

DENSITY-DEPENDENT HABITAT SELECTION AND PERFORMANCE BY A LARGE MOBILE REEF FISH

WILLIAM J. LINDBERG,^{1,5} THOMAS K. FRAZER,¹ KENNETH M. PORTIER,^{2,6} FREDERIC VOSE,^{1,7} JAMES LOFTIN,^{1,8}
DEBRA J. MURIE,¹ DORAN M. MASON,^{3,4} BRIAN NAGY,¹ AND MARY K. HART^{1,9}

¹Department of Fisheries and Aquatic Sciences, University of Florida, 7922 NW 71st Street, Gainesville, Florida 32653 USA

²Department of Statistics, University of Florida–IFAS, Gainesville, Florida 32611 USA

³NOAA Great Lakes Environmental Research Laboratory, Ann Arbor, Michigan 48105 USA

⁴NOAA Atlantic Oceanographic and Meteorological Laboratory, Miami, Florida 33149 USA

Abstract. Many exploited reef fish are vulnerable to overfishing because they concentrate over hard-bottom patchy habitats. How mobile reef fish use patchy habitat, and the potential consequences on demographic parameters, must be known for spatially explicit population dynamics modeling, for discriminating essential fish habitat (EFH), and for effectively planning conservation measures (e.g., marine protected areas, stock enhancement, and artificial reefs). Gag, *Mycteroperca microlepis*, is an ecologically and economically important warm-temperate grouper in the southeastern United States, with behavioral and life history traits conducive to large-scale field experiments. The Suwannee Regional Reef System (SRRS) was built of standard habitat units (SHUs) in 1991–1993 to manipulate and control habitat patchiness and intrinsic habitat quality, and thereby test predictions from habitat selection theory. Colonization of the SRRS by gag over the first six years showed significant interactions of SHU size, spacing, and reef age; with trajectories modeled using a quadratic function for closely spaced SHUs (25 m) and a linear model for widely spaced SHUs (225 m), with larger SHUs (16 standardized cubes) accumulating significantly more gag faster than smaller 4-cube SHUs (mean = 72.5 gag/16-cube SHU at 225-m spacing by year 6, compared to 24.2 gag/4-cube SHU for same spacing and reef age). Residency times (mean = 9.8 mo), indicative of choice and measured by ultrasonic telemetry (1995–1998), showed significant interaction of SHU size and spacing consistent with colonization trajectories. Average relative weight (W_r) and incremental growth were greater on smaller than larger SHUs (mean W_r = 104.2 vs. 97.7; incremental growth differed by 15%), contrary to patterns of abundance and residency. Experimental manipulation of shelter on a subset of SRRS sites (2000–2001) confirmed our hypothesis that shelter limits local densities of gag, which, in turn, regulates their growth and condition. Density-dependent habitat selection for shelter and individual growth dynamics were therefore interdependent ecological processes that help to explain how patchy reef habitat sustains gag production. Moreover, gag selected shelter at the expense of maximizing their growth. Thus, mobile reef fishes could experience density-dependent effects on growth, survival, and/or reproduction (i.e., demographic parameters) despite reduced stock sizes as a consequence of fishing.

Key words: artificial reefs; colonization; density-dependent habitat selection (DDHS); essential fish habitat (EFH); gag; habitat patchiness; habitat quality; *Mycteroperca microlepis*; residency; shelter.

INTRODUCTION

Density-dependent habitat selection (DDHS; Rosenzweig 1981, 1985), along with the ideal-free distribution (IFD; Fretwell and Lucas 1970, Fretwell 1972) and some mating system models (e.g., Verner 1964, Orians 1969), are based on similar reasoning (see MacCall

1990) with roots in optimal foraging theory (Rosenzweig and Abramsky 1997). The general concept is that mobile animals that occupy patchy habitats and exploit patchy resources are expected to choose their location based on the intrinsic quality of habitat patches (i.e., resource quality and abundance) and the density of competitors for those resources. The chosen location is expected to yield greater individual fitness than the immediate alternatives, and proxies for fitness (e.g., growth or fecundity) are generally measured for empirical tests (Morris 1989). As a process, DDHS involves behavioral mechanisms associated with movement (e.g., immigration, emigration, residency, home range, orientation/search, dispersal, etc.) and resource use (i.e., food, shelter, or mates; preferences; and competition).

Manuscript received 17 August 2004; revised 25 July 2005; accepted 17 August 2005. Corresponding Editor: P. S. Levin.

⁵ E-mail: wjl@ufl.edu

⁶ Present address: American Cancer Society, 1599 Clifton Road NE, Atlanta, Georgia 32329 USA.

⁷ Present address: Golder Associates, Inc., 6241 NW 23rd Street, Gainesville, Florida 32606 USA.

⁸ Present address: School of Marine Sciences, University of Maine, Orono, Maine 04473 USA

⁹ Present address: Department of Biology, University of Kentucky, Lexington, Kentucky 40506 USA.

The existence of DDHS, which is expressed at the individual level, has important consequences for population and community dynamics. For example, DDHS can be an important process affecting the coexistence of competing species (Rosenzweig and Abramsky 1997), perhaps including tropical (Robertson 1996) and temperate adult reef fishes (Hixon 1980, Larson 1980, Schmitt and Holbrook 1990, Holbrook and Schmitt 1995). Furthermore, spatially structured populations may be regulated (*sensu* Osenberg and Mittelbach 1996), in part, by DDHS. If so, then field studies of DDHS are essential to spatially explicit population modeling efforts (Conroy et al. 1995, Dunning et al. 1995, Wennergren et al. 1995).

So far, however, the capacity for DDHS has been mostly demonstrated in terrestrial systems, for example, selection of nesting sites by birds (Pleszcynska 1978, Petit and Petit 1996), habitat types by mammals (Morris 1987), and mating/oviposition sites by insects (Parker 1970, 1974). Milinski's (1979, 1984, 1986) laboratory experiments using freshwater fish and contrasting rates of prey inputs clearly showed that fish can choose feeding locations consistent with theory. To date, the capacity for DDHS has been inferred for only a few marine reef fishes, and most have been in the special contexts of settlement (e.g., Sweatman 1983, 1985, Stimson 1990, Schmitt and Holbrook 1996) and mating systems (e.g., Warner and Hoffman 1980*a, b*). Moreover, research on DDHS for reef fishes has been restricted to small, highly site-attached fishes that occupy lower trophic levels of coral reef systems (but see Fishelson et al. 1987). MacCall (1990) and Kramer et al. (1997) reviewed the applicable theory and examples of DDHS (or frequency-dependent habitat selection) by free ranging fishes, but there were few documented marine examples (e.g., juvenile cod, *Gadus morhua* and *G. ogac*, Laurel et al. 2004, but see also Shepherd and Litvak 2004), and none among large, mobile, reef fishes.

Nevertheless, DDHS is an ecological process with profound fisheries management implications, especially for reef fish. Large, mobile, reef fishes are vulnerable to overfishing as they concentrate over specific types of benthic habitat. Not only does this characteristic of their behavior focus fishing effort, it can also make traditional fishery statistics misleading (e.g., Rose and Kulka 1999). Knowledge of how reef fish use patchy reef habitat and the potential consequences on demographic parameters is needed to understand and predict their population and community dynamics. Furthermore, how and why motile reef fish distribute themselves among habitat patches is of the utmost importance for identifying essential fish habitat (EFH).

Much is known about patterns of fish-habitat associations, but much less is known about the underlying mechanisms. While density-independent processes are no doubt important to the distribution and abundance of reef fishes (Doherty and Williams 1988,

Doherty 1991; but see Williams 1991), our current understanding of reef fish ecology also incorporates density-dependent processes and pluralistic causation (Warner and Hughes 1988, Doherty 2002, Forrester et al. 2002, Hixon and Webster 2002, Osenberg et al. 2002, Shima and Osenberg 2003). Studies of density-dependent postsettlement mortality with small, site-attached, reef fish have contributed much to our current thinking about population regulation, yet other density-dependent processes are also important (Levin et al. 2000).

Terrestrial ecologists (e.g., Wiens 1984, 1989, Wiens et al. 1993) have emphasized that ecological relationships among habitat types are important, and in marine ecology, trophic coupling between benthic habitat types is well recognized (Ogden et al. 1973, Parrish 1989, Ambrose and Anderson 1990; see review by Graf 1992). However, to the best of our knowledge, trophic coupling and habitat-selection processes have not been examined together in the same experimental marine system. In general, tests of DDHS have dealt with one resource at a time, typically food or shelter. When food is manipulated, the space between habitat patches is often regarded as an empty impediment to movement. When shelter is manipulated, foraging away from shelter sites may be acknowledged (e.g., Petit and Petit 1996), but is generally not part of the study design. We are building on earlier work (Lindberg et al. 1990, Frazer and Lindberg 1994) to integrate trophic coupling (i.e., among hard-bottom, soft-bottom, and pelagic habitats) with habitat selection for a better understanding of mechanisms regulating reef fish populations.

Here, we test components of DDHS using an experimental reef system in the Gulf of Mexico, and indicate how the interplay between sheltering and feeding habitats (e.g., Werner and Gilliam 1984) mediates individual growth dynamics of gag, *Mycteroperca microlepis*. We selected gag as our study species because of its economic and ecological importance (Turner et al. 2001, Levin and Grimes 2002), its dominance in our study region, and its life history characteristics, behavior, and ecology, which simplified testing habitat-related processes of general consequence for reef fisheries management. Our results support a consistent and strong argument for the importance of DDHS in explaining how reef habitat affects fisheries production and how management actions might affect that relationship.

Predictions and hypotheses

If gag are capable of density-dependent habitat selection (DDHS), then residency times, and therefore gag abundances, should be greatest on reefs that offer the greatest net individual benefits (e.g., greater condition, growth, and/or survival). We first tested effects of habitat patchiness on gag colonization and residency times by manipulating patchiness while controlling habitat complexity, with the expectation that colonization patterns and residency times should be functions of

reef habitat patchiness (size and distance between reefs). Second, we tested whether gag growth and condition are greater on more preferred than less preferred reefs by sampling a subset of reef arrays without replacement. If gag are cueing on food as the basis for DDHS, then gag relative weights and growth rates should either equilibrate among reef types or be greatest on those reef types with the greatest residency times. Alternatively, if this correspondence is not observed, then it can be inferred that gag are cueing on shelter as the primary basis for DDHS.

The results from the first set of experiments generated the general hypothesis that gag growth and condition are density-dependent as a function of shelter availability. To test whether reef habitat, specifically available shelter, limits local densities of gag, and thereby regulates their growth and condition on the shallow continental shelf, we manipulated shelter in otherwise equivalent reef units, and sampled nondestructively. Thus, with reef size held constant, (1) gag densities should decline when shelter volume is reduced, and (2) gag growth and condition should increase when gag densities decline. We also tested, and validated, an assumption that our manipulation of gag shelter did not alter their prey base.

