1		1											
Epinephelus cruentatus														
Epinephelus drummondnayi Epinephelus morio														
Epinephelus nigritus														
Epinephelus niveatus							1							
Equetus acuminatus														
Equetus ianceolatus Fouetus iwamotoi											1		1	
Equetus sp.														
Fistularia tabacaria						[[[
Ginglymostoma cirratum														
Gymnotnorax moringa Haemulon aurolineatum											84		84	
Halichoeres bivittatus	4	2	6	10	10	20	24	23	42	65		1	1	33
Halichoeres sp.						[[[
Hemicaranx amblyrhynchus														
Hemipteronotus novacula				1		1					1	1	2	
Holacanthus ciliaris														
Hyperoglyphe perciformis														
Hypleurochilus bermudensis														
Hypopiectrus sp.														
Lactophrys quadricornis														
Lactophrys trigonus					1	1				[[
Lagodon rhomboides						100								100
Lutjanus campechanus	37	26	52 43	88	51	139	95	32	24	56	11	2/	93	120
Lutjanus synagris	5	5	10		1	1						1	1	2
Monacanthus hispidus														
Monacanthus setifer														
Monocantnidae sp. Mycteroperca microlenis				2		2		1		1				
Mycteroperca phenax	2	2	4	1		1		1	1	2	3		3	2
Opsanus pardus														
Pagrus pagrus	2	14	16	-		07	8	3	-	3	3	10	13	
Parabiennius marmoreus Paralichthys albiqutta	4		4	2	25	2/	26	- /	1	8	25		32	6
Paranthias furcifer														
Pareques umbrosus								1		1				1
Pomacanthus paru Pomacantrus variabilie														1
Priacanthus arenatus														
Rachycentron canadum														
Rhomboplites aurorubens	39	2	41		1	1					122	39	161	28
Rypticus maculatus	2	6	8		2	2	13	4	3	7	1	2	3	1
Sciaenops ocellatus														
Scomberomorus cavalla														
Seriola dumerili	10	1	11				2				1	7	8	
Seriola fasciata	-	-										· ·	. ·	
Seriola rivoliana Seriola zonata	3	3	6								3	1	4	
Serranidae														
Serranus phoebe														
Serranus subligarius														
Stegastes leucostictus														
Stegastes sp.														
Stegastes variabilis														
Stenotomus caprinus														
Synodus foetens														
Unknown small fishes														

Table A1. continued.

Taxon	B16b	B16T	C12	C14a	C14b	C14T	C15	C21	C22	C25	C32	C36	C39
Acanthurus chirurgus													
Aluterus heudeloti			2								1		
Aluterus schoepfi													
Aluterus scriptus													
Anisotremus virginicus Antennarius sp.													
Apogon pseudomaculatus	2	9					29	5	58				
Apogon sp.	40		10	40	0		47		00		40	35	
Balistes capriscus Balistes vetula	18	32	19	12	2	14	17	26	26	2	10		
Balistidae													
Blennidae													
Calamus leucosteus Calamus nodosus													
Calamus proridens													
Calamus sp.													
Canthigaster rostrata Caranx bartholomaei				3	3	6		4	3				
Caranx crysos				2		2	13						
Caranx ruber													
Carcharhinus limbatus													
Carcharhinus sp.													
Centropristis ocyurus	2	2	11							20	1	4	11
Chaetodopterus faber Chaetodop ocellatus			2										
Chaetodon sedentarius													
Chilomycterus atinga													
Chilomycterus schoepti Chromis sp							1						
Chromis enchrysurus				6	7	13	1						
Dasyatis americana													
Decapterus macarellus Diplectrum formosum													٥
Echeneis naucrates													3
Elagatis bipinnulata							4						
Epinephelus cruentatus													
Epinephelus morio													
Epinephelus nigritus													
Epinephelus niveatus												3	
Equetus acuminatus Equetus lanceolatus				2		2					27		5
Equetus iwamotoi													
Equetus sp.													
Fistularia tabacaria Ginglymostoma cirratum													
Gymnothorax moringa													
Haemulon aurolineatum			177							39		124	
Halichoeres bivittatus Halichoeres sp	31	64	16	1	7	8	16	10	73	45	5	34	
Hemicaranx amblyrhynchus													
Hemipteronotus novacula													2
Holacanthus bermudensis Holacanthus ciliaris							1		1				
Hyperoglyphe perciformis													
Hypleurochilus bermudensis													
Hypoplectrus sp.													
Lactophrys quadricomis													
Lactophrys trigonus													
Lagodon rhomboides	46	166	42	E2	20	02	E0	20	140	2	120	24	4
Lutjanus griseus	40	100	43	30	20	50	20	16	4	3	120	34	4
Lutjanus synagris		2						87	1		1		
Monacanthus hispidus													
Monocanthidae sp.									1				
Mycteroperca microlepis								1					
Mycteroperca phenax		2	1	1	1	2		4	1		1		
Pagrus pagrus	1	1	1	29	20	49	63	1	13	42			
Parablennius marmoreus	31	37	16	10	5	15	11	13	37	3		11	
Paralichthys albigutta Paranthias furcifer					1	1							
Pareques umbrosus		1	2					2		2			
Pomacanthus paru		1											
Pomacentrus variabilis Priacanthus arenatus												18	
Rachycentron canadum													
Rhomboplites aurorubens	147	175	174	17	10	27	2	21		46	1	4	
Rypticus maculatus	4	5	4	2	2	4	5	6	3	6	7	4	
Sciaenops ocellatus													
Scomberomorus cavalla	2	2											
Seriola dumerili Seriola fasciata				73	10	83	37	51	29	1			
Seriola rivoliana			1	15	1	15	67	2					
Seriola zonata													
Serranidae													
Serranus prioebe Serranus subligarius													
Sphyraena barracuda													
Stegastes leucostictus													
Stegastes sp. Stegastes variabilis													
Stenotomus caprinus													
Synodus foetens													
I racninocephalus myops													

