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March 12, 1997

Wendy Morrison, Resource Manager
Biscayne National Park
9700 North Canal Drive (SW 328th St.)
Homestead, FL 33030

Dear Ms. Morrison:

In response to your phone request, I am enclosing a final DEP grant project report by Dr. Bill Lindberg, University of Florida. Also enclosed is a brief project summary. Dr. Lindberg's work continues on the Suwannee reef system. He is currently evaluating effects of directed fishing on gag grouper on this artificial reef system. He can be reached at 352-392-9617. Don't hesitate to call me at 904/922-4340 if I can be of additional assistance.

Sincerely,

Jon Dodrill, Environmental Administrator
Office of Fisheries Management
and Assistance Services

/jwd
enclosures

SUWANNEE REGIONAL REEF PROGRAM

-Summary-

Off the mouth of the Suwannee River along Florida's north-central Gulf coast, University of Florida researchers began a program in 1990 to answer many questions regarding the use of artificial reefs for fishery management. Specifically, the program is seeking to answer two important questions: (1) How much fishing can take place at an artificial reef site before the fish caught exceeds the fish produced by that reef? And (2) To what extent can the balance between fish harvested and fish produced be shifted to maximize the sustainable fish populations at managed reef sites? In addition to answering these questions, the research is providing new information to improve reef designs and how to place them for best results.

At the onset of the program, 22 artificial reef sites known as the Suwannee Regional Reef System were developed as the largest experiment of its kind in the nation. Located along the 40-foot depth contour, the reefs are approximately 15 nautical miles offshore and bracket the mouth of the Suwannee River. Each site has six patch reefs spaced either 25, 75, or 225 meters apart. Each of the reefs consists of either four or 16 prefabricated concrete cubes with horizontal 55 gallon drums as central cavities. The reefs were constructed with funds collected from the sale of Florida saltwater fishing licenses.

With funding from the Department of Environmental Protection's Marine Resources Grants Program (saltwater fishing license revenues), the initial study of these reefs from 1991-1995 provided the following findings:

- Although it takes time, gag grouper eventually find that they like living on the artificial reefs. Gag populations increased steadily over the first five years of the project--especially on patch reef with 16 cubes. By the fifth summer of the program, the 16 cube reefs placed 225 meters apart had an average gag population of 400 fish per site. In fact, gag grouper accounted for almost 42% of the total fish weight at all reefs. However, as gag populations increased, the number of black sea bass and adult tomtate decreased from several hundred fish per site to virtually none.
- The total fish abundance and biomass was significantly greater on 16-cube reefs than on 4-cube reefs. But despite having four times as many cubes, there were only two to three times as many fish at the 16-cube sites.
- Some fish that shelter at the reefs and forage over sand bottom had a distinct preference for reefs spaced 225 meters apart. For example, black sea bass, white grunt, cubbyu and gray triggerfish all prepared to maximize the spacing between reefs. On the other hand, adult tomtate and sheepshead, both of which display the same shelter and forage characteristics, did not seem to care about reef spacing.

Suwannee Regional Reef Program Summary

October 1996

Goals for the Program:

- To help resolve the Attraction-Production issue by testing the leading hypotheses for how artificial reefs function ecologically.
- To relate the productivity of fishery species on reefs to behavioral, community, and ecosystem processes (e.g., habitat selection, species interactions, regional productivity, and forcing functions like river outflow) and to fishing pressure.
- To recommend artificial reef design and siting criteria for sustainable fisheries.
- To educate or inform people about what is scientifically known regarding artificial reefs and their applications in an ecosystem context.

Description of the Suwannee Regional Reef System:

- 22 reef sites along the 40 foot depth contour in the northeastern Gulf of Mexico, approximately 15 NM offshore and bracketing the mouth of the Suwannee River.
- The percent cover of natural hard-bottom habitat near these reef sites ranges from 0 to 33%, and rocky outcrops higher than 50 cm are not found in the vicinity.
- Each site has 6 patch reefs in a hexagon spaced at either 25, 75, or 225 m apart.
- Each patch reef has either 4 or 16 prefabricated concrete cubes (35³ inches) with horizontal 55 gallon drums as central cavities; all patch reefs on a site are the same size.
- The core experiment has 4 replicates for each of the 4 combinations of patch reef spacing and size (i.e., 4 & 16 cubes x 25 & 225 m spacing); the remaining sites are earmarked for intrusive experimental manipulations.
- Although others have tested reef size, this is the first experimental system in which reef spacing has also been included in order to test habitat patchiness *per se*.

The General 3-Step Hypothesis That Initiated This Program:

1. We assumed that reef structure provides motile species refuge from predation, and perhaps currents.
 2. Reef-dwelling species that forage off-reef on sand-dwelling benthic prey were expected to create a gradient of prey depletion around their refuge, resulting in a negative feedback to the reef dwellers' energy budgets, residency times, and local abundances.
 3. The patchiness of reef habitat was expected to affect the degree of prey depletion and the intensity of negative feedback, such that smaller, more widely spaced patch reefs may be more favorable to such reef residents than are larger, more closely spaced patch reefs.
- Together, this was termed the "resource mosaic hypothesis" as a specific extension of density-dependent habitat selection theory in behavioral ecology.
 - Results from our initial DEP project led to a broadening of this general hypothesis to also include coupling by gag grouper to pelagic baitfish, with presumably less prey depletion and negative feedback than expected exclusively from benthic prey.

Specific Testable Hypotheses and Descriptive Objectives:

Initial DEP Project (1991-1995)

- H₀: The size and spacing of patch reefs do not affect the abundance of fish.
- H_{alt}: Fish that shelter at reef structure but feed across the adjacent sand plain should be more abundant at widely spaced patch reefs than at closely spaced patch reefs.
- H_{alt}: Small fish that shelter *and* feed directly on a patch reef surfaces should be more abundant on larger patch reefs, but should not be affected by patch reef spacing.
- H_{alt}: Larger patch reefs should have more fish than smaller patch reefs, but the increase in fish abundance with increasing patch reef size should show a diminishing return.
- H₀: Reef age does not affect fish abundance patterns among reef treatments.
- H_{alt}: Effects patch reef size and spacing emerge over time as total fish abundance increases and feedback mechanisms operate.
- H₀: The size and spacing of patch reefs do not affect the abundance of macrobenthos in the adjacent sand plain.
- H_{alt}: Macrobenthos in functional guilds vulnerable to fish predation should increase in density with distance from reefs, and be least abundant around large, closely spaced patch reefs.

Current DEP/MARFIN Project (1995-1998)

- Obj: To determine residency times for juvenile to adult gag (200-800 mm TL) on patch reefs of contrasting sizes and distances apart, and to test the assumption that gag residency times differ with these measures of habitat patchiness.
- Obj: To estimate the frequency of movement between adjacent patch reefs, and to test the assumption that gag move freely among patch reefs spaced tens of meters apart, but move infrequently if at all among patch reefs spaced hundreds of meters apart.
- Obj: To test the assumption that young-of-the-year gag immigrate to intermediate, shallow-water reef habitat during an autumnal pulse of colonization, and to estimate their abundance relative to older cohorts.
- Obj: To confirm or refute that gag of reproductive size classes emigrate from shallow-water reef habitat during late fall-early winter, and immigrate to such habitat during late winter-early spring, as would be consistent with an offshore winter spawning migration.
- H₀: In the absence of directed fishing, gag growth rates and relative weights or condition do not differ among reefs of contrasting patch reef sizes and patch-to-patch distances (i.e., reef habitat patchiness).
- H_{alt}: Gag growth rates and relative weights or condition are greater on reefs supporting higher densities of gag (i.e., larger and perhaps more widely spaced patch reefs).
- H₀: Somatic growth of gag on designed experimental reefs is indistinguishable from somatic growth in the regional stock of gag as a whole.
- H_{alt}: The growth of gag on at least some experimental reef treatments (see prior H_{alt}) is faster, on average, than for the broader regional stock.
- H₀: Fishing pressure has no effect on growth and condition of surviving gag.
- H_{alt}: Reduced densities of gag as a consequence of fishing mortality magnify any effects of habitat patchiness on growth rates and condition of surviving gag.
- Obj: To determine the extent to which reduced gag density, as a consequence of fishing mortality, affects the community structure of local reef fish assemblages.

Initial DEP Project (1991-1995), continued

increased, however, abundances of black sea bass and adult tomtate decreased from several hundreds per reef site to virtually none, with a concurrent loss of reef treatment effects for these species.

- With respect to sand-dwelling macro-invertebrates, the densities of suspension feeders and burrowers within 75 m of reef structure were reduced relative to non-reef control areas. Suspension feeders and surface burrowers, in particular, were significantly affected by reef treatments, but the patterns of those effects are too complex for simple interpretation (i.e., apparently involving several direct and indirect effects).

Current DEP/MARFIN Project (1995-1998)

- The residency "half life" of juvenile to adult gag that have been tagged on Suwannee Regional Reefs to date is approximately 10 months, and as expected, the rank order of residency times among reef treatments corresponds to the rank order of gag abundance.
- Gag move among patch reefs on a site infrequently (0-2 movements per week when sampled at 24 hr intervals), and move significantly less at 225 m reef distances than at 75 or 25 m spacings. Furthermore, resightings of ultrasonically tagged fish suggest that gag stay at or return to a home patch reef.
- An autumnal pulse of immigration by young-of-the-year gag was not obvious during the fall of 1995, but an increased of 18-30 cm gag has been observed in the fall of 1996.
- A synchronous emigration of reproductive size classes was not obvious during late fall 1995, although the lowest average numbers in the largest size classes (i.e., 60-69 cm, 70-79 cm, and 80-89 cm) occurred in November (Dec. and Jan. sampling was missed). June 1996 also showed an increase in the largest size classes compared to prior months.
- Data pertinent to hypotheses regarding somatic growth, condition, and fishing effects will be gathered with the onset of directed fishing in November 1996.

Conclusions from Results to Date:

- The resource mosaic hypothesis survived its initial test. Because of unexpectedly high gag densities, however, the original hypothesis was broadened to include coupling to pelagic as well as benthic prey. These two sources for off-reef prey are expected to differ in their degrees of local prey depletion and density-dependent effects on reef fish.
- One can safely assume that gag residency is long enough and movements localized enough for reef treatment and fishing effects to appear as differences in growth and condition.
- Autumnal immigration by young-of-the-year gag directly onto Suwannee Regional Reefs may depend on year class strength. A highly synchronous emigration during late fall by gag of reproductive sizes has not been obvious; gag in these size classes can overwinter on Suwannee Regional Reefs. A hint of late spring returns of large fish is not yet conclusive.
- We now have a much better, but far from thorough understanding of how warm-temperate reefs function ecologically. While the resource mosaic hypothesis remains viable, others have been disproven. High densities of fish at artificial reefs are not simply a behavioral artifact (Carr and Hixon) and are not dependent on primary and secondary production associated with the reef itself (Bohnsack et al.). Reef structure provides refuge from predation (Hixon and Beets, Herrnkind and Butler), yet trophic linkages to off-reef prey must be important to the production of fishes from reef habitat.

Upcoming FSG Project (1997)

- H_o:** Hydrodynamic conditions induced by reef structure (e.g., turbulence, upwellings, persistent water masses, suspended sediment concentrations) do not differ between large and small patch reefs.
- H_{alt}:** Such conditions are more pronounced around large patch reefs than small ones.
- H_o:** Concentrations of nutrients, particulate organic carbon, and plankton in the water column do not differ between large and small patch reefs, nor between reefs and non-reef controls.
- H_{alt}:** Concentrations of nutrients, particulate organic carbon, and phytoplankton are greater around large patch reefs than small ones, and greater around reefs than non-reef controls, which corresponds to induced hydrodynamic features.
- H_{alt}:** Concentrations of zooplankton are greater around large patch reefs than small ones, and greater around reefs than non-reef controls, corresponding to hydrodynamic features.
- H_o:** Local standing stocks of baitfish at the same reef sites do not differ between large and small patch reefs, and are not correlated with hydrodynamically induced differences in nutrient and plankton concentrations.
- H_{alt}:** Baitfish abundance and biomass is greater at large patch reefs than at small ones, and correspond to hydrodynamic conditions induced by reef structure.
- H_{alt}:** Baitfish abundance and biomass at patch reefs is correlated with nutrient and phytoplankton concentrations.
- H_{alt}:** Baitfish abundance and biomass is correlated with zooplankton concentrations.

Research Findings to Date:

Initial DEP Project (1991-1995)

- As expected for fishes that shelter at reefs and forage over sand, the black sea bass, white grunt, cubbyu, and gray triggerfish were all significantly more abundant on patch reefs spaced at 225 m than at 25 m. Adult tomtate and sheepshead, which also shelter at reefs and forage over sand, were not affected by reef spacing. Adult tomtate, however, were more abundant in summers on 16-cube patch reefs where juvenile tomtate had previously recruited in great swarms, while sheepshead were abundant only in winter spawning aggregations at 16-cube patch reefs.
- As expected for the small fishes very closely associated with reef surfaces, the seaweed blenny and belted sandfish were significantly more abundant on 16-cube patch reefs than on 4-cube reefs. The seaweed blenny was unaffected by patch reef spacing, but the belted sandfish was more abundant at 25 m than at 225 m spacings.
- Total fish abundance and biomass was significantly greater on 16-cube reefs than on 4-cube reefs, but the four-fold difference in reef material yielded only a two- to three-fold difference in fish numbers.
- Reef age significantly affected abundance patterns of fishes among reef treatments but in an unexpected way. Gag increased significantly in abundance over the first five years, and the rate of increase was greater on 16-cube reefs than on 4-cube reefs. The increase in gag corresponded in both time and reef type to an increase in summer baitfish abundance. By the fifth summer, gag abundance at 16-cube x 225 m reefs averaged almost 400 fish per site (rank order of gag abundance: $16 \times 225 > 16 \times 25 > 4 \times 25 = 4 \times 225$) and gag accounted for almost 42% of total fish biomass across all reefs. As abundances of gag

Remaining Research Priorities:

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- Make direct comparisons of growth rates and condition (e.g., relative weights, lipid concentrations, enzyme activity) between reef fish (e.g., gag) occupying Suwannee Regional Reefs and natural hard-bottom habitat of the region.
- Quantify relationships of reef fish abundance (e.g., gag) with pelagic production (primary, secondary and tertiary) and hydrodynamic processes across spatial and temporal scales.
- Characterize and quantify significant pathways of energy flow and material transport in coastal ecosystems using the Suwannee Regional Reefs and contemporary ecological techniques (i.e., stable isotope analyses).
- Test the hypothesis that resident reef fish production (e.g., gag) is tied to the seasonal transport of tertiary production from inshore habitats (e.g., seagrass).
- Experimentally manipulate fish densities (e.g., gag) on replicate patch reefs for a direct test of density-dependence in residency times, growth rates, and condition; fish densities and these measures are expected to re-equilibrate over time.
- Experimentally manipulate reef cavity volume for a direct test of refuge control on gag abundance and reef fish community structure.
- Develop quantitative models of fish abundance and production derived from the research to date and a coupling to regional productivity and ecosystem processes.
- Continue visual fish counts on the Suwannee Regional Reefs, thereby extending the 6-year time-series of *offshore* fisheries independent monitoring in order to:
 - • Determine if reef fish assemblages attain equilibrium or climax conditions;
 - • Distinguish trends in reef fish abundance from natural cycles and variability;
 - • Relate reef fish abundance to *inshore* fisheries independent monitoring;
 - • Identify temporal patterns of abundance indicative of species interactions;
 - Validate quantitative models of reef fish abundance (see above).
- Answer the very practical questions, "*At what level of fishing pressure does the harvest from a reef equal or exceed the fish production attributable to that reef?*" and "*To what extent can that equilibrium point be shifted to maximize sustainable fish production in a managed ecosystem?*"

**Grant Number C-6729
Final Project Report**

**Fundamental Design Parameters for Artificial Reefs:
Interaction of Patch Reef Spacing and Size**

prepared by

Dr. William J. Lindberg, Principal Investigator
Department of Fisheries and Aquatic Sciences
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submitted to

The Office of Fisheries Management and Assistance Services
Division of Marine Resources
Florida Department of Environmental Protection

March 1996

Executive Summary

Artificial reefs are popular among Florida fishermen and designated in Florida Statutes (F.S. Ch. 370.0608) as a fishery enhancement. Florida has the most active artificial reef program in the nation, with nearly 300 built over the past decade and more than half of all reefs sites in the United States. Reef construction expenditures in Florida since 1987 have exceeded 5 million dollars. However, serious questions were raised by fishery scientists more than a decade ago about the true benefits derived from artificial reefs. At issue was whether artificial reefs actually increase fish production or simply concentrate fish, making them easier to catch. In other words, should artificial reefs be considered a tool in fishery conservation or simply another form of fishing gear? This issue became known as the Attraction-Production question, and ultimately motivated the research project reported here.

Researchers are in agreement that this issue cannot be resolved by a direct scientific test at the level of a fish population or fishery stock. Instead, we must come to the truth by a process of elimination, by attempting to disprove the various mechanisms which might explain the abundance of fish at artificial reefs. The Suwannee Regional Reef System (SRRS) was designed and built to test one of the leading hypotheses for how artificial reefs might benefit fish.

Our previous work had given rise to a general three-step hypothesis: (1) We assumed that reefs give fish refuge from predation and perhaps from currents. (2) Reef-dwelling fishes that feed on sand-dwelling prey were expected to deplete their prey around reefs, resulting in a negative feedback to the predators' energy budgets, residency times, and local abundances. (3) The patchiness of reef habitat was expected to affect the degree of prey depletion and the intensity of negative feedback, such that smaller, more widely spaced patch reefs may be more favorable to such reef residents than are larger, more closely spaced patch reefs. The 5-year project reported here experimentally tested the effects of patch reef size and spacing on distribution patterns of potential prey and on the abundances or local standing stocks of reef-associated fishes. As such, this project was an initial test of the general hypothesis, and the first phase of a more comprehensive research program.

The results reported here support our original hypothesis, but also require some modification to it. Reef habitat patchiness significantly affected the densities of benthic invertebrates living in sand around reefs. Patch reef size and spacing significantly affected the abundance of most fishes that were expected to respond to these reef treatments. Effects of patch reef size on fish abundance had previously been tested by other investigators, but ours was the first experiment to also test patch reef spacing. Reef spacing was a critical factor for testing the hypothesis because of its predicted effects on fish abundance. Of the reef-dwelling fishes that could be tested statistically, six can feed over sand, and of these, four (black sea bass, white grunt, gray triggerfish, and cubbyu) were most abundant on the widely spaced patch reefs, as expected. The other two species (tomtate and sheepshead) were unaffected by reef spacing, which we attribute to unique characteristics of their life histories. Patch reef size significantly affected all of these

species except black sea bass and cubbyu. However, a four-fold difference in the amount of reef material generally yielded only a 2-3 fold difference in the number of fish, consistent with what others have found. In addition to reef treatment effects, seasonal differences and trends over time were significant for many species.

The need to modify our original hypothesis comes mostly from results for gag grouper, the top resident predator on these reefs, and the primary target for reef fishermen of the region. Gag significantly increased in abundance over time, becoming the top ranked species in terms of biomass (41.9% of total summer fish biomass) and the most abundant fishery species (averaging as many as 391 per reef). Gag abundance increased at a faster rate on large patch reefs than on small patch reefs, and has not yet leveled off. Concurrently, black sea bass and adult tomtate almost disappeared from these reefs. Herrings (*Clupeidae* spp.) increased in abundance over time and were also most abundant over larger patch reefs. Gag likely feed on herrings to a greater extent than other groupers, and we now hypothesize that gag abundance is not limited by benthic prey production. Because of their gregarious nature and feeding on planktivorous fishes, gag may have the potential to be enhanced by properly designed and well placed artificial reefs. This, however, needs to be fully tested and continued research efforts are warranted.

With respect to the Attraction-Production issue, others have refuted that high densities of fish at artificial reefs are simply an artifact of behavior, and that these fish depend upon primary and secondary production derived directly from within a reef. We hypothesized that reef fish derive substantial support from off the reef, and our initial tests corroborated that hypothesis. Still other investigators have confirmed that refuge from predation is an important function of reef structure, and that shelter can be a bottleneck in the life histories of reef-dwelling species. The bottleneck hypothesis and ours regarding coupling to off-reef production are entirely compatible, and probably explain how reefs function ecologically. A follow-up project to the one reported here is testing other aspects of our original hypothesis (i.e., gag residency, growth, and relative weights), as well as the effects of directed fishing. At this point, we suggest that artificial reefs can contribute biologically to reef fish, but that it remains uncertain whether such gains can offset associated losses to fishing mortality.

Management recommendations and research needs are discussed at the end of this report, with the following being the most important. Proposals for artificial reef construction ought to include explicit management objectives for each reef, so that guidance on reef design and placement can be given, and that reef monitoring can be relevant to decision-making. Any recommendation of reef size will depend on the management objectives for a given reef, and yet optimal sizes need to be determined by future research. Artificial reefs should not be spaced too close together. For patch reef sizes used in the Suwannee Regional Reef System, close spacing may diminish biological returns, and the saturation of an area is theoretically possible. An optimal spacing cannot yet be stated. Artificial reefs have the potential, when properly designed and placed, to be used as conservation tools and as effective fisheries production systems, especially for selected species. However, direct comparisons to natural habitat still need to be made.

Acknowledgments

This research was possible only through the dedicated effort of a highly professional team. Dr. Frederic E. Vose became a valued colleague during this course of study, and we wish him all the best as his career continues with the Florida Marine Research Institute, Cedar Key Field Laboratory. James Loftin has been indispensable as a field biologist, data manager/analyst and, with Dr. Vose's departure, as project coordinator. He too has become a valued colleague. Dr. Martin Posey, University of North Carolina at Wilmington, has been responsible for processing an inordinate number of samples, with help from Mr. Troy Alphin, and has provided substantial expertise in benthic ecology. Dr. Kenneth Portier, Department of Statistics, University of Florida, has generously provided statistical guidance throughout this project, and has been personally participating in the final data analyses. Jason Hale independently assumed responsibility for the necessary research diving technologies and logistics, in addition to his essential role as project biologist. Alan Heck and Charles Jabaly (now also with DEP) performed admirably as project biologists/research divers. Dr. Thomas K. Frazer deserves recognition for participating in the conception of this project, and we welcome him back. The teamwork required to execute an experiment of this scale cannot be overstated.

Research that involves a substantial commitment over an extended period must also have the support and cooperation of administrators with vision and a genuine concern for science, natural resources, and their constituency. Above all, they must possess strong character. Special thanks are due Mr. Jon Dodrill and Dr. Virginia A. Vail, Office of Fisheries Management and Assistance Services, and Mr. Ed Irby, Division of Marine Resources, Florida Department of Environmental Protection. Their counsel, encouragement, and enthusiasm have been sincerely appreciated. This project was sponsored through the Florida Marine Resources Grants Program (grant number C-6729).

The Suwannee Regional Reef System, as the physical facility for this research, was built with funds from the Florida Department of Environmental Protection's Artificial Reef Program (Contract Numbers C-6051, C-7062, and C-7551), with direct cooperation from the Levy County Board of County Commissioners and Ms. Jacqueline Hullander of the Commissioners' staff. Senator George G. Kirkpatrick, Jr. facilitated the initial phase of reef construction.

A great many people, especially those acknowledged above, have contributed substantially to the successful completion of this project. Any shortcomings or errors that might be found, however, are entirely my responsibility.

W.J.L.
March 12, 1996

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Introduction

The purpose for this final report is to convey major findings of a five-year research effort, and to place those findings in a scientific and fisheries management context. This report is not intended to give detailed methods nor exhaustive analyses for all data generated during this project. Several peer-reviewed professional publications will be forthcoming to fulfill that need. Here, the audience is assumed to be professionals in fisheries management who have a technical, biological background but who are not, themselves, conducting research on artificial reefs. Although the issues which justified this project pertain directly to artificial reefs, our findings are also pertinent to natural systems because this work experimentally examines fundamental ecological processes. As such, anyone interested in how habitat characteristics affect reef fish abundance and biomass might also find this report useful.

Status of Artificial Reefs in Florida

Of the 14 coastal states with government-sponsored artificial reef programs, Florida's is obviously the most active (Stone et al. 1991). Over the past decade, nearly 300 reefs were constructed by local governments with funds from DEP's Artificial Reef Program, (Evans 1995). This represents more than half of all reefs built in the United States. For the period from 1987 through 1994, the combined state and federal funding for artificial reefs in Florida exceeded 6.7 million dollars, of which 1.6 million supported research, monitoring, and the development of State plans (Evans 1995).

State funding for artificial reefs has been largely derived from saltwater fishing license revenues, but also from the Florida Boating Improvement Program, the Florida Department of Transportation, and the Florida Aquatic Pollution Recovery Trust Fund (Evans 1995). Florida Statutes created the saltwater fishing license and designated not less than 30% of license revenues to be spent on fishery enhancement (F.S. Ch. 370.0608). Artificial reefs, along with fish hatcheries and fishery statistics, were specified in statute as fishery enhancements.

As evidenced by such government expenditures, artificial reefs are perceived by the public as an asset to recreational fisheries, which is not to say they are perceived as a panacea for all issues affecting fishery stocks. Public support for artificial reefs is further evidenced by the advocacy expressed in popular fishing publications (e.g., *Florida Sportsman*, March 1996). However, the popular-assumption that artificial reefs enhance fishery stocks has been challenged by fishery scientists (e.g., Bohnsack and Sutherland 1985, Bohnsack 1989, Polovina and Sakai 1989, Sato 1985) in what has become known as the Attraction-Production Question. It was the combination of public demand for artificial reefs and fishery management concerns for their potential consequences that justified State investment in this research.

The Attraction-Production Issue¹

Artificial reefs have been popular because they "produce" fish for fishermen. Favorable catch rates and high densities of fish have been taken as proof by the public that artificial reefs benefit fisheries stocks. Obviously, when reefs were built, some fishes became abundant at locations where few or none had previously been caught. Nevertheless, the asserted benefit to fish stocks was very much more an assumption in need of testing than it was a logically valid conclusion. In all likelihood, the assumption was readily accepted because it made artificial reef development compatible with the expressed conservation ethic of most fishermen. More than a decade ago, however, a few concerned fishery scientists challenged that assumption by asking whether artificial reefs actually produced more fish or simply aggregated them, thereby making them easier to locate and catch. This became known as the attraction-production question (Bohnsack and Sutherland 1985).

Prior to that challenge, high densities of fish at artificial reefs were uncritically interpreted as evidence that the amount of hard-bottom habitat was limiting reef fish population size. Hard-bottom was popularly assumed to be the foundation of the food web for reef fish assemblages (i.e., supporting essential primary and secondary production). In that light, an addition of man-made reefs made sense as a way to alleviate a perceived habitat limitation. The assumption of habitat limitation was challenged on logical grounds.

The reasoning went as follows. When reef fishes were unexploited, the existing natural habitat supported an abundance of reef fish, presumably at or near carrying capacity. Fishing mortality then reduced stocks to some lower level, yet the amount of natural habitat remained the same - still capable of supporting higher numbers. Logically, the amount of hard-bottom habitat could not be the factor limiting population size, in which case, the addition of artificial reefs would not benefit fish stocks by alleviating that limitation to produce more fish. Nevertheless, high densities of fish at artificial reefs (see Bohnsack et al. 1991) required an explanation. To this, scientists responded with the question of behavioral attraction, and the inference that high densities were merely an artifact of behavioral preferences leading to intense fishing pressure (see Polovina 1991).

Resolution of the attraction-production issue will require not only rigorous science, but also an education of interested parties as to what would constitute an adequate answer. Most laymen, and perhaps many professionals, seem to believe that science attempts to prove things to be true, when in fact, science advances by proving things (i.e., hypotheses) to be false. Sir Karl Popper, one of the twentieth century's most influential philosophers of science, referred to falsifiability as the "criterion of demarcation" between empirical science and metaphysics (and from pseudoscience). With respect to the attraction-production issue, the reef research community has been engaged in a process tantamount to the testing of multiple working hypotheses, as promoted by Platt's (1964) classic paper on strong inference.

¹ This section is excerpted from a manuscript to be published in *Fisheries* (Nov. 1996), based on a keynote given at the 1995 American Fisheries Society Symposium on artificial reefs. Please do not reprint or publish without approval of the Editor.

While most of our collective research efforts have been focused on limits to fish production, an obvious question has been, "Are artificial reefs inherently more attractive to fish than are natural reefs?" This cuts right to the heart of the challenge that originally began the attraction-production issue. At a recent symposium², Hixon and Carr (Oregon State University) described an elegantly straightforward experiment which refuted the hypothesis that high fish densities were simply an artifact of behavioral preference.