MATERIALS AND METHODS

Study organism

Gag are protogynous hermaphrodites that spawn during late January to early March in deep-water aggregations along the shelf edge break in the north-eastern Gulf of Mexico (Coleman et al. 1996, Koenig et al. 2000, see also Brule et al. 2003). Males primarily exist at deep-water sites and transitional males are not generally found inshore (C. Koenig, *personal communication*). Larval gag settle in shallow seagrass beds (Koenig and Coleman 1998, Koenig and Colin 1999) and other structural habitats nearshore (Keener et al. 1988, Levin and Hay 2003) during late spring to early summer. They grow rapidly (up to 18.6 cm total length [TL]) until emigrating from nursery habitats during the fall of their first year (Ross and Moser 1995). Older and larger juveniles typically reside across a broad shelf area (Bullock and Smith 1991).

On the shallow shelf, gag home ranges around structures are variable (approximately 350 m maximum width [Kiel 2004]). Small groups of gag (2–10 individuals/group) typically meander together (W. Lindberg, *personal observation*), and move closer to rocky shelters with increasing disturbance (e.g., divers or potential predators). With moderate disturbance or threat, gag typically keep structure between themselves and the source, moving through cover and staying close to it. A few may individually move away from reef structure, blanch cryptically, and lie motionless in shallow sand depressions distant from the reef. With intense disturbance or threat, gag pack cavities (Fig. 1) that are otherwise rarely occupied.

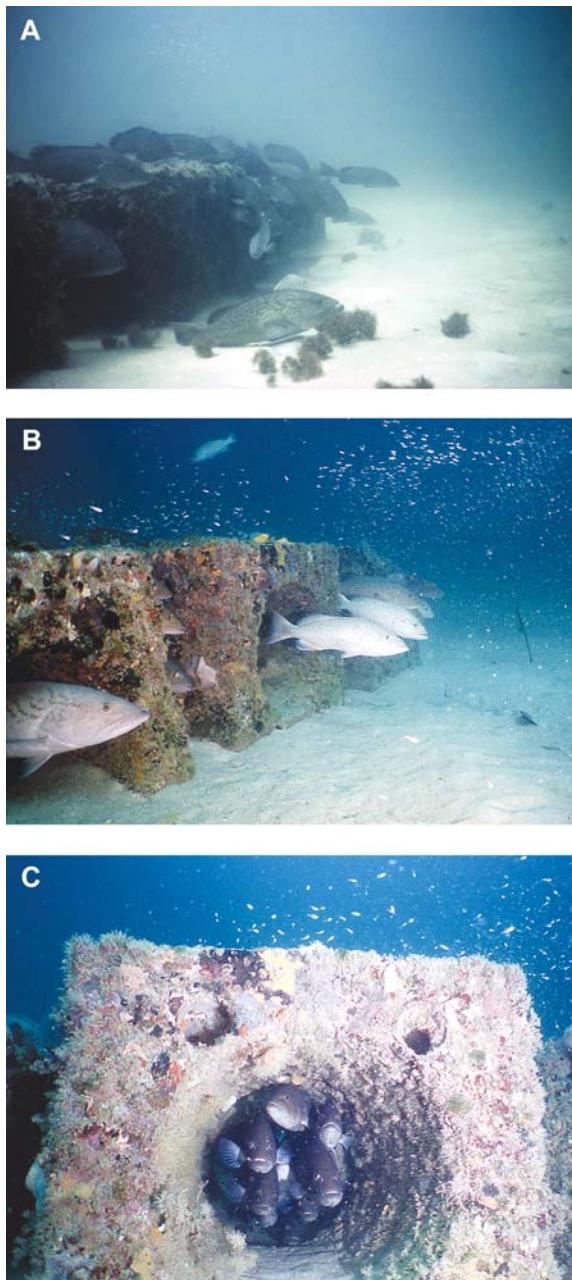


FIG. 1. Numerous gag (A) closely associating with reef structure, (B) emerging from shelter after disturbance, and (C) densely packed within a standard habitat unit (SHU) in response to intense disturbance. Photo credits: (A) J. Hale, (B and C) L. Kellogg.

Gag switch to piscivory with increasing size (Weaver 1996). In all but the coldest months, schooling pelagic planktivores (e.g., Spanish sardine, *Sardinella aurita*; scaled sardine, *Harengula jaguana*; tomtate, *Haemulon aurolineatum*; round scad, *Decapterus punctatus*) are their primary prey (in one study, 67.2–94.8% gross energy consumption; D. Murie, *unpublished data*). On flat, low-

relief, hard-bottom habitat, small groups of gag meander, spatially associated only with schools of pelagic planktivores rather than small hard-bottom features (L. Kellogg, unpublished data). Hobson (1968) described similar prey-tracking behavior for *Mycteroperca rosacea* in the Gulf of California. Gag in the study area also prey on demersal fishes and epibenthic or pelagic macroinvertebrates that dwell in open habitat (e.g., sand perch, *Diplectrum formosum*; pinfish, *Lagodon rhomboides*; *Portunus* crabs; and *Loligo* squid), and to a much lesser extent on reef associated fishes (e.g., black seabass, *Centropristis striata*; white grunt, *Haemulon plumieri*; belted sandfish, *Serranus subligarius*; and pigfish, *Orthopristis chrysoptera*), none of which utilize the cavities manipulated for the shelter experiment (see *Shelter manipulation experiment*) reported here (W. Lindberg, personal observation; D. Murie, unpublished data).

Experimental system

The Suwannee Regional Reef System (SRRS) in the northeastern Gulf of Mexico (Fig. 2A) manipulates reef habitat patchiness, and thus the densities experienced by gag with respect to both sheltering habitat and their surrounding foraging areas (Lloyd 1967, Antonovics and Levin 1980, Lindberg et al. 1990, Walters and Martell 2004). The SRRS consists of 22 hexagonal arrays of standard habitat units (SHUs) (Fig. 2B) located along the 13-m depth contour. The concrete SHUs are either 4-cube or 16-cube squares with aligned central cavities (61 cm diameter) and corner holes (10 cm diameter). Within an array, SHUs are all the same size and spaced at 25, 75, or 225 m. Core areas of gag home ranges (i.e., circular 50% kernels, average radius = 38.3 m, $n = 9$; B. Kiel, unpublished data) do not overlap between SHUs spaced at 225 m, but should overlap among SHUs spaced at 25 m (Fig. 2C). Thus, arrays are the replicates for testing effects of reef patchiness, and total gag abundance per array is a composite measure for the densities experienced due to SHU size and spacing.

Twelve SRRS arrays were built during 1990–1991, giving two initial replicates for each combination of SHU size and spacing. Ten arrays were built during 1992–1993, giving two additional replicates of the 25-m and 225-m treatments for both SHU sizes, plus an additional 4-cube \times 25-m array and 16-cube \times 25-m array. Reef treatments were interspersed geographically by randomizing locations within four strata along the line of reef arrays (north, north-central, south-central, and south).

The SRRS is not a part of the gag nursery habitat inshore where settlement and postsettlement processes occur, but rather it is on the shallow shelf where older and larger juveniles typically reside (Bullock and Smith 1991). Prereproductive females (20–90 cm TL, smaller gag rare) occupy the SRRS and natural hard-bottom habitat across a broad shelf area. Gag large enough to be sexually mature (>60 cm TL; Hood and Schlieder 1992) occupy the SRRS, however, developed gonads

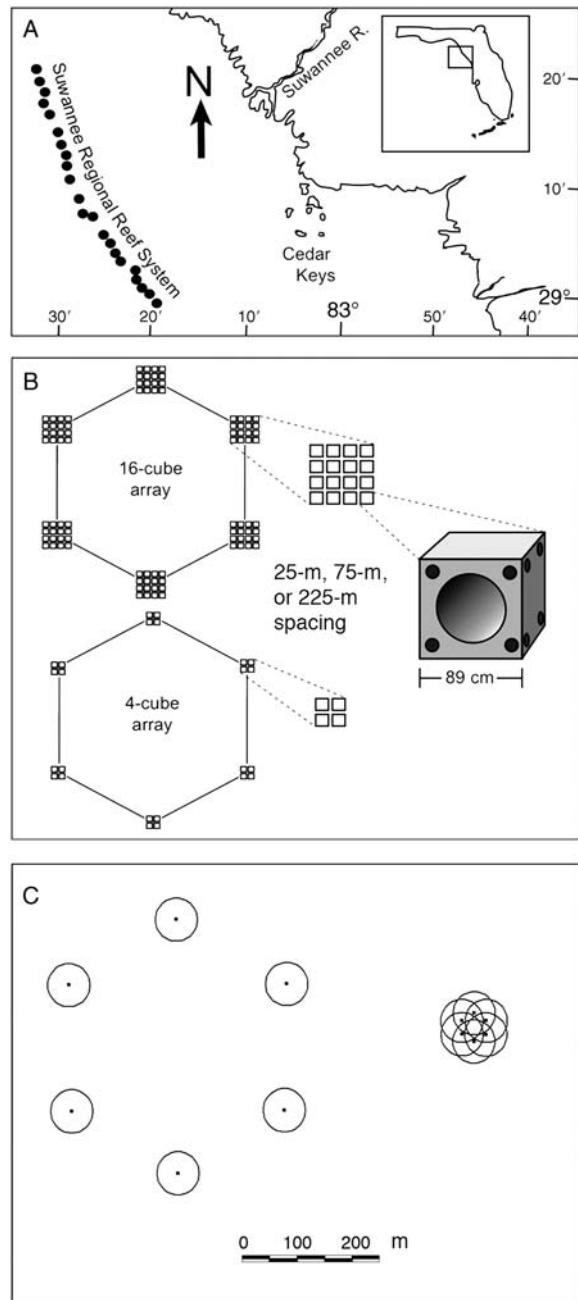


FIG. 2. The Suwannee Regional Reef System (SRRS). (A) Locations of 22 experimental reef arrays offshore from Cedar Key, Florida, USA, along Florida's north-central Gulf coast (inset). (B) Hexagonal arrays of SHUs at each location have equal-sized SHUs, either four or 16 prefabricated concrete cubes, and 25-m, 75-m, or 225-m spacing. (C) Average 50% kernel core areas of gag drawn to scale on 225-m and 25-m arrays (dots represent SHUs; circles represent core area); total core area/array equals 27 687 m² and 15 190 m², respectively.

have not been found in gag sampled from these sites ($n = 81$) during November and December. Fishery returns of ultrasonic tags validated an assumption that maturing gag move naturally through the SRRS.

Percentage of hard bottom was estimated by point-intercept sampling along a 75-m transect line deployed from each SHU in an array; i.e., transect bearings north SHU 0°, northeast SHU 60°, southeast SHU 120°, south SHU 180°, southwest SHU 240°, and northwest SHU 300°. Bottom type was classified as sand or rock at 0.5-m intervals along each transect. The criterion for sand was a depth of at least 5 cm, as determined by metal probe, whereas rock was classified as areas with sand <5 cm deep to rock profiles >10 cm. In summary, the seabed at SRRS reef arrays is typically sand, sand/shell mix, and low-relief limestone, mostly covered with a thin sand veneer. The percentage of cover of hard bottom varies among arrays, but is fairly consistent within any given array.

A localized fish kill in the summer of 1995 affected the five southernmost SRRS sites and reefs were not sampled in winter 1996. In November 1996, the locations of nine SRRS reef arrays were published for access by recreational fishers as part of another experiment on fishing effects.

