INFLUENCE OF HIGH-RESOLUTION SPATIAL INFORMATION ON RESOURCE EXPLOITATION: AN EXAMPLE FROM ANGLER IMPACTS ON ARTIFICIAL REEFS

By

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Exploitation of natural resources is dependent on knowing where to find those resources. Increasingly specific and detailed information regarding the location and relative value of many resources is being continually developed by rapidly advancing technologies in remote sensing. It is generally assumed that such information allows more efficient and directed exploitation of those resources. I evaluated impacts of the public release of detailed geographic information regarding artificial reefs designed for gag grouper (*Mycteroperca microlepis*). Reefs were constructed of concrete cubes approximately 90 cm on a side. Size of reef patches (4-cube and 16-cube, small and large respectively), and distances among patches (25 m and 225 m), were examined. Approximately half of the reef locations were published to the angling community. Reefs were monitored from two years prior to publication to two years-post publication and again six to eight years post-publication.

Impacts on published reef arrays were highest on large, closely spaced reef arrays, and least on small, widely spaced reef arrays. In contrast to pre-publication trends, large reef patches, once published, no longer held more legal gag (>508 mm) than small patches. Six to eight years after publication sub-legal gag (<508 mm) were reduced on the largest, most closely spaced arrays, indicating that these reefs received the highest fishing effort. Large unpublished reefs as well as small, widely spaced reefs showed effects of discovery by anglers in the period six to eight years after other reefs in the study system were made publicly known. The disclosure of locations of previously un-targeted, high-quality habitat led to immediate exploitation of legal gag, with the exception of apparent refuges of small habitat patches, which are inherently more difficult to locate and to fish. Resource managers should take into account the improved efficiency of exploitation made possible by the collection and dissemination of high-resolution geographic habitat data.

CHAPTER 1
INTRODUCTION

Accurate and rapid collection of spatially explicit data regarding the natural environment has been made possible over recent decades by the development of new technologies. Advances in satellite imaging and sensing systems as well as sonic and laser technologies are providing unprecedented detail and information. The utility of high-resolution spatial data to both resource managers and user groups has been clear. It has made possible the quantification of changes in land use and land cover to describe processes such as deforestation and desertification (Pamo, 2004; Leimgruber et. al., 2005) and shoreline changes (Morton et. al., 2005) with much greater accuracy than prior techniques, provided for far more proficient and directed use of natural resources (Pickrill and Todd, 2003), and has opened lines of scientific inquiry previously limited by the technology available (Wright, 1999; Andersen et. al., 2005; Leimgruber et. al., 2005).

In the sea, detailed surveys have been conducted through the use of multi-beam sonar systems (Verlaan, 1997; Pickrill and Todd, 2003) as well as the LIDAR (Laser Imaging Detection and Ranging) optical system (Kincade, 2003). Coupled with Geographic Positioning Systems (GPS), data can be placed very precisely in a spatial context. Such detailed information has already demonstrated its utility in the management, exploration, and understanding of the marine environment. In coastal environments, decisions regarding location of sewage outfalls as well as cable and pipe-line routes have been well founded (Pickrill and Todd, 2003). Side-scan sonar has been used to identify mineral deposits on the ocean floor (Lee and Kim, 2004) and investigate the geo-physical properties of hydrothermal vents and areas of sea-floor spreading (Wright, 1999). In fisheries, LIDAR has been combined with video technology for the remote sensing of schools of capelin (*Mallotus villosus*) and zooplankton densities (Brown et. al. 2002). Detailed maps were created of Brown's Bank in the Northern Atlantic, which were then coupled with biological data to identify key scallop habitats (Kostylev et. al., 2003). As a consequence, commercial trawlers were able to reach quotas in as little as one quarter the time while avoiding fragile or unproductive regions (Pickrill and Todd, 2003).

The availability of such detailed geographic data is clearly a boon to resource managers and those working in the natural environment. Mack (1990) noted, however, that there are unintended uses of new technologies that may only become apparent once a program is well underway. For example, fishery resources are inherently patchy in space, and detailed geographic information collected to other ends has the potential to facilitate their exploitation. In the example of the commercial scallop fishery on Brown's Bank (Kostylev et. al., 2003; Pickrill and Todd, 2003), a quota limited the harvest. New technologies provided information facilitating more efficient harvest without increasing the overall effect on the fishery, and possibly minimized impacts to benthic habitats by reducing the area trawled. Had there been no quota, continued efficient and directed efforts could have led to much greater yields and thus potential overexploitation in the fishery. The development of information increasing the potential for efficient exploitation of natural resources, if not coupled with proper management strategies, creates the possibility of over-exploitation of those resources.

Like the scallop, many marine fishery species are associated with specific habitat types. The current efforts in sea-floor mapping hold the potential of identifying and describing those habitats in great detail, leading to far better understanding of population distributions and identification of essential fish habitats. While clearly useful to managers, to date, there are few documented examples of how fishermen use detailed geographic information of fish habitat. Identification of densely populated habitat among recreational fishermen is commonly achieved through large expenditures of effort in exploring new areas and searching with the limited bottom mapping information and technologies available to the recreational sector. Due to the investment in locating fishing sites, once found, such areas are rarely made public. Although maps are created and bathymetric data are available to recreational anglers, they are typically of coarse scale and limited scope.

The Ideal Free Distribution (IFD), as applied to the distribution of angling effort (Walters and Martell, 2004), predicts that effort will be directed to the most profitable fishing grounds. One assumption of the IFD is complete knowledge of fishing grounds and the relative profitability of each. Increase in awareness of available fishing grounds, as is made possible by detailed bottom mapping, will likely lead to a distribution of angling effort closer to that predicted by the IFD. The predicted consequences are an increase in catch-per-unit-effort (CPUE) in the short-term, and hyper-stability in the long-term as detailed geographic information facilitates exploitation in the face of declining stocks.

Due to the expanse of marine environments and limited ability of recreational anglers to accurately perceive the sea floor, habitat extent is likely a key factor in determining its probability of discovery. Small, isolated habitat patches that support dense local populations of fish are difficult to locate by conventional means, rarely shared if they are discovered, and are likely key habitat features providing refuge for targeted marine species. The uncontrolled dissemination of fine-scale bathymetry could reveal such locations in detail, leading to better-directed and more efficient exploitation of stocks that are patchy in space.

The importance of such refuges is largely unknown, but is potentially critical in the maintenance of a viable fishery. The impacts of both recreational and commercial fishing on populations and assemblages of marine fish have been well documented (Haedrich and Barnes, 1997; Wantiez et. al., 1997; Bianchi et. al., 2000; Roberts et. al., 2001; Bremner et. al., 2003; Coleman et. al., 2004). Fishing generally leads to fewer and smaller fish of the targeted species (Haedrich and Barnes, 1997; Grandcourt, 2003) as well as reduced overall diversity (Albaret and Lae, 2003; Ley et. al., 2002). Protection from fishing, in some cases, has reversed these trends (Roberts, 1994; Wantiez et. al., 1997) and resulted in increased abundance and size of targeted fish as well as increased biodiversity in protected areas. Refuges provide fish the opportunity to become older and larger. Such individuals are of great importance to the welfare of a fishery (Birkeland and Dayton, 2005). For some species, larger and older individuals have been shown to have exponentially higher fecundity (Berkeley et. al., 2004a) and to produce healthier, faster-growing larvae (Conover and Munch, 2002; Berkeley et. al., 2004b), as well as preserving genetic diversity (Hauser et. al., 2002).

As large-scale sea-floor mapping programs are relatively new, studies of such natural, small, isolated, but high quality, habitat features are rare. The use of artificial reef structures to create such locales provides the opportunity to control for habitat features (size, shape, and distribution) that may influence the resulting assemblage of species as well as the exploitation of the resident species by fishers.