By contrast, no single experiment is likely to test fish production or productivity (including survivorship) directly at the levels of breeding populations or fishery stocks. Instead, indirect tests in the deductive traditions of mature sciences like physics are the only route to follow. A sequence of guiding questions has been inherent in the recent research efforts:

1. By what mechanisms or processes *might* artificial reefs enhance fish production (e.g., reduce habitat limitation on larval settlement, alleviate post-settlement demographic bottlenecks, enhance bottom-up production within reefs, or facilitate trophic coupling to off-reef production). These constitute alternative, but not mutually exclusive hypotheses.
2. Are any of these mechanisms or processes affected by characteristics of artificial reefs (e.g., structural complexity, location, reef dimensions, densities or patchiness)? The null hypothesis to be tested is 'no effect' under conditions in which you would most expect an effect from specific ecological processes.
3. Can the rates of processes, confirmed under question 2, be shifted favorably relative to control conditions? Whereas question 2 can be answered by reef-to-reef comparisons, this question requires rate estimates and a contrast to productivity in appropriate natural habitat. The designation of what is appropriate deserves careful consideration.
4. If the answers to questions 2 and 3 are yes, then is the gain in productivity or production sufficient to offset associated fishing mortality? Ultimately, this is the important question for *sustainable* reef fisheries.

These are not easily answered questions, and they increase in difficulty from 1 through 4. Substantial progress has been made but, in deference to other investigators' rights of publication, only highlights of recent research programs can be given here. The importance of Hixon and Carr's most recent contribution was noted above. Earlier work by Hixon and Beets (1993) established refuge from predation as an important function of reef structure. Likewise, earlier work by Bohnsack et al. (1994) impugned the hypothesis that reef habitat for larval fish settlement was limited. Instead, the most highly valued fishes settled elsewhere, and then colonized artificial reefs at later life history stages. Such findings are consistent with the hypothesis that habitat-related bottlenecks could affect

² *Future Artificial Reefs in the U.S. Coastal Ocean: Can Science Resolve the Biological Enhancement Question?*, A Symposium of the 125th Annual Meeting of the American Fisheries Society, Tampa, Florida. August 30, 1995. William Seaman, Jr., Convener.

population demography, but may be alleviated by appropriate artificial structure. To date, the best examples of demographic bottlenecks come from spiny lobsters (Smith and Herrnkind 1992, Butler et al. 1995) and stone crabs (Beck 1995).

While survivorship is an obvious component of production at the population level, production is also commonly considered with respect to assimilation, i.e., maintenance of fish biomass, growth, and reproduction. The source of food which sustains reef fish assimilation should directly affect how artificial reefs function. At the same symposium previously referenced, Bohnsack et al. (NMFS and University of Miami) reported that an absence of on-reef primary and secondary production had no effect on reef fish standing stocks. These negative results are important because they clearly refute the original dogma that justified artificial reefs literally as foundations for the food web supporting reef fish. By eliminating an alternative hypothesis, Bohnsack et al. reinforced our own hypothesis that trophic coupling to off-reef production must be important for reef fish production.

General Hypothesis, Program Goals, and Research Strategy

With the project reported here, we initiated research to test whether ecological processes involved in the trophic coupling between reef fishes and off-reef prey might be enhanced by artificial reefs. Earlier work (Lindberg et al. 1990, Frazer et al. 1991, Frazer and Lindberg 1994) led to a general three-step hypothesis: (1) We assume that reef structure provides motile species refuge from predation, and perhaps from currents. (2) Reef-dwelling species that forage off-reef on sand-dwelling benthic prey are expected to create a gradient of prey depletion around their refuge, resulting in a negative feedback to the reef-dwellers' energy budgets, residency times, and local abundances. (3) The patchiness of reef habitat is expected to affect the degree of prey depletion and the intensity of negative feedback, such that smaller, more widely spaced patch reefs may be more favorable to such reef residents than are larger, more closely spaced patch reefs. Lindberg et al. (1990) termed this the "resources mosaic hypothesis". The theoretical foundation for this hypothesis derives from mating system theory (e.g., Orians 1969, Emlen and Oring 1977), "ideal free distribution" theory (Fretwell 1972, Milinski and Parker 1991), and "density-dependent habitat selection" theory (MacCall 1990), all of which are simply variations of the same reasoning.

Our overall program goals are: to help resolve the Attraction-Production issue by testing one of the leading hypothesis for how artificial reefs might function; to recommend design criteria for artificial reefs to best serve fisheries management objectives; and, to educate or inform people about what is scientifically known regarding artificial reefs and their applications.

Our overall research strategy has been to proceed in phases, to test first for reef treatment effects on fish abundance and biomass, and for reef effects on patterns of potential benthic prey. Then, as warranted, the program would proceed to more directly investigate fish production and rate-determining processes. With respect to the four guiding questions above, this first phase of research concentrates on the first two questions, how might reefs work and can the proposed mechanism withstand testing.

Project Objectives

Objectives for this project were originally stated as the following hypotheses to be tested

1. An interaction exists between patch reef spacing and patch reef size in their effects on:
 - a. species composition, local abundance, and population or community structure;
 - b. distribution of benthic prey species as a function of distance from patch reefs.
2. Reef treatment effects (e.g., differences in fish species abundance or prey densities) become pronounced with time following initial colonization of reefs to an equilibrium number of species, and then fluctuate with seasonal and inter-annual variation.
3. Effects of patch reef spacing and size differ among species or life history stages depending on the extent to which they take refuge on reefs, forage on distinct prey assemblages (e.g., sandy substrate or plankton assemblages), and use reefs for related functions (e.g., mating).
4. Fishing pressure differs with patch reef size and spacing, and is greatest on the larger, closely spaced patch reefs. By agreement, this fourth hypothesis was deferred because the colonization of study reefs by young grouper continued past the first few years. Directed fishing as an experimental treatment is now scheduled for the fall of 1996, as a major part of a follow-up project.

Materials and Methods

The Suwannee Regional Reef System (SRRS)

The SRRS was designed specifically to test the resource mosaic hypothesis (Lindberg et al. 1990, Frazer and Lindberg 1994). The system consists of 22 designed artificial reefs in the eastern Gulf of Mexico, 24-29 km offshore from the mouth of the Suwannee River (Fig. 1). The reef sites are approximately 2 km apart along the 13-meter depth contour.

The bottom at SRRS sites is typically sand with low relief karstified limestone, most of which is covered by a thin veneer of sand. Ledges and small sinks reportedly exist elsewhere in the region, but are rare and have not been encountered during this project. Point-intercept transect sampling at each reef site (see DEP Contract C-8030 for 8 of the 16 reef sites sampled) was used to estimate that rock outcroppings covered 7.6% of the area adjacent to the artificial reefs. Only 21% of that rock exceeded 10 cm in height, with none higher than 50 cm. Most of the hard-bottom was fragmented rather than continuous, with 80% of all rocks one meter wide or less. Only 7% of all outcroppings were greater than 2 m across, with the largest continuous span measuring 12.5 m. Sand habitat between rocks was often less than a meter wide, but extended many tens of meters where outcroppings were scarce. The percent cover of hard-bottom at individual reef sites ranged from 0-33% (Fig. 2).

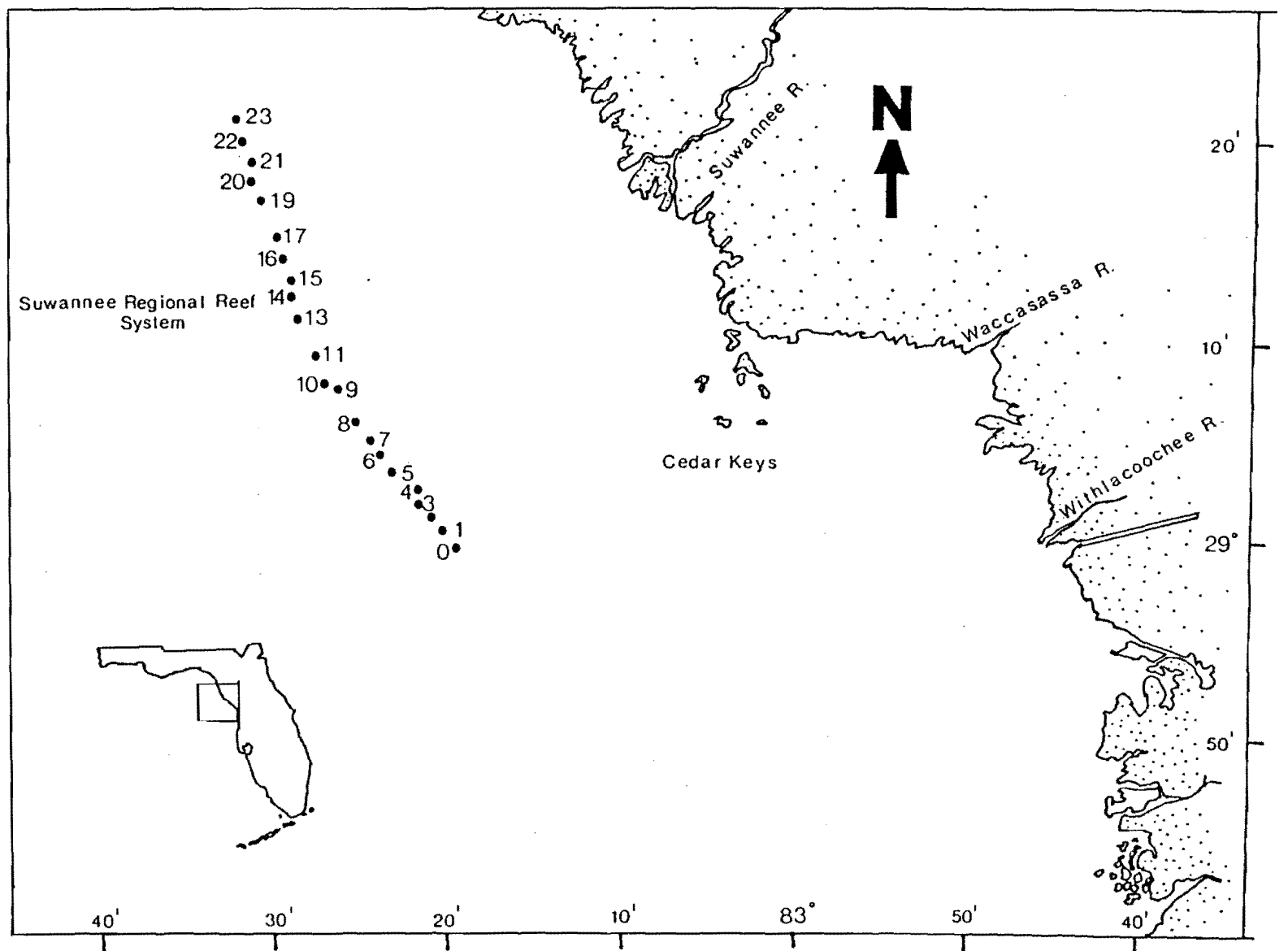


Fig. 1. Vicinity map of the Suwannee Regional Reef System (SRRS) along the 13-m depth contour; offshore from Cedar Key, Florida and the Mouth of the Suwannee River. Sites 12 and 18 were not developed as reefs, and are not shown.

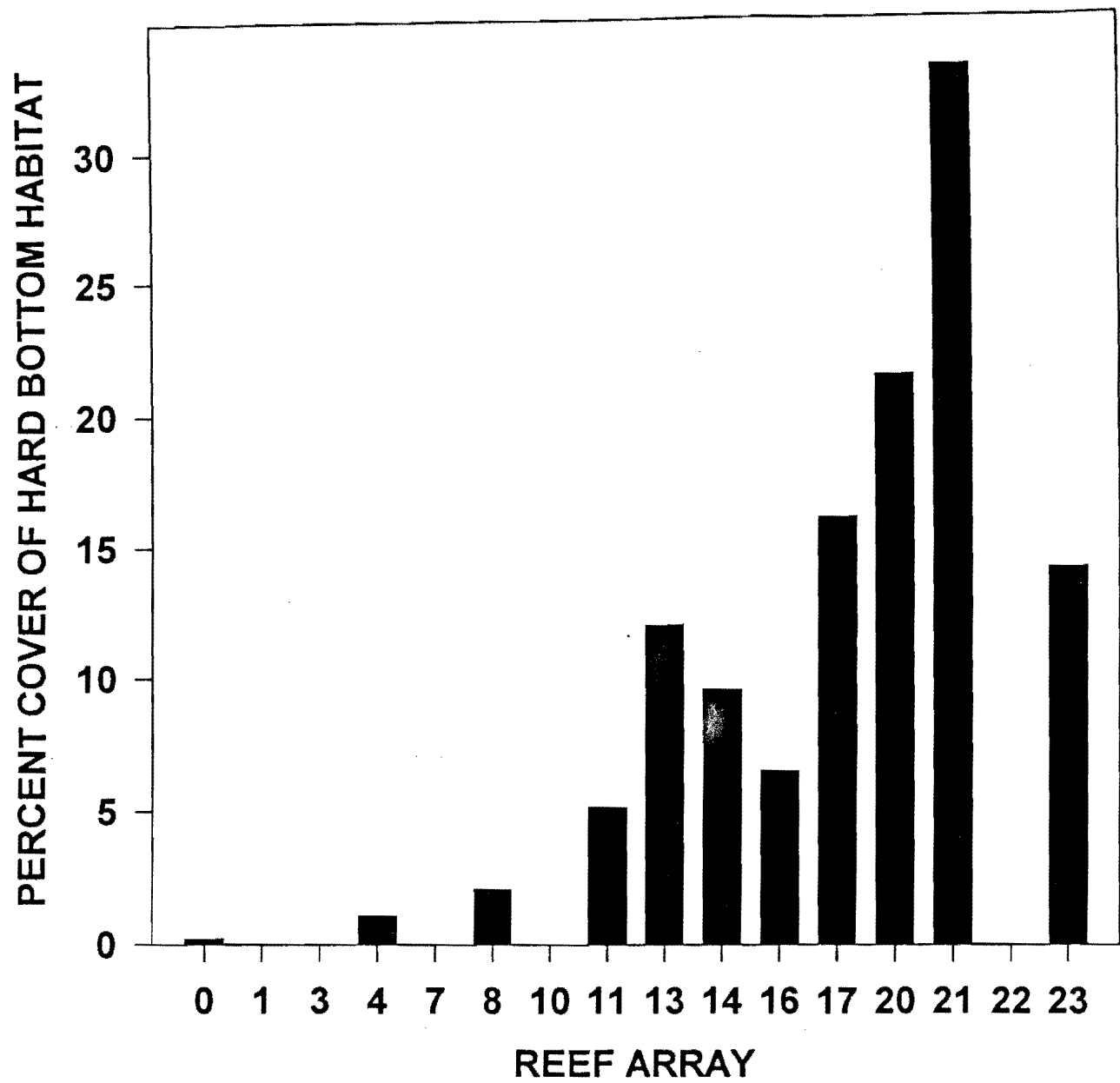


Fig.2. Percentage of hard-bottom cover within each reef site.

The artificial reef structure at each site is configured as a hexagonal array of six patch reefs spaced at either 25 m, 75 m, or 225 m (Fig. 3). Each square patch reef consists of either 4 or 16 prefabricated concrete cubes (volume = $0.7\text{ m}^3/\text{cube}$), and all patch reefs on a given site are the same size (Fig. 3). Overall, a total of 1,320 cubes, with a dry weight of 1,134 kg/cube, were individually positioned underwater by scuba divers which required over 500 hours of bottom-time. Thus, patch reef complexity and composition was controlled while patch reef spacing and size was manipulated. In reference to the SRRS, we use the terms 'patch reef' and 'patch' interchangeably, and the terms 'reef' and 'array' interchangeably.

Twelve reefs were built during 1990-91, giving two initial replicates for each combination of patch reef spacing and size. These were interspersed randomly among odd-numbered reef sites. Eight reefs were built during 1992-93, giving two additional replicates of the 25-m and 225-m spacings for both patch reef sizes. At the same time, two spare reefs were built, with 4 and 16 cubes/patch at 25-m, as replacements in case of unwanted fishing on the more vulnerable designs. These additional replicates and spares were interspersed among the even-numbered reef sites. Only 16 of the 22 reefs were used in this study. Fish data were also collected when possible from the 75 m and two spare arrays, although these were not needed for subsequent analyses.

Fish Censusing

Fish species associated with each patch reef were visually sampled for total counts and size estimates (i.e., minimum, maximum, and estimated average total lengths, cm TL). A routine protocol was used by members of a trained dive team, using scuba, to search methodically around and within each patch reef for 20 minutes. Size estimates were aided by the known dimensions of reef cubes and by meter sticks or scaled T-bars carried by divers (Bohnsack and Bannerot, 1986). Pilot sampling had been conducted to evaluate patch-to-patch, day-to-day, and diver-to-diver variation, and is being reported elsewhere (Vose et al. in press) along with a comparison of this total count method to a modified point census (Bohnsack and Bannerot, 1986). Total counts for each of the 6 patch reefs per array were summed for the total count per replicate reef. The average total length for each species at each patch reef was entered into published length-weight regression equations (e.g., Dawson, 1965; Bohnsack and Harper, 1988), and the resultant weight was multiplied by the number of individuals to yield a biomass estimate for each patch reef. These estimates of biomass per patch reef were summed across patches to yield the total biomass per species per reef replicate. Fish were censused once each summer (mid-June through August) and once each winter (January through March), beginning with summer 1991 and ending with summer 1995.

Benthic Sampling

During summer 1991, winter 1992, summer 1992 winter 1993 and summer 1993, two replicate arrays of each reef type were sampled for macrobenthos along transects from each of 2 randomly chosen patches per array. Along each transect, three core samples were taken by scuba divers at 1 m, 10 m, 25 m, 50 m, and 75 m from the patch reef. Seventy-five meters was chosen as the outer distance to sample because of previous

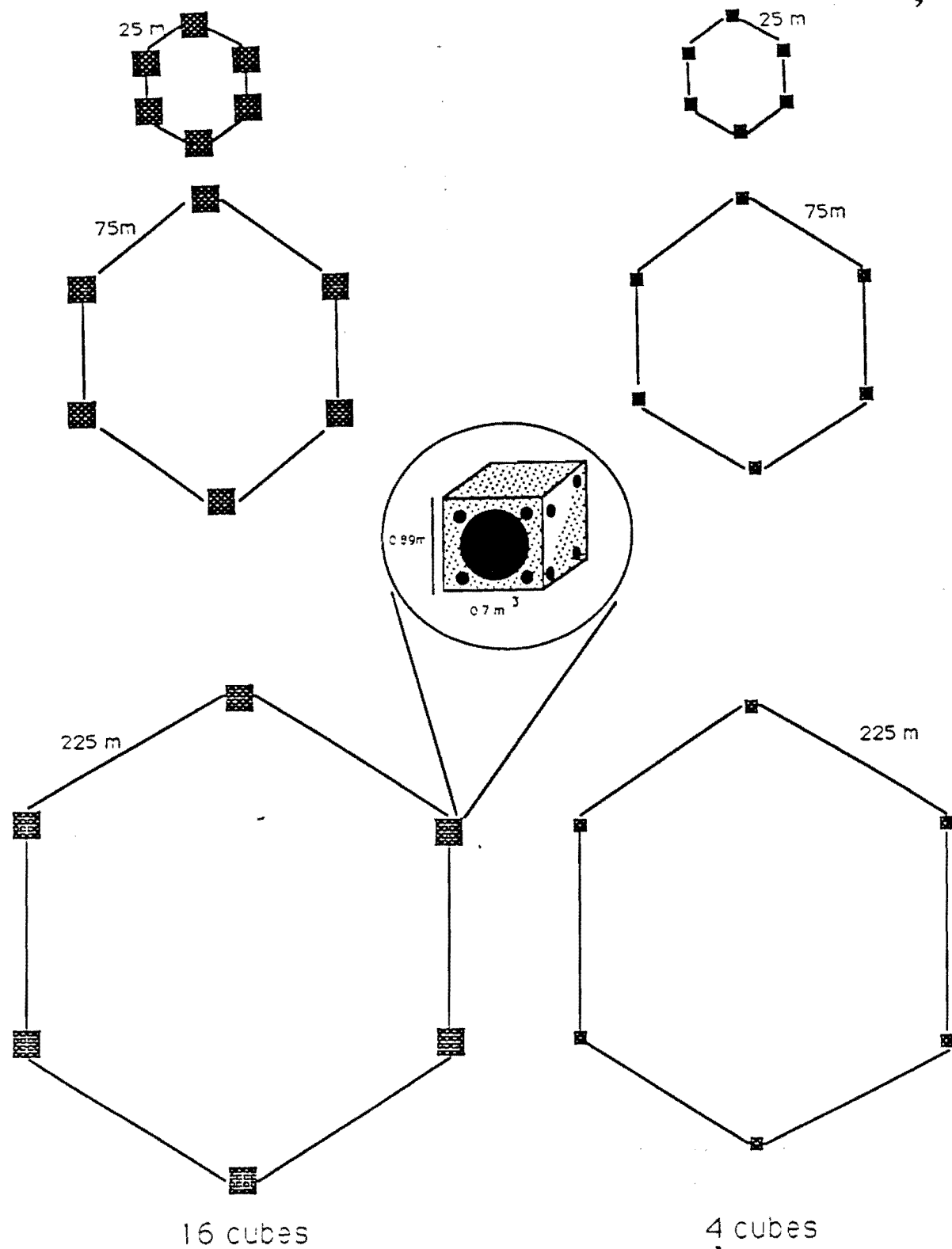


Fig. 3. Artificial reef structure at each site is configured as a hexagonal array of six patch reefs spaced at either 25 m, 75 m, or 225 m. Each square patch reef consists of either 4 or 16 prefabricated concrete cubes (inset).

The formal linear model analysis was limited to fish species, or life history stages, that had an adequate dataset. Fishes were further selected by their daytime use of the reef structure (roughly corresponding to Types A, B, and C of Nakamura 1985), their feeding location (hard-bottom, soft-bottom, and/or pelagic compartments), and their prey types (fish, benthic invertebrates, or plankton). Since these categories are not mutually exclusive, aggregation of species into strict functional guilds for analysis was not attempted. Of the top 20 fish species, 12 that appeared to have important habits (Table 1), relative to the general hypothesis and original objectives, were chosen for statistical analysis.

To test reef effects on benthic infauna, data were aggregated by functional groups. Most infaunal species were rare, only being found during a few sampling periods. Even common taxa were characterized by large fluctuations in abundance between years. Because of this variability, taxonomic difficulties, and problems with interpreting individual species responses to treatment effects, infauna were grouped into guild classifications for analysis of treatment and halo effects. Two types of functional groupings, one based on feeding type and the other on living position, were considered as representative of the fauna. Feeding classifications included suspension feeders, deposit feeders and grazers (predators and algal grazers). Living position classifications included deep burrowers (taxa that burrowed greater than 2 cm below the substrate surface), sedentary organisms (tube builders and species living in permanent burrow systems), and other surface-burrowing taxa (species burrowing within 1 cm of the substrate surface and taxa living on or near the surface). The different functional groups were expected to have different vulnerabilities to predation by reef-dwelling fishes. Species comprising at least 1% of the total individuals sampled during at least one sampling date were grouped into these functional classifications. Groupings were based on published species descriptions, observations, and life history characteristics of related species. Each functional group was composed of at least 5 taxa (Table 2), thereby minimizing effects of individual species.

The distribution of functional groups with respect to distance from patch reefs, among treatments, and between years was initially analyzed using a 3-way ANOVA on log-transformed abundances (log-transformation was found to correct heterogeneity of variances; F-max test). Winter 1993 results were not included in these analyses because of a major storm that impacted the study area, strongly affecting infaunal abundances (Posey et al., in press). Consequently, winter 1992 results were also not included in subsequent analyses because potential seasonal effects could not be adequately examined without seasonal replication. However, the initial analyses indicated strong interannual variability with highly significant interaction effects between year and treatment for all functional groups. Because of these interactions, all analyses were repeated for each year using a 2-way ANOVA with treatment and distance from the reef patch as fixed factors.

Table 1. Fishes with ecological characteristics relative to the general hypotheses and specific objectives of this study.

COMMON NAME	SPECIES NAME	DAYTIME REEF USE ¹	FEEDING LOCATION ²	PREY TYPES ³
Gag Grouper	<i>Mycteroperca microlepis</i>	D	P, S, H	F, B
Red Grouper	<i>Epinephelus morio</i>	D _x	H, S	B, F
Black Sea Bass	<i>Centropristis striata</i>	D _x	S, H	B, F
White Grunt	<i>Haemulon plumieri</i>	D	H, S	B
Gray Triggerfish	<i>Balistes capriscus</i>	D	H, S	B, P
Tomtate (adults)	<i>Haemulon aurolineatum</i>	D	S, H	B, P
Cubbyu	<i>Equetus umbrosus</i>	D _x	H, S	B
Sheepshead	<i>Archosargus probatocephalus</i>	D	H, S	B
Herring	Clupeidae	P	P	P
Round Scad	<i>Decapterus punctatus</i>	P	P	P
Belted Sandfish	<i>Serranus subligarus</i>	C	H	B
Seaweed Blenny	<i>Parablennius marmoreus</i>	C	H	B

¹ C = constant or very close contact with reef structure
D = demersal or hovering near reef, and may take shelter within reef or avoid as disturbed (subscript x indicates close proximity)
P = pelagic, schooling, no direct shelter in reef

² H = hard-bottom, including surfaces of artificial reefs
S = soft-bottom
P = pelagic

³ F = fish
B = benthic invertebrates, including crabs and shrimp
P = plankton

** Note that feeding locations and prey types are listed in a presumed order of preference which likely varies with life history stage, size, and prey availability

Table 2. Functional groups of infaunal organisms classified by feeding mode and living position. Only those taxa representing > 1% of the total organisms for any specific sampling period are included

I. FEEDING GUILDS			
	SUSPENSION FEEDERS	DEPOSIT FEEDERS	GRAZERS
Polychaetes:	<i>Chone americana</i>	<i>Armandi maculata</i> <i>Caulleriella alata</i> <i>Cirrophorus forticirratus</i> <i>Magelona</i> sp. C <i>Paraonis pygoenigmatica</i> <i>Prionospi cristata</i> <i>Prionospio fallax</i> <i>Sphaerosyllis aciculata</i> <i>Spiophanes bombyx</i>	<i>Aricidea cerrutti</i> <i>Aricidea philbinae</i> <i>Aricidea</i> sp. D <i>Glycera</i> sp. <i>Lumbrineris</i> sp. B <i>Nephtys picta</i> <i>Protodorvillea kefersteini</i> <i>Streptosyllis pettiboneae</i>
Bivalves:	<i>Tellina</i> spp. (juv.) <i>Diplodonta punctata</i> Bivalve sp. c		<i>Pitar</i> sp.
Custaceans:		<i>Cyclapsis variana</i>	<i>Ampelisca verilli</i> <i>Bathyporeia</i> sp. <i>Rhepoxgnius epistomus</i> <i>Leptochelia forresti</i>
Other:	<i>Branchiostoma caribaeum</i>	Sipuncula Oligochaeta	Nemertea

Table 2 continued...

II. LIVING POSITION GUILDS			
	SEDENTARY TAXA	DEEP BURROWERS	SURFACE BURROWERS
Polychaetes:	<i>Chone americana</i>	<i>Aricidea cerrutti</i>	<i>Sphaerosyllis aciculata</i>
	<i>Glycera</i> sp.	<i>Aricidea philbinae</i>	<i>Caulleriella alata</i>
	<i>Magelona</i> sp. C	<i>Aricidea</i> sp. D	<i>Cirrophorus forticirratus</i>
	<i>Prionospio cristata</i>	<i>Armandi maculata</i>	<i>Streptosyllis pettiboneae</i>
	<i>Prionospio fallax</i>	<i>Paraonis pygoenigmatica</i>	
	<i>Spiophanes bombyx</i>	<i>Lumbrineris</i> sp. B	
		<i>Nephtys picta</i>	
Bivalves:	<i>Pitar</i> sp.		Bivalve sp. c
	<i>Diplodonta punctata</i>		
Custaceans:	<i>Ampelisca verilli</i>	<i>Rhepoxgnius epistomus</i>	<i>Cyclapsis variana</i>
	<i>Leptochelia forresti</i>	<i>Bathyporeia</i> sp.	
Other:	Sipuncula	Oligochaeta	
		Nemertea	
		<i>Branchiostoma caribaeum</i>	

Results

General Description of the Fish Assemblage

A total of 85 fish species were censused by the total counts throughout the study period, although an additional 20 species were recorded from the SRRS outside that sampling effort (see species list, Appendix A). The cumulative species number increased almost linearly and essentially doubled over the nine sampling seasons (Fig. 4). However, the sampling effort also increased from 8 to 16 reefs for the last four seasons. The average species richness per reef array obviously differed between summer and winter, but remained fairly constant among summers (25-29 species) and among winters (13-16 species) (Fig. 4). Seasonality in the fish fauna was also evident in the total numbers of individuals, all species combined (Fig. 5), and to a lesser extent in the total estimated fish biomass (Fig. 5). A seemingly gradual increase in these measures over time was amplified by a substantial increase for the summer of 1995.