SRRS experiment

Colonization is density dependent and a function of habitat patchiness.—From June 1991–August 1996, fish were censused on the SRRS once each summer (mid-June through August) and winter (January through March). Trained SCUBA divers searched methodically around and then within each SHU for 20 min and visually counted all fish species. The minimum, maximum, and average total length (cm TL) of each fish was estimated using meter sticks or scaled T-bars (Bohnsack and Bannerot 1986). Through winter 1994, only the initially constructed 25-m and 225-m replicates for both SHU sizes were sampled; the 75 m treatments were not sampled because of logistic constraints. Beginning in summer 1994, all 22 reef arrays were sampled, however, the 75-m treatments were not analyzed to retain a balanced experimental design. All reef arrays were surveyed in 1995 and 1996, but the data from arrays affected by the 1995 fish kill were not included in statistical analyses reported here.

For this paper, only summer data from replicates of the 4-cube \times 25-m, 16-cube \times 25-m, 4-cube \times 225-m, and 16-cube \times 225-m treatment combinations were used to test the colonization trajectories for gag. Physically, each treatment had four replicates, but differences in construction dates and the fish kill resulted in unequal sample sizes across the six summers.

A mixed-effects general linear model was used for colonization analyses. SHU-specific gag counts were summed across all SHUs on a reef array and then square-root transformed to produce a reef-specific gag density response. This was combined with a measure of average percentage of hard bottom within 75 m of SHUs in an array. Because measurements over time were taken on the same reefs, temporal correlation in within-reef residuals was assumed and a pooled estimate of the

autocorrelation in temporal residuals was used. A linear time trend was estimated and interactions with SHU size and spacing effects were tested using *F* tests based on restricted maximum likelihood estimates (Littell et. al 1996, Verbeke and Molenberghs 2000). The need for a quadratic time trend was tested and accepted, while more complex model forms, such as those having different slopes for different reef sizes or spacings, were not supported by the data. The assumption of a compound symmetry temporal residual structure fit poorer than the autoregressive structure. Normality of the model residuals was examined graphically with probability plots and formally with a Shapiro-Wilks test. We checked the model test by fitting a generalized linear mixed model for Poisson counts using the GLIMMIX macro (GLMM800.sas; SAS Institute 2003). Test *P* values were very close to the normal mixed-model fits. We used results from the normal mixed model for predictions because of its greater simplicity of form. All computations were performed using procedures in SAS Version 9 (SAS Institute 2003). Only the final significant model results are reported.

Residency is density dependent and a function of habitat patchiness.—Between June 1995 and June 1996, a total of 81 gag (40–75 cm TL) were surgically implanted with uniquely coded ultrasonic tags (20 Sonotronics model CT-82-2, 48 kHz, 14 mo battery life; and 61 Sonotronics model CT-82-3, 75 kHz, 48 mo battery life [Sonotronics, Inc., Tucson, Arizona, USA]). The 48- and 75-kHz tags were interspersed across reef treatments, and labeled to facilitate fishery returns. Five fish per reef array (six on one 16-cube \times 225-m array), each from different SHUs, were captured by hook and line or fish traps, tagged under anesthesia (MS-222), allowed to recover in aerated ambient seawater, and then returned immediately by divers to their original SHU.

At each SRRS array, the presence or absence of tagged fish was determined monthly from July 1995 to August 1997, and then every two months until May 1998, using a Sonotronics ultrasonic receiver and directional hydrophone from the boat. If present, the fish's location was determined specific to SHU location, except for fish on 25-m arrays.

To examine shorter term SHU-to-SHU movements, 20 tagged gag were relocated precisely for three consecutive days over two time periods, 11–13 September and 23–25 September 1996, on arrays with 25-m ($n = 7$ fish), 75-m ($n = 6$ fish), and 225-m ($n = 7$ fish) SHU spacing. Locations of tagged fish were determined using the surface hydrophone from the boat, except on the 25-m site where a diver, positioned centrally in the array, used an underwater ultrasonic receiver (Datasonics DPL-275; Benthos Undersea Systems, Inc. Falmouth, Massachusetts, USA).

Residence time was defined as number of days from tagging to last relocation. Mean residence times of five fish per array and coefficients of variation (cv) per array were used as replicates in two-way ANOVAs, testing

effects of reef type (two sizes \times three distances; $n = 2$ and 3). Coefficients of variation adjusted for small sample sizes (Sokal and Rohlf 1995) gave the same results as unadjusted values, so we report unadjusted results. One fish still present at the end of telemetry sampling was assigned a departure date of 31 May 1998, to factor conservatively into these averages. Our estimates of residence time are also conservative because gag were resident for an unknown period before they were tagged, measured residence times for 20 fish could not exceed the 14-mo battery life of their tags, and the 48-mo tags had a failure rate higher than expected (e.g., five out of six tags initially returned by fishermen had failed within 29 mo). Known tag failures were distributed equally across all reefs arrays.

Gag growth and condition correspondence with reef preference.—Gag performance was contrasted among reef treatments as average relative weight (i.e., fish weight adjusted for length) and as recent growth estimated from otolith marginal increments. In November 1996, at the onset of directed fishing on a subset of SRRS sites, five to 19 fish per reef array ($N = 80$) were collected from six arrays (three 4-cube and three 16-cube). Gag were collected with hook and line or fish traps tended daily. In addition, 54 gag from unspecified natural hard-bottom habitats in the vicinity of the SRRS were obtained from a commercial fisher. Maximum total length and weight was recorded for each fish, with the sagittal otoliths collected and stored dry.

Relative weights, W_r , were calculated as described by Wege and Anderson (1978), using the weight-length relationship reported by Schirripa and Goodyear (1994) for gag in the Gulf of Mexico as the standard. The mean W_r and cv for each array were used as replicates ($n = 3$) in t tests to compare 4-cube and 16-cube treatments. Gag size distributions did not differ between treatments ($P = 0.311$), so the alternative test for W_r proposed by Brenden et al. (2003) was not necessary.

Opaque bands visible in sagittal otoliths are an accurate measure of gag age (Hood and Schlieder 1992). Incremental growth was measured from 0.5-mm transverse sections of otoliths using Image-1 video analysis computer software (Universal Imaging, Inc., Westchester, Pennsylvania, USA). Each otolith was measured along an axis on the proximal (internal) medial surface, from the focus to the distal edge of each opaque growth ring. Incremental growth of each fish (in mm TL) since last annulus formation was then determined by back calculating from the size of fish at capture, as a ratio of otolith marginal increment to axis length. Mean incremental growth per array was compared between 4-cube and 16-cube treatments ($n = 3$) using a t test.

Shelter manipulation experiment

Available shelter was manipulated on four unpublished arrays with 4-cube SHUs spaced at 75 m and 225 m. In late August and early September 2000, screens (2.5

\times 5.1 cm vinyl-coated wire mesh) were secured over the large central cavities of SHUs to create three treatments (Fig. 3): full closure, half closure, and no closure. Eight SHUs of each treatment ($n = 8$) were blocked equally among the four arrays ($N = 24$; Fig. 3). Treatments were distributed symmetrically within arrays, rather than randomly, to control for minor spatial autocorrelation of gag abundance among SHUs prior to manipulation (K. Portier, unpublished analysis).

Shelter volume limits gag density.—All 24 SHUs were censused for fish in May 2000 (premanipulation) and within seven discrete two-week sampling periods in September, October, and December of 2000, and January, April, May, and August of 2001. Sampling was not done when underwater visibility was less than 5 m. A trained SCUBA diver used the census protocol previously described, except fish size estimates were made in 10-cm TL increments. Abundances were tabulated for gag > 50 cm TL (large gag) and gag < 50 cm TL (small gag), corresponding to the approximate size at sexual maturity and legal harvest at the time of study.

Gag growth and condition are regulated by local gag density.—Gag from a subset of replicates of each treatment were sampled with replacement (using fish traps) to obtain measurements for calculating W_r . Total length (cm) and weight (g) were recorded on site for all grouper captured and released (34 gag > 50 cm TL from eight SHUs, and 45 gag < 50 cm TL from 10 SHUs, for a total of 79 gag from 11 SHUs on two SRRS arrays). Gag weight was a calibrated average of 300 readings recorded over a 90-s period using an Ohaus I-10 industrial balance (Ohaus Corporation, Pine Brook, New Jersey, USA) connected to a laptop computer. Gag growth was not estimated from otoliths, owing to the nondestructive sampling with replacement necessary to avoid altering local densities.

Raw census data were square-root transformed ($\sqrt{x+0.5}$) to achieve normality and homogeneity of variances. Repeated-measures mixed-effects linear models (GLMM800.sas; SAS Institute 2003) were used to test for effects of shelter treatments on large gag and small gag for the period of experimental closure. Only data from the seven postmanipulation sampling periods were analyzed. The shelter manipulation was analyzed assuming a split-plot design with array as the main plot and SHU as the split plot. The treatments were factorial, with the main-plot factor being the spacing of SHUs within arrays and the split-plot factor being the closure treatment. An a priori power analysis (K. Portier, unpublished data) concluded that sufficient power would be attained by this design to detect large treatment differences (i.e., residual SD = effect SD), but, because of high variance estimates and limits on replication, detecting small effects (e.g., residual SD = $2 \times$ effect SD) would be unlikely. In the analysis, the treatment effect was split into an array effect and an array-within-spacing effect. Percentage of cover of hard bottom per SHU was included as a fixed-effect covariate. Time was

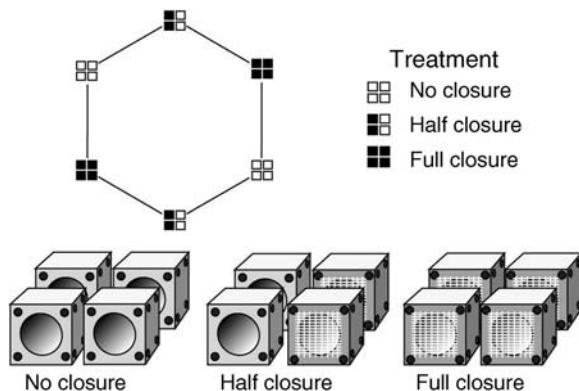


FIG. 3. The shelter experiment had replicate 4-cube SHUs of each treatment uniformly distributed among four SRRS arrays. Screens installed on large central cavities restricted access for large fish without blocking water flow or access for small species.

treated as a repeated measure and all estimable second- and higher-order interactions were included in the model. Follow-up analysis on residual assumptions included graphical (probability and scatter plots) and formal testing (Kolmogorov-Smirnov test with $P > 0.15$) methods. Higher-order interactions were examined with profile plots.

Uncoupling shelter from food experimentally.—On comparable arrays (i.e., 4-cube SHUs spaced at 225 m) that were not part of this shelter experiment, gag ($n=99$) consumed (1) pelagic planktivorous fishes (82% numerical abundance, 84% occurrence, 58% gross energy consumption); (2) SHU-dwelling demersal fishes (2% numerical abundance, 12% occurrence, 29% gross energy consumption); and (3) demersal fish and invertebrates from surrounding benthic habitats (16% numerical abundance, 26% occurrence, 12% gross energy consumption) (D. Murie, unpublished data). On SHUs in this experiment, we compared abundances of major prey types among treatments for (1) and (2) but not (3), as species dwelling away from SHUs could not be affected directly by cavity screening.