The specific characteristics of artificial habitat along with reef placement (Coll et. al., 1998) strongly influence the resulting assemblage of marine life. There are two characteristics of artificial reef use by marine fish that have been widely studied: as shelter and as a food source. Available refuge has been demonstrated to be the dominant structuring influence on the species resident on a reef (Williams and Sale, 1981; Doherty and Sale 1985; Sweatman, 1985; Hixon and Beets, 1989; Eklund, 1997; Lindberg in press) although resident species clearly use the reef as a forage base (Herrera et. al., 2002; Szedlmayer and Lee, 2004). Many top-level predators are transient groups (e.g., jacks, sharks, tunas, mackerels) and would be less-frequently observed at artificial reefs despite their potential for playing a major role in the structuring processes of the resident fish assemblage (Bohnsack et. al., 1994; Carr et. al., 2002).

The use of artificial reefs as refuge is dependent on the shelter characteristics of the structure provided. Many studies have investigated the effects of reef size and design on resulting fish assemblages. Several general trends have been observed. Larger reef structures support higher abundances of fish (Rountree, 1989; Lindberg and Loftin, 1998) though not necessarily at higher densities (per unit reef area) (Bohnsack et. al., 1994; Lindberg and Loftin, 1998). Bohnsack et. al. (1994) found that although there are lower densities at larger reefs, the resident fish are larger on average than on smaller reefs. In contrast, Lindberg et. al. (in press) observed higher growth rates by gag, *Mycteroperca microlepis*, on smaller artificial reef patches. These patterns are likely dependent on the species and system being studied. Size of refuges within a reef has been shown to positively influence the abundance of fish suited to the size of refuge provided (Frazer and Lindberg, 1994; Hixon and Beets, 1989; Hart, 2002). Fish tend to prefer openings close to their own body size (Shulman, 1984). Within reefs, higher habitat complexity increases diversity of the resulting assemblage as adequate shelter is provided for a larger range of species (Charbonnel et. al., 2002; Sherman et. al., 2002; Gratwicke and Speight, 2005). Although resident species also use the reef and surrounding area as a forage base (Herrera et. al., 2002; Szedlmayer and Lee, 2004), several studies have concluded that refuge is the over-riding factor determining abundance of resident fish on artificial reefs (Ecklund, 1997; Lindberg et. al. in press).

For recreational anglers, artificial reefs are widely-known and publicized, easily locatable angling sites. In public surveys, 6.4% (McGlennon and Branden, 1994) to 87% (Ditton and Graefe, 1978) of anglers reported fishing on artificial reefs. The lower end of the spectrum resulted in a fishing intensity (angler hours/unit area) 92-171 times greater than observed on natural substrates (McGlennon and Branden, 1994). While expectations of high catch rates are a motivating factor for selecting artificial reefs (Milon, 1989) only 5 of 27 comparisons by McGlennon and Branden (1994) yielded significantly higher catch rates on artificial habitats, and these were all for pelagic species. Solonsky (1985) demonstrated the significant impact that anglers can have on recreationally targeted game fish on an artificial reef in Monterey Bay. One central reef amidst several others was marked for recreational fishing. After three years, there were significantly fewer rockfish on the marked reef relative to the unmarked reefs surrounding it. Furthermore, tagged fish on the surrounding reefs were observed to move onto the marked reef, but none were observed leaving the marked reef, demonstrating the function of a known artificial reef to attract fish thus increasing their vulnerability to fishing. Turpin and Bortone (2002), who observed artificial reefs before and after they were displaced by hurricanes, also observed a significant increase in lengths of gag, and red snapper, *Lutjanus campechanus*, on these reefs following displacement as anglers no longer knew their locations. The use of artificial reefs in the study reported here offers the additional dimension of high attraction for recreational anglers.

The purpose of this study was to test how the public release of detailed location information regarding patchy habitat impacted the standing stock of gag, a dominant reef-associated, recreationally-targeted species. The specific objectives were: (1) to determine how publication of reef locations to anglers differentially affected abundances of both legal and sub-legal gag across different reef architectures (sizes and spacings), and (2) to determine the impacts of angling over a broad time-scale, including the discovery and exploitation of unpublished reef locations. This evaluation of angling impacts as a function of habitat patchiness and location information provides fishery managers with experimental results pertinent to the management of fisheries in light of the ever-increasing efficiencies that anglers garner through new and developing technologies.

Publication was predicted to lead to rapid reductions of legal gag. A refuge effect on more-widely spaced patches was predicted as these are more difficult to fish as a single unit. Angling impacts were predicted to be greatest on 16-cube arrays as anglers are likely to favor these under the conception that larger habitat patches hold more fish. Discovery of unpublished arrays was expected to be a function of both patch size and spacing. Larger and more-widely spaced patches provide the greatest probability of encounter for searching anglers. Discovery of a single patch should lead to discovery of the entire array as anglers were aware of the reef layouts within the experimental system. Several mechanisms likely affect sub-legal gag abundance. Compensatory responses to predicted decreases in legal gag abundances would lead to an increase in sub-legal gag abundance. Induced immigration and mortality from catch and release would lead to declines in sub-legal gag abundance. Large, closely-spaced arrays were predicted to have the highest fishing effort, thus they were expected to demonstrate the relative importance of these mechanisms.

CHAPTER 2
METHODS

Experimental System

The Suwannee Regional Reef System (SRRS) was constructed from 1990 to 1993 in the northeastern Gulf of Mexico, approximately 20-25 km from the mouth of the Suwannee River (Figure 1A). The building blocks of the SRRS were 89 cm x 89 cm x 89 cm concrete cubes with 60 cm diameter, cylindrical horizontal passages through the centers and 10 cm diameter, horizontal, right-angle tunnels through each of the eight corners (Figure 1B). Cubes were arranged in either 4-cube or 16-cube square reef patches, such that central passages all run in the same direction. Patches were arranged hexagonally, and were spaced 25, 75 or 225 m apart, constituting a reef array (Figure 1B). Reef arrays were spaced one to two km apart along the 13 m depth contour. Twenty-two arrays comprise the entire SRRS, which was designed as a 3 x 2 factorial experiment with three spacing treatments (25m, 75m, 225m) and two patch size treatments (4-cube and 16-cube).

The SRRS was twice affected by perturbations in its initial years. In 1992, locations of four arrays were inadvertently published. In 1995, all fish on the five southernmost arrays were eliminated by a red tide event. This fish-kill effectively reset the fish colonization process on those arrays. Two arrays were both published inadvertently and experienced the fish-kill.

In November of 1996, locations of two to three arrays per treatment group were published for access by the general public. No locations of the 75 m spaced arrays were published and thus the 75 m treatment was excluded from this study. The early perturbations and requirements of other on-going research projects warranted restrictions on randomization when selecting arrays for publication, e.g. inadvertently published arrays were assigned to the 'published' treatment.

Study Organism

Gag, *Mycteroperca microlepis*, is a dominant reef-associated, demersal fish species in the Western Atlantic ranging from New England to Brazil, including the Gulf of Mexico (McErlean, 1963). As protogynous hermaphrodites, female gag mature at 3-6 years old and 538 to 795 mm TL (Hood and Schlieder 1992; Harris and Collins 2000). In two studies, no males younger than five or smaller than 875 mm TL were observed (Hood and Schlieder 1992; Harris and Collins 2000). By age 11, males comprised 50% of the age class. Transition from female to male is hypothesized to be socially mediated (Koenig et. al. 1999; Coleman et. al. 2002) but is debated (Kenchington, 1999). Gag reach sizes between 1100 and 1200 mm and ages ranging into the early twenties (Hood and Schlieder 1992; Collins et. al. 1998).