Table A2. Fishes identified and enumerated over unreported artificial reefs off northwest Florida in the northern Gulf of Mexico during summer 2008. Modules at a given site were sampled separately if they were greater than 8 m apart. Abundances at those sites are reported for each module (a,b) and also summed (T) between modules.

Taxon	A12	A19	A20	A31	A34	A35	A36	A53	A56	B1a	B1b	B1T	B2	B3
Acanthurus chirurgus														
Aluterus heudeloti													4	2
Aluterus schoepfi	2												2	2
Aluterus scriptus														
Anisotremus virginicus							1							
Apogon pseudomaculatus	47		2	42	112	21		1	23	15	8	23		1
Apogon sp.				100	617						8	8		
Balistes capriscus		1			3	1	1	5		4	2	6	1	7
Balistidae														
Blennidae														
Calamus leucosteus														
Calamus proridens														
Calamus sp.														1
Canthigaster rostrata	12		7	1	2			7	3				5	6
Caranx crysos	13			9			114						11	23
Caranx ruber														
Carcharhinus limbatus														
Carcharhinus pumbeus Carcharhinus sp.														
Centropristis ocyurus		41				77	33			2	2	4		
Chaetodipterus faber													2	1
Chaetodon ocenatus Chaetodon sedentarius													2	
Chilomycterus atinga	1		İ											
Chilomycterus schoepfi														
Chromis sp.	1		1	1	2						1	1	1	
Dasyatis americana	<u> </u>		<u> </u>											
Decapterus macarellus						672			564					
Echeneis naucrates									1					
Elagatis bipinnulata														
Epinephelus cruentatus						1								
Epinephelus drummondhayi				1	1									
Epinephelus nigritus														
Epinephelus niveatus							1						1	
Equetus acuminatus		18		7			1			6	1	7		12
Equetus ianceolatus		10		/			· ·			0		1		12
Equetus sp.														
Fistularia tabacaria														
Gingiymostoma cirratum Gymnothorax moringa	-													
Haemulon aurolineatum	153	55				80	19	121	63	1	153	154	95	
Halichoeres bivittatus	14		5	164	80			11	4					46
Halichoeres sp. Hemicarany amhlyrhynchus						3								
Hemipteronotus novacula														
Holacanthus bermudensis									1					
Holacanthus ciliaris Hyperoglyphe perciformis														
Hypleurochilus bermudensis														
Hypoplectrus sp.														
Kyphosus sectator														
Lactophrys trigonus														
Lagodon rhomboides														
Lutjanus campechanus	56	4	28	91	29	1	34	56	10	47	13	60	47	30
Lutianus synagris	2	1	15				2			4	1	5	5	23
Monacanthus hispidus			İ											
Monacanthus setifer														
Mycteroperca microlepis						1								4
Mycteroperca phenax														
Opsanus pardus			<u> </u>							-		<u> </u>		
Parablennius marmoreus	4	19	10	13	3/	22	15	10	12	4	29	33	3	1
Paralichthys albigutta	<u> </u>													
Paranthias furcifer														
Pomacanthus paru		1				2								11
Pomacentrus variabilis														
Priacanthus arenatus														
Rhomboplites aurorubens		28	129			31	6	6	1	10	26	36	4	
Rypticus maculatus	2	10	5	6	6	6	4	4	2	3	2	5	6	
Sardinella aurita						6336								
Sciaenops oceilatus Scomberomorus cavalla														
Seriola dumerili	4	1	77	5			3	9					24	53
Seriola fasciata													2	
Seriola rivoliana Seriola zonata	-		2	14									1	3
Serranidae														
Serranus phoebe														
Serranus subligarius			-											
Stegastes leucostictus	1		-											
Stegastes sp.	1													
Stegastes variabilis		3			1			7						
Synodus foetens	1		-			1	-							
Trachinocephalus myops														
Unknown small fishes			1											