Specifically, we measured pelagic prey fish abundance on two of the four reef arrays in mid July, early August, late August, and early October of 2002. The transducer of a Simrad EY500 120 KHz echosounder (Puget Sound Instrument Company, Inc., Tacoma, Washington, USA) was mounted on a 1-m tow body and towed alongside the research vessel at a depth of approximately 1 m at approximately 2.5 m/s. Acoustic transects traversed each SHU along random headings at least five times to ensure full ensonification of schools present. Equipment performance was monitored using an oscilloscope and digital echogram recorder. Raw digitized acoustic signals were time-marked and geocoded using differential GPS (DGPS) with submeter accuracy. Routine calibrations were performed using a tungsten carbide reference sphere (Foote 1990).

Estimates of total pelagic fish abundance were determined for each transect (five transects per SHU) and combined to estimate abundance for each SHU. Raw acoustical data were processed using Echoview software (Sonardata, Hobart, Australia) to estimate fish school volume, relative fish density within the school, and relative total biomass. Fish schools were identified and delimited into two-dimensional regions, with each region comprised of several (4–157) 2-m horizontal bins. Each two-dimensional bin within a school was converted to a three-dimensional volume by assuming a spherical geometric shape; total volume of the school was determined by summing across bin volumes (Coetzee 2000). Relative fish density was determined by echo-squared integration (Powell and Stanton 1983, Thorne 1983) on the identified school. Relative total biomass was determined by multiplying relative biomass density by school volume. Relative biomass estimates were \log_{10} transformed and used in a repeated-measures analysis of variance (SAS Institute 2003) to test for differences in relative abundance between shelter treatments.

We tested SHU-dwelling demersal prey with tomtate (*H. aurolineatum*) and white grunt, using square root-transformed ($\sqrt{x+0.5}$) census data from December 2000 and January 2001, and analyzed the data with repeated measures, treatment by blocks ANOVA (SAS Institute 2003). We also censused and analyzed black seabass and belted sandfish abundances for direct and indirect effects from differences in gag abundance (Hart 2002), and those results are in another manuscript. Here, we note that black seabass were most abundant on full-closure treatments where gag numbers were significantly reduced, and belted sandfish showed treatment effects positively correlated with gag only when black seabass, the intermediate predator, was episodically present in January 2001.

Thus, we validated an assumption that closures of large cavities within SHUs would not directly affect major prey types. While indirect community responses might affect minor prey species, any cascading effects due to changes in gag abundance would not violate our assumption. However, without a thorough community analysis comparing these treatments, we cannot conclusively uncouple shelter availability from prey availability.

RESULTS

SRRS experiment

Colonization is density dependent and a function of habitat patchiness.—Gag colonized the reef arrays of contrasting habitat patchiness in a manner consistent with DDHS and an interplay between sheltering habitat and the surrounding foraging area. SHU size, spacing, and age (i.e., colonization period) interacted significantly to affect gag abundance (Table 1), and the nature of those interactions confirmed density-dependent colonization by this motile reef fish. Larger SHUs accumu-

TABLE 1. Mixed-model ANOVA results for summer gag counts (square-root transformed) from the Suwannee Regional Reef System, testing the effects of reef size (4-cube and 16-cube standard habitat units [SHUs]), spacing (25 m and 225 m), and reef age (1–6 yr) on colonization shown in Fig. 4.

Effect	Type	Numerator		Denominator		Chi-square		F ratio	
		df	df	χ^2	P	F	P		
Size \times spacing \times age	linear	4	40	38.34	<0.0001	9.59	<0.0001		
Size \times spacing \times age	quadratic	4	40	9.90	0.0422	2.47	0.0597		
Average hard bottom		1	12	3.31	0.0690	3.31	0.0940		
Fixed effect	Type	Size	Spacing	Estimate	SE	df	t	P	
Intercept				9.9028	0.9694	12	10.22	<0.0001	
Size \times spacing \times age	linear	4	25	4.6017	3.4963	40	1.32	0.1956	
Size \times spacing \times age	quadratic	4	25	-4.5736	2.1645	40	-2.11	0.0409	
Size \times spacing \times age	linear	4	225	7.9796	3.0010	40	2.66	0.0112	
Size \times spacing \times age	quadratic	4	225	-0.7596	1.9732	40	-0.38	0.7023	
Size \times spacing \times age	linear	16	25	5.3981	3.3640	40	1.60	0.1164	
Size \times spacing \times age	quadratic	16	25	-5.5026	2.3797	40	-2.31	0.0260	
Size \times spacing \times age	linear	16	225	16.0614	3.0754	40	5.22	<0.0001	
Size \times spacing \times age	quadratic	16	225	-0.1229	2.1144	40	-0.06	0.9539	
Average hard bottom				5.4587	3.0018	12	1.82	0.0940	

lated gag much faster than smaller SHUs, yet the large, closely spaced, SHUs saturated by year 3 (Fig. 4). The colonization trajectories of closely spaced SHUs were quadratic for both SHU sizes (Table 1). In contrast, the trajectories through time for widely spaced SHUs were

linear (Table 1), with indications of saturation beginning between years 5 and 6 (Fig. 4). The appendix explains how to predict abundance from Table 1.

Residency is density dependent and a function of habitat patchiness.—Gag showed high site fidelity and prefer-

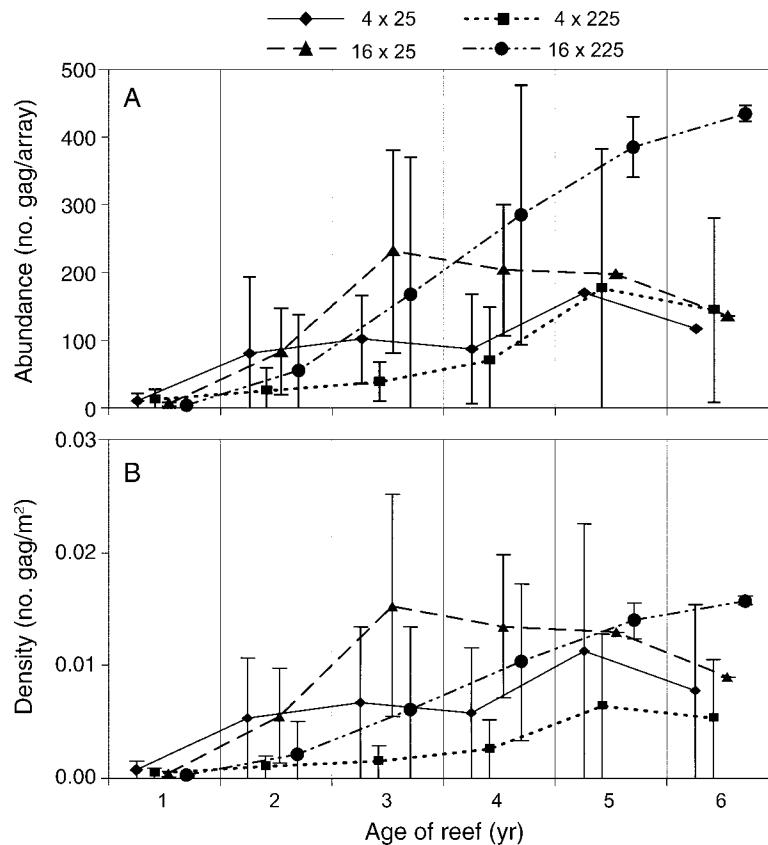


FIG. 4. Colonization trajectories of SRRS treatment combinations based on (A) gag total abundance per array (mean \pm SD) and (B) gag density per array (mean \pm SD, total abundance/m² total core area; see Fig. 2C). Key: 4 \times 25, 4-cube SHUs spaced at 25 m; 16 \times 225, 16-cube SHUs spaced at 225 m, etc. The means at each reef age have been offset so error bars are distinguishable.

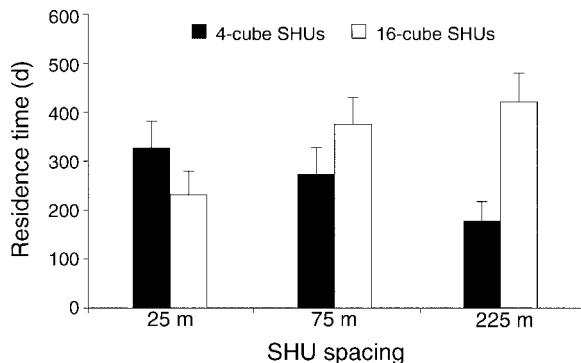


FIG. 5. Residence times (mean + SE) of 81 ultrasonically tagged gag on SRRS reef treatments, showing significant interaction ($P < 0.001$) of standard habitat unit (SHU) size and spacing.

ences among reef arrays of contrasting habitat patchiness (Fig. 5). Average residency time was 298 d ($n = 81$ fish; residency = $83.6 - 0.19t + 0.000117 t^2$, where t is time in days; $r^2 = 0.994$). However, SHU size and spacing interacted significantly to affect residency times ($P < 0.001$, Fig. 5). Residency times were greater on 16-cube SHUs than 4-cube SHUs, except at the 25-m spacing where gag moved freely among SHUs. For the 16-cube SHUs, residency times increased significantly with SHU spacing ($P < 0.05$), while for the 4-cube SHUs, the opposite was true ($P < 0.05$). Residency time coefficients of variation for replicate reef arrays were not affected by SHU size and spacing ($P = 0.234$).

Frequency of movement between SHUs in an array was significantly affected by SHU spacing ($P = 0.019$ using daily telemetry data), with greater movement among SHUs that were more closely spaced. Over two three-day periods, fish movement did not differ significantly between the 25-m and 75-m treatments (median 2.0 vs. 1.5 movements/d), but the 225-m treatment had no recorded movements of gag among SHUs. In addition, from monthly telemetry data, more than five times as many gag moved among SHUs within an array at 75 m than at 225 m (averages of 40.4 % and 7.9%, respectively; $P < 0.001$), with no significant effect of SHU size ($P = 0.966$).

Among the 81 gag originally implanted with ultrasonic tags and monitored monthly for residency times, there were 31 cases involving 29 individuals where the fish left and subsequently returned. The average time absent was 101 d (range = 26–397 d), with error in that estimate acknowledged due to coarse sampling intervals. The return frequencies were dependent on reef treatments ($\chi^2 = 5.266$, $df = 2$, $P \approx 0.076$). For 16-cube reefs, the 25-m treatment had fewer returns than expected, while the 75-m and 225-m treatments had more than expected. For 4-cube reefs, the 225-m treatment had fewer returns than expected, while the other two treatments had more. This qualitative pattern of gag returns was consistent with the interaction of SHU size and spacing that affected

residency times (Fig. 5). No ultrasonically tagged gag were recorded as moving from one array to another.

Although not intended as a mark–recapture study, 23 of the original 81 ultrasonically tagged gag were reported from the fishery. Of these, seven were caught on the SRRS after some arrays were opened to public fishing in November 1996. The remainder had emigrated mostly to the west or northwest of their release points (Fig. 6), consistent with maturing gag transiting the shallow shelf over time. Two were recaptured in the western Gulf, and these reports were confirmed with direct telephone calls by the senior author to the reporting fishers.

Gag growth and condition are lower on preferred habitats.—We assumed that an average residency time of 298 d for gag at SHUs was long enough for measurable performance factors, such as growth and condition, to be attributable to reef treatments.