Gag form spawning aggregations of 10's to 100's of individuals (Coleman et. al., 1996). Aggregations have been observed along the shelf edge break in the Northwest Gulf of Mexico in 50-120 m (Coleman et. al. 1996; Koenig et. al., 1999), on deep (70-100 m) reefs off the Atlantic coast of Florida (Gilmore and Jones, 1992), and have been recently reported on the Campeche Bank, Yucatan, Mexico (Brule et. al., 2003). Gag spawn from late December through April with peak spawning in February and March (Hood and Schlieder 1992; Collins et. al. 1998). Currents carry gag larvae inshore where they settle in seagrass beds and oyster bars (Ross and Moser, 1995). Average larval duration is approximately 43 days (Keener et. al. 1988). Gag spend their first summer growing in inshore habitats where their diet is composed primarily of crustaceans (Bullock and Smith 1991; Weaver 1996). In the late summer and fall, gag move to deeper water and take up residency on near-shore reefs and live-bottom where their diet shifts to decapod crustaceans and fishes (Bullock and Smith 1991; Weaver 1996). It is in these habitats that gag reach legally harvestable size and are first targeted by fishers. Gag continue to grow and mature in these environments before moving to spawning grounds as mature adults. The natural annual mortality rate is unknown but is assumed to be M=0.15 for stock assessment purposes (Turner et. al. 2001). It is during their transition across the shallow continental shelf that juvenile to sub-adult pre-reproductive females take up residency on the SRRS

Sources of Data

Gag present on each SRRS patch were counted once each Summer from 1995 to 1998 and 2002 to 2004 by trained SCUBA divers (see Lindberg et. al., in press for details). Types of data collected changed over the years of sampling as the research questions being addressed changed. I worked with a historical data set (1995 to 1998) and participated in data collection during the 2002 to 2004 period. From 1995 to 1996 the total number of gag on each patch reef were counted and divers visually estimated the length of the largest and smallest gag as well as the average size of gag. In 1997 and 1998, counts were divided into total number of legal (>20" or 508 mm) and sub-legal (<20" or 508 mm) gag. In 2002 through 2004, gag were individually assigned to 10 cm size groups. The 50-59 cm size group was further divided into gag from 50-55 cm and 56-59 cm in order to determine the number of legal and sub-legal gag on a patch. This coincided with an increase in the legal size of recreationally harvestable gag from 20" (508 mm) to 22" (559 mm) that occurred on June 19, 2000 (Turner et. al., 2001). For this investigation, all data were converted to counts of legal and sub-legal gag by array. Legal and sub-legal counts were estimated for 1995 and 1996 from percentages of legal and sub-legal gag observed on unpublished arrays of the same architecture in 1997. This is based on a necessary assumption that the proportions of legal and sub-legal gag on patches of like architecture and presumed level of fishing effort is consistent over time (1995-1997) and space (among unpublished arrays). These approximations were further adjusted based on the size estimates for the largest and smallest gag (i.e., if the largest gag observed was smaller than the legal limit, all gag were considered sub-legal). Patch reef counts were summed for each array, as the arrays rather than the patches are the proper replicates for this study.

Suitability of Data

Preliminary analyses were conducted to establish the suitability of data to be used. Reef arrays were constructed from 1990-1993. Within arrays, data from 1995 and 1996 were compared for significant differences. None were found and thus variable reef age was determined not to be a significant factor influencing gag abundances. In 1995 a fish-kill event eliminated all fish on the five southern-most reef arrays. The fish-kill was investigated as a treatment effect within reef architectures. Data were excluded from the final model for all architecture/year combinations in which the fish-kill treatment was significant. This resulted in the exclusion of data from all fish-killed arrays in 1995. In 1996 legal counts on four-cube arrays were considered recovered and included in further analyses. Analysis indicated all affected arrays had recovered by 1997. In 1992, several array locations were inadvertently published. Due to low replication and the impacts of the fish-kill, I was unable to evaluate this effect.

Experimental Design

Three variables were investigated in a repeated measures 2 x 2 x 2 x 3 factorial design for their effects on gag abundance on the SRRS: patch spacing (25 m or 225 m between patches within an array), patch size (4 or 16 cubes per patch), publication of locations for public fishing (published or not), and time period. Annual counts were nested within three different time periods (time relative to the publication of array locations). "Pre" consists of data collected in 1995 and 1996, prior to publication. "Acute" consists of data collected in 1997 and 1998, the period immediately following publication. "Chronic" consists of data taken in 2002 through 2004, six to eight years following publication.

Statistical Analyses

All analyses were conducted independently on legal and sub-legal gag count data. To satisfy the assumptions of normality and homogeneity of variances, all count data were square root transformed.

Data not excluded by the preliminary analyses were entered in a four-way repeated-measures, mixed-model Analysis of Variance (ANOVA) to determine significant interactions and main effects. Alternate correlation structures for the effect of year nested within period were tested, but none improved the model over a zero-correlation model. The Kenward-Rogers method was used to estimate the degrees of freedom for the appropriate F-test for fixed effects. Follow-up analyses were done by pair-wise comparisons of least square means provided for each treatment by the model. Residuals were plotted in a Q-Q plot and against predicted values to examine model fit. Akaike's information criterion as well as mean square error values were compared between treatment levels to investigate error structure in the model. All statistical analyses were performed in SAS version 8 (SAS Institute Inc. 2002, Cary, NC). An alpha value of 0.05 was used for determining statistical significance. Due to the low replication and thus low suspected power of these tests, the alpha value was not adjusted to maintain an experiment-wise error rate of 0.05.

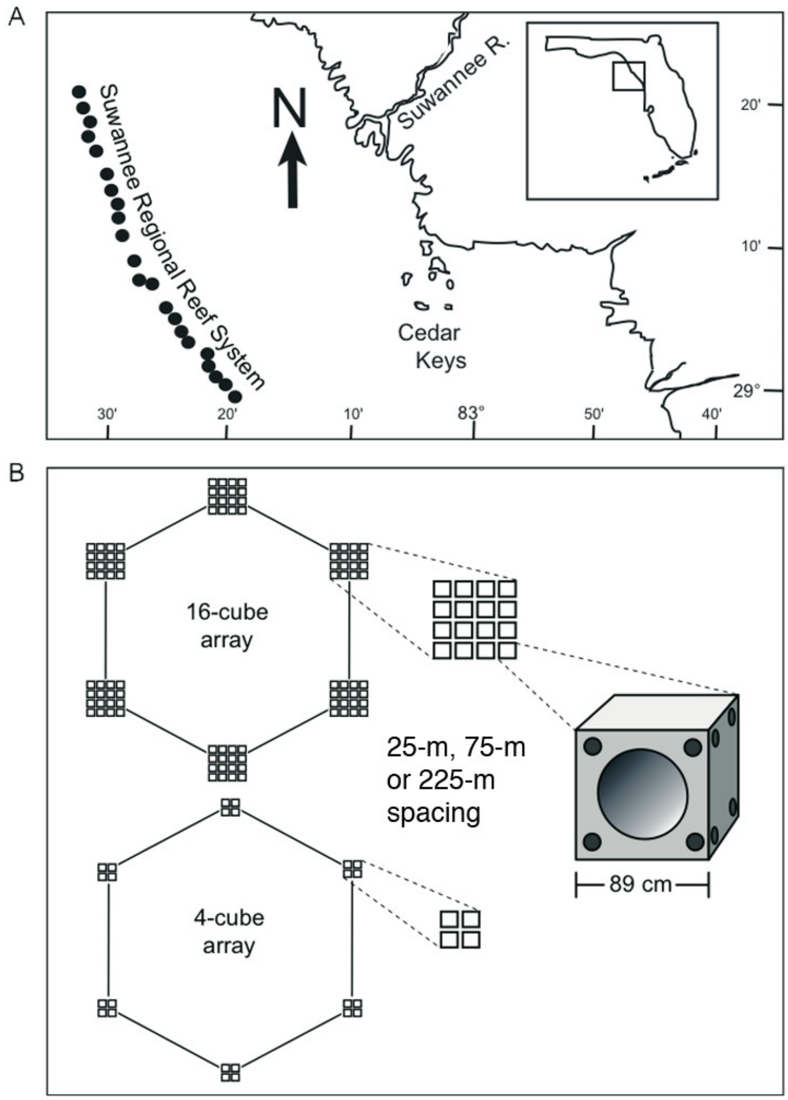

Figure 1. Design of the Suwannee Regional Reef System (A) Location of SRRS in the Big Bend region of Florida (inset). (B) Design of a component artificial reef block and layout of an SRRS array.