Table A2. continued.

Taxon	B4a	B4b	B4T	B7a	B7b	B7T	B8	B9a	B9b	B9T	B11a	B11b	B11T	B16a
Acanthurus chirurgus														
Aluterus heudeloti														
Aluterus schoenfi														
Aluterus scriptus														
Anisotremus virginicus														
Antennarius sp.					2	2								
Apogon sp.					1	1								
Balistes capriscus	1		1				1	13	3	16	3	8	11	13
Balistes vetula														
Blennidae														
Calamus leucosteus														
Calamus nodosus														
Calamus proridens														
Canthigaster rostrata		3	3		1	1								2
Caranx bartholomaei		5	5									[
Caranx crysos	21	3	24					345	1	346		83	83	78
Carcharbinus limbatus														
Carcharhinus plumbeus														
Carcharhinus sp.														
Centropristis ocyurus														
Chaetodon ocellatus								2		2				
Chaetodon sedentarius	3		3											
Chilomycterus atinga														
Chilomycterus schoepfi Chromis sp														
Chromis enchrysurus					2	2								
Dasyatis americana														
Decapterus macarellus														
Echeneis naucrates												-		
Elagatis bipinnulata														
Epinephelus cruentatus														
Epinephelus drummondhayi														
Epinephelus nigritus														
Epinephelus niveatus							1							
Equetus acuminatus														
Equetus lanceolatus							2	1		1	2	1	3	
Equetus sp.														
Fistularia tabacaria												[
Ginglymostoma cirratum														
Haemulon aurolineatum							38	1	2	3	19		19	
Halichoeres bivittatus					8	8		34	15	49	5	5	10	26
Halichoeres sp.														
Hemicaranx amblyrhynchus Heminteropotus povacula														
Holacanthus bermudensis											1	1	2	
Holacanthus ciliaris														
Hyperoglyphe perciformis														
Hypieurocnilus bermudensis Hypoplectrus sp.														
Kyphosus sectator														
Lactophrys quadricornis														
Lactophrys trigonus														
Lutjanus campechanus	50	21	71	90	38	128	77	16	11	27	31	63	94	65
Lutjanus griseus	15	11	26	3	1	4					3	4	7	
Lutjanus synagris		3	3	1		1					15	10	25	2
Monacanthus nispidus												-		
Monocanthidae														
Mycteroperca microlepis	1		1						1	1				1
Opsanus pardus								1	1	2	1	1	2	2
Pagrus pagrus	6	21	27				2	51	27	78	30	2	32	5
Parablennius marmoreus	3	9	12	15		15		2	1	3	5	8	13	3
Paralichthys albigutta														
Pareques umbrosus	2		2											2
Pomacanthus paru														
Pomacentrus variabilis	ļ]		<u> </u>											
Rachycentron canadum														
Rhomboplites aurorubens	8	451	459					14		14	12	2	14	125
Rypticus maculatus	4	4	8	6		6	14	5	4	9	1	3	4	3
Sardinella aurita														
Scomberomorus cavalla														
Seriola dumerili	37	44	81				6	1		1	11	3	14	9
Seriola fasciata											1		1	
Seriola rivoliana Seriola zonata	4	9	13								2	-	2	
Serranidae														
Serranus phoebe														
Serranus subligarius														
Stegastes leucostictus														
Stegastes sp.														
Stegastes variabilis														
Stenotomus caprinus Synodus foetens														
Trachinocephalus myops														
Unknown small fishes														

Table A2. continued.