The top 20 species per sampling season are listed in rank order, based on abundance and biomass, for summers and winters in Tables 3, 4, 5, and 6, respectively. For the summers, the top five species comprised 93% to 98.5% of total fish numbers (Table 3) and 61.6% to 81.7% of total fish biomass (Table 4), pooled across all reefs. For the winters, the top five species comprised 68.4% to 88.7% of total fish numbers (Table 5) and 76.1% to 92.4% of total fish biomass (Table 6). The most obvious seasonal contrasts are the higher abundances of tomtate, Clupeidae spp., round scad, and Spanish sardines in the summers, and the much higher abundance and biomass rankings of sheephead in the winters.

A shift in fish community structure over time is most evident in biomass rankings. For example, gag increased from ninth in summer 1991, to third in summer 1992, and then to first for the remaining three summers (Table 4). Gag biomass showed a similar increase over consecutive winters, but shared the top two rankings with sheephead (Table 6). By contrast, black sea bass rankings decreased from third, to fifth, to sixteenth and fifteenth over consecutive summers (Table 4), and from first, to third, to fourth, and fifth over consecutive winters (Table 6). The increase in gag and decrease in black sea bass is also evident in their average numbers per reef (Fig. 6). Of particular interest, is that gag more than doubled in abundance between summer 1994 and summer 1995, coinciding with a substantial increase in the abundance of herrings (Clupeidae spp. and Spanish sardines, combined) (Fig. 6). Changes over time for these and other species are addressed in the context of reef treatment effects below.

Effects of Natural Hard-Bottom on Reef Fish Abundances

Results from the summer of 1994 are used here as an example of relationships between fish on artificial reefs and surrounding natural hard-bottom habitat. During that season, a total of 61 fish taxa were recorded. Twenty-four species did not meet the many assumptions required for ANCOVA, usually because they occurred infrequently. The

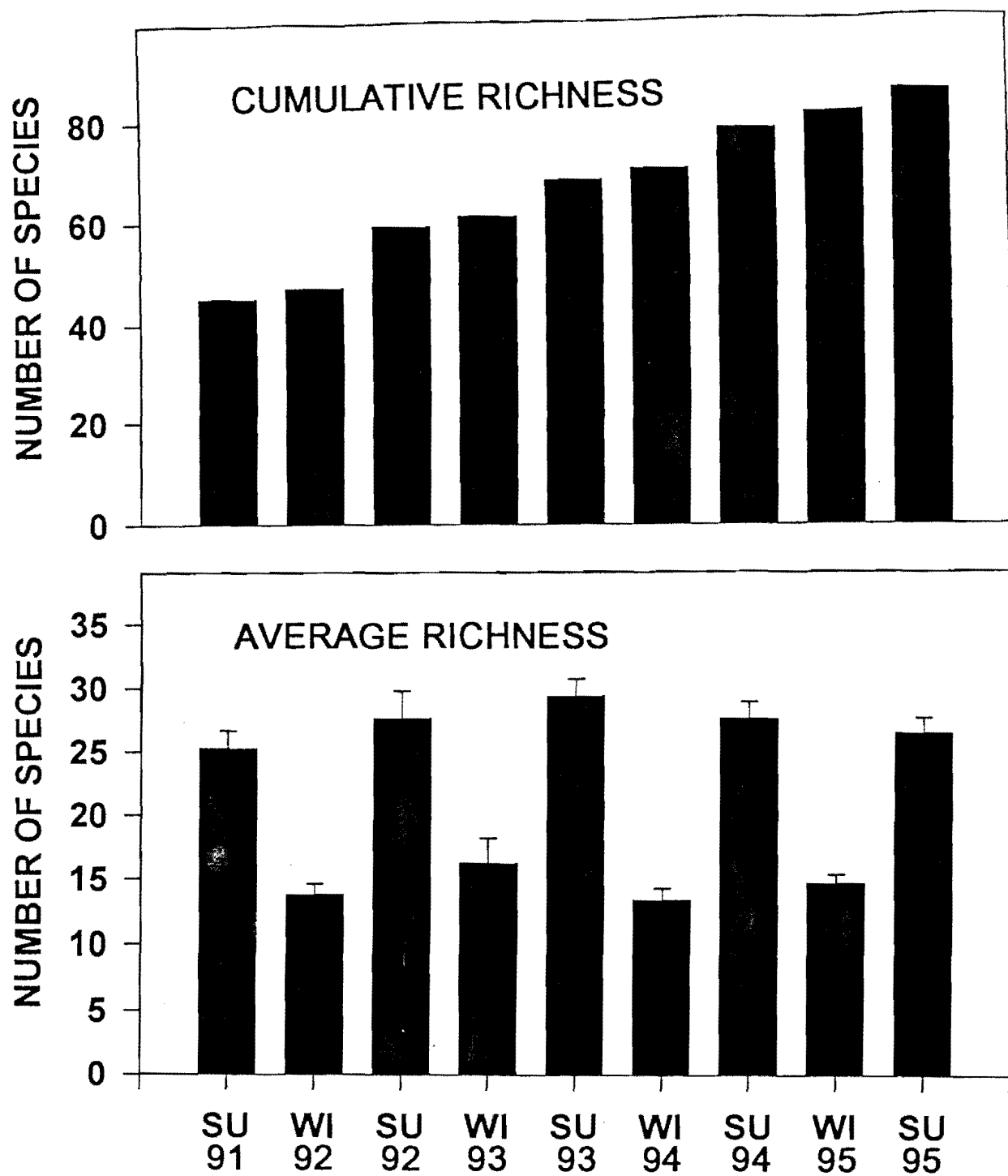


Fig. 4. (Upper) Total number of fish species censused during summer and winter (1991-95), and (Lower) average number of fish species present at each reef array, irrespective of spatial configuration, during the same sampling periods.

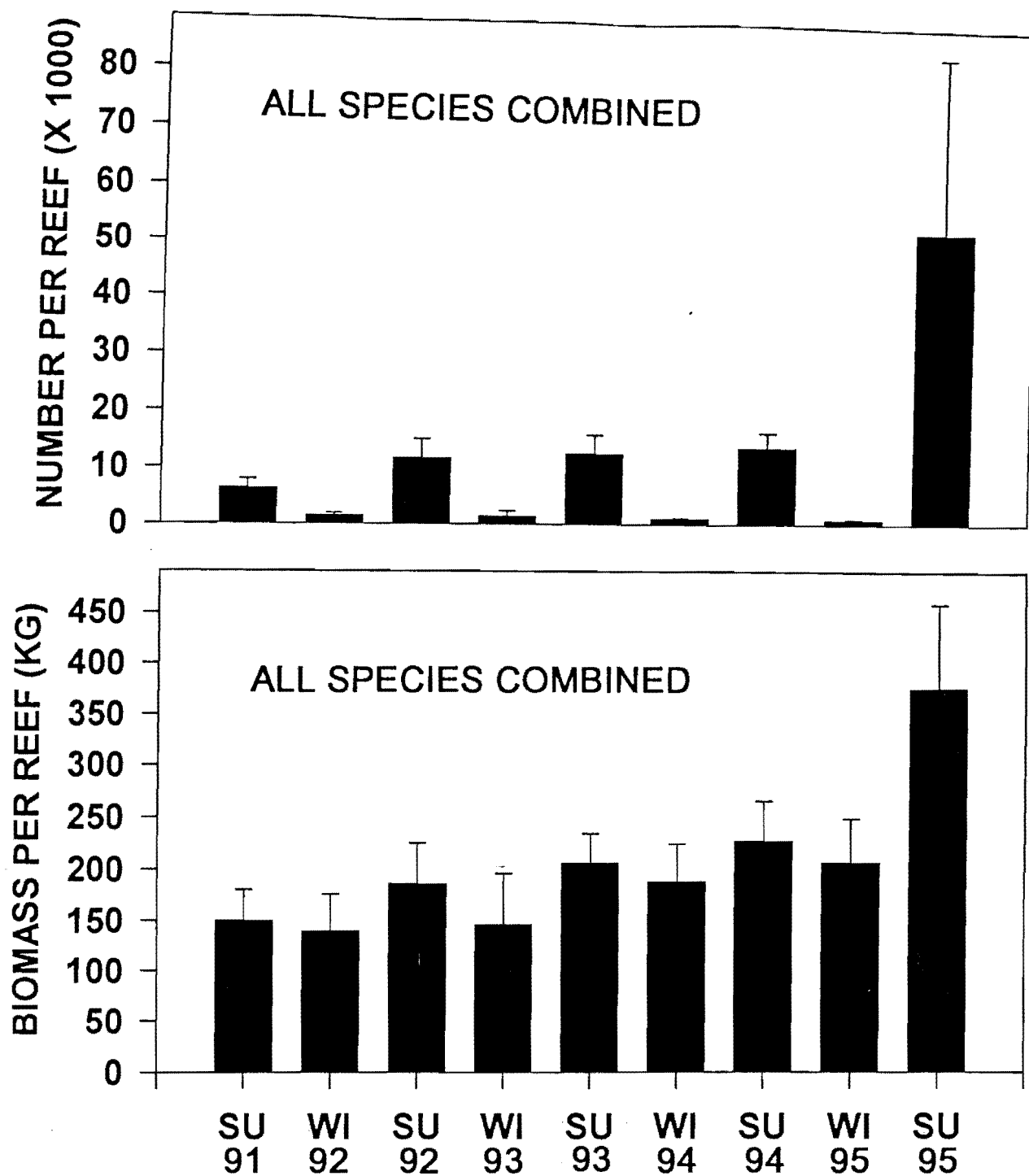


Fig. 5. (Upper) Mean numbers of fish censused at each reef array, irrespective of spatial configuration, and (Lower) the mean estimated total fish biomass present at each reef array during summer and winter (1991-95).

Table 3. Relative abundances of the twenty most common species censused during summer sampling periods (1991 – 1995).

SUMMER 1991			SUMMER 1992		SUMMER 1993		SUMMER 1994		SUMMER 1995	
RANK	COMMON NAME	% ABUN	COMMON NAME	% ABUN	COMMON NAME	% ABUN	COMMON NAME	% ABUN	COMMON NAME	% ABUN
1	tomtate	70.3%	tomtate	60.4%	tomtate	46.8%	Clupeidae spp.	49.5%	Clupeidae spp.	83.7%
2	round scad	17.3%	Clupeidae spp.	21.5%	Clupeidae spp.	36.4%	tomtate	39.1%	tomtate	13.2%
3	black sea bass	2.2%	round scad	9.7%	round scad	10.3%	round scad	2.9%	round scad	0.7%
4	pigfish	1.6%	Spanish sardine	1.5%	cubbyu	1.7%	cubbyu	1.3%	unidentified juv.	0.5%
5	cubbyu	1.6%	cubbyu	1.2%	white grunt	0.9%	Spanish sardine	1.3%	gag	0.5%
6	Spanish sardine	1.3%	white grunt	1.2%	belted sandfish	0.5%	unidentified juv.	1.1%	Spanish sardine	0.3%
7	white grunt	0.9%	black sea bass	0.8%	slippery dick	0.5%	white grunt	1.0%	white grunt	0.3%
8	slippery dick	0.8%	seaweed blenny	0.7%	gag	0.5%	slippery dick	0.7%	slippery dick	0.2%
9	Atlantic spadefish	0.8%	slippery dick	0.5%	seaweed blenny	0.3%	gag	0.6%	cubbyu	0.2%
10	Clupeidae spp.	0.6%	greater amberjack	0.4%	sand perch	0.3%	seaweed blenny	0.6%	belted sandfish	0.2%
11	belted sandfish	0.5%	pigfish	0.4%	sand diver	0.2%	belted sandfish	0.5%	seaweed blenny	0.1%
12	greater amberjack	0.5%	belted sandfish	0.4%	spottail pinfish	0.2%	black sea bass	0.3%	Atlantic spadefish	<0.1%
13	spottail pinfish	0.3%	Atlantic spadefish	0.3%	Atlantic spadefish	0.2%	Atlantic spadefish	0.2%	Spanish mackerel	<0.1%
14	seaweed blenny	0.2%	spottail pinfish	0.3%	black sea bass	0.2%	spottail pinfish	0.2%	crested blenny	<0.1%
15	Atlantic bumper	0.2%	gag	0.1%	blue runner	0.1%	greater amberjack	0.1%	whitespotted soapfish	<0.1%
16	sand perch	0.2%	gray triggerfish	<0.1%	gray snapper	0.1%	Spanish mackerel	<0.1%	black sea bass	<0.1%
17	blue runner	0.1%	sand perch	<0.1%	gray triggerfish	0.1%	blue runner	<0.1%	leopard toadfish	<0.1%
18	gag	0.1%	gray snapper	<0.1%	greater amberjack	0.1%	sand perch	<0.1%	gray triggerfish	<0.1%
19	planehead filefish	<0.1%	leopard toadfish	<0.1%	southern sennet	<0.1%	gray triggerfish	<0.1%	spotted goby	<0.1%
20	whitespotted soapfish	<0.1%	littlehead porgy	<0.1%	Spanish mackerel	<0.1%	sheepshead	<0.1%	sand perch	<0.1%
		99.6%		99.7%		99.6%		99.6%		99.9%
Number of reefs = 8			Number of reefs = 8		Number of reefs = 8		Number of reefs = 16		Number of reefs = 12	
Number of species = 45			Number of species = 50		Number of species = 47		Number of species = 57		Number of species = 54	
Total abundance = 51185			Total abundance = 95191		Total abundance = 101377		Total abundance = 221687		Total abundance = 627327	

Table 4. Rank ordering of taxa based on their relative contribution to total fish biomass during summer sampling periods (1991 – 1995).

SUMMER 1991			SUMMER 1992		SUMMER 1993		SUMMER 1994		SUMMER 1995	
RANK	COMMON NAME	% MASS	COMMON NAME	% MASS	COMMON NAME	% MASS	COMMON NAME	% MASS	COMMON NAME	% MASS
1	tomtate	39.0%	greater amberjack	24.0%	gag	32.7%	gag	29.9%	gag	41.9%
2	round scad	17.0%	tomtate	21.4%	nurse shark	11.9%	greater amberjack	11.6%	Clupeidae spp.	20.1%
3	black sea bass	7.3%	gag	9.5%	white grunt	9.0%	nurse shark	7.7%	jewfish	11.1%
4	white grunt	6.7%	white grunt	6.5%	tomtate	7.9%	white grunt	6.9%	nurse shark	5.1%
5	Atlantic spadefish	5.3%	black sea bass	6.4%	jewfish	5.3%	Atlantic spadefish	5.5%	Atlantic spadefish	3.5%
6	greater amberjack	5.0%	round scad	5.9%	gray triggerfish	3.6%	jewfish	4.3%	tomtate	3.2%
7	pigfish	4.4%	Atlantic spadefish	5.3%	cubbyu	3.2%	round scad	3.9%	white grunt	3.0%
8	cubbyu	3.6%	gray triggerfish	4.2%	greater amberjack	3.2%	tomtate	3.4%	Spanish mackerel	2.6%
9	gag	3.1%	cubbyu	2.9%	Clupeidae spp.	2.9%	Spanish sardine	3.2%	red grouper	1.9%
10	Spanish sardine	2.7%	jewfish	2.9%	red grouper	2.6%	gray triggerfish	2.4%	gray triggerfish	1.3%
11	Atlantic bumper	1.0%	Clupeidae spp.	2.9%	Atlantic spadefish	2.4%	cubbyu	2.3%	cobia	1.1%
12	blue runner	0.6%	Spanish sardine	1.2%	round scad	2.4%	red grouper	2.1%	great barracuda	0.7%
13	red grouper	0.6%	sheepshead	0.8%	Spanish mackerel	2.3%	Spanish mackerel	1.9%	cubbyu	0.7%
14	spottail pinfish	0.6%	gray snapper	0.8%	gray snapper	2.0%	Clupeidae spp.	1.9%	leopard toadfish	0.6%
15	gulf flounder	0.4%	littlehead porgy	0.7%	blue runner	1.9%	black sea bass	1.9%	black sea bass	0.5%
16	littlehead porgy	0.3%	spottail pinfish	0.7%	black sea bass	1.9%	blue runner	1.6%	hogfish	0.4%
17	slippery dick	0.3%	leopard toadfish	0.7%	sheepshead	1.0%	crevalle jack	1.4%	sheepshead	0.4%
18	gray triggerfish	0.3%	pigfish	0.5%	leopard toadfish	0.5%	great barracuda	1.3%	gray snapper	0.4%
19	sand perch	0.2%	red grouper	0.4%	sand diver	0.5%	cobia	1.2%	Spanish sardine	0.3%
20	gray snapper	0.2%	gulf flounder	0.4%	littlehead porgy	0.4%	sheepshead	1.1%	southern stingray	0.2%
		98.7%		98.1%		97.5%		95.7%		98.8%
Number of reefs = 8			Number of reefs = 8		Number of reefs = 8		Number of reefs = 16		Number of reefs = 12	
Number of species = 44			Number of species = 50		Number of species = 47		Number of species = 57		Number of species = 54	
Total biomass = 1200 KG			Total biomass = 1488 KG		Total biomass = 1646 KG		Total biomass = 3626 KG		Total biomass = 4504 KG	

Table 5. Relative abundances of the twenty most common species censused during winter sampling periods (1991 – 1995).

WINTER 1992			WINTER 1993		WINTER 1994		WINTER 1995	
RANK	COMMON NAME	% ABUN	COMMON NAME	% ABUN	COMMON NAME	% ABUN	COMMON NAME	% ABUN
1	black sea bass	26.4%	tomtate	65.9%	cubbyu	22.5%	unidentified juv.	23.2%
2	pigfish	22.1%	black sea bass	8.1%	spottail pinfish	17.2%	tomtate	23.0%
3	spottail pinfish	20.6%	cubbyu	6.6%	black sea bass	10.5%	gag	14.0%
4	tomtate	9.6%	spottail pinfish	4.1%	white grunt	10.4%	sheepshead	11.5%
5	cubbyu	6.8%	white grunt	4.0%	pigfish	7.8%	white grunt	8.8%
6	white grunt	6.3%	sheepshead	2.5%	sheepshead	6.8%	cubbyu	5.0%
7	Atlantic spadefish	2.9%	gag	1.9%	tomtate	5.8%	black sea bass	4.1%
8	sheepshead	2.0%	seaweed blenny	1.7%	round scad	5.7%	belted sandfish	2.9%
9	belted sandfish	0.7%	Atlantic spadefish	1.5%	gag	5.1%	seaweed blenny	2.2%
10	sand perch	0.5%	belted sandfish	1.2%	red porgy	2.5%	spottail pinfish	1.4%
11	seaweed blenny	0.5%	round scad	0.4%	seaweed blenny	1.6%	Atlantic spadefish	0.8%
12	gag	0.4%	gray triggerfish	0.3%	belted sandfish	1.6%	gray triggerfish	0.7%
13	slippery dick	0.3%	pigfish	0.3%	Atlantic spadefish	0.6%	leopard toadfish	0.6%
14	round scad	0.2%	leopard toadfish	0.2%	sand perch	0.4%	red grouper	0.3%
15	planehead filefish	<0.1%	gray snapper	0.2%	leopard toadfish	0.3%	pigfish	0.3%
16	gray snapper	<0.1%	sand perch	0.2%	Clupeidae spp.	0.3%	hogfish	0.2%
17	gulf flounder	<0.1%	red grouper	0.2%	red grouper	0.2%	jackknife-fish	0.2%
18	leopard toadfish	<0.1%	planehead filefish	0.1%	hogfish	0.1%	tiger goby	0.1%
19	jackknife-fish	<0.1%	slippery dick	0.1%	black drum	<0.1%	crested blenny	0.1%
20	greater amberjack	<0.1%	tiger goby	<0.1%	gray triggerfish	<0.1%	spotted dragonet	<0.1%
		99.8%		99.7%		99.6%		99.5%
Number of reefs = 8			Number of reefs = 4		Number of reefs = 16		Number of reefs = 16	
Number of species = 30			Number of species = 31		Number of species = 38		Number of species = 42	
Total abundance = 11872			Total abundance = 5790		Total abundance = 16207		Total abundance = 13142	

Table 6. Rank ordering of taxa based on their relative contribution to total fish biomass during winter sampling periods (1991 – 1995).

WINTER 1992			WINTER 1993		WINTER 1994		WINTER 1995	
RANK	COMMON NAME	% MASS	COMMON NAME	% MASS	COMMON NAME	% MASS	COMMON NAME	% MASS
1	black sea bass	24.1%	gag	26.4%	sheepshead	29.4%	sheepshead	38.1%
2	pigfish	16.2%	sheepshead	25.9%	gag	29.3%	gag	37.5%
3	sheepshead	15.8%	black sea bass	12.6%	white grunt	13.9%	white grunt	12.2%
4	white grunt	11.7%	white grunt	11.2%	black sea bass	5.8%	gray triggerfish	2.3%
5	spottail pinfish	8.3%	Atlantic spadefish	4.6%	cubbyu	5.4%	black sea bass	2.3%
6	Atlantic spadefish	7.2%	red grouper	3.4%	spottail pinfish	5.1%	red grouper	1.8%
7	gag	5.6%	spottail pinfish	3.2%	pigfish	2.9%	Atlantic spadefish	1.6%
8	tomtate	4.5%	cubbyu	2.9%	tomtate	2.3%	cubbyu	0.8%
9	cubbyu	3.9%	jewfish	2.6%	round scad	1.8%	hogfish	0.6%
10	gulf flounder	0.7%	gray triggerfish	2.5%	red grouper	1.2%	jewfish	0.6%
11	red grouper	0.6%	tomtate	2.3%	Atlantic spadefish	0.9%	leopard toadfish	0.5%
12	sand perch	0.3%	black drum	0.6%	black drum	0.5%	tomtate	0.4%
13	greater amberjack	0.3%	leopard toadfish	0.4%	nurse shark	0.4%	spottail pinfish	0.4%
14	leopard toadfish	0.1%	gray snapper	0.4%	hogfish	0.3%	greater amberjack	0.3%
15	gray snapper	0.1%	pigfish	0.3%	leopard toadfish	0.3%	black drum	0.2%
16	planehead filefish	<0.1%	gulf flounder	0.2%	gray triggerfish	0.2%	blue angelfish	0.1%
17	jackknife-fish	<0.1%	planehead filefish	0.1%	sand perch	0.1%	pigfish	<0.1%
18	Echeneis spp.	<0.1%	sand perch	0.1%	blue angelfish	<0.1%	polka-dot batfish	<0.1%
19	slippery dick	<0.1%	hogfish	<0.1%	gray snapper	<0.1%	belted sandfish	<0.1%
20	round scad	<0.1%	round scad	<0.1%	planehead filefish	<0.1%	planehead filefish	<0.1%
		99.9%		99.9%		99.9%		99.9%
Number of reefs = 8			Number of reefs = 4		Number of reefs = 16		Number of reefs = 16	
Number of species = 29			Number of species = 31		Number of species = 38		Number of species = 42	
Total biomass = 1115 KG			Total biomass = 532 kg		Total biomass = 2998 kg		Total biomass = 3293 kg	

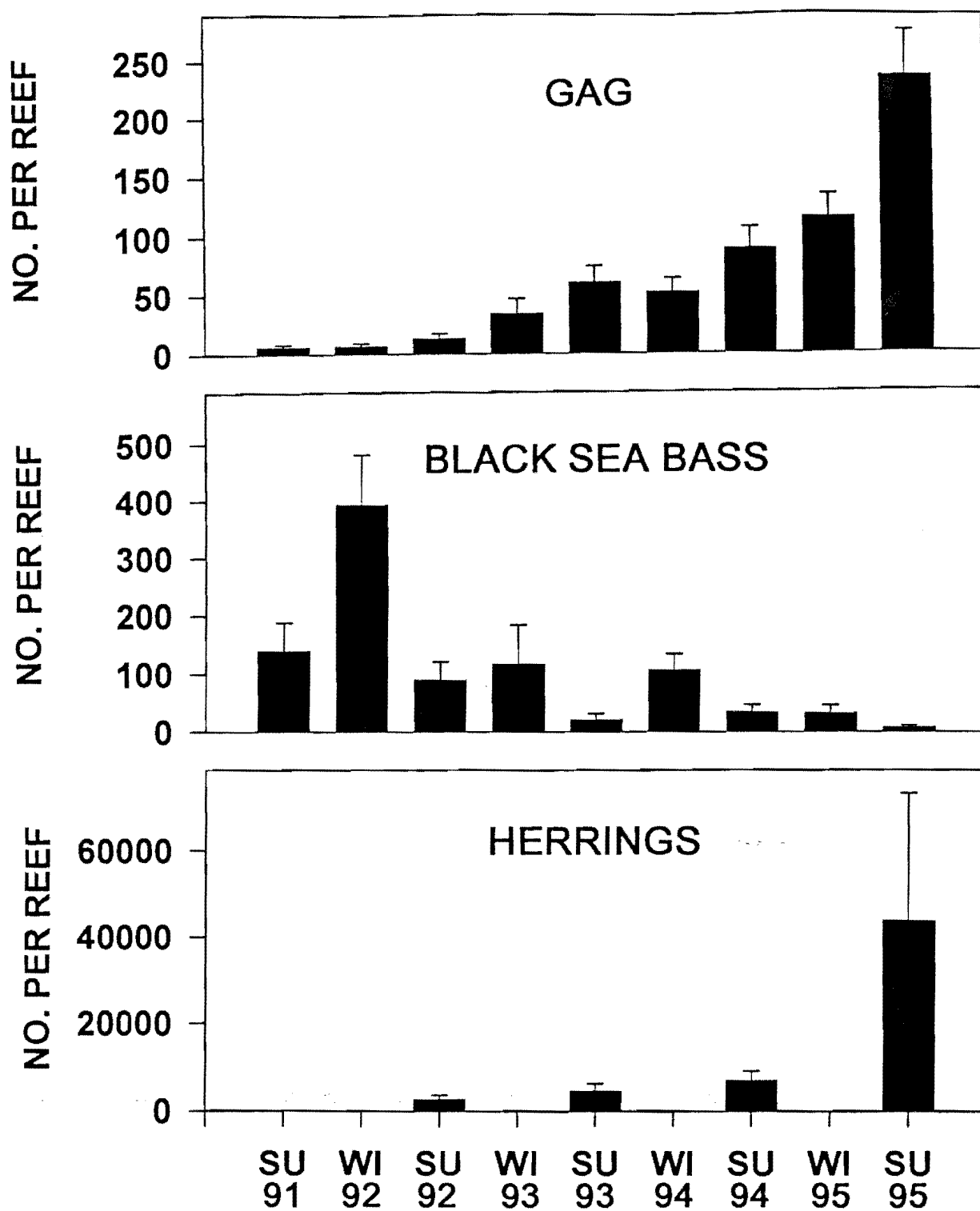


Fig. 6. Mean numbers of gag, black sea bass, and herrings (*Clupeidae* sp.) at each reef array, irrespective of spatial configuration, for summer and (1991-95).

relationship between fish numbers at the artificial reefs and the percent cover of adjacent hard-bottom habitat could be tested for 37 taxa.

A significant positive relationship existed for just 8 species (Table 7): cubbyu, white grunt, nurse shark, gag, red grouper, Atlantic spadefish, Clupeidae spp., and Spanish mackerel. A significant negative relationship existed for 3 species (Table 7): black sea bass, leopard toadfish, and seaweed blennies. However, fish abundance was not significantly associated with adjacent hard-bottom ($p \geq 0.05$) for the remaining 26 species (Table 7).

Reef Treatment and Time Effects on Fishes

Gag abundance increased over time ($p = 0.0001$), and gag were slightly more abundant in summer than in winter ($p = 0.0021$). Patch reef size significantly interacted with the time trend ($p = 0.0002$), such that gag abundance increased faster on 16-cube reefs than on 4-cube reefs (Fig. 7). By the summer of 1995, gag attained an average of 391 individuals per 16-cube x 225-m reef array. Over that same 5-year span, the minimum and median sizes of gag, averaged among all reefs, remained the same while the average maximum size tended to increase (Fig. 8).