CHAPTER 3
RESULTS

Legal Gag

The four-way interaction of patch size, patch spacing, publication and time period was significant (p=0.0083, Table 2) for legal-sized gag abundances on the SRRS. The results of follow-up comparisons below explain this four-way interaction. The interaction is partitioned chronologically with steady-state comparisons within time periods and transitional comparisons between time periods. Mean square errors were examined between treatment levels and determined not to be significantly different between levels of any treatment. Residual analysis indicated good model fit. The significant model was run using untransformed data in order to generate least square means and error estimates for use in figures to better convey the results.

Pre-publication Time Period (Initial Conditions)

Arrays were not selected randomly for publication and thus there were pre-existing differences between arrays selected for the published and unpublished treatments. Arrays that experienced the fish-kill and those that were inadvertently published were given priority as 'published' treatments in order to maintain a valid 'unpublished' treatment to compare against. To-be-published 4 x 225 m arrays had significantly fewer legal gag than their not-to-be-published counterparts even before their publication (p=0.0008).

Beyond the perturbations, there was a distributional pattern on the unpublished arrays dependent on the size and spacing of arrays (Figure 2). Within spacing treatments, 16-cube arrays had a higher abundance of legal gag than 4-cube arrays (25 m p=0.0002;

225 m p=0.0009). Within 4-cube arrays, there was a higher abundance of legal gag on 225 m arrays than 25 m arrays (p=0.0314).

Transition from "Pre" to "Acute" Time Periods

The publication of array locations significantly impacted the abundances of legal-sized gag for 16-cube arrays (Figure 3) for both spacing treatments (25 m p<0.0001; 225 m p<0.0001). Four-cube published arrays, however, did not change significantly following publication (25 m p=0.3378; 225 m p=0.3898), (Figure 4). There was a significant increase in legal gag abundance on unpublished 4 x 25 m arrays (p=0.0071), and thus no difference in the "acute" period between unpublished 4-cube arrays based on their spacing (p=0.6264). This was the only significant change on any of the unpublished array treatments.

Within "Acute"

The effect of publication on legal gag was most pronounced for arrays with larger reef patches (Figure 5). The number of legal gag on published 16-cube arrays, however, was not significantly different than the number of legal gag on published 4-cube arrays (25 m p=0.5977; 225 m p=0.2462) or unpublished 4-cube arrays (25 m p=.0004 [greater abundance on four-cube arrays]; 225 m p=0.2380). Unpublished arrays maintained the size-dependent difference of more legal gag on 16-cube than 4-cube arrays (25 m p=0.0005; 225 m p<0.0001). In the "acute" period a pattern emerged of more legal gag on unpublished 4-cube arrays relative to published 4-cube arrays for both spacing treatments (25 m p=0.0044; 225 m p=0.0249). More widely spaced arrays were hypothesized to be more difficult to fish and although there were more legal gag on published 16-cube arrays at the 225 m spacing, the difference was not significant (p=0.0737).

Transition from "Acute" to "Chronic"

Following the initial impacts of publication observed in the "acute" period, none of the published arrays experienced significant changes (Figures 3 and 4). On unpublished arrays, decreases indicative of discovery by anglers were observed. Although 4-cube, 25-meter arrays did not change (p=0.2764), 4-cube arrays at the 225-meter spacing declined significantly (p=0.0483) (Figure 4). Sixteen-cube arrays experienced a significant reduction in legal gag between the "acute" and "chronic" periods at both spacing treatments (25m p=0.0010; 225m p<0.0001) (Figure 3).

Within "Chronic"

Despite the decrease on unpublished 16-cube, 25 m arrays, these arrays still held significantly more legal gag in the "chronic" period than did the published 16 cube, 25 m arrays (p=0.0003) (Figure 6). Reductions on unpublished arrays lead to there being no difference in legal gag abundances between 16-cube, 225 m arrays and their published counterparts (p=0.0872). Sixteen-cube arrays, both published and unpublished, did not show any difference by spacing (pub, p=0.1246; unpub, p=0.4132).

Four-cube arrays showed a different pattern of gag abundance in the "chronic" period than the "acute." Although there were still more legal gag on the unpublished 4-cube, 25 m than the published 4 cube, 25 m arrays (p=0.0214), 4-cube, 225 m arrays showed no difference between published and unpublished treatments (p=0.7808) (Figure 6). As with the 16-cube arrays, this was the result of a significant decrease on the unpublished arrays. Within publication treatments, spacing was not significant on 4-cube arrays (published p=0.4519; unpublished p=0.0872)

In the "chronic" period, patch size was no longer significant for any treatment. Effects of publication continued to be significant for 25 m arrays (4-cube p=0.0214; 16-

cube p=0.0003), however, 225 m arrays no longer showed any differences by publication (4-cube p=0.7808; 16-cube p=0.1812)

Sub-Legal Gag

There was a significant main effect of time period (p<0.0001) for sub-legal gag (Table 4). The three-way interaction between publication, patch size, and patch spacing was also significant (p=0.0513) (Table 4) given the low replication and thus low expected power of this test. Mean square error was examined between treatment levels and determined not to be significantly different between levels of any treatment. Residual analysis indicated good model fit. The significant model was run using untransformed data in order to generate least square means and error estimates for use in figures to better convey the results.

The significant main effect of time period was manifested as a trend of decreasing abundance of sub-legal gag. Although the decrease was not significant from the “pre” to the “acute” period (p=0.5617), it was significant from “acute” to “chronic” (p=0.0001).

The significant effect of publication in the three-way interaction was only on 16-cube, 25 m arrays. There were more sub-legal gag on the unpublished than published arrays (p=0.0151) (Figure 7).

In most cases, there were more sub-legal gag on 16-cube arrays than on 4-cube arrays. This held true for unpublished arrays (25 m p=0.0101; 225 m p=0.0017) as well as published 225 m arrays (p=0.0003), but not for published 25 m arrays (p=0.6966).

Patch spacing had the most involved interaction determining sub-legal gag abundance (Figure 8). There was a significant interaction with publication as spacing had no significant effect on unpublished arrays (4-cube p=0.3868; 16-cube p=0.5679). Patch spacing and patch size interacted to affect patterns of sub-legal gag abundance on published arrays. There were more sub-legal gag on published 16-cube arrays at the 225 m spacing than the 25 m spacing (p=0.0125). The opposite was true for the published 4-cube arrays with more sub-legal gag on 25 m arrays than 225 m arrays (p=0.0188).

Table 1. Type 3 tests of fixed effects for legal gag

Covariance Parameters	Subject	Estimate	Std. Err.	Z value	Pr Z
Reef		1.1787	0.6847	1.72	0.0462
Year (Period)	Reef	2.3078	0.3555	6.49	<0.0001

Four-way interaction	Num DF	Den DF	F-value	Pr>F
Pd*Fishing*Size*Dist	2	85.3	5.08	0.0083

Three-way interactions	Num DF	Den DF	F-value	Pr>F
Pd*Fishing*Size	2	85.3	15.85	<0.0001
Pd*Fishing*Dist	2	85.3	4.01	0.0217
Pd*Size*Dist	2	85.3	2.72	0.0716
Fishing*Size*Dist	1	10.5	1.59	0.2344

Two-way interactions	Num DF	Den DF	F-value	Pr>F
Pd*Fishing	2	85.3	27.51	<0.0001
Pd*Size	2	85.3	36.64	<0.0001
Pd*Dist	2	85.3	6.21	0.0030
Fishing*Size	1	10.5	3.22	0.1014
Fishing*Dist	1	10.5	0.60	0.4549
Size*Dist	1	10.5	4.39	0.0613

Main Effects	Num DF	Den DF	F-value	Pr>F
Period	2	85.3	39.43	<0.0001
Fishing	1	10.5	48.20	<0.0001
Size	1	10.5	43.84	<0.0001
Distance	1	10.5	4.19	0.0664

Table 2. Type 3 tests of fixed effects for sub-legal gag.

