Florida State University Libraries

Electronic Theses, Treatises and Dissertations The Graduate School

2006

The Life History, Reproductive Ecology, and Demography of the Red Porgy, Pagrus Pagrus, in the Northeastern Gulf of Mexico

Douglas Alan Devries

Follow this and additional works at the FSU Digital Library. For more information, please contact lib-ir@fsu.edu

THE FLORIDA STATE UNIVERSITY

COLLEGE OF ARTS AND SCIENCES

THE LIFE HISTORY, REPRODUCTIVE ECOLOGY, AND DEMOGRAPHY OF THE RED PORGY, *Pagrus pagrus*, IN THE NORTHEASTERN GULF OF MEXICO

By

DOUGLAS ALAN DEVRIES

A Dissertation submitted to the
Department of Biological Science
in partial fulfillment of the
requirements for the degree of
Doctor of Philosophy

Degree Awarded:
Spring Semester, 2006

The members of the Committee approve the Dissertation of Douglas A. DeVries defended on December 5, 2005.

_____
Joseph Travis
Professor Co-Directing Dissertation

_____
Christopher C. Koenig
Professor Co-Directing Dissertation

_____
Duane Meeter
Outside Committee Member

_____
John S. Elam
Committee Member

_____
Churchill B. Grimes
Committee Member

_____
Don R. Levitan
Committee Member

Approved:

_____
Timothy S. Moerland, Chair, Department of Biological Science

_____
Joseph Travis, Dean, College of Arts and Sciences

The Office of Graduate Studies has verified and approved the above named committee members.

For my parents,

Peter and Arlene DeVries

my wife,

Kristin

and Dr. Keitz Haburay,

who got me hooked on making a career of studying fish

ACKNOWLEDGEMENTS

I owe a huge debt of gratitude to many current and former colleagues at the Panama City Laboratory of the National Marine Fisheries Service. I thank Churchill Grimes for giving me the opportunity to begin a career with the National Marine Fisheries Service, for much encouragement and support (scientific, moral, financial, and logistical) from my earliest days at the lab to develop professionally and pursue a PhD, for all his efforts to establish a cooperative institute with the FSU Biology Department, for allowing me to devote much of my time and effort to working towards this degree, and last but not least, for serving as a valuable member of my committee, providing much advice and constructive comments for many long years. Herb Kumpf, as lab director after Churchill, was also extremely supportive and encouraging throughout his tenure. I especially thank him for providing the vessel and equipment I needed to conduct my research and for allowing me the freedom to collect the samples I needed many miles from land. I thank Pete Sheridan for his patience, support, and for allowing me the time and freedom to complete this project.

A special thanks to fellow students and "Fish Guys" Andy David and Bob Allman, without whose friendship, encouragement, and help I probably would not have made it through those 3 semesters of commuting to Tallahassee 2-3 times a week, the 6 AM departures, the 4 PM Friday Nat Hist seminars, the all nighters for statistics classes, multivariate statistics, graduate reviews, committee meetings, and of course, prelims. I thank Andy also for all his help in designing, building, and maintaining the aquaculture facilities and his always good advice and assistance with maintaining my fish in captivity.

Extra special thanks to Chris Palmer and Bill Walling for all their help in the field and lab, for sacrificing their backs and kidneys on all those 12-14 hr, 35 mile trips offshore, all for the sake of red porgy. Thanks also to Bill for all the help with the captive fish and processing histo samples. A host of other coworkers, interns, and volunteers also helped out in the field and lab, including John Brusher, Joe Mikulas, Clare Mangum, and Dan Harris. Alan Collins spent many hours passing on his knowledge of fish reproduction and reproductive histology, providing sound advice, and answering unending questions. Thanks to Beverly Barnett and Bill Kline for helping so much in processing histo and

otolith samples. I thank Gary Fitzhugh for being a good friend, a great sounding board, a constant source of stimulating scientific discussions and good ideas, always encouraging, being very patient with my slow progress, and for letting me use his boat and shop.

Very special thanks are due to my co-chairs Joe Travis and Chris Koenig for teaching me much, never giving up on me, and for being a constant source of support, encouragement, and advice for 10 long years. Chris's enthusiasm, insight, creativity, and extensive work on gag first inspired me to explore the world of protogyny and reproductive ecology. Joe has been an extraordinary teacher, advisor, mentor, advocate, and friend. I greatly appreciate all the time he invested in me, his willingness to take on such a nontraditional student, his always insightful, constructive, positive feedback, and his great sense of humor. Every meeting I had with Joe was uplifting and I can't imagine having a better major professor.