Red grouper also increased in abundance over time ($p = 0.0292$) and were significantly more abundant at 16-cube reefs than at 4-cube reefs ($p = 0.0327$) (Fig. 9). By the summer of 1995, red grouper were distributed essentially as one fish per patch on each of the 16-cube x 225-m reef arrays.

Black sea bass abundance was greater in winter than in summer ($p = 0.0001$), but decreased substantially over time ($p = 0.0001$) (Fig. 10). The time trend and season significantly interacted ($p = 0.0001$) such that the decline was more dramatic for winters than for summers. Superimposed on these changes with time was an effect of patch reef spacing ($p = 0.0278$), with abundances greater on reefs with 225-m spacing than on those with 25-m spacing. The average winter abundance of black sea bass on 16-cube reefs spaced at 225-m declined from 702 in 1992 to 30 in 1995. Over the 5-year period, the minimum and median sizes of black sea bass, averaged among all reefs, tended to increase while the average maximum size showed relatively little change (Fig. 11).

In contrast to the serranids above, white grunt abundance showed no significant trends over time. They were, however, more abundant in winter than in summer ($p = 0.0001$) (Fig. 12), and the seasonal effect interacted significantly with both patch reef size ($p = 0.0001$) and patch reef spacing ($p = 0.0438$). Typically within seasons, the 16-cube patch reefs spaced at 225-m had the highest abundances of white grunt, averaging 160 across winters and 90 across summers.

Gray triggerfish were more abundant in summer than in winter ($p = 0.0001$), and increased in abundance over time ($p = 0.0173$). Independent of these time effects, patch reef size and spacing interacted significantly ($p = 0.0211$), such that abundances were greatest on 16-cube x 225-m reefs (Fig. 13). The average summer abundance of gray triggerfish on

Table 7. Fishes showing a significant relationship between Summer 1994 abundance and the percent cover of natural hard bottom habitat. A positive slope indicates more fish were found on reefs with larger amounts of surrounding hard bottom habitat.

COMMON NAME	SPECIES NAME	SLOPE	TYPE III- F	PROB > F
cubbyu	<i>Equetus umbrosus</i>	+	68.34	0.0001
white grunt	<i>Haemulon plumieri</i>	+	49.28	0.0001
nurse shark	<i>Ginglymostoma cirratum</i>	+	24.37	0.0004
gag	<i>Mycteroperca microlepis</i>	+	21.15	0.0008
red grouper	<i>Epinephelus morio</i>	+	12.28	0.0049
Atlantic spadefish	<i>Chaetodipterus faber</i>	+	7.86	0.0172
leopard toadfish	<i>Opsanus pardus</i>	-	7.67	0.0182
herrings	Clupeidae spp.	+	6.99	0.0228
Spanish mackerel	<i>Scomberomorus maculatus</i>	+	6.37	0.0283
black sea bass	<i>Centropristis striata</i>	-	5.82	0.0345
seaweed blenny	<i>Parablennius marmoreus</i>	-	5.60	0.0374

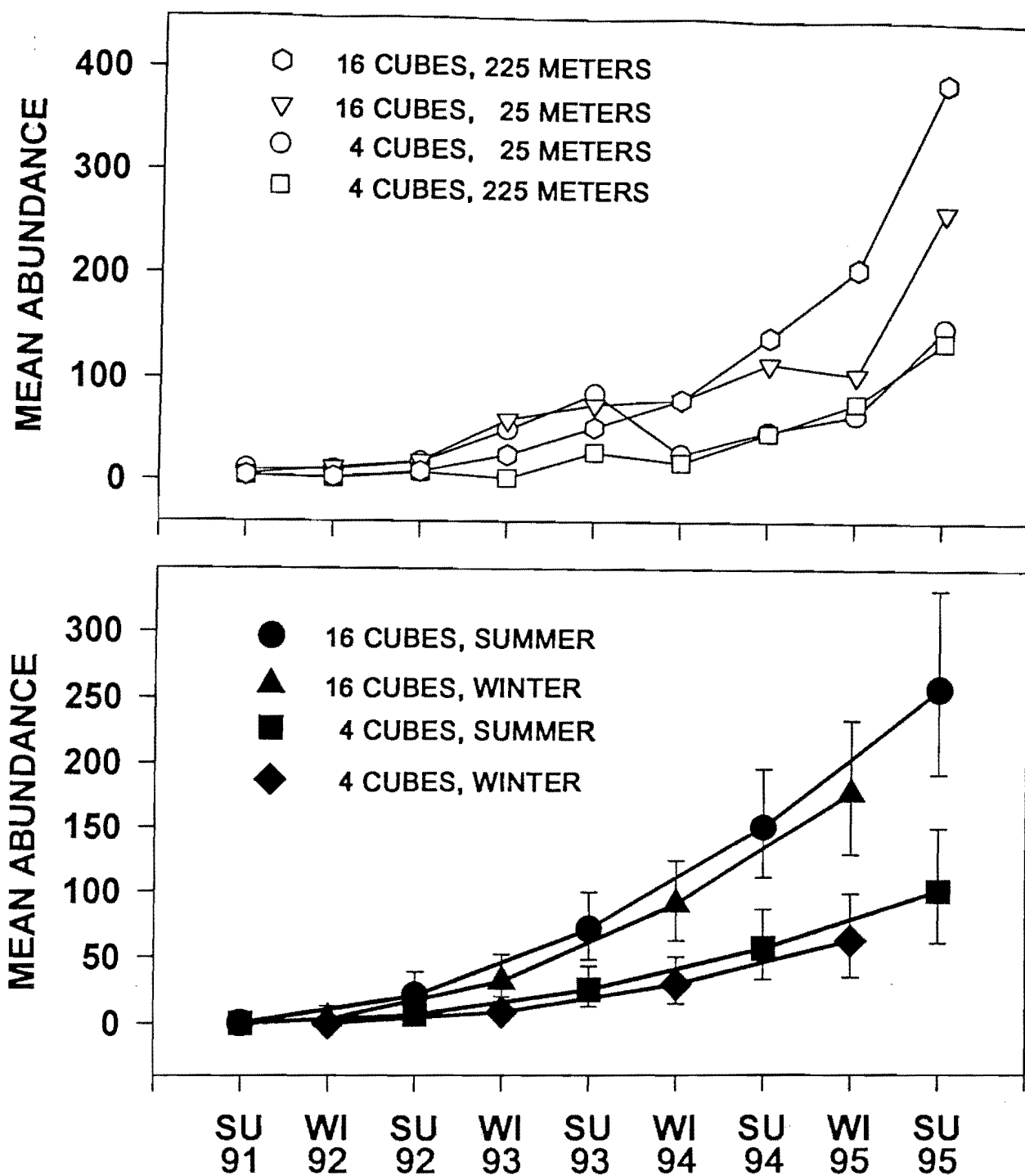


Fig. 7. (Upper) Mean numbers of gag per reef treatment for summer and winter during 1991 through 1995. (Lower) Predicted means generated from a model incorporating only significant fixed-factor effects as identified in the legend (see text for further details with regard to the analysis); 95% confidence intervals are given for each predicted value.

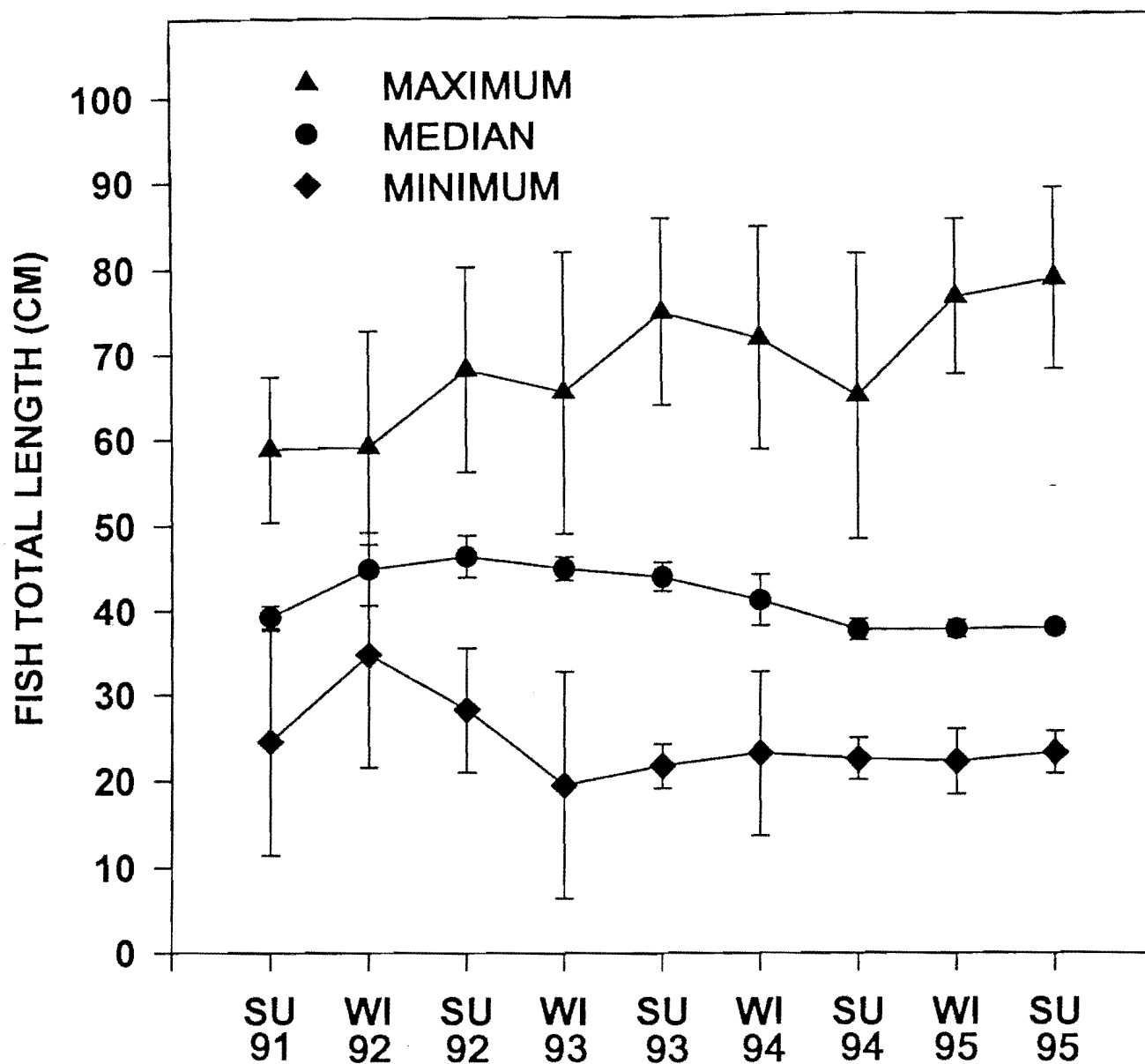


Fig. 8. Estimated total lengths (cm) of gag censused during summer and winter (1991-95), irrespective of reef treatment. Error bars represent 95% confidence intervals around minimum, maximum, and median values.

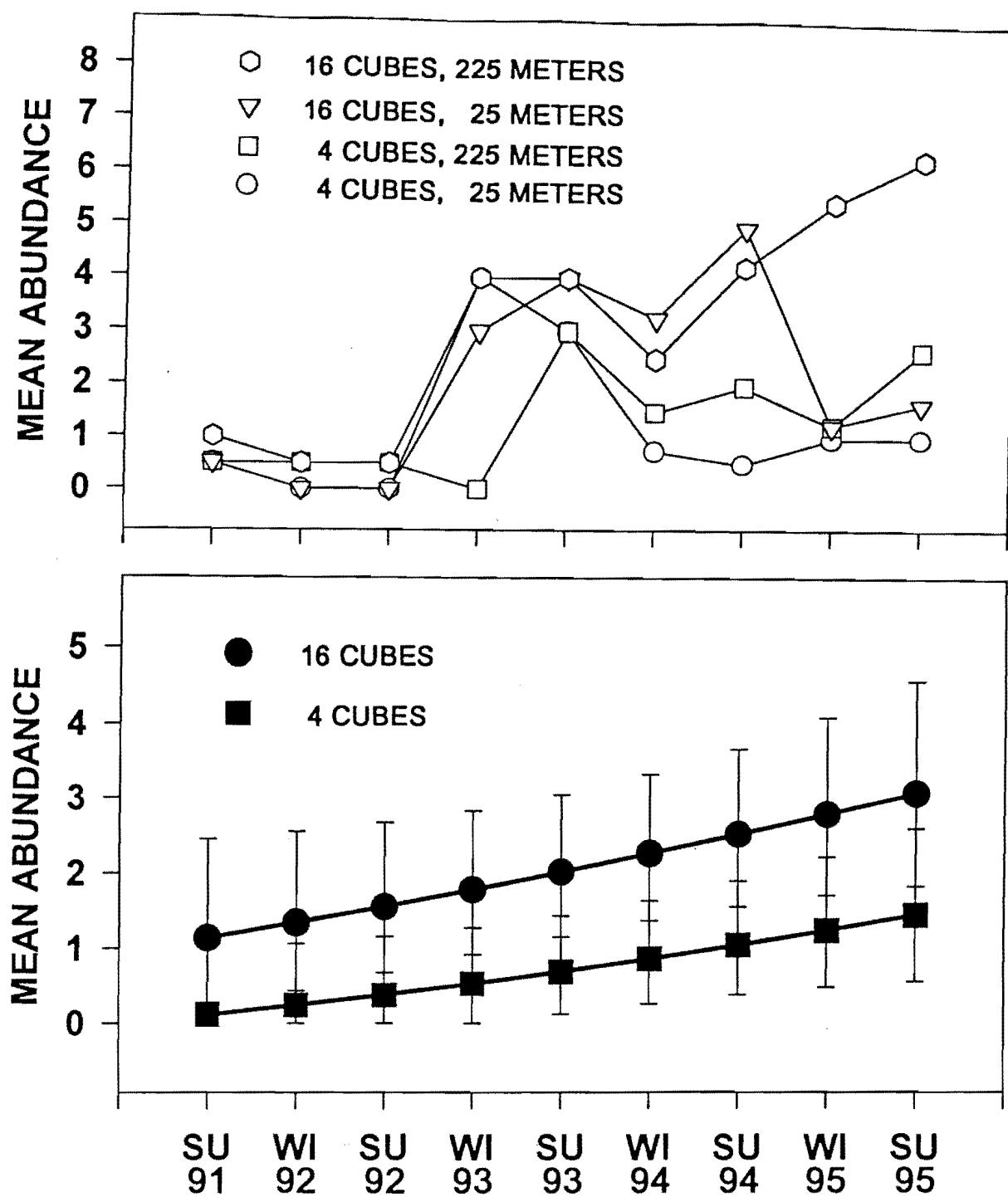


Fig. 9. (Upper) Mean numbers of red grouper per reef treatment for summer and winter during 1991 through 1995. (Lower) Predicted means generated from a model incorporating only significant fixed-factor effects as identified in the legend (see text for further details with regard to the analysis); 95% confidence intervals are given for each predicted value.

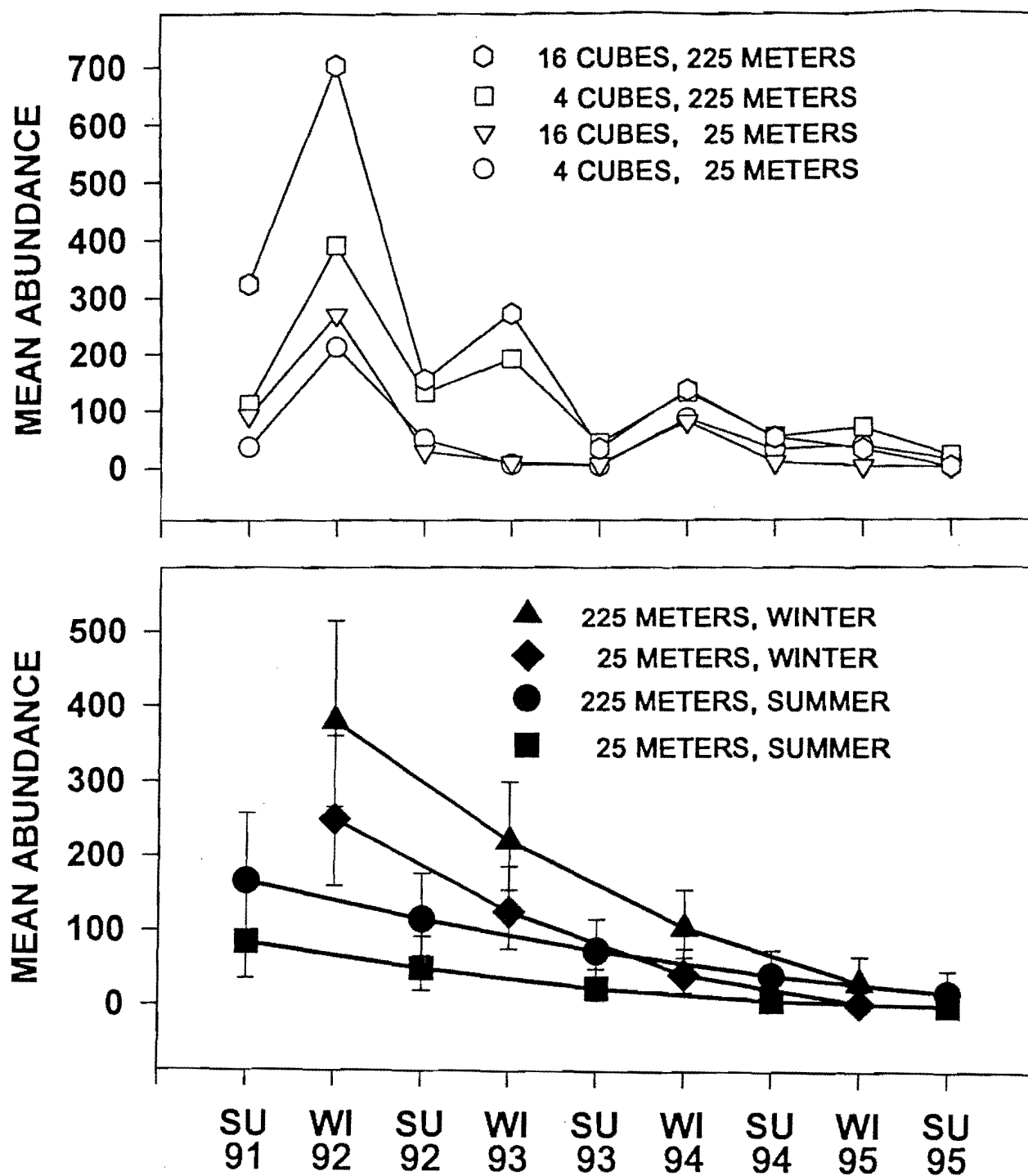


Fig. 10. (Upper) Mean numbers of black sea bass per reef treatment for summer and winter during 1991 through 1995. (Lower) Predicted means generated from a model incorporating only significant fixed-factor effects as identified in the legend (see text for further details with regard to the analysis); 95% confidence intervals are given for each predicted value.

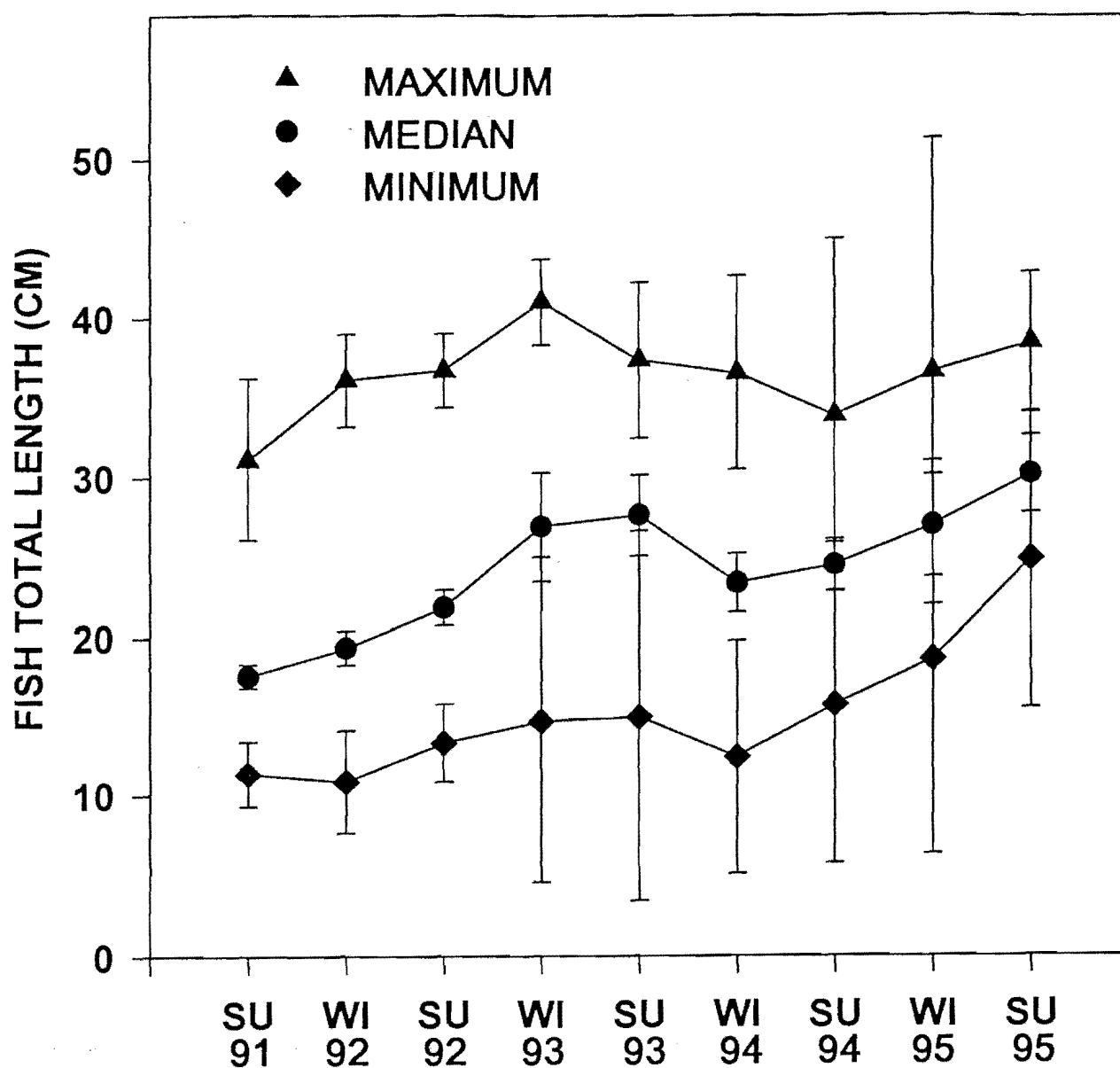


Fig. 11. Estimated total lengths (cm) of black sea bass censused during summer and winter (1991-95), irrespective of reef treatment. Error bars represent 95% confidence intervals around minimum, maximum, and median values.

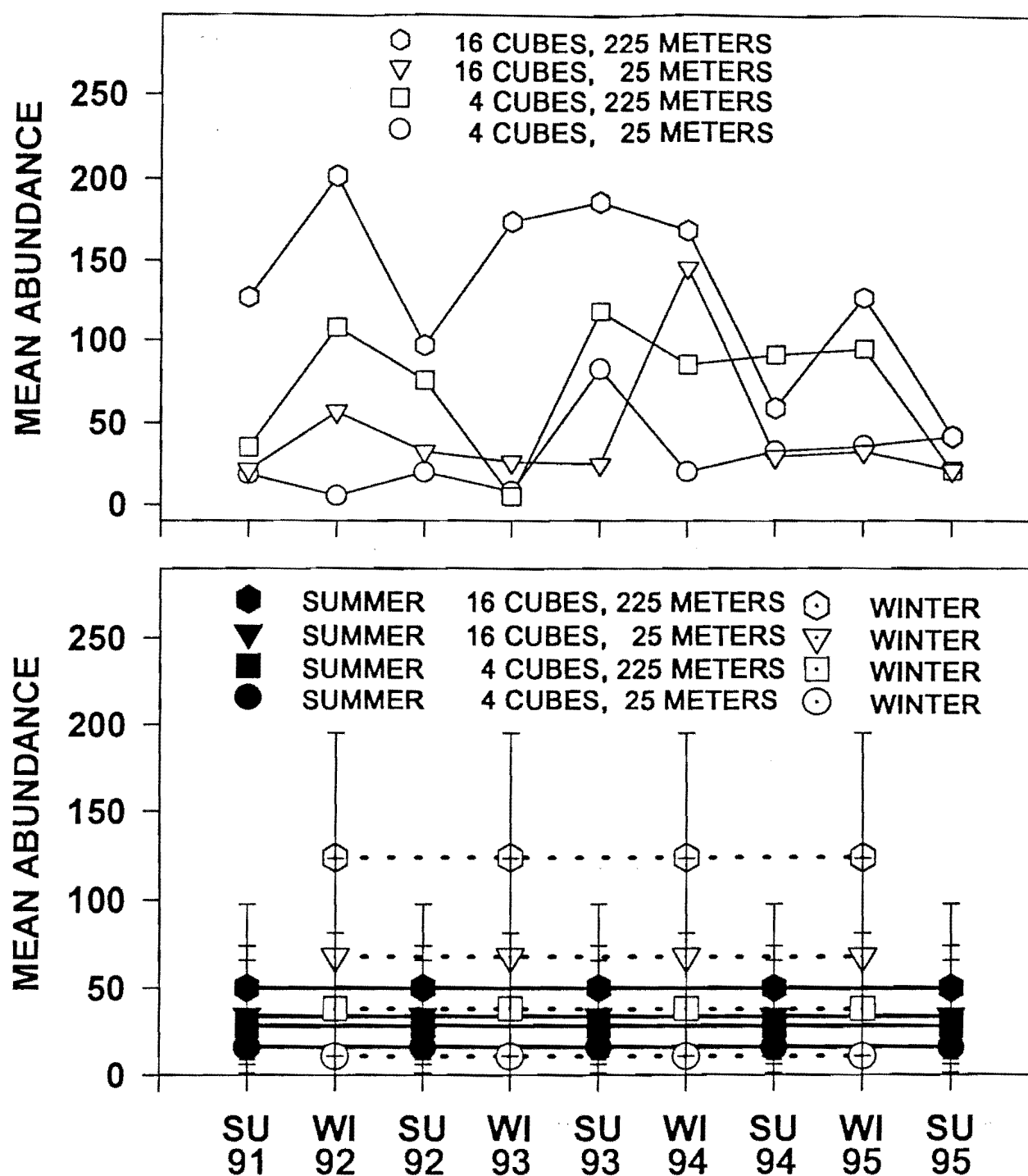


Fig. 12. (Upper) Mean numbers of white grunt per reef treatment for summer and winter during 1991 through 1995. (Lower) Predicted means generated from a model incorporating only significant fixed-factor effects as identified in the legend (see text for further details with regard to the analysis); 95% confidence intervals are given for each predicted value.