Gag condition, as measured by average relative weights (W_t) was significantly affected by reef type ($P = 0.025$, Fig. 7A). Gag from the 4-cube SHUs were significantly heavier for their lengths than were those from 16-cube SHUs (104.2% vs. 97.7%). Follow-up comparisons involving the 54 commercially caught fish from natural hard-bottom habitat could not be statistically tested because fishing sites had been pooled in the catch. However, average relative weights of these fish were indistinguishable from fish from the 16-cube SHUs (Fig. 7A). Relative weights were significantly more variable on 4-cube than 16-cube SHUs (mean cv = 7.18% and 4.72%, respectively, $P = 0.028$), which is to be expected if colonization was from a common pool and assimilation was greater on 4-cube SHUs, despite the shorter mean residency times. Gag average incremental growth from otoliths was also greater on 4-cube SHUs



FIG. 6. Geographic distribution of 23 tag returns from the fishery for 81 gag implanted with ultrasonic transmitters and released on the SRRS. Open circles represent seven fish recaptured on the SRRS and indicate the general release points. Solid circles are recapture locations for gag that emigrated. The two open squares are locations of known gag spawning aggregations closed to fishing by the Gulf of Mexico Fishery Management Council.

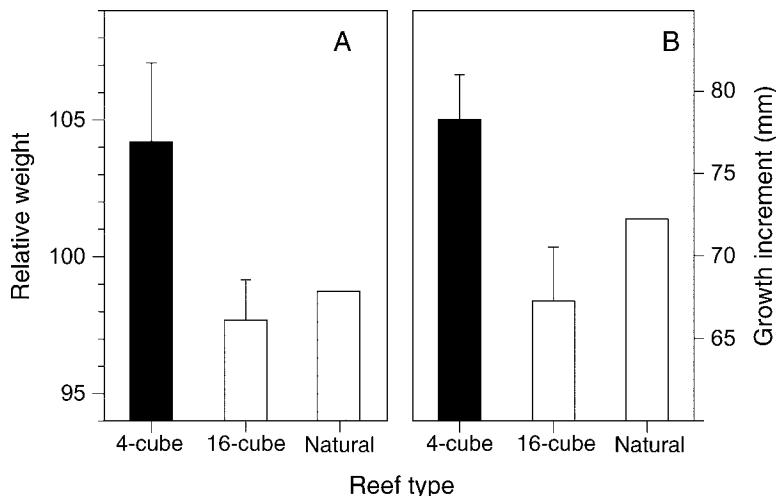


FIG. 7. Performance of gag as (A) relative weights (mean ± SE) and (B) incremental growth in total length (mean ± SE) for SRRS arrays ($n = 3$) with small vs. large SHUs, and compared to natural reefs of the region (15 gag/SRRS array; 54 gag in one sample from natural habitat).

than on 16-cube SHUs ($P = 0.059$, $1 - \beta = 0.450$, Fig. 7B). For these data, gag from the SRRS had been previously exposed to little or no fishing pressure (i.e., density reductions), whereas the fishing history of the natural hard-bottom was unknown, but presumed exploited.

Shelter manipulation experiment

Shelter volume limits gag density.—Abundance of gag >50 cm TL showed a significant response to the closure treatments (Table 2). Abundance shifted as expected, with highest abundances at no-closure sites and lowest at full-closure sites (Fig. 8A). By the first postmanipulation sampling periods, i.e., September and October 2000, large gag had redistributed and by December 2000 and January 2001, large gag showed a pronounced response to treatment. In April and May 2001, abundance had dropped significantly and the treatment effect was weak. A significant interaction between

percentage of hard bottom and treatment suggests that the strength of the treatment response was, at least partially, a function of the surrounding habitat (Table 2). To further examine this interaction, data were partitioned between arrays with higher and lower percentages of nearby hard bottom (Fig. 9A and B,

TABLE 2. Analysis of covariance results from the shelter closure experiment for gag > 50 mm total length (TL).

Effect	df	F	P
Spacing	1	1.32	0.3699
Array (spacing)	2	0.74	0.2307
Treatment	2	5.12	0.0294*
Spacing × treatment	2	1.12	0.3626
Hard bottom	1	1.85	0.1766
Spacing × hard bottom	1	3.93	0.0504
Treatment × hard bottom	2	4.85	0.0099*
Spacing × treatment × hard bottom	2	2.12	0.1253
SHU (array (spacing) × treatment)	10	1.18	0.1186
Time	6	4.69	0.0111*
Time × spacing	6	0.87	0.5468
Time × array (spacing)	12	1.37	0.0853
Time × treatment	12	1.23	0.2731
Time × spacing × treatment	12	0.68	0.7702
Error	96		

* $P \leq 0.05$, $MSE = 0.4922$.

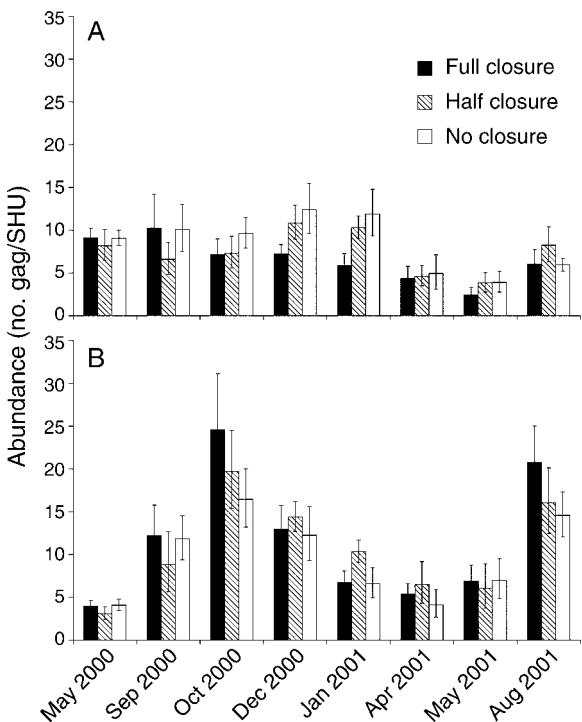


FIG. 8. Abundances of gag per SHU per sampling period (mean ± SE) for three treatments: no cavities closed, half of the large cavities closed, and all such cavities closed for (A) gag >50 cm TL and (B) gag <50 cm TL. May 2000 was pretreatment, and cavities were closed in late August 2000.

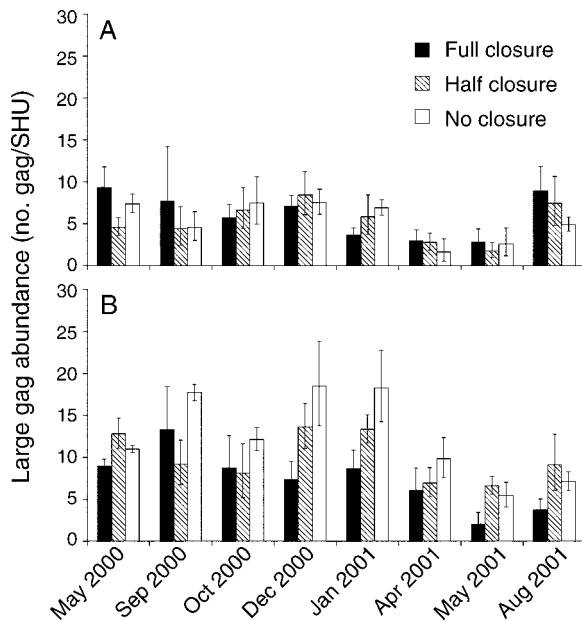


FIG. 9. Abundances per sampling period (mean \pm SE) for large gag (> 50 cm TL) on SHUs with no large central cavities closed, half of the large central cavities closed, and all such cavities closed from (A) two SRRS arrays with average percentage of surrounding natural hard bottom of 33% and 35% ($n = 6$ /array) and (B) two SRRS arrays with average percentage of surrounding natural hard bottom of 6% each ($n = 6$ /array). May 2000 was pretreatment, and cavities were closed in late August 2000.

respectively). This revealed a strong response to shelter treatments for large gag (>50 cm TL) on SHUs with little nearby hard bottom. Small gag abundance did not respond to shelter manipulations, but in October 2000 and August 2001 abundance peaked, suggesting periodic movement onto these reefs (Fig. 8B).

Gag growth and condition are regulated by local density.—Condition, calculated as W_r , was affected as

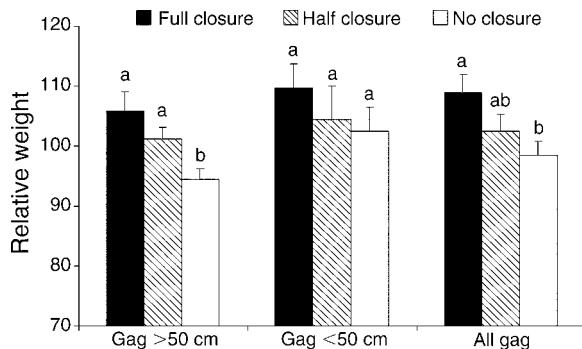


FIG. 10. Relative weights of large (>50 cm TL), small (<50 cm TL), and all gag from the three reef cavity treatments (grand mean \pm SE). Different letters above the histograms indicate pairwise comparisons that differ significantly ($P < 0.05$) within that size class.

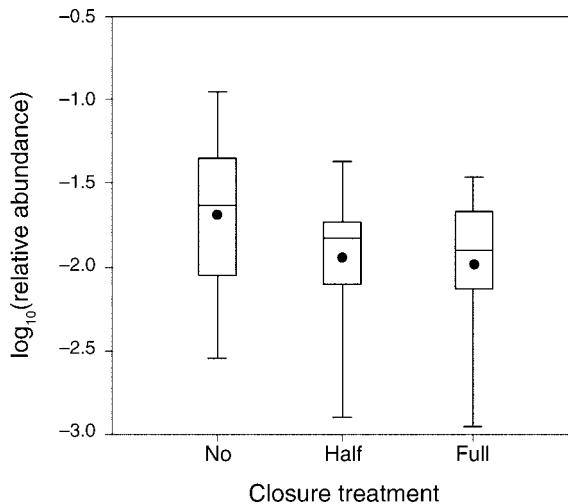


FIG. 11. Log-transformed relative abundance of pelagic prey fishes with respect to reef closure treatment for summer 2001 (dot, mean; horizontal line, median; bottom box, 25% quartile; upper box, 75% quartile; and vertical bar, range).

predicted for large gag (>50 cm TL, $P = 0.0418$, with full closure \approx half closure \geq no closure; Fig. 10), but no differences were found for small gag (<50 cm TL, $P = 0.4583$), or for all gag combined ($P = 0.0710$). However, in pairwise comparisons for all gag combined, the full-closure treatment was significantly greater than the no-closure treatment ($P = 0.0260$, Fig. 10).

Prey abundance is not altered by experimental shelter manipulation.—Relative abundance of pelagic prey fishes did not differ across the three closure treatments (Fig. 11), nor did shelter closures affect the winter abundance of white grunt ($P = 0.920$) or tomtate >8 cm TL (schooling tomtate <8 cm were included in the pelagic prey analysis). The larger tomtate occurred on too few replicates to test statistically, but were similarly distributed among closure treatments. Thus, prey fish abundance could not account for differences in gag abundance and condition between treatments.