My other committee members – Don Levitan, John Elam, and Duane Meeter – no doubt never imagined they were signing up for a 10 yr term, were also very patient and encouraging, and provided much sound advice and different perspectives. Duane Meeter's courses on ANOVA and regression were unquestionably the two most useful, enjoyable statistics classes I ever had. Don Levitan's questions and comments were always challenging and thought - provoking.

I especially thank David Wyanski, and also Pat Harris, Oleg Pashuk, Scott Meister, and Kathy Grimball at the South Carolina Marine Resources Research Institute for teaching me so much about the reproductive histology and ageing of red porgy, and for so generously processing 700 histological samples for free. Deb Murie at the University of Florida kindly revealed the mysteries of breaking and burning otoliths. Peter Hood generously provided all his raw data and otolith sections from his groundbreaking study of red porgy in the Gulf. Bob Dixon at the NMFS Beaufort lab graciously provided many years of Gulf red porgy data from the Headboat Survey. Ken Sulac and George Dennis with USGS Gainesville provided many specimens from sites as far west as Alabama and allowed me to participate in some of their cruises. I owe much thanks to Judy Bowers, who cheerfully guided me safely through the bureaucratic mazes of the graduate school and biology department of FSU for these 10 long years.

I am greatly indebted to the National Marine Fisheries Service for giving me the privilege of pursuing my PhD and for providing all of my funding and logistical support.

And finally, I want to thank my parents, my three daughters – Rachel, Ashley, and Laura, and most of all my wonderful wife and best friend Kristin, for unending encouragement and support, and for putting up with a dad and husband who spent way too much time away from home fooling around with red porgies for too many years

TABLE OF CONTENTS

List of Tables viii
List of Figures x
Abstract xiv

INTRODUCTION 1

1. SIZE AND SEX SELECTIVITY IN HOOK AND LINE SAMPLING FOR RED PORGY 5

2. ASPECTS OF REPRODUCTION IN RED PORGY IN THE NORTHEASTERN GULF OF MEXICO 17

3. SMALL SCALE SPATIAL HETEROGENEITY IN LIFE HISTORY TRAITS AND DEMOGRAPHICS OF *PAGRUS PAGRUS* (SPARIDAE), A PROTOGYNOUS REEF FISH IN THE NORTHEASTERN GULF OF MEXICO 54

4. SPATIAL VARIABILITY IN MATURITY, RATES AND TIMING OF SEX CHANGE, AND SEX RATIOS OF *PAGRUS PAGRUS* (SPARIDAE) IN THE NORTHEASTERN GULF OF MEXICO 92

CONCLUSIONS 117

APPENDIX A. SUPPLEMENTARY FIGURES 122

APPENDIX B. SUPPLEMENTARY TABLES 142

REFERENCES 147

BIOGRAPHICAL SKETCH 160

LIST OF TABLES

Table 1.1. Results of two different runs tests for size selectivity in hook and line collections of red porgy (Sokal and Rohlf 1969, Zar 1999). α=0.05. ns = not significant 12

Table 1.2. Results of runs tests for sex selectivity in hook and line collections of red porgy (Sokal and Rohlf 1969, Zar 1999). The test for dichotomized data was used to examine sex selectivity in two ways – considering all transitionals as males and all as females. α=0.05. ns = not significant.....13

Table 2.1. Macroscopic and histological gonad maturity stages assigned to female red porgy. Numbers in parentheses following histological stage names indicate stage number.....42

Table 3.1. Depth, location, bottom temperature range, and sampling information for the nine standard sites.....79

Table 3.2. Results of Kolmogorov-Smirnov 2-sample tests of overall size and age distributions among nine standard sites. Numbers in bold indicate sites which were not significantly different.....80

Table 3.3. Least squares and Robson-Chapman estimates of annual survival (S) and instantaneous total mortality (Z) rates of red porgy for the standard sites. The least squares S was calculated as e^{-Z} and the Robson-Chapman Z was calculated as –lnS 81

Table 3.4. Site specific estimates of instantaneous natural mortality (M) and conditional natural mortality (n, which = $1-e^{-M}$) rates calculated using Pauly's (1980) equation. For one set of estimates, the L_∞ and k used in the Pauly equation were derived from a von Bertalanffy growth equation in which t_0 was not constrained, while for the second set of estimates, t_0 was constrained to 0. An overall pooled bottom water temperature of 22.4°C was used in all calculations.....82