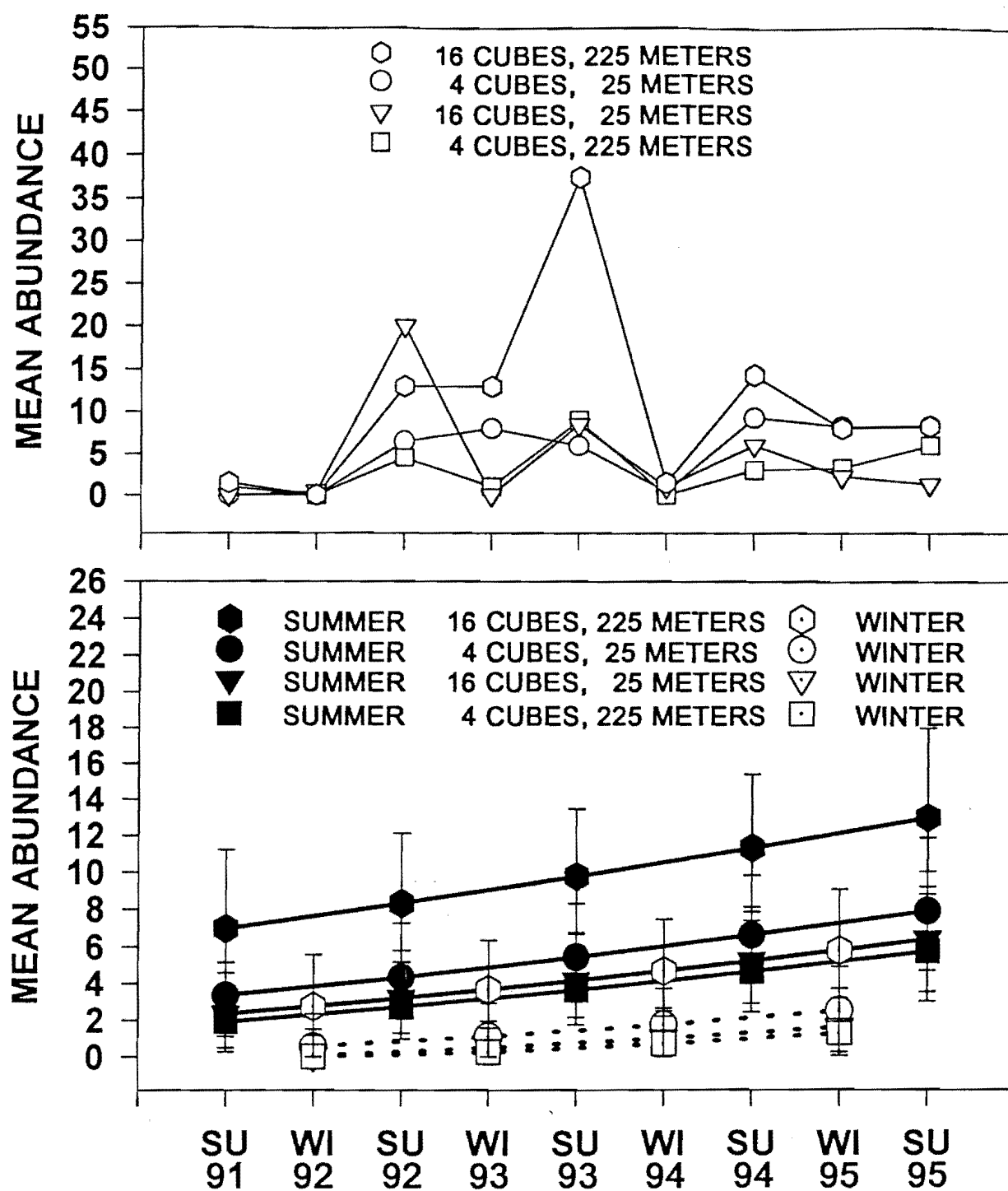


Fig. 13. (Upper) Mean numbers of gray triggerfish per reef treatment for summer and winter during 1991 through 1995. (Lower) Predicted means generated from a model incorporating only significant fixed-factor effects as identified in the legend (see text for further details with regard to the analysis); 95% confidence intervals are given for each predicted value.

this favored reef type peaked at 38 fish per reef during the summer of 1993, but never rose above 14 for any other season.

Tomtate adults decreased significantly over time ($p = 0.0001$), and were more abundant in summer than in winter ($p = 0.0001$). However, the time trend and season effect interacted ($p = 0.0026$), such that abundance declined to a greater extent across summers than across winters (Fig. 14). Initially, tomtate adults were more abundant on 16-cube reefs than on 4-cube reefs ($p = 0.0025$), but this size effect interacted with the time trend ($p = 0.0019$) by disappearing as adult tomtate became scarce. By the summer of 1995, an average of 13 adult tomtate per reef were censused among all reefs, regardless of design.

Cubbyu were more abundant in summer than in winter ($p = 0.0093$), but showed no significant trends over time (Fig. 15). They were consistently more numerous on 225-m reefs than on 25-m reefs. Patch reef spacing had a greater contribution to the best fitting model than did season, but because of variability over time it yielded a marginal probability ($p = 0.0749$).

Sheepshead abundance increased over time ($p = 0.0001$), and that trend significantly interacted with season ($p = 0.0045$) (Fig. 16). Likewise, sheepshead abundance was significantly greater on 16-cube reefs than on 4-cube reefs ($p = 0.0001$), and that treatment effect significantly interacted with season ($p = 0.0001$). Over time, sheepshead increasingly aggregated on 16-cube reefs in the winter, attaining an average 176 per reef by the winter of 1995. The winter increase in abundance was attributable to an influx of large fish, as evidenced by the seasonal contrast in maximum sizes, averaged across all reefs (Fig. 17).

The abundance of herrings, family Cludeidae, increased over time ($p = 0.0010$), and that trend interacted with both season and patch reef size in 2-way ($p = 0.0001$ and $p = 0.0030$, respectively) and 3-way ($p = 0.0028$) interaction effects. These fishes were absent in winter, and over the summers increased in abundance to a greater degree on 16-cube reefs than on the 4-cube reefs (Fig. 18). The overall trend was amplified by exceptionally high averages from 16-cube x 25-m reefs during the summer of 1995. Round scad, as another schooling planktivore, was much more abundant in summer than winter ($p = 0.0001$), but showed a decreasing trend over time ($p = 0.0316$) that interacted with season ($p = 0.0446$), i.e. they were absent in winter and decreased in numbers over the summers.

The abundance of belted sandfish increased over time ($p = 0.0001$) and was greater in summers than in winters ($p = 0.0001$) (Fig. 19). They were more abundant on 16-cube reefs than 4-cube reefs ($p = 0.0005$), and that effect interacted with season ($p = 0.0308$) so the contrast between patch reef sizes was greater in the summer than in the winter. Belted sandfish were also more abundant on 25-m reefs than on 225-m reefs ($p = 0.0465$). Their summer numbers on the 16-cube x 25-m reefs increased from an average of 44 per array in 1991 to 134 per array in 1995. Seaweed blenny, as another small fish very closely associated with the reef surface, also increased in abundance over time ($p = 0.0001$), was

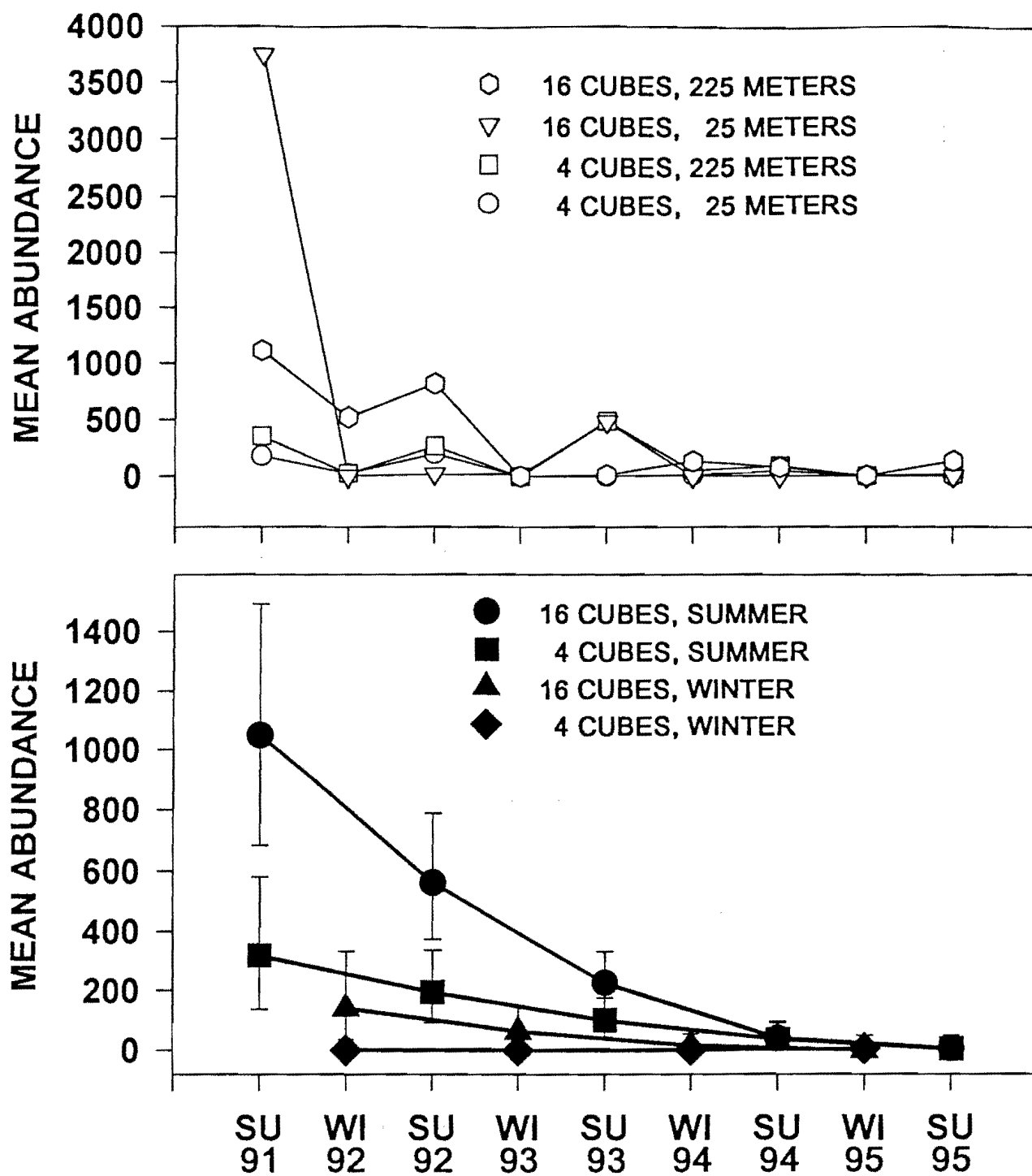


Fig. 14. (Upper) Mean numbers of tomtate (adults) per reef treatment for summer and winter during 1991 through 1995. (Lower) Predicted means generated from a model incorporating only significant fixed-factor effects as identified in the legend (see text for further details with regard to the analysis); 95% confidence intervals are given for each predicted value.

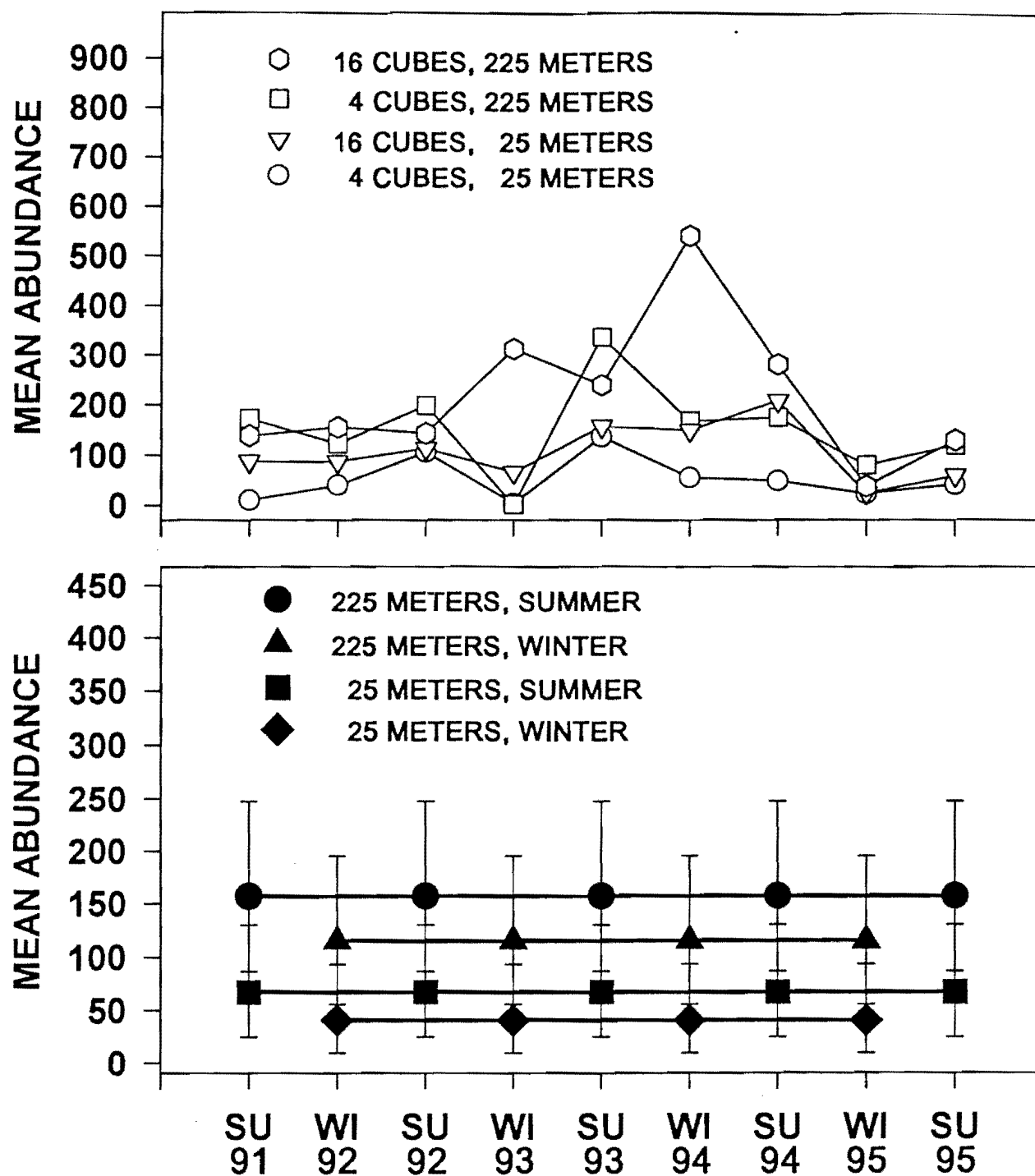


Fig. 15. (Upper) Mean numbers of cubbyu per reef treatment for summer and winter during 1991 through 1995. (Lower) Predicted means generated from a model incorporating only significant fixed-factor effects as identified in the legend (see text for further details with regard to the analysis); 95% confidence intervals are given for each predicted value.

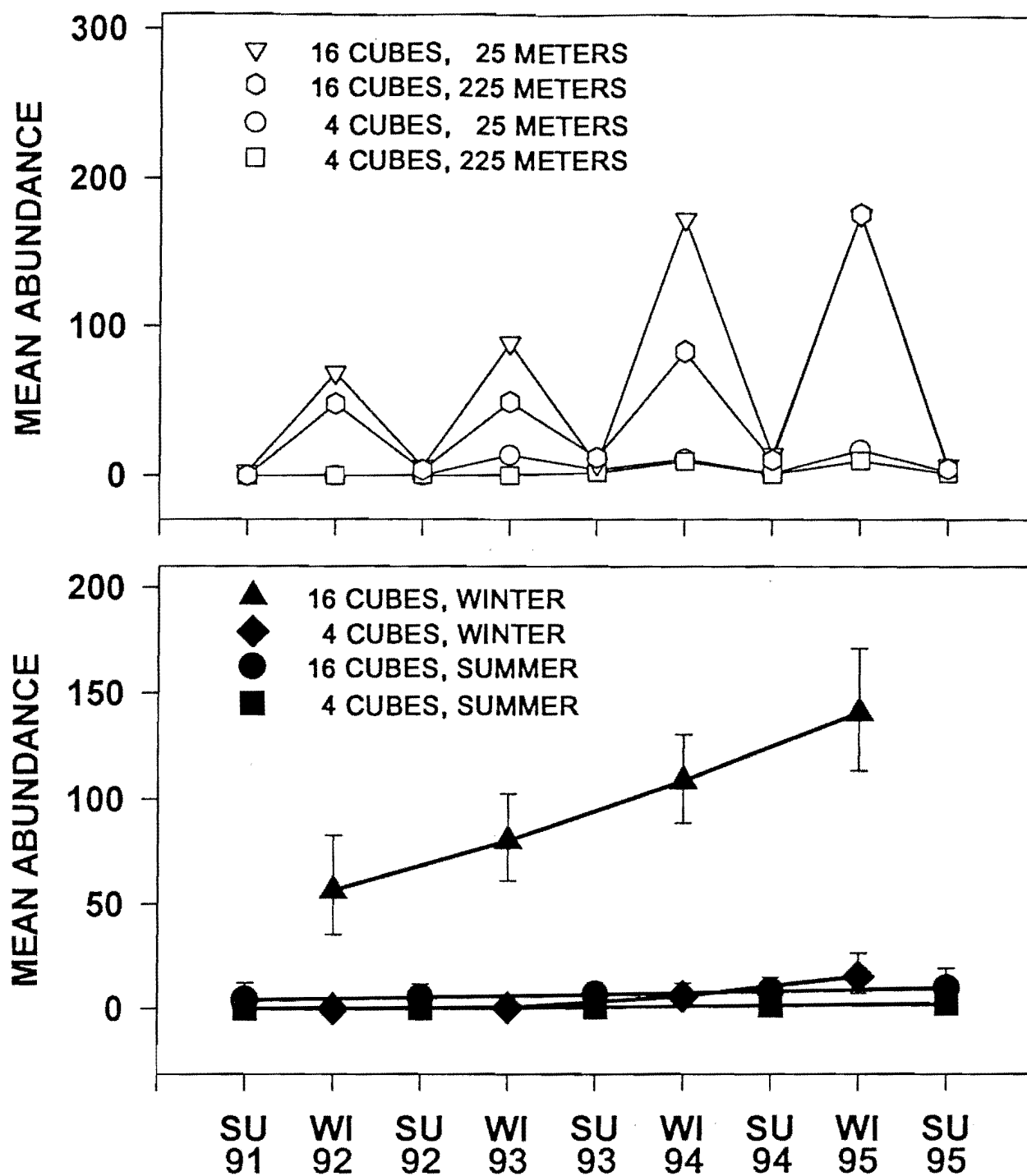


Fig. 16. (Upper) Mean numbers of sheephead per reef treatment for summer and winter during 1991 through 1995. (Lower) Predicted means generated from a model incorporating only significant fixed-factor effects as identified in the legend (see text for further details with regard to the analysis); 95% confidence intervals are given for each predicted value.

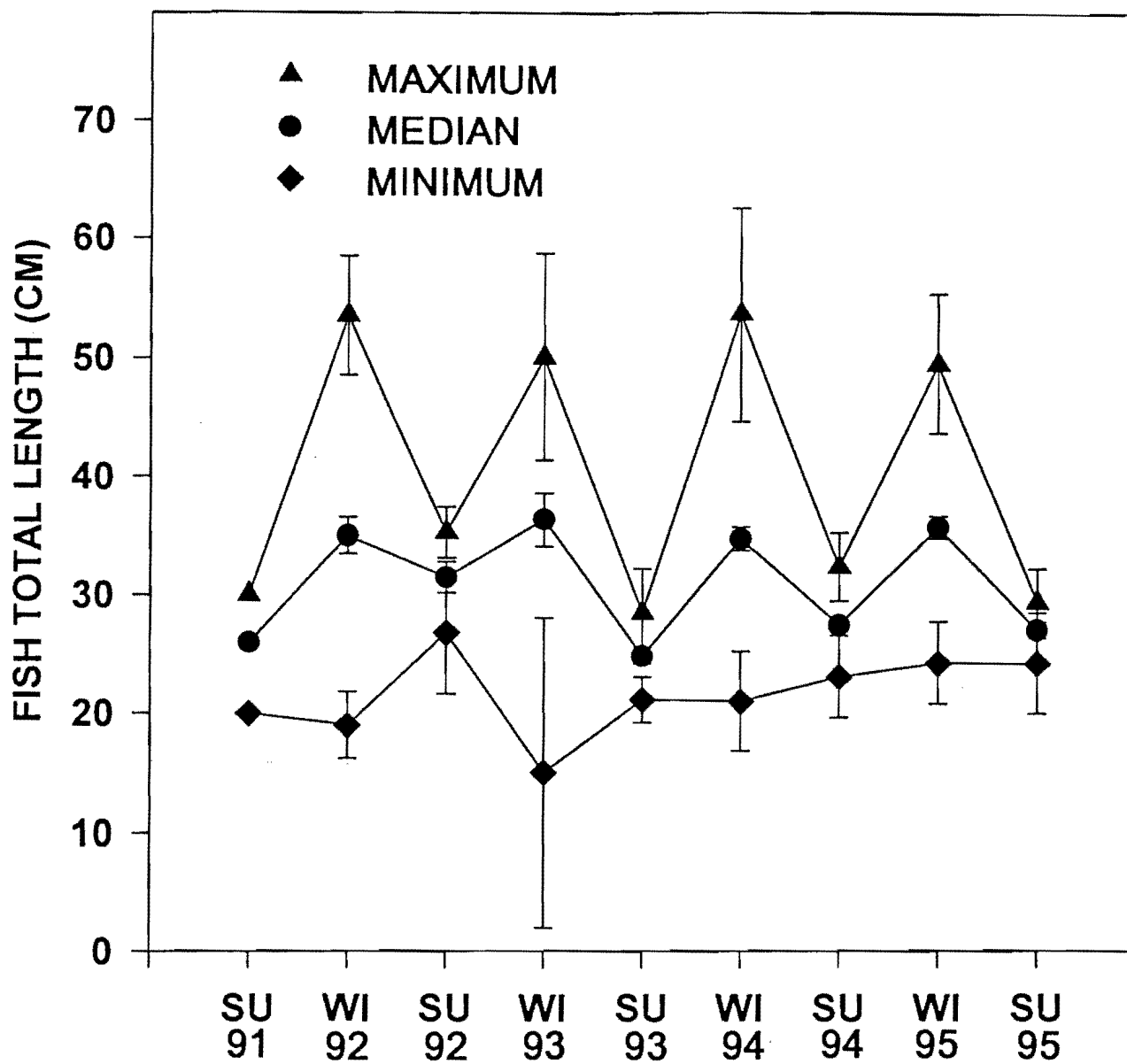


Fig. 17. Estimated total lengths (cm) of sheephead censused during summer and winter (1991-95), irrespective of reef treatment. Error bars represent 95% confidence intervals around minimum, maximum, and median values.

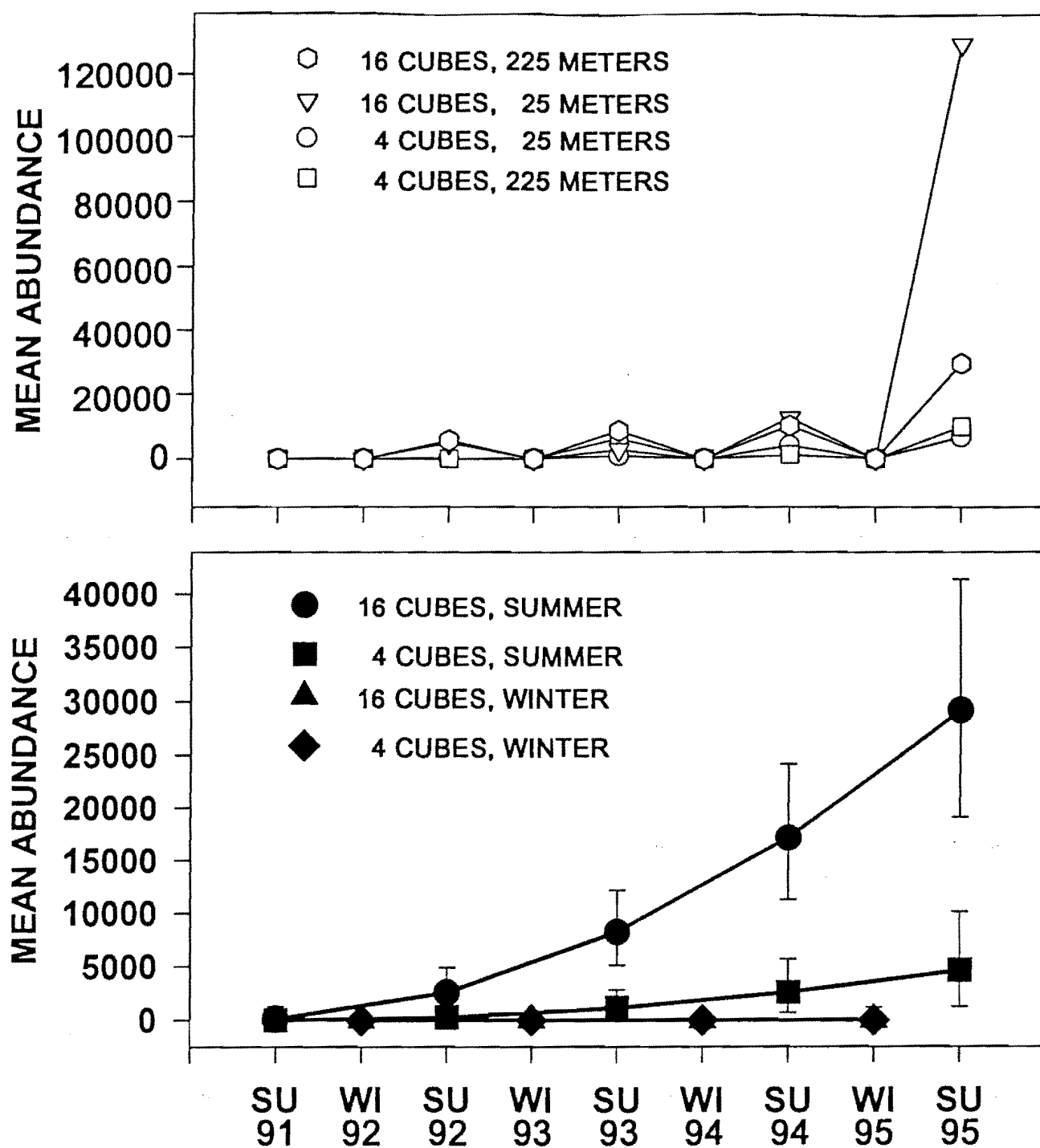


Fig. 18. (Upper) Mean numbers of herring (family Clupeidae) per reef treatment for summer and winter during 1991 through 1995. (Lower) Predicted means generated from a model incorporating only significant fixed-factor effects as identified in the legend (see text for further details with regard to the analysis); 95% confidence intervals are given for each predicted value.

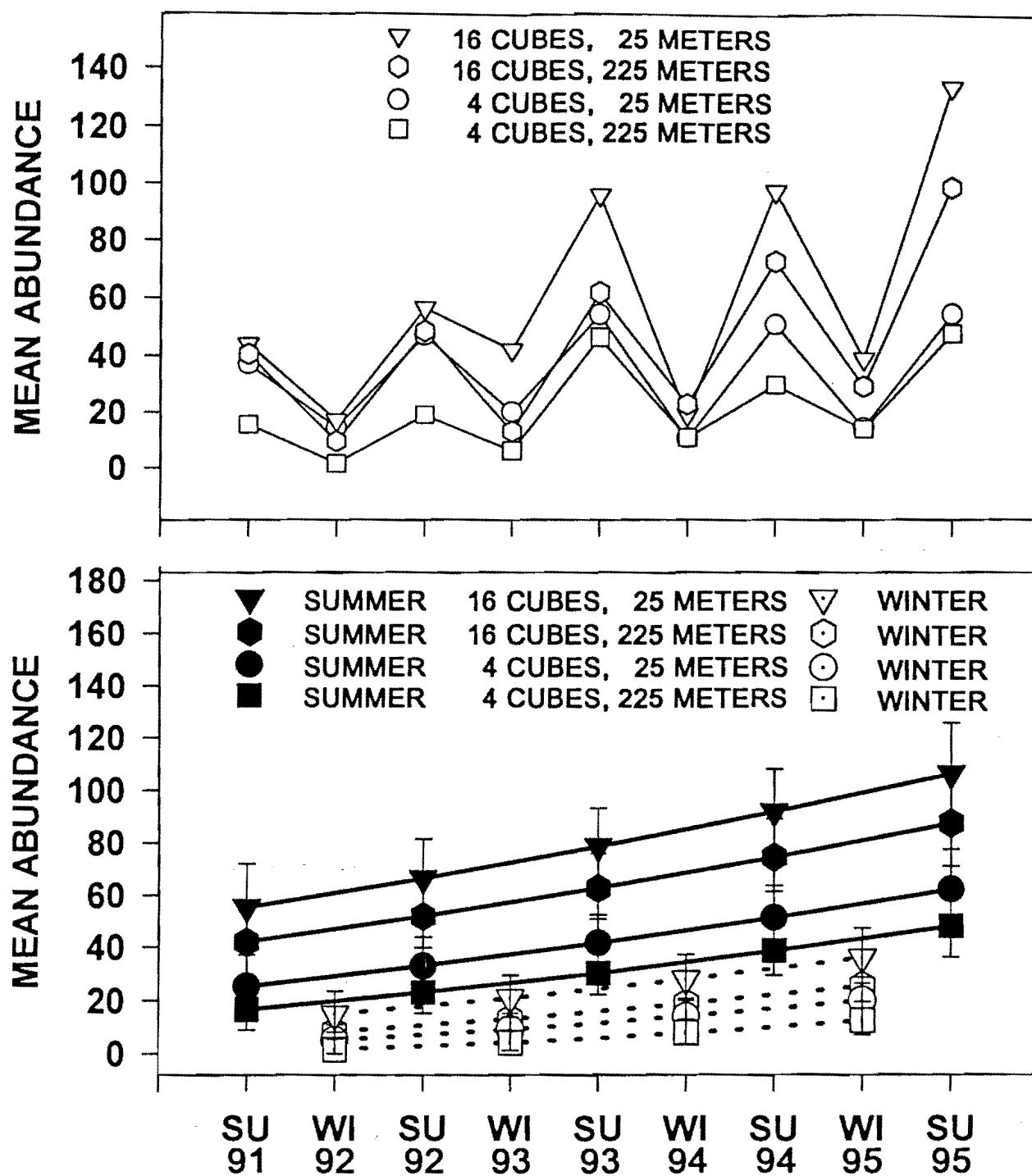


Fig. 19. (Upper) Mean numbers of belted sandfish per reef treatment for summer and winter during 1991 through 1995. (Lower) Predicted means generated from a model incorporating only significant fixed-factor effects as identified in the legend (see text for further details with regard to the analysis); 95% confidence intervals are given for each predicted value.

more abundant in summer than in winter ($p = 0.0001$), and had higher numbers on 16-cube reefs than on 4-cube reefs ($p = 0.0006$).