DISCUSSION

While it is generally recognized that density-dependent ecological processes play an important role in fish population dynamics, and, in turn, have important implications for fisheries management, density-dependent habitat selection has not been adequately considered in the ecology of mobile reef fishes that support economically important fisheries. Investigating whether gag, an ecologically important and valued commercial and recreation fish, exhibit DDHS and how reef habitat and gag density interact to affect fish growth and condition has important management implications. As habitat management becomes increasingly integrated with fisheries management (e.g., Magnuson-Stevens Fishery Management and Conservation Act

mandating essential fish habitat [EFH] and NMFS guidelines for EFH [*available online*]),¹⁰ the predictability of habitat effects on rates of growth, survival, reproduction, and production will become increasingly important. In particular, spatial and temporal variation in these rates will be determined by changes in population size (MacCall 1990) and independent factors such as intrinsic habitat quality (*sensu* Kramer et al. 1997). Important independent factors to be considered will be those characteristics of habitat that are exploited by mobile fishes through various adaptations, including the behavioral and ecological components of DDHS that we tested.

Our study found that gag are capable of DDHS since patterns in residency times among reef types indeed matched patterns of abundance, as expected (Turchin 1998), and density-dependent colonization depended on habitat patchiness. However, the greatest relative weights and growth increments did not correspond to the reef types with the greatest residency times and abundances. Instead, these measures of production were greatest on the smaller, more widely scattered SHUs.

In fishes, differences in condition and growth presumably affect demographic rates (e.g., Lambert and Dutil 2000, Marteinsdottir and Begg 2002, but see also McIntyre and Hutchings 2003, Koops et al. 2004), and are sometimes used as proxies for fitness (e.g., Hughes and Grand 2000, Munday 2001). Since gag growth and condition were lowest on preferred reefs, we can infer that gag are cueing on something other than food for DDHS. If gag are selecting habitat initially on the basis of shelter rather than food, and if growth and condition are negatively density dependent, then, importantly, subsequent reproductive success may involve significant trade-offs between the shelter requirements and feeding ecology of prereproductive gag (e.g., Werner and Gilliam 1984, Grand and Dill 1997, Sih 1997, Walters and Korman 1999, Dahlgren and Eggleston 2000, Walters 2000).

The results from our shelter-closure experiment supported the hypotheses that reef habitat, specifically available shelter, can limit local densities of gag, and thereby regulate their growth and condition in shallow continental shelf habitats. Our results are even more compelling because of the low power of this relatively large-scale experiment, determined a priori. Only major, not subtle, differences could be detected, and all of the observed differences among treatments were in the expected directions. Furthermore, these differences were not likely due to unrecognized treatment effects on prey abundance because we accounted for prey species comprising most of the consumption by gag in this system.

At the most basic level, our findings that gag select habitat in a density-dependent manner, combined with

the likelihood of cryptic density dependence among reef fishes (Shima and Osenberg 2003, Overholtzer-McLeod 2004), argues against relying on observational sampling and mapping alone for the identification of EFH. Results from our shelter experiment also reinforce that differences in fish densities expected among habitats can vary over time (see Osenberg et al. 2002), and with the context of surrounding habitat. This challenges the incipient field of marine landscape ecology to move quickly past spatial correlations for mapping habitat associations and abundance patterns, and toward an integration of spatial processes into practical fisheries models of population and community dynamics (e.g., Mason and Brandt 1999).

Moreover, any assessment of EFH or potential marine protected areas for prereproductive gag must take into account the spatial distribution of suitably sized shelter, as that might constitute a demographic bottleneck (e.g., Beck 1995, 1997) mediated through energetic processes (Jones and McCormick 2002) rather than numeric responses (e.g., St. Mary et al. 2000, Halpern 2004). Many others have noted the importance of shelter to reef fishes (e.g., Shulman 1985, Hixon and Beets 1993, Frazer and Lindberg 1994, Jones and McCormick 2002), and here we connected shelter to density and density to condition and growth.

Gag population dynamics are spatially stage structured with highly variable reproductive parameters (Collins et al. 1998, Turner et al. 2001). Our tag returns from the fishery confirm an export of SRRS gag to the broader stock, consistent with maturing females transiting the continental shelf (Bullock and Smith 1991, Hood and Schlieder 1992). Female size and age at first reproduction are highly variable (570–980 mm TL [Collins et al. 1998]; 3–6 yr [Hood and Schlieder 1992]), and batch fecundity estimates (BFE) are most strongly related to total length ($BFE = 1.773 \times 10^3(TL) - 1.119 \times 10^6$, $r^2 = 0.60$, size range = 690–1065 mm TL [Collins et al. 1998]). The number of batches per year increases with age, but varies interannually (Collins et al. 1998). We found differences of 6% in condition and 15% in growth for prereproductive females from contrasting reef treatments (Fig. 7). All other things being equal, and given the equation just cited, a 15% difference in TL would yield a 58% difference in fecundity at the upper end of the size range for first reproduction; fecundity differences would be even more substantial toward the lower end of the size range. However, this is overly simplistic. For example, it is not yet known whether higher growth rates experienced at any given location are finite gains offset by subsequent use of less favorable habitat, or if they help to set individual growth trajectories (see Armsworth and Roughgarden 2005) with reproduction and management consequences (see Alonzo and Mangel 2004, 2005). We infer that habitat-related differences in growth and condition of gag incurred during their prereproductive transition across the shelf may contribute to variation in the age of first

¹⁰http://www.nmfs.noaa.gov/habitat/habitatprotection/efh/efh_guidelines.htm

reproduction and batch fecundity, but not to the interannual variation in batches per year reported by Collins et al. (1998). The latter is more likely related to interannual variation in condition experienced by reproductively active females further offshore. Efforts to estimate the distribution of reef habitat quality across the shelf and to model these spatial dynamics within the gag population are now underway.

The existence of DDHS and interaction between the size and spacing of reef habitats also has important implications for artificial reef applications. The diminishing return of gag abundance and performance with increasing SHU size and decreasing SHU spacing suggests that, if reefs are built ostensibly to enhance gag stocks rather than enhancing fishing success (Lindberg and Relini 2000), then they ought to be small, widely scattered patch reefs with appropriately sized cavities. Such reefs can enhance the biological production of gag locally, while the individuals are in residence. Our results also suggest that the attraction–production issue pertaining to artificial reefs is a false dichotomy (Lindberg 1997), in that high densities of fish like gag result from processes such as DDHS rather than behavioral artifacts (Bohnsack 1989). Whether or not artificial reefs are ecological traps (*sensu* Schlaepfer et al. 2002) depends on associated fishing mortality. To evaluate their potential contributions to regional stocks (e.g., Grossman et al. 1997), the relationships between numeric and energetic processes must be much better known (Persson et al. 1997, Jones and McCormick 2002). Whether or not enhanced local production on smaller reefs actually translates into numerically enhanced regional stocks has not yet been tested.

Concluding remarks

The internal consistency of our results from a decade of field experiments confirms DDHS as an important process in the ecology of gag. However, it is important to make the distinction between ecological pattern and process when applying DDHS to marine fisheries. Here, we tested DDHS as a process without implying an ideal free distribution (IFD), which is a pattern expected from DDHS given certain assumptions (Fretwell 1972, McCall 1990). Recently, Shepherd and Litvak (2004) critiqued the application of IFD theory to marine fisheries, and questioned the existence of DDHS in marine fishes. While we generally agree with their critique, especially the need for appropriate nulls when inferring process from pattern, we also note they frequently used IFD and DDHS synonymously. For gag, we do not necessarily expect the equilibrium of an IFD to be manifested at the geographic scale of the stock. In another study, experimentally displaced gag returned to resident reefs from 3 km away, well beyond the core of their home range (Kiel 2004), so at least gag have the potential to compare habitat patches and make choices accordingly. However, the assumptions of IFD theory are clearly not met at broader geographic scales

(Lima and Zollner 1996, Kennedy and Gray 1997). Instead, we suggest gag exercise DDHS in their residency-emigration decisions, which, given the trade-offs between sheltering and feeding, could have profound effects on spatial dynamics within the population.

ACKNOWLEDGMENTS

The authors are grateful for the collaboration of many colleagues, staff, and students who have contributed to this program, including Martin Posey, Jason Hale, Charlie Jabaly, Allen Heck, Troy Alphin, Doug Marcinek, Mark Butler, Raymond Kurz, Loren Kellogg, Brian Kiel, and Stephen Larsen. We thank Charles Jacoby, Micheal Allen, Sophia Balcomb, Philip Levin, and two anonymous reviewers for critiques that significantly improved this paper. The Suwannee Regional Reef System was constructed with funds from the Florida Artificial Reef Program, Florida Fish and Wildlife Conservation Commission (formerly in the Department of Environmental Protection), under contract numbers C-6051, C-7062, and C-7551 with cooperation from the Levy County Board of County Commissioners. We thank Virginia Vale, Jon Dodrill, James Townsend, and the late George G. Kirkpatrick, Jr. for facilitating development of this study system. The Florida Department of Environmental Protection sponsored SRRS research from 1991 to 1995 through Grant Number C-6729 (to W. J. Lindberg). The Florida Department of Environmental Protection, Marine Resources Grants Program (Grant No. MR-073 to W. J. Lindberg) and the National Marine Fisheries Service, MARFIN Program (Grant No. NA57FF0288 to W. J. Lindberg) jointly sponsored movement studies and experimental contrasts in growth and condition. The National Marine Fisheries Service, MARFIN Program (Grant No. NA97FF0350 to W. J. Lindberg, T. K. Frazer, and K. M. Portier) sponsored the shelter-closure experiment, and the Florida Sea Grant College Program (Grant No. NA16RG-2195, L/LR-B-53 to W. J. Lindberg, D. J. Murie, and D. M. Mason) sponsored the associated hydroacoustic analysis. This work is a product of the Florida Agricultural Experiment Station, Journal Series No. R-10744.