Taxon	B16b	B16T	C12	C14a	C14b	C14T	C15	C21	C22	C25	C32	C36a	C36b	C36T	C39
Acanthurus chirurgus															
Aluterus heudeloti				4	3	7		2							
Aluterus schoepfi						,		2			2	2		4	
Aluterus scriptus															
Anisotremus virginicus															
Antennarius sp. Apogon pseudomaculatus									10	29		28	78	106	1
Apogon sp.									7	20		20		100	
Balistes capriscus	1	14	13	16	6	22	14	32	29		8				1
Balistes vetula															
Blennidae															
Calamus leucosteus															
Calamus nodosus															
Calamus proridens				3	1	4									
Canthigaster rostrata		2		1	4	5	3	8	5						
Caranx bartholomaei															
Caranx crysos	265	343		16		16	533	145	1						
Carcharhinus limbatus															
Carcharhinus plumbeus															
Carcharhinus sp.															
Centropristis ocyura Chaetodinterus faber			6								2	2	3	5	10
Chaetodon ocellatus	1	1		2		2	1								
Chaetodon sedentarius			1												
Chilomycterus atinga															
Chromis sp.															
Chromis enchrysurus			4								1				
Dasyatis americana															
Diplectrum formosum													3	3	3
Echeneis naucrates															5
Elagatis bipinnulata															
Epinephelus cruentatus															
Epinephelus morio															
Epinephelus nigritus															
Epinephelus niveatus												1		1	
Equetus acuminatus Equetus lanceolatus			2		1	1		2			24				2
Equetus iwamotoi															_
Equetus sp.															
Fistularia tabacaria															
Gymnothorax moringa							1								
Haemulon aurolineatum			77								13	131	9	140	
Halichoeres bivittatus	17	43	6				15		93	80	19	5	3	8	
Halichoeres sp. Hemicaranx amblyrhynchus															
Hemipteronotus novacula															1
Holacanthus bermudensis							1		2						
Holacanthus ciliaris								1							
Hypleurochilus bermudensis								1							
Hypoplectrus sp.															
Kyphosus sectator															
Lactophrys quadricomis															
Lagodon rhomboides															
Lutjanus campechanus	43	108	30	18	3	21	162	41	58	2	57	37	2	39	10
Lutjanus griseus		2	4	9	11	20	13	18	1		9				
Monacanthus hispidus			· · ·												
Monacanthus setifer															
Monocanthidae Mucteroperca microlenis		1		4		1		2	2						
Mycteroperca phenax	2	4	1	1	1	2	1	3			1				
Opsanus pardus										2					
Pagrus pagrus	3	8	3	18	27	45	14	3	14	70					
Paralichthys albigutta	5	0	0				2	4	4	4	1	1		1	
Paranthias furcifer															
Pareques umbrosus	1	3								3					
Pomacantnus paru Pomacentrus variabilis															
Priacanthus arenatus							1								
Rachycentron canadum															
Rhomboplites aurorubens	10	135	109	3	12	15	1	390	252	7	£	12	21	33	
Sardinella aurita	3	•		2	4	4	4	U	U	,	0	3		1	
Sciaenops ocellatus															
Scomberomorus cavalla															
Seriola dumerili Seriola fasciata	6	15		1	12	13	2	3			2	1		1	
Seriola rivoliana				3	2	5	1	3	2						
Seriola zonata															
Serranidae Serranus phoebe															
Serranus subligarius															
Sphyraena barracuda															
Stegastes leucostictus															
Stegastes variabilis												6	2	8	
Stenotomus caprinus														-	
Synodus foetens															
Unknown small fishes															