Description of Sand-Dwelling Macrobenthos

Just under 600 taxa were identified from core samples taken from the Suwannee Regional Reef System (Appendix B). This represents one of the highest infaunal diversities reported from benthic communities in either the Gulf of Mexico or from shallow areas along the Atlantic coast of the United States. The most speciose groups were polychaetes, with 226 species, and crustaceans, with 125 species. Although numbers of species were high on all sampling dates, many species were relatively rare and even common species exhibited strong temporal variations in abundance (Table 8). The number of species increased linearly with the sampling effort, despite over 1000 cores being processed to date (Fig. 20).

Initial analysis of functional groups indicated highly significant interannual variation in abundances of organisms and in species composition of the functional groups. In general, abundances of most groups were highest in 1992. Abundances were lowest in 1991, perhaps reflecting residual effects from construction of the reef arrays. Abundances of most groups were also lower in 1993 compared to 1992, possibly reflecting significant reductions in abundance of many taxa following the March 1993 storm of the century (Posey et al. in press); when seas driven by 95 mph winds strongly disturbed bottom sediments. Not surprisingly, given variations in species composition and abundances, highly significant interactions existed between treatment effects and year for all functional groups examined. Thus, analyses of treatment and distance effects were made for each year separately.

Reef Treatment Effects on Macrobenthos

To test the hypothesis that predation by reef-associated predators depleted food near reefs (the "halo" of infauna reported around some natural reef systems), abundances of each functional group were compared among the 5 distances sampled: 1 m, 10 m, 25 m, 50 m, and 75 m from the reef. No significant differences in abundance were found between distances for any functional groups examined in either 1991 or 1993. Similarly, there were no significant interactions between distance effects and treatment effects. In 1992, however, some distance effects existed. Among feeding types, suspension feeders displayed a trend towards lowest abundance immediately adjacent to patch reefs (Fig 21), with higher abundances in control areas or 75 m from reefs. Other feeding types did not show significant differences with distance from reefs. Deep burrowing forms were characterized by a mixed pattern, with lower abundance immediately adjacent to and 50 m from patch reefs (Fig. 21). Tube-building and near-surface dwellers did not exhibit significant differences among distances. There were no significant interactions between distance from the reef and reef treatment in 1992.

Table 8. Mean numbers ($\pm$ SE) of dominant and total infauna per 0.01 m² for seasonal sampling periods in 1991-1993. The total number of infaunal species identified is provided as are measures of diversity (H') and evenness (J).

	SUMMER 1991	WINTER 1992	SUMMER 1992	WINTER 1993	SUMMER 1993
Dominant Taxa	<i>Oikopleura</i> sp. 2.28 (0.74)	oligochaeta 4.98 (0.35)	<i>Glycera</i> sp. ^P 5.15 (0.59)	<i>Paraonis pygoenigmatica</i> ^P 1.99 (0.39)	<i>Branchiostoma caribaeum</i> 3.24 (0.32)
	<i>Branchiostoma caribaeum</i> 1.95 (0.15)	<i>Glycera</i> sp. ^P 3.43 (0.43)	<i>Branchiostoma caribaeum</i> 4.06 (0.34)	oligochaeta 1.34 (0.35)	bivalve sp. A ^m 2.20 (0.29)
	oligochaeta 1.54 (0.14)	<i>Prionospio fallax</i> ^P 2.01 (0.13)	<i>Cirriphorus forticirratu</i> s ^P 2.37 (0.30)	<i>prionospio cristata</i> ^P 1.12 (0.26)	<i>prionospio cristata</i> ^P 1.86 (0.41)
	<i>Glycera</i> sp. ^P 1.14 (0.20)	<i>Spiophanes bombyx</i> ^P 1.81 (0.14)	oligochaeta 2.32 (0.24)	<i>Branchiostoma caribaeum</i> 1.00 (0.20)	<i>Cirriphorus forticirratu</i> s ^P 1.84 (0.29)
	<i>Synelmis</i> sp. B ^P 1.05 (0.09)	<i>Armandia maculata</i> ^P 1.73 (0.12)	bivalve sp. A ^m 1.79 (0.14)	<i>Prionospio fallax</i> ^P 0.82 (0.18)	oligochaeta 1.82 (0.28)
Total Fauna	27.96 (1.58)	40.32 (1.08)	47.56 (1.43)		43.44 (1.79)
Total Species	300	325	347	374	292
Diversity (H')	1.817	1.732	1.791	2.267	1.89
Evenness (J)	0.734	0.690	0.705	0.881	0.77

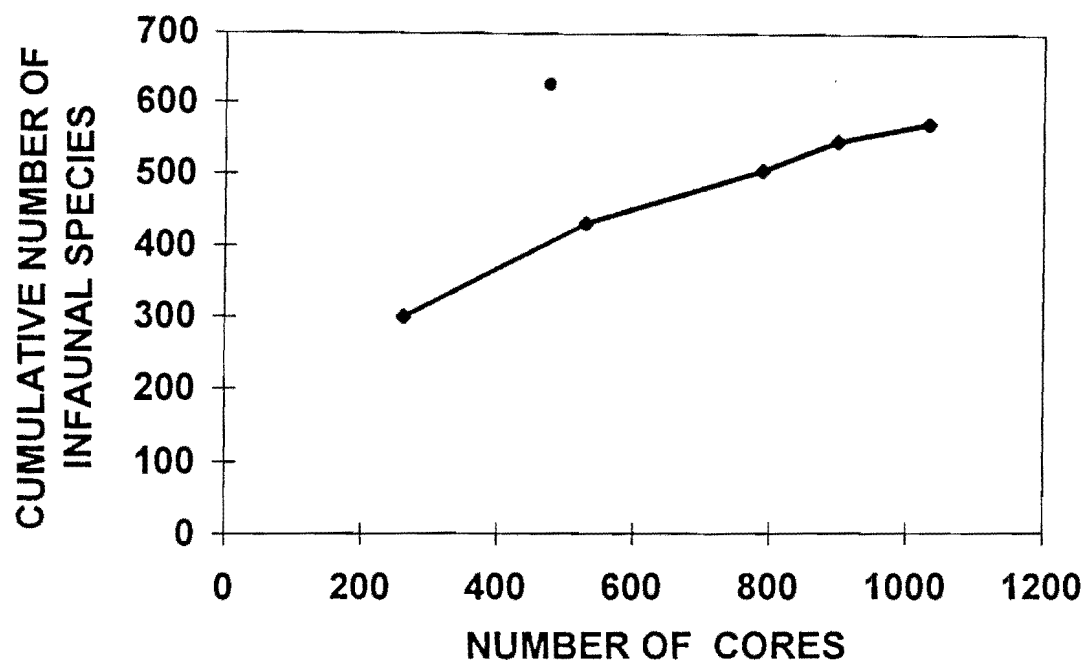


Fig. 20. Cumulative number of infaunal species as a function of sampling effort.

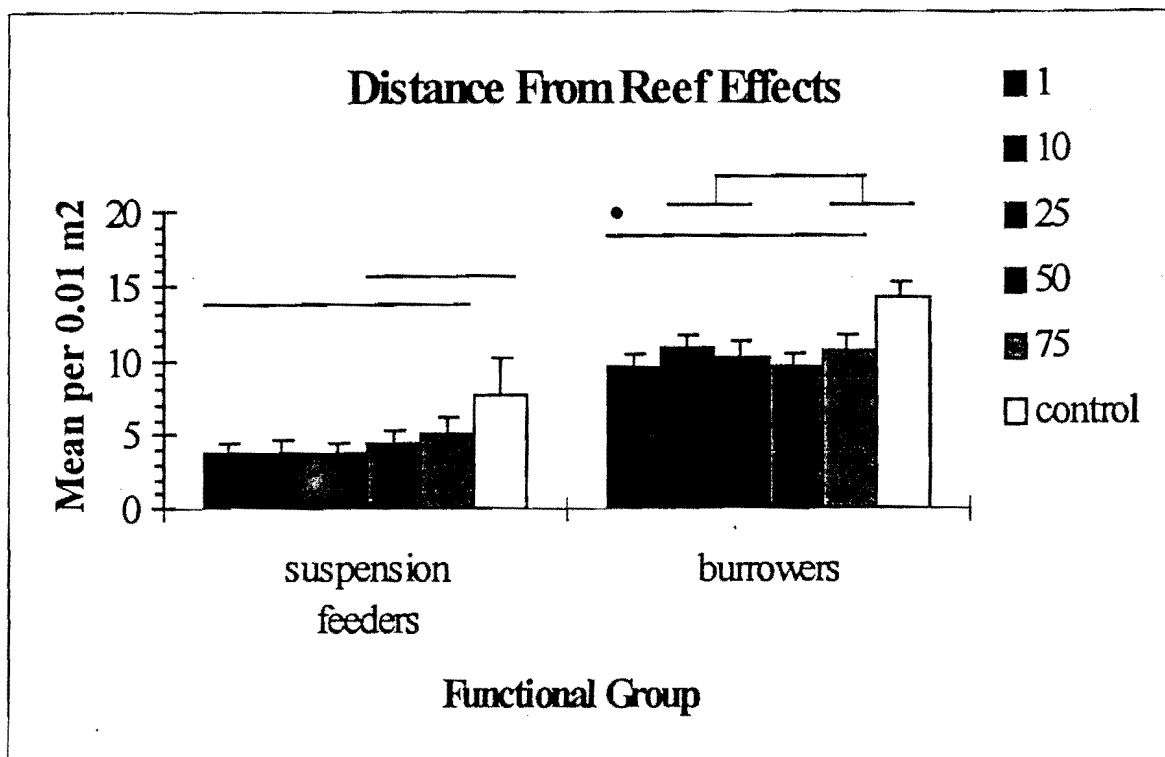


Fig. 21. Abundances of suspension feeders and deep burrowers at 5 distances from a reef and in control areas during 1992. Bars indicate mean per 0.01 m² ($\pm$ SE). Bars connected by a line do not differ significantly ($p < 0.05$; Tukey's Studentized Range comparison)

Conflicting predation pressures with respect to infaunal abundances may exist at varying distances from a reef patch. Juvenile clams, *Mercenaria mercenaria*, placed at 10 m from a patch reef exhibited high survivorship even after 72 hours (Fig. 22). However, clams 75 m from that reef had significantly lower survivorship, i.e., over 80% mortality within 24 hours. Remains of the clams in trays were similar to those previously observed following predation by blue crabs, *Callinectes sapidus*, (M. Posey, unpubl. data), and project divers reported seeing portunid crabs (*Portunus* sp.) at 75 m from the reef. By contrast, no *Portunus* were observed within 25 m of any reef, and juvenile grouper inhabiting reefs of the region were found to have crabs as part of their diet (F. Vose, personal observation). These results suggest a potentially important indirect effect of reef predators. Small predators, such as portunid crabs, may be the major predator on some small infauna. Abundances of these small predators may be significantly reduced close to the reef because of predation by reef-dwelling predators. An enhancement of some infauna close to reefs may result from indirect predation effects.

The experimental reef treatments represented a gradient from closely-spaced, larger patch reefs to widely-spaced, smaller patch reefs. Additionally, control sites represented sandflat areas quite distant from reefs. During 1991, infaunal abundances were lower than during either of the two subsequent years, and infaunal responses to reef treatments were mixed. Among feeding guilds, deposit feeders and suspension feeders both showed significant treatment effects (Fig. 23, Table 9), while among functional groups based on living position, only surface burrowers showed significant treatment effects (Fig. 24, Table 9). Surface burrowers had the clearest pattern with highest numbers adjacent to 16-cube patch reefs spaced at 25 m (i.e., 16-cube x 25-m reefs) and lower, though relatively even, abundances among the other reef treatments and control plots. Deposit feeders also had highest numbers near 16-cube x 25-m reefs, but had intermediate abundances near 4-cube x 225-m reefs and control areas, and lower abundances near 16 x 225 and 4 x 25 reef treatments. The suspension feeders showed a mixed pattern, with lowest numbers near 4-cube x 225-m reefs, but relatively higher abundances at control areas and near other reef treatments.

All functional groups exhibited significant treatment effects for the 1992 sampling season. Grazers, suspension feeders, and sedentary infauna all had lowest numbers near 16-cube x 25-m reefs, with higher abundances among the other reef treatments and control areas (Figs. 23 and 24). By contrast, surface burrowers had highest numbers near 16-cube x 25-m reefs compared to other reef treatments and controls (the same pattern as observed for this group in 1991). Deep burrowers and deposit feeders showed a mixed pattern, with lowest numbers near 16-cube x 225-m reefs and relatively higher abundances in control areas and near 16 x 25 or 4 x 225 reef treatments.

Final processing of samples is ongoing for 4-cube reefs sampled in 1993. However, comparisons among 16-cube reefs and controls indicate significant spacing effects for all functional groups (Figs. 23 and 24, Table 9). Deposit feeders and surface burrowers both had highest numbers adjacent to patch reefs with 25-m spacing, and lower abundances near 225-m spaced reefs and controls. For surface burrowers, this pattern is the same as

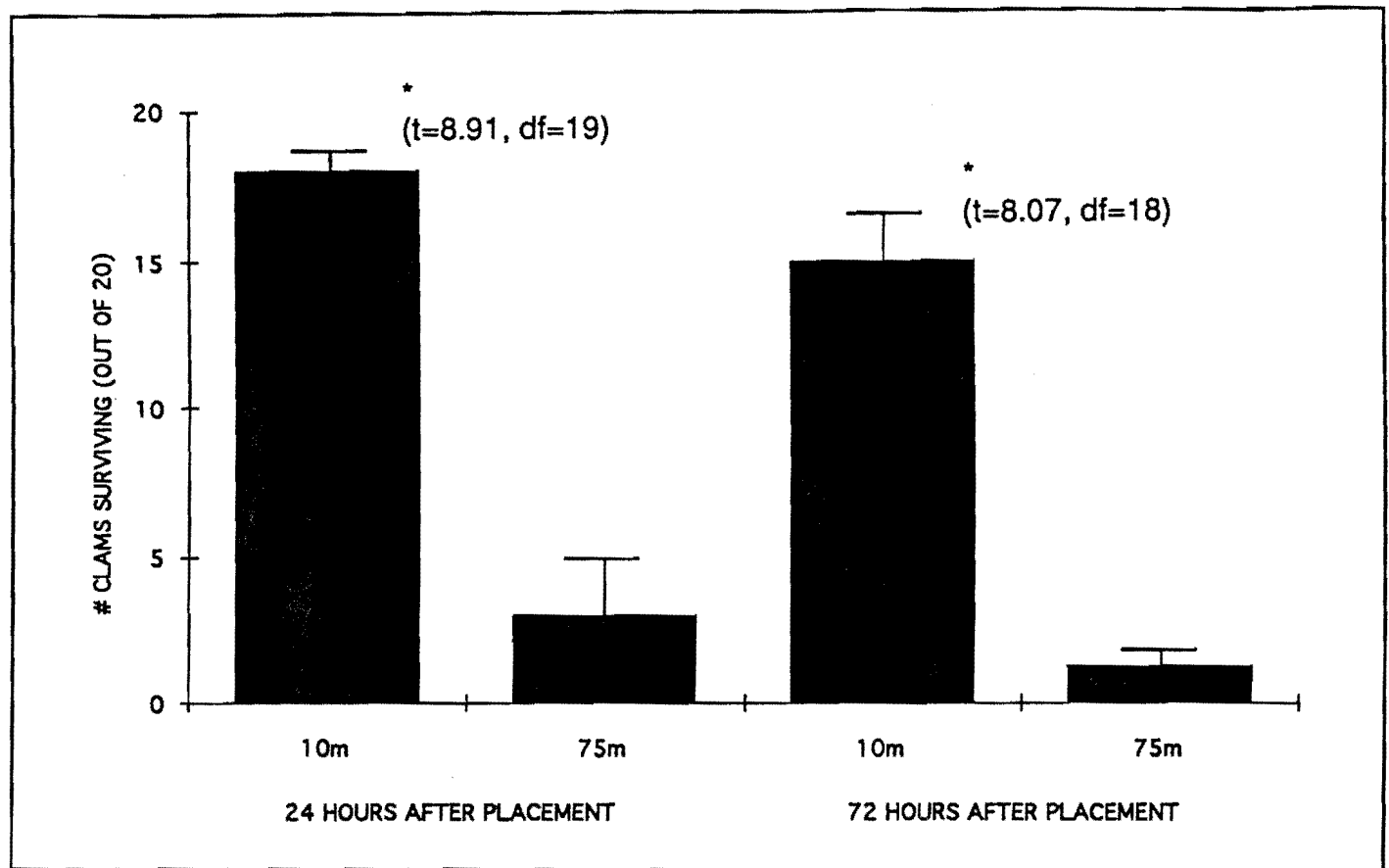


Fig. 22. Survivorship of juvenile *Mercenaria mercenaria* placed at two distances from a reef patch. Bars indicate mean number (n=10) surviving (+ SE). Significance levels (* $p < 0.05$) are from a t-test.

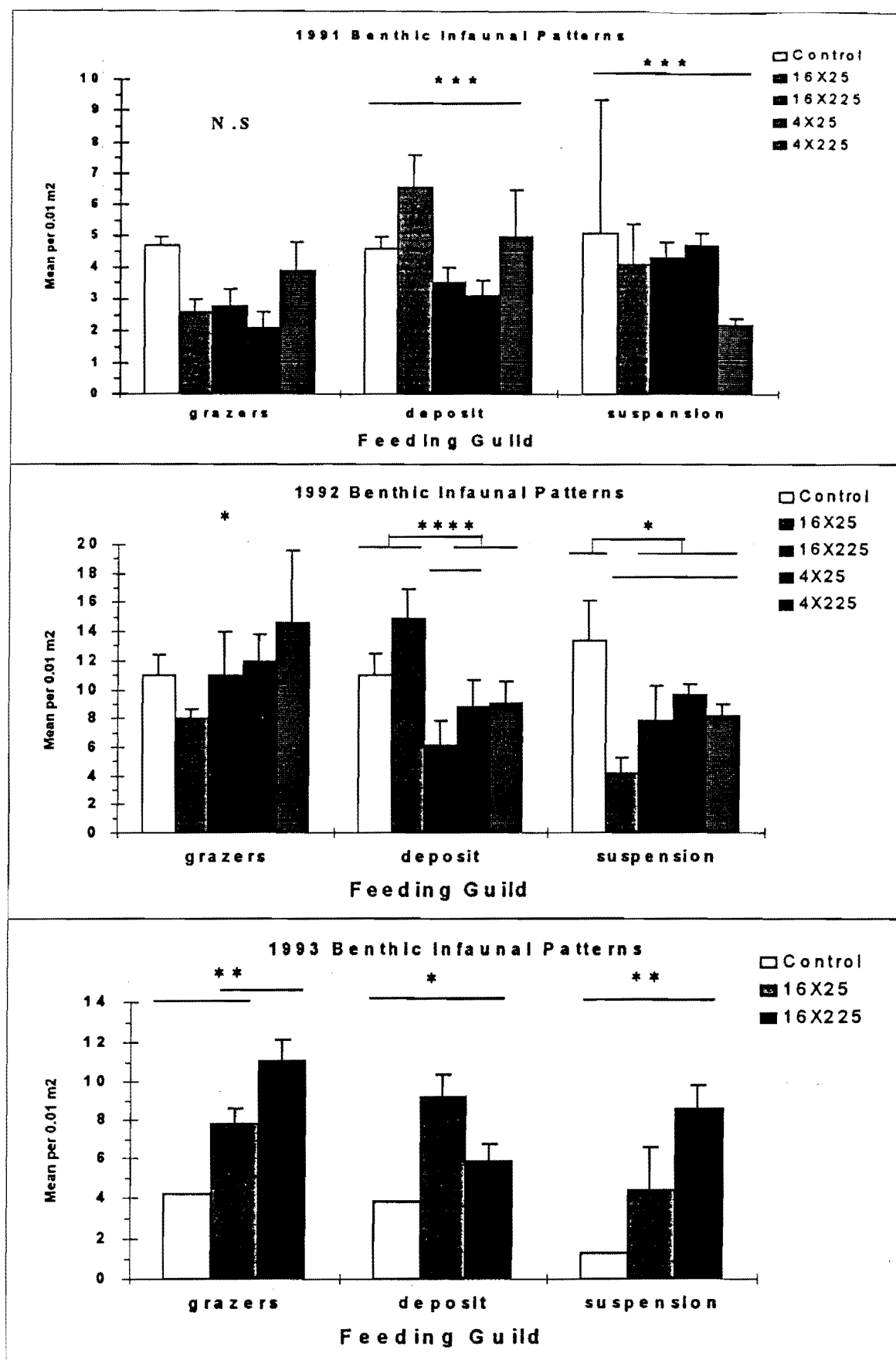


Fig. 23: Abundances of grazer, deposit feeder, and suspension feeder feeding guilds in each of 5 reef treatments during 1991, 1992, and 1993. Bars indicate mean per 0.01 m² (+ 1 SE). Bars connected by a line do not differ significantly ($p < 0.05$, Tukey's Studentized Range comparison). Significance levels are from Analysis of Variance (* $p < 0.05$; ** $p < 0.01$; *** $p < 0.001$; **** $p < 0.0001$).

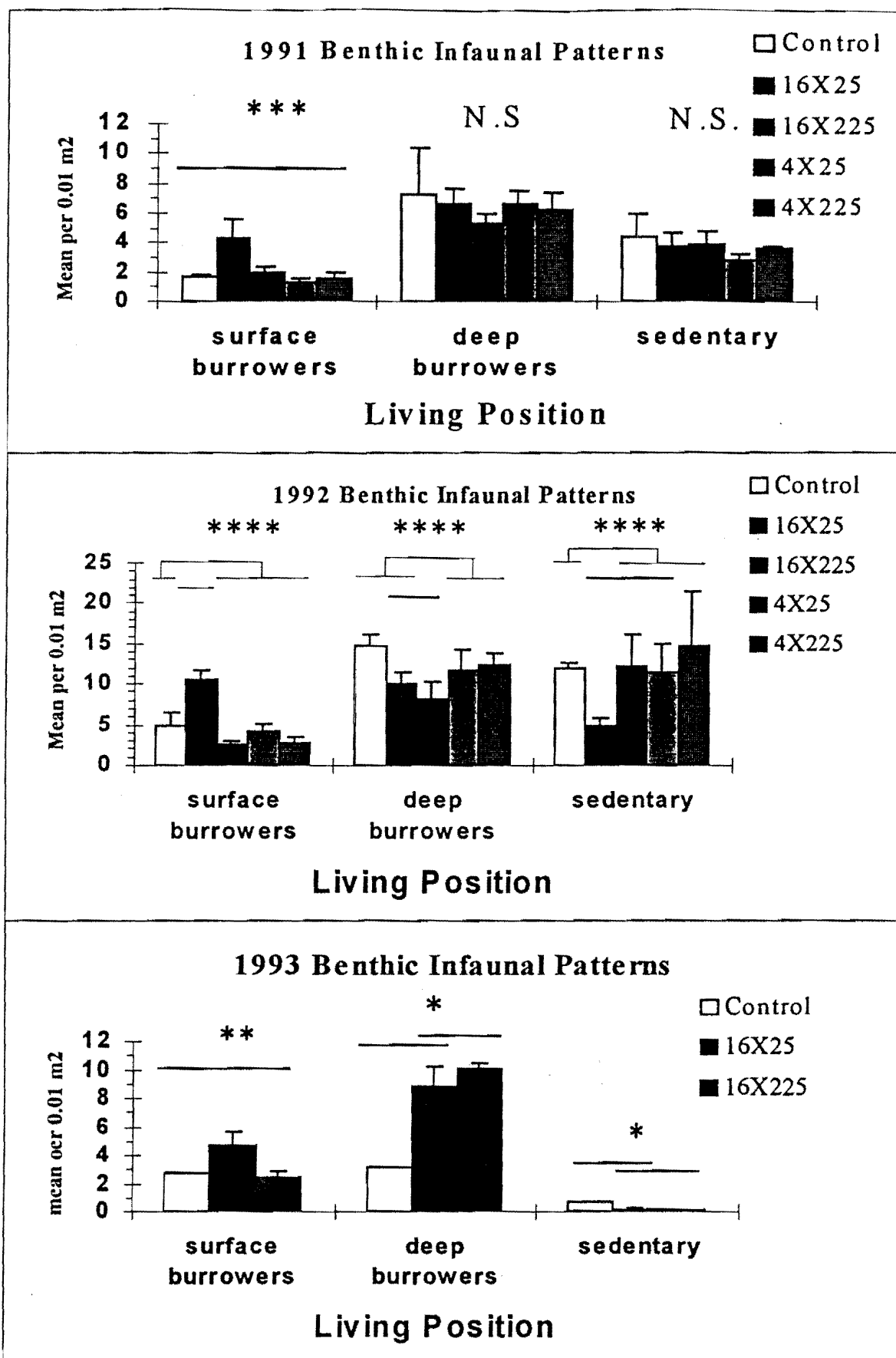


Fig. 24: Abundances of surface burrower, deep burrower, and sedentary living position guilds in each of 5 reef treatments during 1991, 1992, and 1993. Symbols as in Fig. 23.

Table 9. Results of 2-way ANOVA with distance from patch and reef treatment as main effects: F-values are given for each factor in the model; the associated degrees of freedom for distance, treatment and interaction effects are 5, 4 and 12, respectively.

YEAR	FUNCTIONAL GROUP	DISTANCE	TREATMENT	INTERACTION
1991	GRAZERS	0.16	1.43	1.18
	DEPOSIT FEEDERS	0.45	7.35	0.62
	SUSPENSION FEEDERS	0.38	4.86	0.32
	SURFACE BURROWERS	0.19	7.18	0.46
	DEEP BURROWERS	0.44	0.68	0.70
	SEDENTARY	1.13	0.76	0.48
1992	GRAZERS	0.37	3.31	0.46
	DEPOSIT FEEDERS	0.59	7.79	0.34
	SUSPENSION FEEDERS	1.90	2.40	0.49
	SURFACE BURROWERS	1.72	18.41	1.80
	DEEP BURROWERS	1.50	7.27	0.64
	SEDENTARY	0.47	5.04	0.49
1993	GRAZERS	0.84	7.62	5.09
	DEPOSIT FEEDERS	0.32	3.70	2.10
	SUSPENSION FEEDERS	0.10	7.50	0.23
	SURFACE BURROWERS	1.72	5.45	2.65
	DEEP BURROWERS	0.17	3.42	0.79
	SEDENTARY	0.67	2.89	0.60

seen in 1991 and 1992. Highest numbers for deposit feeders near 16 x 25 reefs is also consistent with what was observed for this group in 1992. Grazers, suspension feeders, and deep burrowers all had highest numbers near 225-m spaced reefs, intermediate abundances near 25-m spaced reefs, and lowest abundances in control areas. Sedentary organisms had highest numbers in control areas, intermediate abundances near 25-m spaced reefs, and lowest abundances near 225-m spaced reefs.