LITERATURE CITED

- Alonzo, S. H., and M. Mangel. 2004. The effects of size selective fisheries on the stock dynamics of and sperm limitation in sex-changing fish. *Fisheries Bulletin* **102**:1–13.
- Alonzo, S. H., and M. Mangel. 2005. Sex-change rules, stock dynamics, and the performance of spawning-per-recruit measures in protogynous stocks. *Fisheries Bulletin* **103**:229–245.
- Ambrose, R. F., and T. W. Anderson. 1990. Influence of an artificial reef on the surrounding infaunal community. *Marine Biology* **107**:41–52.
- Antonovics, J., and D. A. Levin. 1980. The ecological and genetic consequences of density-dependent regulation in plants. *Annual Review of Ecology and Systematics* **11**:411–452.
- Armsworth, P. R., and J. E. Roughgarden. 2005. The impact of directed versus random movement on population dynamics and biodiversity patterns. *American Naturalist* **165**:449–465.
- Beck, M. W. 1995. Size-specific shelter limitation in stone crabs: a test of the demographic bottleneck hypothesis. *Ecology* **76**:968–980.
- Beck, M. W. 1997. A test of the generality of the effects of shelter bottlenecks in four stone crab populations. *Ecology* **78**:2487–2503.
- Bohnsack, J. A. 1989. Are high densities of fishes at artificial reefs the result of habitat limitation or behavioral preference? *Bulletin of Marine Science* **44**:631–645.
- Bohnsack, J. A., and S. P. Bannerot. 1986. A stationary visual census technique for quantitatively assessing community

- structure of coral reef fishes. NOAA Technical Report NMFS 41. U.S. Department of Commerce, Miami, Florida, USA.
- Brenden, T. O., B. R. Murphy, and J. B. Birch. 2003. Statistical properties of the relative weight (W_r) index and an alternative procedure for testing W_r differences between groups. *North American Journal of Fisheries Management* **23**:1136–1151.
- Brule, T., C. Deniel, T. Colas-Marruto, and X. Renan. 2003. Reproductive biology of gag in the southeastern Gulf of Mexico. *Journal of Fish Biology* **63**:1505–1520.
- Bullock, L. B., and G. B. Smith. 1991. Seabasses (Pisces: Serranidae). *Memoirs of the Hourglass cruises* 8(2). Florida Marine Research Institute, St. Petersburg, Florida, USA.
- Coetzee, J. 2000. Use of a shoal analysis and patch estimation system (SHAPES) to characterize sardine schools. *Aquatic Living Resources* **13**:1–10.
- Coleman, F., K. Koenig, and L. A. Colins. 1996. Reproductive styles of shallow-water grouper (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. *Environmental Biology of Fishes* **47**: 129–141.
- Collins, L. A., A. G. Johnson, C. C. Koenig, and M. Scott Baker, Jr. 1998. Reproductive patterns, sex ratio, and fecundity in gag, *Mycteroperca microlepis* (Serranidae), a protogynous grouper from the northeastern Gulf of Mexico. *Fishery Bulletin* **96**:415–427.
- Conroy, M. J., Y. Cohen, F. C. James, Y. G. Matsinos, and B. R. Maurer. 1995. Parameter estimation, reliability, and model improvement for spatially explicit models of animal populations. *Ecological Applications* **5**:17–19.
- Dahlgren, C. P., and D. B. Eggleston. 2000. Ecological processes underlying ontogenetic habitat shifts in a coral reef fish. *Ecology* **81**:2227–2240.
- Doherty, P. J. 1991. Spatial and temporal patterns in recruitment. Pages 261–292 in P. F. Sale, editor. *The ecology of fishes on coral reefs*. Academic Press, New York, New York, USA.
- Doherty, P. J. 2002. Variable replenishment and the dynamics of reef fish populations. Pages 327–355 in P. F. Sale, editor. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, New York, New York, USA.
- Doherty, P. J., and D. M. Williams. 1988. The replenishment of coral reef fish populations. *Oceanography and Marine Biology* **26**:487–551.
- Dunning, J. B., Jr., D. J. Stewart, B. J. Danielson, B. R. Noon, T. L. Root, R. H. Lamberson, and E. E. Stevens. 1995. Spatially explicit population models: current forms and future uses. *Ecological Applications* **5**:3–11.
- Fishelson, L., W. L. Montgomery, and A. A. Myrberg, Jr. 1987. Biology of surgeonfish *Acanthurus nigrofuscus* with emphasis on changeover in diet and annual gonadal cycles. *Marine Ecology Progress Series* **39**:37–47.
- Footo, K. G. 1990. Spheres for calibrating an eleven frequency acoustic measurement system. *Journal du Conseil International pour l'Exploration de la Mer* **46**:284–286.
- Forrester, G. E., R. R. Vance, and M. A. Steele. 2002. Simulating large-scale population dynamics using small-scale data. Pages 275–301 in P. F. Sale, editor. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, New York, New York, USA.
- Frazer, T. K., and W. J. Lindberg. 1994. Refuge spacing similarly affects reef associated species from three phyla. *Bulletin of Marine Science* **55**:388–400.
- Fretwell, S. D. 1972. *Populations in a seasonal environment*. Princeton University Press, Princeton, New Jersey, USA.
- Fretwell, S. D., and H. J. Lucas, Jr. 1970. On territorial behavior and other factors influencing habitat distribution in birds. *Acta Biotheoretical* **19**:16–36.
- Graf, G. 1992. Benthic-pelagic coupling: a benthic view. *Oceanography and Marine Biology Annual Review* **30**:149–190.
- Grand, T. C., and L. M. Dill. 1997. The energetic equivalence of cover to juvenile coho salmon (*Oncorhynchus kisutch*): ideal free distribution theory applied. *Behavioral Ecology* **8**: 437–447.
- Grossman, G. D., G. P. Jones, and W. Seaman, Jr. 1997. Do artificial reefs increase regional fish production? A review of existing data. *Fisheries* **22**:17–23.
- Halpern, B. S. 2004. Habitat bottlenecks in stage-structured species: hermit crabs as a model system. *Marine Ecology Progress Series* **276**:197–207.
- Hart, M. K. 2002. Habitat-mediated direct and indirect effects among three Serranid fishes. Thesis. University of Florida, Gainesville, Florida, USA.
- Hixon, M. A. 1980. Competitive interactions between California reef fishes of the genus *Embiotoca*. *Ecology* **61**:918–931.
- Hixon, M. A., and J. P. Beets. 1993. Predation, prey refuges, and the structure of coral-reef fish assemblages. *Ecological Monographs* **63**:77–101.
- Hixon, M. A., and M. S. Webster. 2002. Density dependence in reef fish populations. Pages 303–325 in P. F. Sale, editor. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, New York, New York, USA.
- Hobson, E. S. 1968. Predatory behavior of some shore fishes of the Gulf of California. Research Report 73. U.S. Fish and Wildlife Service, Washington, D.C., USA.
- Holbrook, S. J., and R. J. Schmitt. 1995. Compensation in resource use by foragers released from interspecific competition. *Journal of Experimental and Marine Biology and Ecology* **185**:219–233.
- Hood, P. B., and R. A. Schlieder. 1992. Age, growth, and reproduction of gag, *Mycteroperca microlepis* (Pisces: Serranidae), in the Eastern Gulf of Mexico. *Bulletin of Marine Science* **51**:337–352.
- Hughes, N. F., and T. C. Grand. 2000. Physiological ecology meets the ideal-free distribution: predicting the distribution of size-structured fish populations across temperature gradients. *Environmental Biology of Fishes* **59**:285–298.
- Jones, G. P., and M. I. McCormick. 2002. Numerical and energetic processes in the ecology of coral reef fishes. Pages 221–238 in P. F. Sale, editor. *Coral reef fishes: dynamics and diversity in a complex ecosystem*. Academic Press, New York, New York, USA.
- Keener, P., G. D. Johnson, B. W. Stender, E. B. Brothers, and H. R. Beatty. 1988. Ingress of postlarval gag, *Mycteroperca microlepis* (Pisces: Serranidae), through a South Carolina Barrier inlet. *Bulletin of Marine Science* **42**:376–396.
- Kennedy, M., and R. D. Gray. 1997. Habitat choice, habitat matching and the effect of travel distance. *Behaviour* **134**: 905–920.
- Kiel, B. L. 2004. Homing and spatial use of gag grouper, *Mycteroperca microlepis*. Thesis, University of Florida, Gainesville, Florida, USA.
- Koenig, C. C., and F. C. Coleman. 1998. Absolute abundance and survival of juvenile gags in seagrass beds of the northeast Gulf of Mexico. *Transactions of the American Fisheries Society* **127**:44–55.
- Koenig, C. C., F. C. Coleman, C. B. Grimes, G. R. Fitzhugh, K. M. Scanlon, C. T. Gledhill, and M. Grace. 2000. Protection of fish spawning habitat for the conservation of warm-temperate reef-fish fisheries of shelf-edge reefs of Florida. *Bulletin of Marine Science* **66**:593–616.
- Koenig, C. C., and P. L. Colin. 1999. Distribution, abundance and survival of juvenile gag grouper, *Mycteroperca microlepis* (Pisces: Serranidae), in seagrass beds of the northeast Gulf of Mexico. *Proceedings of the Annual Gulf and Caribbean Fisheries Institute* **45**:37–54.
- Koops, M. A., J. A. Hutchings, and T. M. McIntyre. 2004. Testing hypotheses about fecundity, body size and maternal condition in fishes. *Fish and Fisheries* **5**:120–130.
- Kramer, D. L., R. W. Rangeley, and L. J. Chapman. 1997. Habitat selection: patterns of spatial distribution from