Covariance Parameters	Subject	Estimate	Std. Err.	Z Value	Pr Z
Reef		1.0481	0.7444	1.41	0.0795
Year (Period)	Reef	3.6065	0.5661	6.37	<0.0001

Four-way interaction	Num DF	Den DF	F-value	Pr>F
Pd*Fishing*Size*Dist	2	83.9	1.53	0.2222

Three-way interactions	Num DF	Den DF	F-value	Pr>F
Pd*Fishing*Size	2	83.9	2.75	0.0695
Pd*Fishing*Dist	2	83.9	1.25	0.2928
Pd*Size*Dist	2	83.9	1.24	0.2937
Fishing*Size*Dist	1	10.5	4.83	0.0513

Two-way interactions	Num DF	Den DF	F-value	Pr>F
Pd*Fishing	2	83.9	0.50	0.6088
Pd*Size	2	83.9	2.88	0.0615
Pd*Dist	2	83.9	0.24	0.7852
Fishing*Size	1	10.5	1.34	0.2719
Fishing*Dist	1	10.5	0.01	0.9252
Size*Dist	1	10.5	13.23	0.0042

Main Effects	Num DF	Den DF	F-value	Pr>F
Period	2	83.9	12.44	<0.0001
Fishing	1	10.5	4.15	0.0675
Size	1	10.5	38.63	<0.0001
Distance	1	10.5	0.02	0.8831

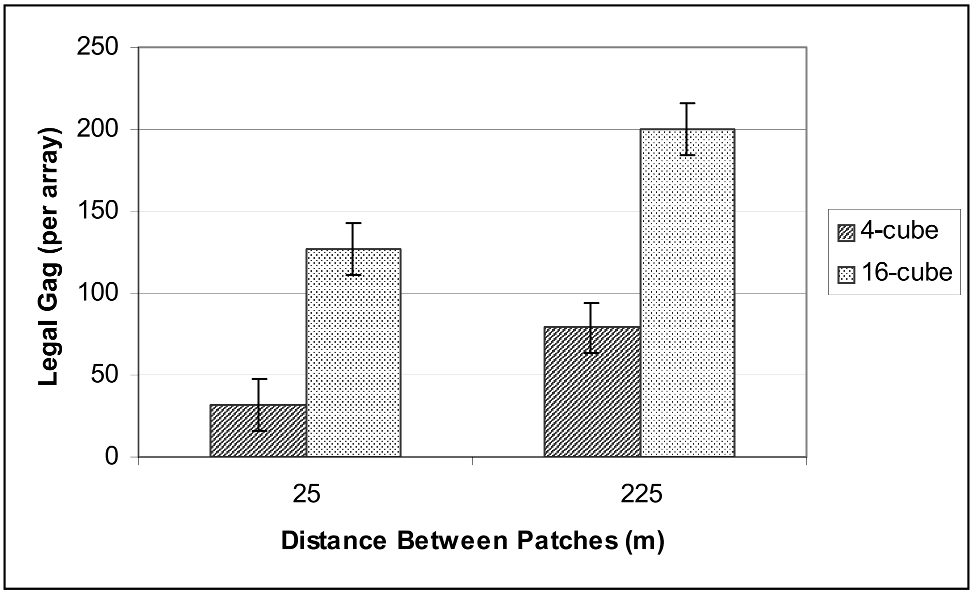

Figure 2. Pre-publication distribution of legal gag grouper on the SRRS. Data are drawn from not-to-be-published arrays due to the influence of pre-publication perturbations on to-be-published arrays.

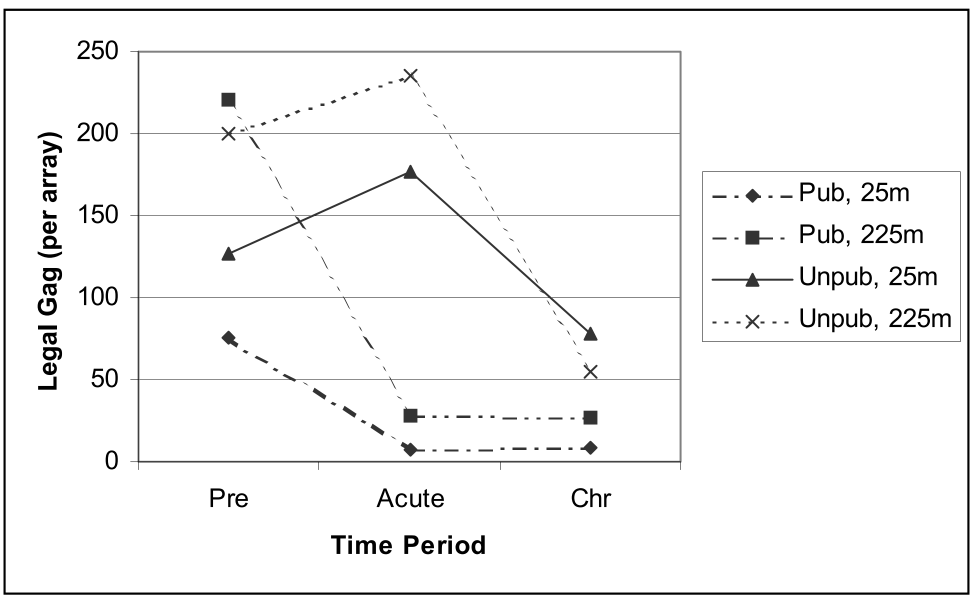

Figure 3. Chronology of impacts to legal gag on 16-cube arrays of the SRRS by array architecture and publication status.

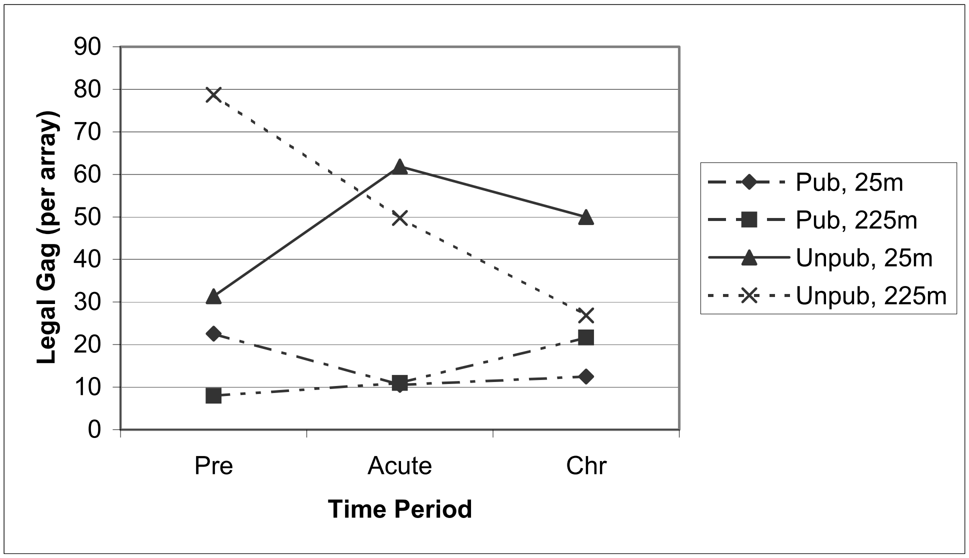

Figure 4. Chronology of impacts to legal gag on four-cube arrays of the SRRS by array architecture and publication status.