Discussion

Our first question is whether the resource mosaic hypothesis, stated on page 4, should be rejected, retained, or modified based on results from this first phase of research. If there had been no reef treatment effects on either the fishes or benthos, then clearly rejection would be in order. If all the original expectations, expressed as objectives on page 5, had been fully corroborated, then the general hypothesis would have been confirmed, but we would have gained relatively little new insight (the greater the scientific insight, the greater the opportunity for effective resource management). Given our results, the resource mosaic hypothesis must be retained for further testing, but modified to incorporate a direct coupling to pelagic as well as benthic prey production, and the effects of complex predator-prey relationships.

The need to modify our thinking comes from the striking increase in gag abundance over time. We attribute that trend to four factors that are reasonable to assume or test: (1) the superior quality of refuge provided by the SRRS compared to natural habitat in the vicinity, (2) the gregarious nature of gag compared to other groupers, like red grouper, (3) the apparent preference for, and availability of, schooling planktivorous fishes (e.g., herrings, family Cludeidae) as prey for gag, unlike many other serranids, and (4) the relative absence of directed fishing pressure on the Suwannee Regional Reef System. Of these, the fourth may be least consequential to the trend because most of the gag were sublegal and less vulnerable to fishing mortality anyway. The claim of superior refuge quality is supported by our extensive bottom surveys in the region for reef site selection and estimates of percent cover for hard-bottom. Gag were most abundant on the 16-cube reefs, the same as herrings. Herrings have been commonly regurgitated by gag during our 1995 tagging of efforts on the SRRS, and are in the diets of gag from natural habitat of the region (D. Weaver, unpubl. MS thesis). Because herrings disappear in winter while gag remain, we now have several additional hypotheses regarding seasonal shifts in gag diets, feeding compartments, energy budgets, movements and residency, but these need not be elaborated here.

An ability by gag, as the top resident piscivore, to shift between demersal and pelagic prey would affect the detail but not the general logic of our original hypothesis. For one thing, we expected any negative feedback to gag to be mediated through intermediate predators like black sea bass and grunts. The prediction of benthic prey depletion and negative feedback to predators was derived from a premise similar to a fixed input model in ideal

free distribution theory (i.e., that predation would eventually exceed benthic prey production near reefs). However, pelagic prey availability may be more akin to a continuous input model with less potential for depletion and more potential for attaining higher local standing stocks. The theoretical implications of such prey switching are not yet worked out, but some practical implications are discussed below.

Nevertheless, high densities of gag would be expected to assert top-down controls on the abundance of other reef fishes. Black sea bass and adult tomtate in particular declined as gag increased. Others like white grunt and cubbyu showed no trend over time, while some like belted sandfish and blennies increased. We suspect that white grunt, and perhaps cubbyu, are not prime prey for gag. We suggest that belted sandfish, in particular, are prey to black sea bass and that their increase is due, in part, to a decline of black sea bass caused by gag predation. Such complex predation effects are also indicated by results from the benthos, as discussed below. Menge (1995) estimated that 40% of the changes in community structure for rocky intertidal systems were attributable to indirect effects. Indirect effects must also be considered now for reef systems.

While many investigators have examined effects of reef size (e.g., Bohnsack et al. 1994) and some have considered effects of distance from natural reef tracts (e.g., Molles 1978), these have mostly been in the context of island biogeography theory. Few, if any, have examined artificial reefs in the context of density-dependent habitat selection (MacCall 1990). In this context, patch reef spacing ought to affect the resultant patterns, especially considering our hypothesis of prey depletion and negative feedback (see e.g., Bernstein et al. 1991).

In addition to gag and red grouper, we selected for analysis six demersal species which were expected to be affected by patch reef spacing (black sea bass, white grunt, gray triggerfish, tomtate, cubbyu, and sheepshead). We also selected for analysis two pelagic taxa (herrings and round scad) and two small fishes that dwell on reef surfaces (belted sandfish and seaweed blennies). For these last four taxa, an effect of patch reef spacing was not expected. Four of the six species that apparently feed over sand were affected by reef spacing, while only one of the four fishes not involved in that coupling were affected. Black sea bass, white grunt, gray triggerfish, and cubbyu were all more abundant on reefs spaced at 225 m, as expected. Belted sandfish were more abundant at 25-m reefs, consistent with a release from predation by black sea bass. Tomtate and sheepshead were affected by patch reef size but not spacing, which we attribute to idiosyncrasies of their life histories. Tomtate fry apparently settle directly onto reef structure in large schools and small juveniles are more abundant on the larger patch reefs. We suspect that adult tomtate numbers reflect juvenile settlement patterns and attrition during the growing season. Sheepshead, on the other hand, aggregate as adults in the winter apparently for spawning, but otherwise occur in low numbers on the SRRS (Vose et al. manuscript in revision). As such, sheepshead patterns reflect mating strategies rather than feeding and sheltering processes. Taken together, these results clearly support our general hypothesis.

The benthic component of this research was designed to test several predictions that follow from an hypothesis of trophic connections between reef communities and adjacent sandflat habitats. First, lower infaunal abundances were predicted close to the reef structure. This halo of reduced infaunal abundances would result from predation by reef-associated predators on infauna immediately adjacent to a reef. Such halos have been reported for temperate natural reef systems. Second, we predicted that lowest infaunal abundances would be associated with the largest, most tightly packed reef patches and would be greater near small reefs spaced widely apart. This would result from greater concentrations of predators and greater depletion of food resources near densely packed reefs. Intermediate densities may occur adjacent to large, widely spaced patches or small, closely spaced patches, depending on the relative influence of these variables.

The benthic community found associated with reef and control sites in the SRRS presented several advantages and problems for testing these ideas. First, this community is among the most diverse (numbers of species and evenness) reported for shallow shelf habitats in either North America or Europe. This diversity made interpretation of individual species responses difficult. However, it also allowed formation of functional groups containing a minimum of 5 common species per group. Second, the community exhibited strong interannual variability. This variation prevented determination of long-term infaunal responses to reef placement and made comparisons between years, even on a qualitative level, difficult. Finally, the experimental evidence from clam outplants suggests that this community may, trophically, be much more complex than many of the temperate communities examined in other studies. In particular, small intermediate predators residing off-reef may play an important role in regulating the abundances of some infauna.

Limited evidence for a halo of reduced infaunal abundance adjacent to a reef was observed for one functional guild, suspension feeders. This group showed a consistent progression towards lower abundances as one moved closer to a patch reef. Most of these suspension feeders included small, juvenile clams and tube-dwelling polychaetes, all of which might be susceptible to predation by epibenthic fish and crustaceans. Size-specific predation on clams is suggested by results of the outplant experiment compared to results from the core sampling. Deep burrowing infauna also displayed a distance from reef effect on abundances, but the pattern was not one of a steady change correlated with distance. The lack of strong halo effects for most other taxa may reflect the complex interactions between larger reef-associated predators and smaller, intermediate off-reef predators. Reef predators may have conflicting effects on benthos, directly reducing abundances of infauna near a reef through direct predation and indirectly enhancing numbers near a reef by preying on intermediate predators such as crabs. The balance of these conflicting pressures ultimately determines whether infaunal abundances are reduced, enhanced, or not significantly changed immediately adjacent to a patch reef.

Treatment effects (effects of patch reef spacing and size) were strong for all functional groups. One of the most consistent and pronounced treatment effects was enhancement of surface burrowers near large, closely spaced reef patches. This effect was observed during all three years of sampling. Surface burrowers included a variety of shallow burrowers, some of them deposit feeding polychaetes, scavenging amphipods, and arrow worms (cephalochordates). Most of these taxa are good burrowers and hence may have some protection from predation by epibenthic predators. Many of these taxa, especially amphipods and deposit feeding polychaetes, would be able to utilize detrital and algal food washed onto the sand from the reef itself. Their enhancement immediately adjacent to the reef may reflect this ability to utilize reef-exported food while having some protection from reef predators.

Treatment effects for other functional guilds were not as predictable. Suspension feeders (mainly juvenile clams living near the surface) and sedentary infauna tended to have lower abundances associated with large, closely spaced patch reefs. This distribution is consistent with the susceptibility of these organisms to predation by epibenthic predators (living near the sediment surface or having a permanent tube or burrow connection with the surface). However, the pattern was variable between years. Other functional groups showed patterns that were highly variable between years or else had highest abundance associated with reefs of intermediate combinations of patch size and spacing. Higher abundances in intermediate treatments may reflect the influence of conflicting effects of reef-associated predators on infauna.

Relevance to the Attraction-Production Issue

This first phase of research had the potential to disprove the resource mosaic hypothesis, and thereby eliminate from further consideration one mechanism by which artificial reefs might benefit fish. At this point, the hypothesis, and therefore the possibility of enhancement by reefs, remains viable. Yet, we must consider our first test to be weak relative to the attraction-production issue because, so far, we have tested only local fish abundances, standing stocks, and infaunal densities rather than direct measures of production or productivity. Fortunately, alternative hypotheses about how artificial reefs might function have been tested by others and rejected (e.g. inherent attractiveness of artificial reefs over natural reefs, Hixon and Carr AFS Symposium; bottom-up enhancement of primary and secondary production, Bohnsack et al. AFS Symposium; limitation of larval fish settlement habitat, Bohnsack et al. 1994). So, in keeping with Platt's (1964) concept of strong inference, we tentatively accept that ecological processes by which reef fish are coupled to off-reef prey production might be enhanced by artificial reefs.

While claiming that our original hypothesis has survived its first large-scale test, we must also be clear that it requires modification. The phenomenal increase in gag abundance on the Suwannee Regional Reef System over the 5 years of this project was unanticipated. In part, we attribute that increasing abundance to superior shelter characteristics of the reef cubes compared to most natural hard-bottom habitat of the region. In this respect, our thinking about

how reefs function merges, in general, with Herrnkind and Butler's hypothesis³ regarding demographic bottlenecks. With respect to our hypothesis of benthic prey depletion, negative feedback, and effects of habitat patchiness, some fish species responded to reef treatments as expected, but gag did not.

It appears that our patch reefs fostered a localized abundance and persistence of schooling planktivorous fishes (e.g., herring) during the warmer months, and that resident gag could feed perhaps to satiation from such pelagic production. Treatment effects on the gag and baitfish indicate that reefs can manipulate such relationships. Although our general hypothesis must now be altered to include coupling to pelagic, as well as to benthic prey production, it is important to recognize that pelagic production ought to be less prone to localized prey depletion than the off-reef benthic production.

Our results to date, and the logical framework in which these data are interpreted, suggest that an enhancement of biological production (i.e., growth and survivorship) by artificial reefs might be possible. Whether such production would be sufficient to offset fishing mortality remains to be seen. Furthermore, a very real possibility exists that our findings might not apply to all artificial reefs. For instance, gag may be more amenable than the top reef-dwelling predators of other systems to a switching between benthic and pelagic prey. The SRRS was also built to bracket a suspected influence of Suwannee River outflow on regional productivity, whereas other reef systems might not draw from comparable pelagic production. Obviously, we must be careful not to extrapolate beyond the inference space of this study.

Fundamental Design Parameters for Artificial Reefs

Our definition of parameter is "any of a set of physical properties whose values determine the characteristics or behavior of a system."⁴ For artificial reefs, fundamental design parameters would be common properties that can be controlled during site selection, materials selection, or placement to affect the performance of reefs relative to their management objectives. Implicitly, management objectives must be defined for the consideration of design parameters to have any merit. For this discussion, we assume the general objectives are related to fishery species, either to benefit the fish or the fishermen.

We know that the size distribution and abundance of cavity space will affect the size distribution, abundance and, to some extent, the species composition of fish residing on reefs (Hixon and Beets 1993). Therefore, reef structural complexity is one fundamental design parameter. We know from hydrodynamics that cubes create turbulence in a flow field, whereas horizontal cylinders or domes tend to create lift (P. Sheng, Dept of Coastal and Oceanographic Engineering, University of Florida, personal communication). Therefore, cubes should be more stable. Furthermore, we suspect that turbulence and associated hydrodynamic features affect the presence and persistence of plankton and planktivores above reefs (Otake et al. 1991, Sheng et al. proposal pending). Therefore,

³ Presented at the AFS Symposium cited in footnote 2, and implicit in Butler et al. 1995.

⁴ Meriam-Webster Dictionary, 1974.

geometric shape related to hydrodynamic influences may be another aspect of fundamental design.

We know also that patch reef size, in its horizontal dimensions, affects the local abundance and biomass of fish, but that there is an overall diminishing return with increasing reef size (Bohnsack et al. 1994), e.g., 16-cube reefs held more fish than 4-cube reefs, but not a four-fold difference. Reef size is a fundamental design parameter that, in part, determines the design options for structural complexity and hydrodynamic effects. Reef size may also be the main parameter determined by management objectives (e.g., larger reefs may favor fishermen but give less bang-for-the-buck in biological returns). The optimization of reef size in the horizontal plane remains to be worked out.

Reef size in the vertical plane is referred to as profile or vertical relief (Bohnsack et al. 1991). For benthic or demersal reef fishes, an optimal relief seems to be around 1 m (Molles 1978, Patton et al. 1985), which is one reason for the size of the SRRS cubes. In our case, however, the cubes included a large horizontal cavity which was covered to accommodate grouper habits. This is in contrast to the open-topped cubes of similar size used by Bohnsack et al. (1994). Obviously, profile is also related to structural complexity.

Given the results of this project, patch reef spacing must now be considered a fundamental design parameter. Overall, our greatest numbers occurred on 16-cube patch reefs spaced at 225 m, but that arbitrary combination is likely not optimal. Again, the reef spacing to be chosen, in conjunction with size, will likely depend on the management objectives.

A functional corollary of patch reef spacing is ecological setting. Hixon and Carr inferred from their experiment on behavioral preference for natural versus artificial patch reefs that the locations of artificial reefs probably account for their observed high densities of fish. On a local scale, this inference is consistent with our general hypothesis regarding the coupling to off-reef benthic production. Furthermore, some important reef fishes were positively associated with the amount of surrounding hard-bottom. Natural habitat in the region generally lacked quality refuge for fishery species, which were scarce during the site surveys preceeding reef construction. Proximity to, or placement upon hard-bottom might be an effective design parameter for specific management objectives.

On a broader scale, the placement of artificial reefs relative to features that affect regional production might also be a design consideration. We positioned the SRRS so as to bracket the Suwannee River outflow with the intent of eventually examining its influence. Observed variation in water color and salinity across the SRRS, plus satellite imagery, confirmed that these reefs intercepted the Suwannee plume. We can speculate that the observed spike in Cludeidae abundance during the summer of 1995 was related to high river flow the previous autumn (Fig. 25) when Gulf menhaden, *Brevoortia patronus*, were likely spawning in the region (Lassuy 1983). Alternative hypotheses for the abundance of herrings exist, but if reef placement can enhance the production of fishery species like gag by capitalizing on their prey distributions, then strategic placement is worth considering.

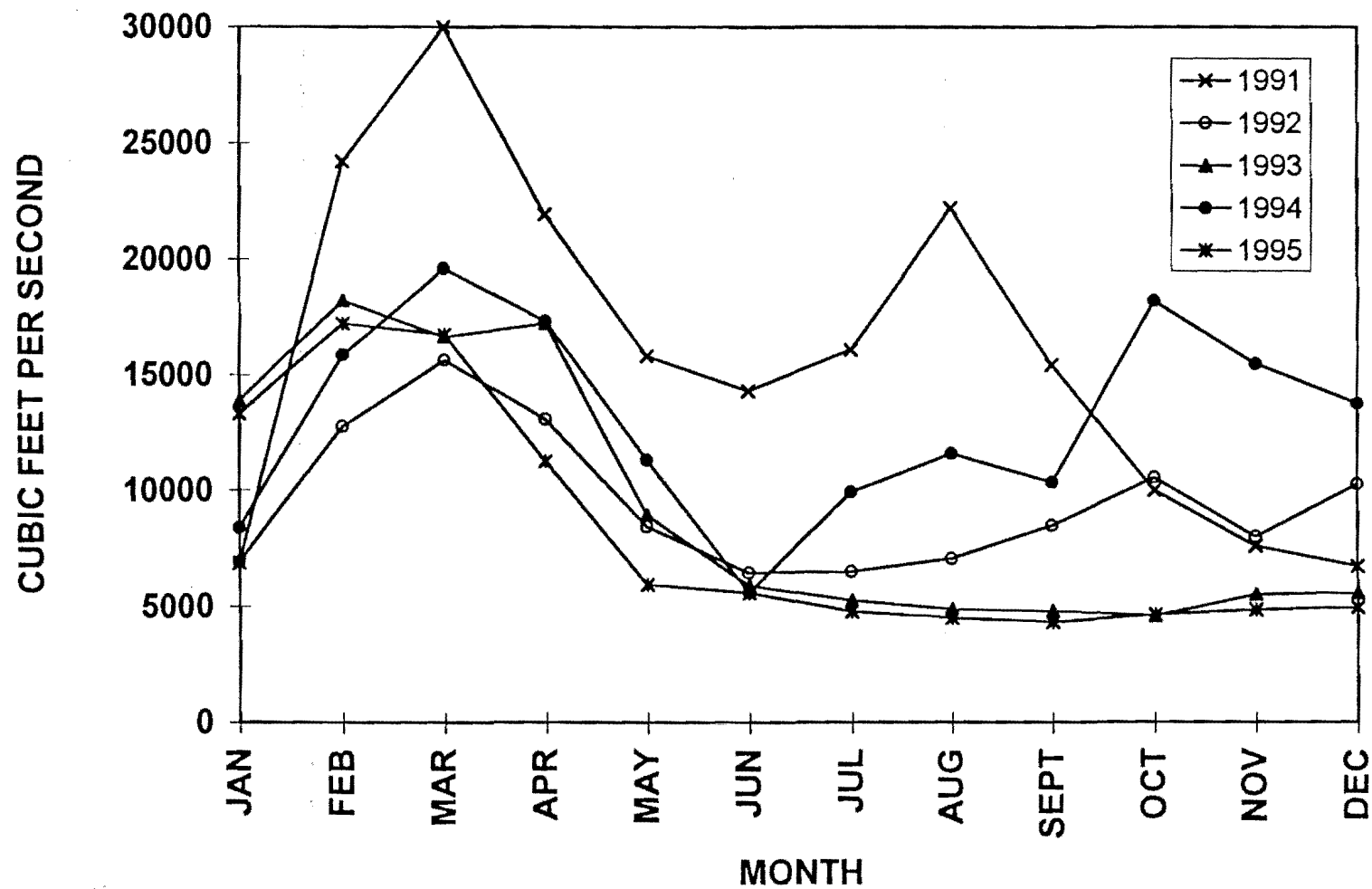


Fig. 25. Mean monthly discharge (cubic feet per second) for the Suwannee River for 1991 through 1995

Management Implications and Recommendations

Artificial reefs have potential to affect ecological processes that, in turn, affect fishery species. However, our ability to manipulate those processes for predictable outcomes is still in its infancy. With all the recent research, we can say that predator-prey relationships, foraging efficiencies, habitat selection, survivorship, and in some cases reproduction, are likely being affected, but we cannot yet assign values to the potential gains in biological production nor say that the gains outweigh the losses. With respect to the guiding questions listed on page 3, the field as a whole is moving from questions 1 and 2 to questions 3 and 4, from what are the ecological processes being manipulated to what is the extent of the effects and how do they compare to unmanipulated natural conditions or to the fishery harvest. We feel confident that the fish densities and catch rates at artificial reefs, which fishermen recognize, are not simply consequences of an artifact or anomaly. However, at our current state of knowledge we can only give general guidance for how to use the scientific results in support of fishery management.

The first recommendation cannot be overstated. Every artificial reef ought to have specific management objectives explicitly stated to justify its construction. Professionals do not design or build things without knowing what their clients want to accomplish. Throughout the United States, artificial reef programs seem to ignore the need for management objectives, or treat them superficially. At the extremes, if reefs are to be justified as enhancements to benefit fishery stocks, consistent with a conservation ethic, then those proposing the reefs should say so and explain how that might be accomplished. Likewise, if reefs are justified as enhancements to fishing *per se*, i.e., as a fishing gear, then those proposing the reefs should say that, too, and be honest about their intent. The design recommendations for these two extremes might be very different.

A requirement for explicit objectives in proposals for reef funding would also create a "teachable moment" between professional staff and user groups, during which time underlying values can be clarified and good stewardship fostered. This benefit is entirely consistent with Florida's Ecosystem Management policy. Explicit management objectives would give professional staff a basis for feedback to local reef builders on such matters as reef locations and configurations. Management objectives also assure an effective context for the monitoring of artificial reefs to evaluate their performance. Without objectives or criterion measures, monitoring is simply data collection with little relevance to decision-making.

Design considerations for the Suwannee Regional Reef System, in addition to the experiment built into the system, included a desire to enhance the biological production of gag. That motivated the architecture of cubes and patch reefs, and their placement along the 40 foot depth contour. In all honesty, though, the extent to which this objective *appears* to have been met was unanticipated because of what was unknown about gag at the time of construction. The extent to which abundant juvenile gag on the SRRS might contribute to regional stocks remains unknown, but it is obvious that the more we know about any target species, the better we can tailor reefs to serve enhancement functions.

Some general recommendations regarding design parameters are possible. Artificial reefs ought to be structurally complex, with an abundance and variety of cavity spaces, including cavities of a size and orientation appropriate for the species being targeted. A likely trade-off, depending on the management objective, may be that complex reefs are more difficult to fish. Structural complexity, in concert with reef size and profile, should also promote turbulence by interfering with hydrodynamic flow. Flat, broad surfaces perpendicular to flow are probably better than curved or narrow surfaces, or surfaces parallel to flow.

Our recommendations on patch reef size are less certain. If reefs are built to serve the fisherman directly, then large patch reefs may be preferred. They are easier to find, easier to fish, and have a greater density of fish under the boat. In general, however, if reefs are built to serve the fish, then many small patch reefs rather than a few large ones may be preferred. Harvestable size classes of some fish might, however, have lower size limits for patch reefs they will occupy. For gag, in particular, a recommendation of patch reef size is confounded by the positive relationship of baitfish abundance with reef size. The difference in rates of increase for gag between 16-cube and 4-cube reefs suggests that larger patch reefs may also be better biologically. On the other hand, cavity space within a reef might eventually set a limit on resident gag stocks. We are at a disadvantage in recommending reef sizes specific for gag because of the pelagic coupling that became evident, and because we only had two patch reef sizes to compare. Bohnsack et al. (1994) compared reefs across four sizes (1, 2, 4, and 8 cubes) and found the same general diminishing return. Unfortunately, their cubes were open-topped and grouper were not common; gag did not occur at their site in south Florida, so no guidance can be derived from their study.

In general, we recommend that discrete patch reefs be spaced apart rather than close together. The apparent dependence of reef fish on off-reef prey production suggests that it may be possible to saturate an area with reef material and suffer a diminishing return with continued development (see Sato 1985). An optimal spacing cannot be estimated from available data, but in all likelihood that would depend on the overall productivity of the region in which reefs are built. For that and other reasons, it may be wise to locate reefs in areas where base productivity may be high, but where poor natural reef habitat may not allow sufficient numbers of reef fish to exploit that productivity. Such was the reasoning for the Suwannee Regional Reefs.

Future Research Directions

The initiative has already been taken to build upon results of this project. A follow-up project is underway to test reef treatment effects on the growth and relative weights of gag on the SRRS, and to test the effects of fishing on these measures of production. The new project is being sponsored jointly by the Marine Resources Grants Program (DEP) and the MARFIN Program (NMFS). One component still missing from this new work is

an adequate sampling from natural hard-bottom habitat of the region to compare gag production from experimental artificial reefs to appropriate natural controls. The addition of this component would be in keeping with the third guiding question (p. 3) for resolving the Attraction-Production issue.

New research proposals are also pending with the University of Florida's Interdisciplinary Research Initiative and the Florida Sea Grant College Program for an initial test of the relationship between clupeid abundance on the SRRS, hydrodynamic turbulence around patch reefs, and planktonic production (Y. P. Sheng, Principal Investigator, E. Philips and W. Lindberg, Associate Investigators). If funded these projects would also complement, in a limited way, the need to investigate thoroughly the influence of the Suwannee River on regional marine production. That effort is being initiated through a proposed Nature Coast Ecosystem Management Area, in partnership with the Florida Marine Research Institute/DEP, the Suwannee River Water Management District, and the Department of Fisheries and Aquatic Sciences/UF. One component still missing from the work being proposed is a hydrodynamic circulation model for the region, which would be essential to estimate the pelagic production potentially available to the SRRS and surrounding benthos. A circulation model for the region would also serve DEP's Shellfish Monitoring Program and the Fisheries Independent Monitoring Program, which is just getting underway at the Cedar Key Field Laboratory.

We have long recognized the need to relate abundances of juvenile fishes inshore with the abundances older fish offshore. This would greatly improve the predictive capability to be gained from long-term monitoring programs such as DEP's. However, to do so the 5-year database reported in this document would have to be extended beyond the summers of 1996 and 1997, which is the extent of the second research phase noted above. Consideration ought to be given to continued summer fish censusing on the Suwannee Regional Reef System.

The striking outcome of this research program to date is the recognition that gag have true potential for enhancement because of their gregarious nature, high site fidelity (Loftin et al. 1996), and predation on planktivores. Patch reef size is an obvious parameter that affects gag abundance and possibly growth, survivorship, and energy reserves. The ability to optimize patch reef size for gag production, however, will require a contrast across a wide range of possible patch reef sizes. Future artificial reef construction in the Big Bend region could, with planning and forethought, create the infrastructure that would allow optimal reef sizes for gag to be determined. The successful completion of the Big Bend Regional Reef Project during 1995 demonstrates that such planning and execution is possible.

Within the context of each major research direction noted above is a myriad of scientific questions that have significance to fisheries management, in general, and to the application of artificial reef technology, in particular. The opportunity to discuss or propose any of these questions would be welcome.

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Appendix A. Fish species recorded at the Suwannee Regional Reefs from 1991-1995. Family assignments, common names, and species authorities included follow **Common and Scientific Names of Fishes from the United States and Canada, Fifth edition**. American Fisheries Society, 1991.

FAMILY	SCIENTIFIC NAME	COMMON NAME
Antennariidae	<i>Antennarius ocellatus</i> (Block & Schneider, 1801)	ocellated frogfish
Apogonidae	<i>Astrapogon alutus</i> (Jordan & Gilbert, 1882)	bronze cardinalfish
Balistidae	<i>Balistes capriscus</i> Gmelin, 1789	gray triggerfish
Balistidae	<i>Monacanthus hispidus</i> (Linnaeus, 1766)	planehead filefish
Batrachoididae	<i>Opsanus pardus</i> (Goode & Bean, 1879)	leopard toadfish
Belonidae	<i>Strongylura</i> sp.	needlefish sp..
Blenniidae	<i>Hypleurochilus geminatus</i> (Wood, 1825)	crested blenny
Blenniidae	<i>Parablennius marmoreus</i> (Poey, 1876)	seaweed blenny
Bothidae	<i>Ancylopsetta quadrocellata</i> Gill, 1884	ocellated flounder
Bothidae	<i>Bothus ocellatus</i> (Agassiz, 1831)	eyed flounder
Bothidae	<i>Bothus robinsi</i> Topp & Hoff, 1972	twospot flounder
Bothidae	<i>Paralichthys albigutta</i> Jordan & Gilbert, 1882	gulf flounder
Callionymidae	<i>Diplogrammus pauciradiatus</i> (Gill, 1965)	spotted dragonet
Carangidae	<i>Caranx crysos</i> (Mitchill, 1815)	blue runner
Carangidae	<i>Caranx hippos</i> (Linnaeus, 1766)	crevalle jack
Carangidae	<i>Chloroscombrus chrysurus</i> (Linnaeus, 1766)	Atlantic bumper
Carangidae	<i>Decapterus punctatus</i> (Cuvier, 1829)	round scad
Carangidae	<i>Oligoplites saurus</i> (Schneider, 1801)	leatherjack
Carangidae	<i>Seriola dumerili</i> (Risso, 1810)	greater amberjack
Carangidae	<i>Seriola rivoliana</i> Valenciennes, 1833	almaco jack
Carangidae	<i>Seriola zonata</i> (Mitchill, 1815)	banded rudderfish
Carcharhinidae	<i>Carcharhinus leucas</i> (Valenciennes, 1841)	bull shark
Clinidae	<i>Paraclinus marmoratus</i> (Steindachner, 1876)	marbled blenny
Clinidae	<i>Starksia ocellata</i> (Steindachner, 1876)	checkered blenny
Clupeidae	<i>Harengula jaguana</i> Poey, 1865	scaled sardine

Appendix A. Continued.