- behavioural decisions. Pages 37–80 in J. G. J. Godin, editor. Behavioural ecology of teleost fishes. Oxford University Press, Oxford, UK.
- Lambert, Y., and J. D. Dutil. 2000. Energetic consequences of reproduction in Atlantic cod (*Gadus morhua*) in relation to spawning level of somatic energy reserves. Canadian Journal of Fisheries and Aquatic Sciences **57**:815–825.
- Larson, R. J. 1980. Competition, habitat selection, and the bathymetric segregation of two rockfish (*Sebastes*) species. Ecological Monographs **50**:221–239.
- Laurel, B. J., R. S. Gregory, J. A. Brown, J. K. Hancock, and D. C. Schneider. 2004. Behavioural consequences of density-dependent habitat use in juvenile cod *Gadus morhua* and *G. ogac*: the role of movement and aggregation. Marine Ecology Progress Series **272**:257–270.
- Levin, P. S., and C. B. Grimes. 2002. Reef fish ecology and grouper conservation and management. Pages 377–389 in P. F. Sale, editor. Coral reef fishes: dynamics and diversity in a complex ecosystem. Academic Press, New York, New York, USA.
- Levin, P. S., and M. E. Hay. 2003. Selection of estuarine habitats by juvenile gags in experimental mesocosms. Transactions of the American Fisheries Society **132**:76–83.
- Levin, P. S., N. Tolimieri, M. Nicklin, and P. F. Sale. 2000. Integrating individual behavior and population ecology: the potential for habitat-dependent population regulation in a reef fish. Behavioral Ecology **11**:565–571.
- Lima, S. L., and P. A. Zollner. 1996. Towards a behavioral ecology of ecological landscapes. Trends in Ecology and Evolution **11**:131–135.
- Lindberg, W. J. 1997. Can science resolve the attraction-production issue? Fisheries **22**:10–13.
- Lindberg, W. J., T. K. Frazer, and G. R. Stanton. 1990. Population effects of refuge dispersion for adult stone crabs (*Xanthidae*, *Menippe*). Marine Ecology Progress Series **66**: 239–349.
- Lindberg, W. J., and G. Relini. 2000. Integrating evaluation into reef project planning. Pages 195–235 in W. Seaman, Jr., editor. Artificial reef evaluation: with application to natural marine habitats. CRC Press, Boca Raton, Florida, USA.
- Littell, R. C., G. A. Milliken, and W. W. Stroup. 1996. SAS system for mixed models. SAS Institute, Cary, North Carolina, USA.
- Lloyd, M. 1967. Mean crowding. Journal of Animal Ecology **36**:1–30.
- MacCall, A. D. 1990. Dynamic geography of marine fish populations. Books in recruitment fishery oceanography. Washington Sea Grant Program, University of Washington Press, Seattle, Washington, USA.
- Marteinsdottir, G., and G. A. Begg. 2002. Essential relationships incorporating the influence of age, size and condition on variables required for estimation of reproductive potential in Atlantic cod, *Gadus morhua*. Marine Ecology Progress Series **235**:235–256.
- Mason, D. M., and S. B. Brandt, editors. 1999. Space, time and scale: new perspectives in fish ecology and management. Canadian Journal of Fisheries and Aquatic Sciences **56** (Supplement 1).
- McIntyre, T. M., and J. A. Hutchings. 2003. Small-scale temporal and spatial variation in cod (*Gadus morhua*) life history. Canadian Journal of Fisheries and Aquatic Sciences **60**:1111–1121.
- Milinski, M. 1979. An evolutionary stable feeding strategy in sticklebacks. Zeitschrift für Tierpsychologie **51**:36–40.
- Milinski, M. 1984. Competitive resource sharing: an experimental test of a learning rule for ESSs. Animal Behavior **32**: 233–242.
- Milinski, M. 1986. A review of competitive resource sharing under constraints in sticklebacks. Journal of Fish Biology (Supplement A) **29**:1–14.
- Morris, D. W. 1987. Tests of density-dependent habitat selection in a patchy environment. Ecological Monographs **57**:269–281.
- Morris, D. W. 1989. Density dependent habitat selection: testing the theory with fitness data. Evolutionary Ecology **3**: 80–94.
- Munday, P. L. 2001. Fitness consequences of habitat use and competition among coral-dwelling fishes. Oecologia **128**:585–593.
- Ogden, J. C., R. A. Brown, and N. Salesky. 1973. Grazing by the echinoid *Diadema antillarum* Philippi: formation of halos around West Indian patch reefs. Science **182**:715–717.
- Orians, G. H. 1969. On the evolution of mating systems in birds and mammals. American Naturalist **103**:589–603.
- Osenberg, C. W., and G. G. Mittelbach. 1996. The relative importance of resource limitation and predator limitation in food chains. Pages 134–148 in G. A. Polis and K. O. Winemiller, editors. Food webs: integration of patterns and dynamics. Chapman and Hall, London, UK.
- Osenberg, C. W., C. M. St. Mary, R. J. Schmitt, S. J. Holbrook, P. Chesson, and B. Byrne. 2002. Rethinking ecological inference: density dependence in reef fishes. Ecology Letters **5**:715–721.
- Overholtzer-McLeod, K. L. 2004. Variance in reef spatial structure masks density dependence in coral-reef fish populations on natural versus artificial reefs. Marine Ecology Progress Series **276**:269–280.
- Parker, G. A. 1970. The reproductive behaviour and the nature of sexual selection in *Scatophaga stercoraria* L. II. The fertilization rate and the spatial and temporal relationships of each sex around the site of mating and oviposition. Journal of Animal Ecology **39**:205–228.
- Parker, G. A. 1974. The reproductive behaviour and the nature of sexual selection in *Scatophaga stercoraria* L. IX. Spatial distribution of fertilization rates and evolution of male search strategy within the reproductive area. Evolution **28**:93–108.
- Parrish, J. D. 1989. Fish communities of interacting shallow-water habitats in tropical oceanographic regions. Marine Ecology Progress Series **58**:143–160.
- Persson, L., S. Diehl, P. Eklöv, and B. Christensen. 1997. Flexibility in fish behaviour: consequences at the population and community levels. Pages 316–343 in J. G. J. Godin, editor. Behavioural ecology of teleost fishes. Oxford University Press, Oxford, UK.
- Petit, L. J., and D. R. Petit. 1996. Factors governing habitat selection by prothonotary warblers: field tests of the Fretwell-Lucas models. Ecological Monographs **66**:367–387.
- Pleszcynska, W. K. 1978. Microgeographic prediction of polygyny in the lark bunting. Science **201**:935–937.
- Powell, L. A., and T. K. Stanton. 1983. A programmable microcomputer-based sonar echo processor for real-time processing. IEEE Journal of Oceanic Engineering, **8**:280–287.
- Robertson, D. R. 1996. Interspecific competition controls abundance and habitat use of territorial Caribbean damselfishes. Ecology **77**:885–899.
- Rose, G. A., and D. W. Kulka. 1999. Hyperaggregation of fish and fisheries: how catch-per-unit-effort increased as the northern cod (*Gadus morhua*) declined. Canadian Journal of Fisheries and Aquatic Science **56**:118–127.
- Rosenzweig, M. L. 1981. A theory of habitat selection. Ecology **62**:327–335.
- Rosenzweig, M. L. 1985. Some theoretical aspects of habitat selection. Pages 517–540 in M. L. Cody, editor. Habitat selection in birds. Academic Press, San Diego, California, USA.
- Rosenzweig, M. L., and Z. Abramsky. 1997. Two gerbils of the Negev: a long-term investigation of optimal habitat selection and its consequences. Evolutionary Ecology **11**:733–756.
- Ross, S. W., and M. L. Moser. 1995. Life history of juvenile gag, *Mycteroperca microlepis*, in North Carolina estuaries. Bulletin of Marine Science **56**:222–237.

- SAS Institute. 2003. SAS version 9. SAS Institute, Cary, North Carolina, USA.
- Schirripa, M. J., and C. P. Goodyear. 1994. Status of the gag stocks of the Gulf of Mexico. Contribution No. MIA-93/94-61. U.S. National Marine Fisheries Service, Southeast Fisheries Science Center, Miami Laboratory, Miami, Florida, USA.
- Schlaepfer, M. A., M. C. Runge, and P. W. Sherman. 2002. Ecological and evolutionary traps. *Trends in Ecology and Evolution* **17**:474–480.
- Schmitt, R. J., and S. J. Holbrook. 1990. Population responses of surperch released from competition. *Ecology* **71**:1653–1665.
- Schmitt, R. J., and S. J. Holbrook. 1996. Local-scale patterns of larval settlement in a planktivorous damselfish: Do they predict recruitment? *Marine and Freshwater Research* **47**:449–463.
- Shepherd, T. D., and M. K. Litvak. 2004. Density-dependent habitat selection and the ideal free distribution in marine fish spatial dynamics: considerations and cautions. *Fish and Fisheries* **5**:141–152.
- Shima, J., and C. W. Osenberg. 2003. Cryptic density dependence: effects of covariation in density and site quality in reef fish. *Ecology* **84**:46–52.
- Shulman, M. J. 1985. Recruitment of coral reef fishes: effects of distribution of predators and shelter. *Ecology* **66**:1056–1066.
- Sih, A. 1997. To hide or not to hide? Refuge use in a fluctuating environment. *Trends in Ecology and Evolution* **12**:375–376.
- Sokal, R. R., and F. J. Rohlf. 1995. *Biometry: the principles and practice of statistics in biological research*. Third edition. Freeman, New York, New York, USA.
- Stimson, J. S. 1990. Density dependent recruitment in the reef fish *Chaetodon miliaris*. *Environmental Biology of Fishes* **29**:1–13.
- St. Mary, C. M., C. W. Osenberg, T. K. Frazer, and W. J. Lindberg. 2000. Stage structure, density dependence, and the efficacy of marine reserves. *Bulletin of Marine Science* **66**:675–690.
- Sweatman, H. P. A. 1983. Influence of conspecifics on the choice of settlement sites by larvae of two pomacentrid fishes (*Dascyllus aruanus* and *D. reticulatus*) on coral reefs. *Marine Biology* **75**:225–229.
- Sweatman, H. P. A. 1985. The influence of adults of some coral reef fishes on larval recruitment. *Ecological Monographs* **55**:469–485.
- Thorne, R. E. 1983. Assessment of population abundance by hydroacoustics. *Biological Oceanography* **2**:253–262.
- Turchin, P. 1998. *Quantitative analysis of movement: measuring and modeling population redistribution in animals and plants*. Sinauer Associates, Sunderland, Massachusetts, USA.
- Turner, S. C., C. E. Porch, D. Heinemann, G. P. Scott, and M. Ortiz. 2001. Status of gag in the Gulf of Mexico, Assessment 3.0. Contribution SFD 01/02–134. U.S. National Marine Fisheries Service, Southeast Fisheries Science Center, Sustainable Fisheries Division, Miami, Florida, USA.
- Verbeke, G., and G. Molenberghs. 2000. *Linear mixed models for longitudinal data*. Springer-Verlag, New York, New York, USA.
- Verner, J. 1964. Evolution of polygamy in the Long-billed Marsh Wren. *Evolution* **18**:252–261.
- Walters, C. 2000. Natural selection for predation avoidance tactics: implications for marine and community dynamics. *Marine Ecology Progress Series* **208**:309–313.
- Walters, C., and J. Korman. 1999. Linking recruitment to trophic factors: revisiting the Beverton-Holt recruitment model from a life history and multispecies perspective. *Reviews in Fish Biology and Fisheries* **9**:187–202.
- Walters, C. J., and S. J. D. Martell. 2004. *Fisheries ecology and management*. Princeton University Press, Princeton, New Jersey USA.
- Warner, R. R., and S. G. Hoffman. 1980a. Local population size as a determinant of mating system and sexual composition in two tropical marine fishes (*Thalassoma* spp.). *Evolution* **34**:508–518.
- Warner, R. R., and S. G. Hoffman. 1980b. Population density and the economics of territorial defense in a coral reef fish. *Ecology* **61**:772–780.
- Warner, R. R., and T. Hughes. 1988. The population dynamics of reef fishes. Pages 149–155 in J. H. Choat, et al., editors. *Proceedings of the Sixth International Coral Reef Symposium*, Australia. Executive Committee, Townsville, Australia.
- Weaver, D. C. 1996. *Feeding ecology and ecomorphology of three sea basses (Pisces: Serranidae) in the northeastern Gulf of Mexico*. Thesis. University of Florida, Gainesville, Florida, USA.
- Wege, G. J., and R. O. Anderson. 1978. Relative weight (W_t): a new index of condition for largemouth bass. Pages 79–91 in G. Novinger and J. Dillard, editors. *New approaches to the management of small impoundments*. Special publication 5. American Fisheries Society, North Central Division, Bethesda, Maryland, USA.
- Wennergren, U., M. Ruckelshaus, and P. Kareiva. 1995. The promise and limitations of spatial models in conservation biology. *Oikos* **74**:349–356.
- Werner, E. E., and J. F. Gilliam. 1984. The ontogenetic niche and species interactions in size-structured populations. *Annual Review of Ecology and Systematics* **15**:393–425.
- Wiens, J. A. 1984. On understanding a non-equilibrium world: myth and reality in community patterns and processes. Pages 154–172 in D. R. Strong, Jr., D. Simberloff, L. G. Abele, and A. B. Thistle, editors. *Ecological communities: conceptual issues and evidence*. Harper and Row, New York, New York, USA.
- Wiens, J. A. 1989. Spatial scaling in ecology. *Functional Ecology* **3**:385–397.
- Wiens, J. A., N. C. Stenseth, B. Van Horne, and R. A. Ims. 1993. *Ecological mechanisms and landscape ecology*. *Oikos* **66**:369–380.
- Williams, D. M. 1991. Patterns and processes in the distribution of fishes on coral reefs. Pages 437–474 in P. F. Sale, editor. *The ecology of fishes on coral reefs*. Academic Press, San Diego, California, USA.

APPENDIX

Procedures for using the fitted linear model (Table 1) to predict mean gag abundances (*Ecological Archives* A016-029-A1).