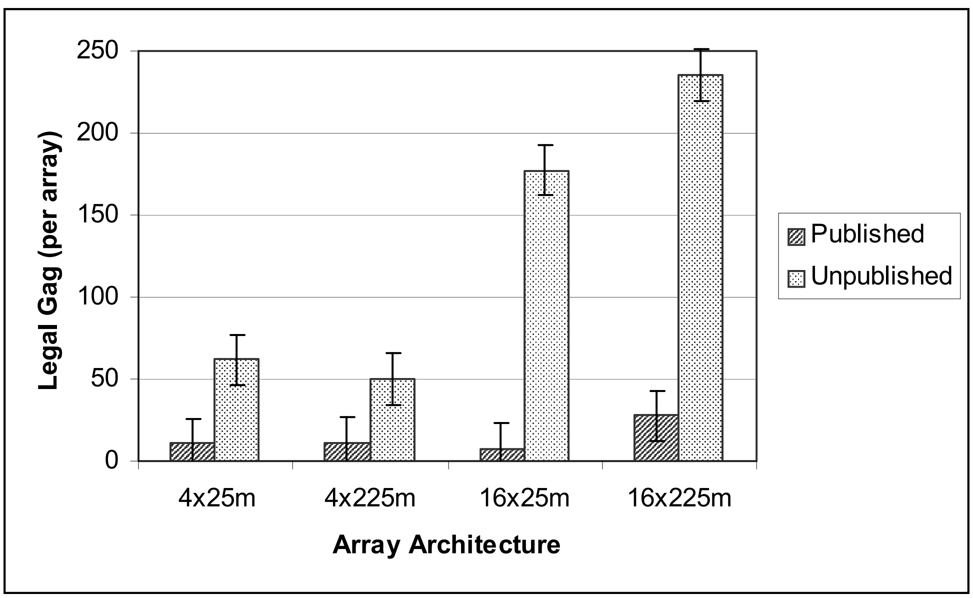

Figure 5. Abundance of legal gag per array within the "acute" period by array architecture and publication status.

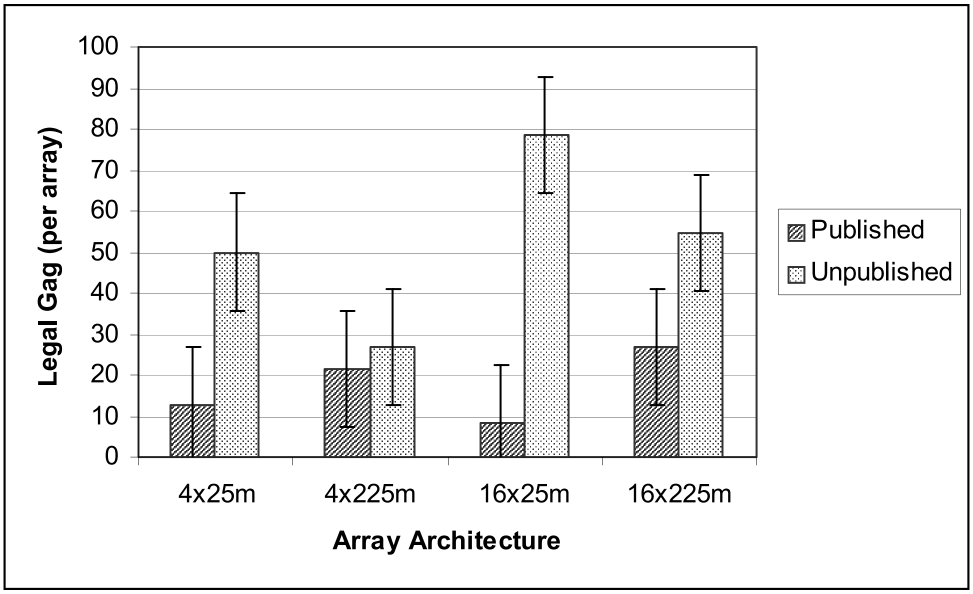

Figure 6. Abundance of legal gag per array within the “chronic” period by array architecture and publication status.

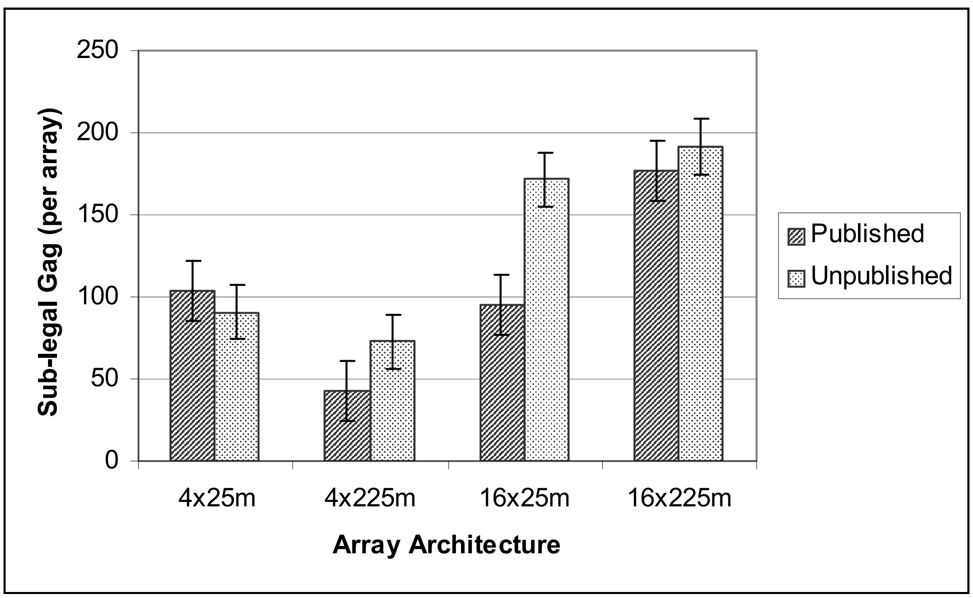

Figure 7. Abundance of sub-legal gag per array, by array architecture and publication status, averaged across all time periods.

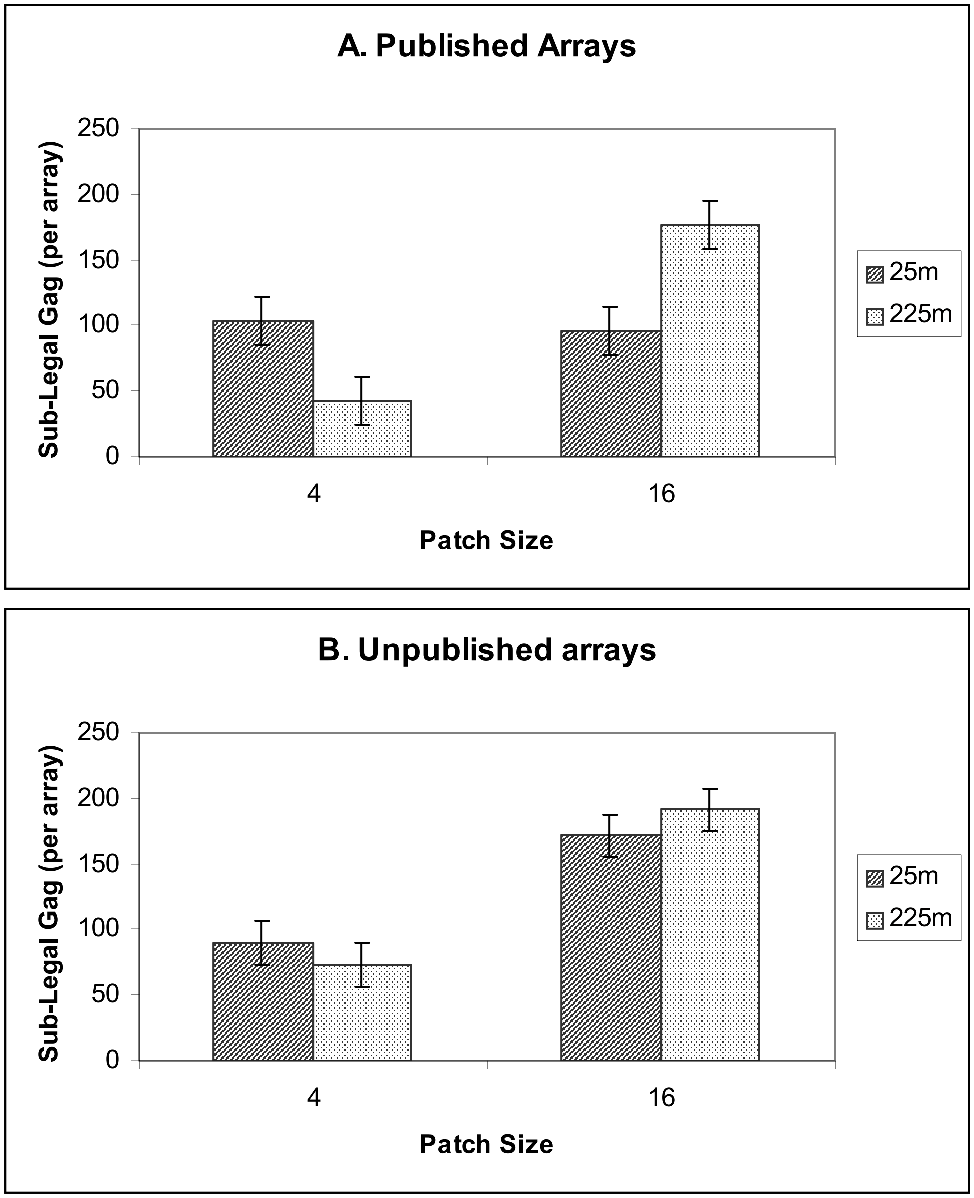

Figure 8. Abundance of sub-legal gag per array, by array architecture on (A) published and (B) unpublished arrays.