FAMILY	SCIENTIFIC NAME	COMMON NAME
Congridae	<i>Conger oceanicus</i> (Mitchill, 1814)	conger eel
Dactyloscopidae	<i>Dactyloscopus moorei</i> (Fowler, 1906)	speckled stargazer
Dasyatidae	<i>Dasyatis americana</i> Hildebrand & Schroeder, 1928	southern stingray
Dasyatidae	<i>Dasyatis centroura</i> (Mitchill, 1815)	rougetail stingray
Dasyatidae	<i>Gymnura micrura</i> (Shneider, 1801)	smooth butterfly ray
Echeneidae	<i>Echeneis naucrates</i> Linnaeus, 1758	sharksucker
Ephippidae	<i>Chaetodipterus faber</i> (Broussonet, 1782)	Atlantic spadefish
Gadidae	<i>Urophycis regia</i> (Walbaum, 1792)	spotted hake
Gerridae	<i>Eucinostomus</i> sp.	mojarra sp.
Gobiesocidae	<i>Gobiesox strumosus</i> Cope, 1870	skilletfish
Gobiidae	<i>Coryphopterus punctipectophorus</i> Springer, 1960	spotted goby
Gobiidae	<i>Gobiosoma longipala</i> Ginsburg, 1933	twoscale goby
Gobiidae	<i>Gobiosoma macrodon</i> Beebe & Tee-Van, 1928	tiger goby
Gobiidae	<i>Ioglossus calliurus</i> Bean, 1882	blue goby
Gobiidae	<i>Microgobius carri</i> Fowler, 1945	Seminole goby
Haemulidae	<i>Haemulon aurolineatum</i> Cuvier, 1830	tomtate
Haemulidae	<i>Haemulon plumieri</i> (Lacepede, 1801)	white grunt
Haemulidae	<i>Orthopristis chrysoptera</i> (Linnaeus, 1766)	pigfish
Labridae	<i>Halichoeres bivittatus</i> (Bloch, 1791)	slippery dick
Labridae	<i>Halichoeres caudalis</i> (Poey, 1860)	painted wrasse
Labridae	<i>Hemipteronotus novacula</i> (Linnaeus, 1758)	pearly razorfish
Labridae	<i>Lachnolaimus maximus</i> (Walbaum, 1792)	hogfish
Lutjanidae	<i>Lutjanus campechanus</i> (Poey, 1860)	red snapper
Lutjanidae	<i>Lutjanus griseus</i> (Linnaeus, 1758)	gray snapper
Lutjanidae	<i>Lutjanus synagris</i> (Linnaeus, 1758)	lane snapper
Mullidae	<i>Mullus auratus</i> Jordan & Gilbert, 1882	red goatfish
Muraenidae	<i>Gymnothorax saxicola</i> Jordan & Davis, 1891	honeycomb moray

Appendix A. Continued.

FAMILY	SCIENTIFIC NAME	COMMON NAME
Ogcocephalidae	<i>Ogcocephalus radiatus</i> (Mitchill, 1818)	polka-dot batfish
Ophichthidae	<i>Ahila egmontis</i> (Jordan, 1884)	key worm eel
Ophichthidae	<i>Ophichthus puncticeps</i> (Kaup, 1860)	palespotted eel
Ophidiidae	<i>Lepophidion brevibarbe</i> (Cuvier, 1829)	blackedge cusk-eel
Ophidiidae	<i>Ophidion</i> sp.	cusk-eel
Opistognathidae	<i>Opistognathus</i> sp.	spotfin jawfish
Ostraciidae	<i>Lactophrys quadricornis</i> (Linnaeus, 1758)	scrawled cowfish
Pomacanthidae	<i>Holacanthus bermudensis</i> Goode, 1876	blue angelfish
Pomacentridae	<i>Pomacentrus variabilis</i> Castelnau, 1855	cocoa damselfish
Rachycentridae	<i>Rachycentron canadum</i> (Linnaeus, 1766)	cobia
Rajidae	<i>Raja eglanteria</i> Bosc, 1802	clearnose skate
Rhincodontidae	<i>Ginglymostoma cirratum</i> (Bonnaterre, 1788)	nurse shark
Scaridae	<i>Nicholsina usta</i> (Valenciennes, 1839)	emerald parrotfish
Sciaenidae	<i>Equetus lanceolatus</i> (Linnaeus, 1758)	jackknife-fish
Sciaenidae	<i>Equetus umbrosus</i> Jordan & Eigenmann, 1889	cubbyu
Sciaenidae	<i>Odontoscion dentex</i> (Cuvier, 1830)	reef croaker
Sciaenidae	<i>Pogonias cromis</i> (Linnaeus, 1766)	black drum
Sciaenidae	<i>Sciaenops ocellatus</i> (Linnaeus, 1766)	red drum
Scombridae	<i>Euthynnus alletteratus</i> (Rafinesque, 1810)	little tunny
Scombridae	<i>Scomberomorus cavalla</i> (Cuvier, 1829)	king mackerel
Scombridae	<i>Scomberomorus maculatus</i> (Mitchill, 1815)	Spanish mackerel
Scorpaenidae	<i>Scorpaena brasiliensis</i> (Cuvier, 1829)	barbfish
Serranidae	<i>Centropristis ocyurus</i> (Jordan & Evermann, 1887)	bank sea bass
Serranidae	<i>Centropristis striata</i> (Linnaeus, 1758)	black sea bass
Serranidae	<i>Diplectrum formosum</i> (Linnaeus, 1766)	sand perch
Serranidae	<i>Epinephelus itajara</i> (Lichtenstein, 1822)	jewfish
Serranidae	<i>Epinephelus morio</i> (Valenciennes, 1828)	red grouper

Appendix A. Continued.

FAMILY	SCIENTIFIC NAME	COMMON NAME
Serranidae	<i>Mycteroperca microlepis</i> (Goode & Bean, 1879)	gag
Serranidae	<i>Mycteroperca phenax</i> Jordan & Swain, 1884	scamp
Serranidae	<i>Rypticus maculatus</i> Holbrook, 1855	whitespotted soapfish
Serranidae	<i>Serraniculus pumilio</i> Ginsburg, 1952	pygmy sea bass
Serranidae	<i>Serranus subligarius</i> (Cope, 1870)	belted sandfish
Soleidae	<i>Gymnachirus melas</i> (Nichols, 1916)	naked sole
Soleidae	<i>Symphurus urospilus</i> (Ginsburg, 1951)	spottail tonguefish
Sparidae	<i>Archosargus probatocephalus</i> (Walbaum, 1792)	sheepshead
Sparidae	<i>Calamus proridens</i> Jordan & Gilbert, 1884	littlehead porgy
Sparidae	<i>Diplodus holbrooki</i> (Bean, 1878)	spottail pinfish
Sparidae	<i>Lagodon rhomboides</i> (Linnaeus, 1766)	pinfish
Sparidae	<i>Pagrus pagrus</i> (Linnaeus, 1758)	red porgy
Sphyraenidae	<i>Sphyraena barracuda</i> (Walbaum, 1792)	great barracuda
Sphyraenidae	<i>Sphyraena picudilla</i> Poey, 1860	southern sennet
Syngnathidae	<i>Cosmocampus albirostris</i> (Kaup, 1856)	whitenose pipefish
Syngnathidae	<i>Hippocampus erectus</i> Perry, 1810	lined seahorse
Syngnathidae	<i>Syngnathus pelagicus</i> Linnaeus, 1758	sargassum pipefish
Syngnathidae	<i>Syngnathus springeri</i> Herald, 1942	bull pipefish
Synodontidae	<i>Synodus intermedius</i> (Agassiz, 1829)	sand diver
Tetraodontidae	<i>Chilomycterus schoepfi</i> (Walbaum, 1792)	striped burrfish
Tetraodontidae	<i>Sphoeroides nephelus</i> (Goode & Bean, 1882)	southern puffer
Tetraodontidae	<i>Sphoeroides spengleri</i> (Bloch, 1782)	bandtail puffer
Triglidae	<i>Prionotus martis</i> Ginsburg, 1950	barred searobin
Triglidae	<i>Prionotus rubio</i> Jordan, 1886	blackwing searobin

Appendix B. Organisms collected in cores near the Suwannee Regional Reefs from 1991 – 1994. Only taxonomic levels used for sorting specimens are reported.

PHYLUM CNIDARIA	ORDER ISOPODA
CLASS ANTHOZOA	34 Anthuridae sp. A
1 anemone	35 Anthuridae sp. B
CLASS HYDROZOA	36 Anthuridae xeranthura
2 actinula	37 Cassidisca lunifrons
PHYLUM ARTHROPODA	38 Cyathura (burbanki)
ORDER ACARINA (MITE)	39 Dynamenella (angulata)
CLASS PYCNOGONIDA	40 Edotea montosa
3 Callipallene brevirostris	41 Ericsonella filiformis
CLASS MALACOSTRACA	42 Eurydice littoralis
ORDER STOMATOPODA	43 Haliophasma germinata
4 Squilla sp.	44 Haliophasma germinata
ORDER TANAIDACEA	45 Isopoda sp. A
5 Leptochelia forresti	46 Isopoda sp. B
ORDER AMPHIPODA	47 Lysidia minetta
6 Ampelisca Cristata microdentata	48 Munna fabrici
7 Ampelisca vadacum	49 Paracerceius sp.
8 Ampelisca (romigi)	50 Ptilanthura (tricarina)
9 Ampelisca (typica)	51 Serolis mgrayi
10 Amphilocheus neupobitanus	52 Xenanithura brevitelson
11 Amphipoda sp. E	CLASS CIRRIPIEDIA
12 Ampithoe longimana	53 Balanus (trigonus) cirripedia
13 Ampithoe longimana	INFRAORDER BRACHYURA
14 Aoridae sp. A	54 Brachyura sp.
15 Apheus sp.	55 Brachyura sp. A
16 Argissa hematipes	56 Cryptopodia concava
17 Carinabatea sp.	57 Ebalia cariosa
18 Cerapus tubularis	58 Euchirograpsus americanus
19 Elasmopus sp. (pectinicus)	59 Goneplacidae sp.
20 Hyale sp.	60 Heterocrypta granulata
21 Isaeidae sp.	61 Hypoconcha sabulosa
22 Lysianassidae sp. B	62 Inachinae sp.
23 Maera danae	63 Ovalipe sp.
24 Melita sp. B	64 Pinnixia sp.
25 Melitidae sp. A	65 Portunus sp.
26 Microdeutopus anamalus	66 Euprognatha sp.
27 Microprotopus sp.	67 Euryplax nitida
28 Oedicerotida sp. A	68 megalops larvae
29 Phtisica sp.	ORDER DECOPODA
30 Pontogeneiidae sp. A	69 Cronius tumidulus
31 Rhachotropis sp.	70 Mesorhoea sexpinosa
32 Stenothoe crassicornis	FAMILY ALBUNIDAE
33 Synopiidae sp.	71 Lepidopa websteri

Appendix B. Continued.

FAMILY MYSIDAE		PHYLUM BRYOZOA	
72	<i>Mysidopsis mortenseni</i>	106	<i>Cupuladria</i>
FAMILY PAGURIDAE		107	<i>Leptochelia filum</i> (Tanaidacea)
73	<i>Pagarus annulipes</i>	108	<i>Nebalia</i> sp.
74	<i>Pagarus hendersoni</i>	109	<i>Schizoporella</i> sp.
75	<i>Paguridae zoea</i>	PHYLUM MOLLUSCA	
76	<i>Paguristes hummi</i>	CLASS POLYPLACOPHORA	
FAMILY UPOGEBIIDAE		110	<i>Acanthochitona pygmaea</i>
77	<i>Upogebia affinis</i>	111	<i>Chaetopleura apiculata</i>
FAMILY CALLIANASSIDAE		112	<i>Chiton</i>
78	<i>Callianassa biformis</i>	113	<i>Polyplacophora</i> sp.
79	<i>Callianassa</i> sp.	CLASS GASTROPODA	
FAMILY CAPRELLIDAE		114	<i>Gastropoda</i> sp. T
80	<i>Duetella mayeri</i>	115	<i>Acteon punctostraitus</i>
81	<i>Luconacia incerta</i>	116	<i>Admete</i> sp.
INFRAORDER CARIDAE		117	<i>Arene tricarinata</i>
82	<i>Alpheus formosus</i>	118	<i>Atys</i> sp.
83	<i>Automate evemanni</i>	119	<i>Bulla eburnia</i>
84	<i>Automate gardineri</i>	120	<i>Calyptreaea</i> sp.
85	<i>Latreutes fucorua</i>	121	<i>Cancellaria reticulata</i>
86	<i>Leptoalpheus forceps</i>	122	<i>Cerithium</i> sp.
87	<i>Leptochela serratorbita</i>	123	<i>Conus (floridanus)</i>
88	<i>Neopontonides beaufortensis</i>	124	<i>Crepidula maculosa</i>
89	<i>Ogyrides alphaerostris</i>	125	<i>Epitonium</i> sp.
90	<i>Parapenaeus politus</i>	126	<i>Gastropoda</i> sp. A
91	<i>Periclemenes</i> sp.	127	<i>Gastropoda</i> sp. B
92	<i>Processa bermudensis</i>	128	<i>Gastropoda</i> sp. C
93	<i>Processa vicina</i>	129	<i>Gastropoda</i> sp. D
94	<i>Sicyonia dorsalis</i>	130	<i>Gastropoda</i> sp. E
95	<i>Sicyonia stimpsoni</i>	131	<i>Gastropoda</i> sp. R
96	<i>Sicyonia typica</i>	132	<i>Gastropoda</i> sp. S
97	<i>Trachypenaeus constrictus</i>	133	<i>Gastropoda</i> sp. U
CLASS INSECTA		134	<i>Marginella</i> sp.
98	<i>Collembola</i>	135	<i>Melarellidae</i>
99	<i>Diperta</i>	136	<i>Mitrella lunata</i>
100	<i>Ellipes minuta</i>	137	<i>Nassarius</i> sp.
101	<i>Ephemeroptera</i>	138	<i>Naticidae</i> sp.
102	<i>Hemiptera</i>	139	<i>Oliva sayana</i>
103	<i>Hymenoptera</i>	140	<i>Oliva</i> sp.
104	<i>Orthoptera</i>	141	<i>Olivella</i> sp.
PHYLUM BRACHIOPODA		142	<i>Ostomia</i> sp.
105	<i>Glottidea albida</i>	143	<i>Parahaustorius longimerus</i>
		144	<i>Photis reinardi</i>

Appendix B. Continued.

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|----------------|----------------------------|-------------------------|-------------------------|
| 145 | Pleurobranchidae sp. | 187 | Divaricella sp. |
| 146 | Rhepoxgnius epistomus | 188 | Fimbria fimbriata |
| 147 | Rudilemboides naglei | 189 | Laevicardium laevagatum |
| 148 | Stenothoe minuta | 190 | Laevicardium pictum |
| 149 | Strombiformis (bilineatus) | 191 | Lucina floridana |
| 150 | Synchelidium heplacjeles | 192 | Lucina nassula |
| 151 | Synchelidium maculatum | 193 | Lyonsia sp. |
| 152 | Tiron sp. | 194 | Macrocallista maculata |
| 153 | Vitrinella (hemphilli) | 195 | Mitrella lunata |
| 154 | Odostomia sp. | 196 | Modiolus sp. |
| CLASS BIVALVIA | | 197 | Nuculana sp. |
| 155 | Arca sp. | 198 | Pandora trilineata |
| 156 | Arcopsis adamsi | 199 | Panope bitruncata |
| 157 | Bivalvia sp. A | 200 | Periploma margaritaceum |
| 158 | Bivalvia sp. B | 201 | Pitar sp. |
| 159 | Bivalvia sp. C | 202 | Pleuromeris tridentata |
| 160 | Bivalvia sp. D | 203 | Plicatula sp. |
| 161 | Bivalvia sp. E | 204 | Semele sp. |
| 162 | Bivalvia sp. F | 205 | Solemya velum |
| 163 | Bivalvia sp. G | 206 | Tellina aequistriata |
| 164 | Bivalvia sp. H | 207 | Tellina idae |
| 165 | Bivalvia sp. I | 208 | Tellina listeri |
| 166 | Bivalvia sp. J | 209 | Tellina (bodegensis?) |
| 167 | Bivalvia sp. K | 210 | Thyasira arisinuata |
| 168 | Bivalvia sp. L | 211 | Thyasira trisinuata |
| 169 | Bivalvia sp. M | 212 | Trachycardium sp. |
| 170 | Bivalvia sp. N | CLASS SCAPHAPODA | |
| 171 | Bivalvia sp. O | 213 | Cadulus sp. |
| 172 | Bivalvia sp. P | 214 | Dentalium sp. |
| 173 | Bivalvia sp. Q | PYLUM NEMERTEA | |
| 174 | Bivalvia sp. R | 215 | Cerebratulus lacteus |
| 175 | Bivalvia sp. S | PHYLUM PHORONIDA | |
| 176 | Bivalvia sp. T | 216 | Phoronis sp. |
| 177 | Bivalvia sp. U | PHYLUM PLATHYHELMINTHES | |
| 178 | Bivalvia sp. V | 217 | Platyhelminthes sp. |
| 179 | Chama sp. | PHYLUM ANNELIDA | |
| 180 | Chione sp. | CLASS OLIGOCHAETA | |
| 181 | Cooperella atlantica | 218 | Oligochaete sp. |
| 182 | Crassinella sp. | CLASS POLYCHAETA | |
| 183 | Crassostrea lunulata | 219 | Acistrosyllis hartmanae |
| 184 | Crassostrea virginica | 220 | Aglaophamus verrilli |
| 185 | Crenella divaricata | 221 | Ammotrypane pallida |
| 186 | Cyclocardia sp. | 222 | Ampharete sp. A |

Appendix B. Continued.

223	Ampharete sp. B	266	Cirriformia sp. B
224	Ampharetidae sp. A	267	Cirrophorus forticirratus
225	Ampharetidae sp. B	268	Diopatra cuprea
226	Amphicteis gunneri	269	Diopatra ornata
227	Amphicteis scaphobranchiata	270	Diopatra papollata
228	Amphictene sp. A	271	Diopatra sp. *
229	Amphitritinae sp.	272	Dispio uncinata
230	Anaitides longipes	273	Dorvellidae sp. A
231	Anaitides sp.	274	Dorvillea sp. A
232	Ancistrosyllis sp. C	275	Dorvilleidae spp.
233	Ancistrosyllis sp. B	276	Dorvilleidae (sociabilis)?
234	Apomatus	277	Driloneris sp.
235	Arabella iricolor	278	Ehlersia sp.
236	Arenicolidae sp.	279	Eteone lactea
237	Aricidea (Acmira) sp. A	280	Eteone sp.
238	Aricidea (Acmira) cerrutti	281	Euclymone sp. A
239	Aricidea (Acmira) lopezi	282	Eulalia bilineata
240	Aricidea (Acmira) philbinae	283	Eunice vittata
241	Aricidea (Acmira) sp. C	284	Eurythoe sp.
242	Aricidea (Acmira) sp. D	285	Eusyllis sp.
243	Aricidea (Acmira) taylori	286	Exogone dispar
244	Aricidea (Allia) sp. A	287	Exogone sp.
245	Aricidea (Allia) suecica	288	Fabriciola trilobata
246	Aricidea (Aricidea) wassi	289	Fimbriostenelais longipinnis
247	Armandia agilis	290	Genetyllis sp.
248	Armandia maculata	291	Genus A (Polynoidea)
249	Axiothella mucosa	292	Genus B (Ampharetidae)
250	Axiothella sp.	293	Glycera sp.
251	Axiothella sp. A	294	Goniadella sp.
252	Brania clavata	295	Goniadides carolinae
253	Brania sp.	296	Grubeulepis mexicana
254	Brania wellfleetensis	297	Grubeulepis sp. A
255	Brania (swedmarki)	298	Gymnonereis crosslandi
256	Cabira inserta	299	Gymnonereis sp.
257	Capitella capitata	300	Gyptis brevipalpa
258	Capitellidae sp. A	301	Gyptis vittata
259	Cautleriella alata	302	Hesione sp.
260	Ceratocephale crosslandi	303	Hesionidae sp.
261	Ceratocephale oculata	304	Hesiura sp. A
262	Ceratonereis sp.	305	Heteropodarke heteromorpha
263	Chaetozone sp. A	306	Heteropodarke sp. A
264	Chaetozone sp. C	307	Heteropodarke sp.
265	Chone americana	308	Hydroides microtus

Appendix B. Continued.

309	<i>Inbergonuphis gorgonensis</i>	352	<i>Melinna</i> sp.
310	<i>Isolda pulchella</i>	353	<i>Mesochaetopterus capensis</i>
311	<i>Kefersteinia cirrata</i>	354	<i>Micromaldane</i> sp.
312	<i>Kesun</i> sp.	355	<i>Micromaldane</i> sp.
313	<i>Kinberginereis simoni</i>	356	<i>Microphthalamus hamosus</i>
314	<i>Kinberginereis</i> sp.	357	<i>Microspio pigmentata</i>
315	<i>Kinbergonuphis fragilis</i>	358	<i>Mooreonuphis nebulosus</i>
316	<i>Kinbergonuphis pulchra</i>	359	<i>Mooreonuphis pallidul</i>
317	<i>Kinbergonuphis</i> sp.	360	<i>Mooreonuphis</i> sp.
318	<i>Kinbergonuphis vermillionensis</i>	361	<i>Myriochele oculata</i>
319	<i>Kinbergonuphis virgata</i>	362	<i>Mystides borealis</i>
320	<i>Laonice cirrata</i>	363	<i>Neanthes acuminata</i>
321	<i>Leitocapitella</i> sp.	364	<i>Nematoneris hebes</i>
322	<i>Leitoscoloplos robustus</i>	365	<i>Neoheteromastus lineus</i>
323	<i>Leitoscoloplos fargilis</i>	366	<i>Nephtys magellanica</i>
324	<i>Lepidonotus subleuis</i>	367	<i>Nephtys bucera</i>
325	<i>Loima medusa</i>	368	<i>Nephtys parva</i>
326	<i>Loima viridis</i>	369	<i>Nephtys picta</i>
327	<i>Lumbrineris coccinea</i>	370	<i>Nephtys squamosa</i>
328	<i>Lumbrineris latreilli</i>	371	<i>Nereidae</i> spp.
329	<i>Lumbrineris</i> sp. A	372	<i>Nereidae</i> sp. A
330	<i>Lumbrineris</i> sp. B	373	<i>Nereidae</i> sp. B
331	<i>Lumbrineris</i> sp. C	374	<i>Neries falsa</i>
332	<i>Lumbrineris</i> sp. D	375	<i>Neries palsa</i>
333	<i>Lumbrineris verrilli</i>	376	<i>Nicon</i> sp.
334	<i>Lysianopsis alba</i>	377	<i>Notomastus americanus</i>
335	<i>Lysidice ninetta</i>	378	<i>Notomastus lobatus</i>
336	<i>Lysilla</i> sp.	379	<i>Odontosyllis enopla</i>
337	<i>Lysippe capensis</i>	380	<i>Odontosyllis</i> sp. A
338	<i>Macroclymene</i> sp.	381	<i>Onuphidae</i>
339	<i>Magelona pettiboneae</i>	382	<i>Onuphidae</i> sp. A
340	<i>Magelona</i> sp. A	383	<i>Onuphis eremita parva</i>
341	<i>Magelona</i> sp. B	384	<i>Onuphis eremits oculata</i>
342	<i>Magelona</i> sp. C	385	<i>Onuphis vermillionensis</i>
343	<i>Magelonidae</i>	386	<i>Onuphis (chinensis)?</i>
344	<i>Malacoceros sanderhorsti</i>	387	<i>Ophelia denticulata</i>
345	<i>Maldanidae</i> sp.	388	<i>Ophelina acuminata</i>
346	<i>Maldanidae</i> sp. A	389	<i>Ophelina cylindrica</i> data
347	<i>Malmgreniella</i> sp B	390	<i>Ophiodromus</i>
348	<i>Mastobranchus</i> sp.	391	<i>Opisthodonta</i> sp.
349	<i>Mastobranchus</i> sp.	392	<i>Orinia riseri</i>
350	<i>Mediomastus californiensis</i>	393	<i>Owenia</i> sp.
351	<i>Megelomma vesiarlosum</i>	394	<i>Owenia</i> sp. A

Appendix B. Continued.

395	<i>Paleanotus heteroseta</i>	438	<i>Scolecopsis squamata</i>
396	<i>Paleanotus</i> sp. A	439	<i>Scolecopsis texana</i>
397	<i>Paranaitis speciosa</i>	440	<i>Scoloplos (ameceps)</i>
398	<i>Paranthanais (polynoides)</i>	441	<i>Scoloplos rubra</i>
399	<i>Paraonidae</i> sp. A	442	<i>Scoloplos</i> sp. B
400	<i>Paraonis fulgens</i>	443	<i>Scoloplos (capensis)</i>
401	<i>Paraonis pygoenigmatica</i>	444	<i>Serpula</i> sp.
402	<i>Parapionosyllis</i> sp. A	445	<i>Sigambra bassi</i>
403	<i>Paraprionospio pinnata</i>	446	<i>Sigambra tentaculata</i>
404	<i>Paraprionosyllis longicirrata</i>	447	<i>Sphaerosyllis aciculata</i>
405	<i>Pectinaria gouldii</i>	448	<i>Sphaerosyllis longicauda</i>
406	<i>Pectinaria regalis</i>	449	<i>Spio pettiboneae</i>
407	<i>Pettiboneia</i> sp. A	450	<i>Spio</i> sp.
408	<i>Pholoe</i> sp.	451	<i>Spiochaetopterus costarum</i>
409	<i>Phyllodoce arenae</i>	452	<i>Spionidae</i> sp.
410	<i>Phyllodoce</i> sp. D	453	<i>Spionidae</i> sp. A
411	<i>Phyllodocidae</i> sp. A	454	<i>Spiophanes bombyx</i>
412	<i>Pionosyllis gesae</i>	455	<i>Streblospio benedicti</i>
413	<i>Pista</i> sp.	456	<i>Streptosinigera heteroseta</i>
414	<i>Plakosyllis</i> sp.	457	<i>Streptosyllis pettiboneae</i>
415	<i>Platynereis</i> sp.	458	<i>Syllidae</i> sp. A
416	<i>Poecilochaetus johnsoni</i>	459	<i>Syllidae</i> sp. B
417	<i>Polychaeta</i> sp. B	460	<i>Syllidae</i> sp. C
418	<i>Polychaeta</i> sp. C	461	<i>Syllides</i> sp.
419	<i>Polycirrus haematodes</i>	462	<i>Syllis cornata</i>
420	<i>Polycirrus</i> sp.	463	<i>Synelmis</i> sp. A
421	<i>Polydortes</i> sp.	464	<i>Synelmis</i> sp. B
422	<i>Polydora socialis</i>	465	<i>Terrebellidae</i> sp.
423	<i>Polydora</i> sp.	466	<i>Tharyx</i> cf. <i>annulosus</i>
424	<i>Polynoidae</i> sp. A	467	<i>Therochaeta</i> sp. A
425	<i>Potamilla peniformis</i>	468	<i>Travisia hobsonae</i>
426	<i>Prionospio apoprionospio dayi</i>	469	<i>Trichobranchus glacialis</i>
427	<i>Prionospio apoprionospio pygmaea</i>	470	<i>Trypanosyllis parvidentat</i>
428	<i>Prionospio minuspio cirrifera</i>	471	<i>Trypanosyllis</i> sp.
429	<i>Prionospio minuspio</i> sp.	PHYLUM ECHIURA	
430	<i>Prionospio (prionospio) cristata</i>	472	<i>Echiura</i> sp.
431	<i>Prionospio (prionospio) fallax</i>	PHYLUM SIPUNCULA	
432	<i>Protodorvillea kefersteini</i>	473	<i>Sipuncula</i> sp.
433	<i>Rullierinereis</i> sp.	PHYLUM PRIAPULIDA	
434	<i>Sabella microthalma</i>	474	<i>Priapulida</i> sp.
435	<i>Sabellaria</i> sp. A	PHYLUM CHAETOGNATHA	
436	<i>Sabellides</i> sp. A	475	<i>Sagitta</i> sp.
437	<i>Schishomeringo</i> sp.		

Appendix B. Continued.

PHYLUM ECHINODERMATA

SUBCLASS ASTEROIDEA

476 *Astropecten articulatus*

SUBCLASS OPHUROIDEA

477 *Amphipolis squamata*

SUBCLASS ECHINOIDEA

478 heart urchin

479 sand dollar

480 urchin

CLASS HOLOTHUROIDEA

481 *Cucumariidae* sp.482 *Leptosynapta* sp.

PHYLUM CHORDATA

483 *Oikopleura* sp.484 *Branchiostoma caribaeum*

485 fish eggs

486 fish larvae