CHAPTER 4
DISCUSSION

The SRRS was designed to examine how spatial components of habitat structure affect gag abundance. The subsequent publication of several array locations introduced directed fishing effort as an additional factor. Although no data were collected regarding fishing effort or angler behavior, differences between published and unpublished treatments are assumed to be due to directed fishing. Further, inferences are possible regarding angler behavior based on observed gag abundances on the SRRS. In a survey of recreational anglers in Dade County, FL, over 28% used artificial reef sites, motivated by expectations of high catch rates (Milon, 1989). Fishing effort usually is positively related with fish abundance that "represents a cumulative statistical summation of the effects of individual fisher choices" (Walters and Martell, 2004, p.205). For recreational anglers this leads to a roughly linear relationship between fish abundance and angling effort (Walters and Martell, 2004). On the SRRS this relationship is complicated by the rapid depletion of localized standing stocks of legal gag. The reduction in abundance lowers the benefit to anglers of selecting particular arrays and offers feedback to their decision-making process, but must have a lag as new experiences are likely slow to modify initial impressions and expectations.

This experiment effectively demonstrated the ability of anglers to remove the vast majority of legally harvestable fish from published artificial reefs over the course of only a few years. Once published, size of reef patches had no impact on abundance of legal gag, indicating both large and small patches were fished down to a similar level. Over the six to eight years following publication and the initial rapid reductions in legal gag, effort was apparently redirected to locating unpublished reef arrays. Changes on unpublished reef arrays can likely be attributed to discovery by anglers as they were proportional to predicted impacts based on architecture. Large and widely-spaced patches (those most prone to discovery) experienced declines in abundance, while reef arrays composed of small closely-spaced patches did not change. Patterns in sub-legal gag abundance are driven by significant declines on the most heavily fished arrays (published, 16-cube, 25 m spaced).

Several studies have reported higher abundances of fish on larger habitat patches or patches providing more refuge (de Boer 1978; Roberts and Ormond 1987; Hixon and Beets, 1989; Rountree, 1989; Kuwamura et. al. 1994, Eggleston et. al. 1998; Abelson and Shlesinger 2002). The initial conditions observed on the SRRS with regard to array architecture are thus not surprising. Studies of gag home range on the SRRS (Kiel 2004) and residency (Lindberg et. al. in press) have indicated that reef patches spread 25 m apart are collectively used as a single home-site whereas 225 m spaced patches are used independently.

The fact that fishing had both an immediate and significant impact on the largest aggregations of gag is not surprising. Reductions in catch assumed to be reflective of similar reductions in abundance were observed by Grandcourt (2003) in monitoring the exploitation of a virgin stock of crimson jobfish, *Pristipomoides filamentous*, a shelf-edge hook and line fishery. There are also numerous examples in the literature of comparisons between both recreationally and commercially fished and un-fished areas in which there are more fish and larger fish in protected areas than unprotected ones (Roberts, 1994;

Jennings and Polunin, 1996; Wantiez et. al., 1997, Guidetti et. al., 2005, Kamukuru et. al., 2005) as well as declines over time of exploited stocks (Haedrich and Barnes, 1997; Fogarty and Murawski 1998; McClanahan and Mangi, 2001; Albaret and Lae 2003; Laurans et. al., 2004). Solonsky (1985) demonstrated the significant impact of fishing on artificial reefs in Monterey Bay, CA. A single marked reef was constructed amidst other unmarked reefs. Observed abundance of legal-sized rockfish on the marked reef was reduced after three years of fishing effort relative to the unmarked reefs. Furthermore, tagged fish were observed to move from unmarked reefs to the marked reef, but not vice versa, indicating the potential 'sink' quality of a fished artificial reef. Similar movements of fish (from natural to artificial reefs, but not back) were observed in Puerto Rico (Fast and Pagan, 1974). On the SRRS we had the unique opportunity to examine the manner in which variable spatial qualities of reefs interact with fishing effort to determine the abundance of a targeted species.

Although 25 and 225 m published 16-cube arrays experienced significant declines in abundance of legal gag following publication, the predicted refuge effect of more widely spaced arrays was only marginally significant in the "acute" period. There are several potential mechanisms for such a refuge effect. Since gag treat 25 m arrays as a single home-site, fishing effort, even when focused on a single patch, is effectively fishing the entire array due to the movement of gag among patches. There is also a significant margin of error for non-anchored fishing techniques (drift-fishing or trolling) on 25 m arrays. Should the boat's course not take it over the intended patch, it is far more likely to encounter gag on another patch, or between patches. Furthermore, 25 m spaced arrays are likely to be more appealing to spear-fishermen who can easily swim between patches in search of legal gag. All of these factors likely contribute to higher attractiveness to anglers of 25 m arrays relative to 225 m arrays. An additional consideration is that 225 m spaced patches may recruit more gag as a result of their larger footprint, simply by an increased chance of encounter by gag, however, immigration rates and residence times under fished conditions, relative to removal rates by anglers are unknown.

While the publication of array locations led to a rapid depletion of legal gag on 16-cube patches, 4-cube patches did not change significantly with publication. Both their smaller size and lower abundances of gag make them more difficult to locate and fish effectively. Furthermore, the four cube arrays were likely less attractive to anglers based on the common conception that smaller reefs hold fewer fish. Although there was no significant change on the published four-cube arrays between the “pre” and “acute” periods, there was a significant effect of publication within the “acute” period (more legal gag on unpublished arrays). Keeping in mind that there were randomization restrictions in assignment of publication treatments because of earlier perturbations, the effect of publication on four-cube arrays may have been to maintain low abundances on these arrays, rather than to depress them below their pre-publication levels.

The immediacy of the decrease in gag abundances following publication is further emphasized by the fact that none of the published treatments demonstrated any significant further decreases between the “acute” and “chronic” periods. A new equilibrium abundance appears to have been reached in which legally harvestable fish were maintained at low levels by fishing activities. The increase in the minimum size of recreationally harvestable gag between the “acute” and “chronic” periods had the potential to further decrease abundances of legal gag as those between 508 and 550 mm would be considered sub-legal in the “chronic” period. There was, however, a significant decrease of sub-legal gag between these periods, indicating that this was a minimal effect in relation to the other processes affecting abundances of legal and sub-legal gag on the SRRS.

Because the SRRS represents only a way-point in the spatially stage-structured life history of gag, there is a constant immigration to and emigration from the reefs. In studies done prior to introducing the publication treatment, mean residence time for an individual gag was 9.8 months (Lindberg et. al. in press). It is assumed that newly arriving gag make a decision as to whether to stay or not based on current conditions on the patch. Although density-dependent habitat selection has been confirmed for gag (Lindberg et. al., in press), the exact influence of the standing stock of gag on an array in the decision making process of newly arriving gag is unknown. On arrays depleted by fishing, it seems reasonable that newly arrived legal-sized gag would find themselves among the dominant fish present and be more likely to stay on the reef than if there was a full compliment of un-fished legal gag present. In this manner there may be a higher percentage of newly arrived gag deciding to stay on published patches, thus making themselves vulnerable to fishing, than on unpublished patches or patches prior to publication. Fully understanding the rate at which gag arrive, and the proportion of those taking up residence, as well as criteria important in making such a decision, would be a big step forward in understanding the implications of fishing on habitat selection and habitat-specific mortality risk.

The tendency of gag to aggregate in specific habitats known to recreational anglers fits the definition of an 'ecological trap' (Schlaepfer et. al., 2002). The concept of ecological traps has most widely been applied to terrestrial environments. Ecological traps result when an organism makes a mal-adaptive habitat selection, due most frequently to an anthropogenic change or manipulation of the environment, based on cues that over evolutionary time were correlated with improved fitness. In the marine environment, the tendency of many game-fish species to associate with structure can be interpreted as an ecological trap. Once discovered by anglers, high quality habitat (both artificial and natural) will continue to attract and aggregate both fish and the anglers targeting them. In the case of the SRRS, the artificial reef patches are high quality habitat (Lindberg et. al. in press) providing gag both refuge and a prey base. The outcome, however, is an aggregation accurately predictable in space, leading to the removal of the majority of legally harvestable gag. The decision to take up residence on published patches of the SRRS seems to meet the criteria of an ecological trap (Schlaepfer et. al. 2002), but could only be conclusively defined as such with complete knowledge of the overall reproductive success of gag taking up residence on the SRRS relative to those inhabiting natural hard-bottom habitats.

One of the most telling results is the lack of any significant difference between size treatments of both published and unpublished arrays during the "chronic" period. While other factors such as catch-ability of legal gag and by-catch of under-sized gag factor into the benefit to anglers of fishing an array, the primary focus is assumed to be harvest of legal gag, and each size of reef provides similar potential harvest at its new equilibrium abundance. This indicates that the additional shelter on 16-cube patches does not provide gag any greater protection from fishing relative to the four-cube arrays. Also, when constructing reefs for the benefit of the gag, the additional investment in construction materials is not justified by its potential to house more legal gag under conditions where recreational fishing will occur.

The predictable impacts of fishing on the SRRS extend beyond the published arrays. Ultimately the unpublished arrays of the SRRS are all predicted to become discovered. Thus the rate of progression from their un-fished state in the pre-publication period and "acute" period to their moderately-fished state in the "chronic" period is an indication of their combined ease of discovery and subsequent value as fishing sites. Between the "acute" and "chronic" periods, unpublished 16-cube arrays, in both spacing treatments, experienced significant declines in legal gag. This is believed to be due to increased fishing effort, most likely from directed efforts in response to declining catches on published arrays, but also possibly due to simple chance, to locate sites that were known to exist. Sixteen-cube arrays would be the most susceptible to discovery as they have a larger footprint than four-cube arrays, and larger aggregations of gag, thus providing the largest targets for searching anglers. Of the four-cube arrays, only the 225-meter spaced treatments showed significant effects of discovery. The probability of a searching angler encountering an array is higher on more-widely and systematically spaced arrays where there is likely less overlap of the areas used by gag on different patches. As the types of array architectures within the SRRS were publicly known, discovery of one patch within an array should be interpreted as discovery of the array as a whole.

Impacts of directed fishing extended beyond the removal of legally-harvestable gag to the sub-legal gag. All comparisons involving published, 16-cube, 25-meter arrays demonstrated the impacts of fishing pressure on sub-legal gag. This treatment apparently received the highest level of fishing effort and thus was the first to demonstrate effects of that angling pressure trickling down to the sub-legal gag. First, there were more sub-legal gag on unpublished arrays of this architecture than published arrays. Second, there was no difference between this treatment and 4-cube, published arrays at the 25-meter spacing. In all other treatment combinations, 16-cube arrays held more sub-legal gag than 4-cube arrays as would be expected by the amount of shelter provided. Finally, published, 25-meter spaced, 16-cube arrays had fewer sub-legal gag than the more widely-spaced, published, 16-cube arrays, a pattern that was not observed among the unpublished arrays. Hooking mortality, illegal harvest, and induced emigration are all potential mechanisms by which sub-legal gag may be affected. No data were collected to determine the relative importance of these mechanisms. Catch and release associated mortality from recreational anglers has been measured to be as high as 20 % from headboat fisheries (R. Dixon, NMFS, personal communication). These gag, however, were caught from a minimum depth of 25 m where there is a greater effect of swim bladder expansion than occurs on the SRRS in 13 m of water, and they were not followed beyond release. Both depth-related effects as well as hooking effects contribute to release mortality. In a study of depth-related capture-release mortality on gag, where gill or gut-hooked fish were not included, no gag caught from 20 m of water showed any adverse depth-related effects of being caught (C. Koenig, FSU, unpublished data). Hooking mortality on another serranid, *Epinephelus quoyanus*, in shallow waters (<2m) of the Great Barrier Reef, where depth related effects were not a factor, was found to be highest at 5.1% when bait-fishing with single hooks (Diggles and Ernst, 1997). Actual catch and release mortality on the SRRS is likely close to this figure, as bottom-fishing with natural bait is a very common technique. It is likely that many legal gag are hooked several times before being landed and that sub-legal gag are both hooked and landed without being harvested from the system. Beyond hooking mortality, the role these experiences play in modifying behavior and possibly residence times of surviving gag may be of importance.

The main effect of time period on sub-legal gag abundance manifested itself in a decreasing trend over time. The only significant change, however, was from the "acute" period to the "chronic" period. The lack of an interaction with publication makes interpretation somewhat troublesome. It is possible that there were simply several years of smaller year-classes of gag colonizing the SRRS. The continued directed angling efforts both on published and unpublished arrays following the "acute" period, however, certainly contributed to the decline.

This study has revealed an interaction of spatial qualities of habitat and angling pressure, mediated by detailed information of those habitat qualities, in determining local abundances of a targeted reef-dependent species. The relative benefit to gag that occupy small patches of artificial habitat are clear. Widely-spaced patches within an array increase the probability of a single patch being discovered. Discovery of a single patch, in this case, should lead to discovery of the array as a whole as anglers are familiar with the layout of patches in the SRRS. While the end results have been demonstrated there is still uncertainty in the precise mechanisms, and their relative importance, combining to produce the observed patterns. Identifying and quantifying these mechanisms would be important for applying the results of this study to management decisions for gag, other fish and other systems. Additional information regarding the usage and opinions of the SRRS in the angling community could validate several of the assumptions and inferences made herein as well as increase the applicability of conclusions drawn in this study. The publication of detailed geographic information in this case allowed anglers to select or disregard fishing sites according to their expectations of success based on habitat architecture. The continued development of such detailed information regarding natural habitats will enhance efficiencies in the exploitation of natural resources.

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BIOGRAPHICAL SKETCH

The author was born in Washington, D.C. During his early years he was fascinated by the fish, frogs, turtles and insects that he caught and raised and watched in his neighborhood streams and ponds. As early as pre-school he was the tender of the class aquarium. His first exposure to the scientific method came from Stanley Edwards, his science teacher from fourth through sixth grades. Mr. Edwards effectively conveyed his own passion for the sciences and natural world.

During summer vacation following his sophomore year of high school, he began volunteering for Dr. Marjorie Reaka-Kudla, a coral reef biologist at the University of Maryland. Being invited on a two-week research trip to the Florida Keys as a 16-year-old who was half way through high-school convinced him he was in the right field. Involvement in her research continued through his high school years.

He attended the University of California at Santa Barbara from which he graduated in 1998 with a Bachelor of Science degree in aquatic sciences. After graduation he returned to the University of Maryland, this time working with Dr. David Secor of the University's Chesapeake Biological Laboratory. Following three years as a faculty research assistant he decided to return to school in pursuit of a master degree. The opportunity to again work beneath the water drew him to the University of Florida where he studied under Dr. William J Lindberg.

Following graduation he has accepted a position in Gainesville, FL, with Golder Associates, an environmental consulting firm.