Table 3.5. Site specific estimates of instantaneous fishing mortality (F) and exploitation (u) rates derived from both maximum likelihood and least square estimates of Z and 2 estimates of M - the overall pooled Pauly estimate of 0.36 and the site specific estimates based on von Bertalanffy k and L_∞ where t_0 was unconstrained. A is the annual mortality rate and equals 1-S, where S = annual survival = e^{-Z} ; and u=FA/Z. Estimates of u assume a Type 2 fishery in which fishing and natural mortality operate concurrently. Symbols and formulae follow Ricker (1975).....83

Table 4.1. Results of two series of paired logistic regressions of proportions of females in transition on location. Two models were used - in one, total length was included, along with location, as a main effect; and in the second, age replaced length as a second main effect. Numbers in bold indicate significant differences. J248 = John's 248, E R = Elbo Reef, G B = Good Bottom, R D G = Ridge, SIG = Sig1_2, W G = Whoopi Grounds, and I R = Ivy's Reef 109

Table 4.2. Results of paired logistic regressions of proportions of males (i.e., sex ratio) on location. Two models were used - in one, total length was included, along with location, as a main effect; and in the second, age replaced length as a second main effect. Numbers in bold indicate significant differences. J248 = John's 248, E R = Elbo Reef, G B = Good Bottom, R D G = Ridge, SIG = Sig1_2, W G = Whoopi Grounds, and I R = Ivy's Reef. FTC = failed to converge 110

Table B.1. Median and mean total lengths, standard errors, and size ranges for the nine standard sites by sex and overall. M = males, F = females, T = transitionals 143

Table B.2. Site specific von Bertalanffy growth parameters and associated statistics 144

Table B.3. Results of Tukey's HSD test of mean size at age among the standard sites for ages 2-7. Lower case letters in bold indicate sites which were not significantly different at α=0.05. BA = Benny Allen, ER = Elbo Reef, GB = Good Bottom, IR = Ivy's Reef, J248 = John's 248, RDG = Ridge, S1_2 = Sig1_2, WG = Whoopi Grounds.....145

Table B.4. Mean age (yr) and standard error for each site by sex. Ages are ordered from oldest to youngest for each sex. BA = Benny Allen, ER = Elbo Reef, GB = Good Bottom, IR = Ivy's Reef, J248 = John's 248, RDG = Ridge, SIG = Sig1_2, WG = Whoopi Grounds 146

LIST OF FIGURES

Figure 1.1: Plots of individual size (TL mm) versus capture order for selected collections from Good Bottom and Ivy's Reef 14

Figure 1.2: Plots of individual sex versus capture order for selected collections from Good Bottom and Ivy's Reef. Transitionals were considered males 15

Figure 1.3. Overall length frequency distributions of red porgy from NMFS stationary video surveys since 1996 and from all hook and line collections in this study 16

Figure 2.1: Locations of all red porgy collections by gear. Numbers associated with depth contours are depths in meters 43

Figure 2.2: Gonadosomatic indices (GSI) for male and female red porgy from the north-eastern Gulf of Mexico.....44

Figure 2.3: Monthly percent frequencies of reproductive stages in female red porgy. Cort. alv. = cortical alveolar, Migratory Nuc. = migratory nucleus (= early FOM) 45

Figure 2.4. A. Percentages of stage 4 (early FOM) and stage 5 (late FOM) female red porgies by site for Dec - Feb only. B. Percentages of female red porgy with POF's by site during Dec-Feb. Numbers at top of bars are sample sizes 46

Figure 2.5: Size at maturity ogives and 95% C.L. using a LOESS regression model for female red porgy in the northeastern Gulf of Mexico. Mature fish were defined in two ways: the presence of vitellogenic oocytes (≥ maturity stage 3) or the presence of POF's. Only fish collected during the spawning season, Dec-Feb, were included in the analysis 47

Figure 2.6: Proportions of mature female red porgy at age in the northeastern Gulf of Mexico. Maturity was defined as the presence of vitellogenic oocytes (≥ maturity stage 3) and the presence of POF's. Only fish collected during the spawning season, Dec-Feb, were included in the analysis 48

Figure 2.7: Monthly percentages of female red porgies in transition. Numbers above each box indicate the number of collections for that month. Only collections with >5 fish were included in analysis 49

Figure 2.8: Overall length and age frequency distributions, by sex, of all red porgies collected by hook and line 50

Figure 2.9. Overall percent frequency distribution of female red porgy in transition, Mar-Nov, by size (A) and by age (B). Numbers above bars indicate total number of females in that size or age interval.....51

Figure 2.10. Color patterns of male and female adult red porgies. Note especially the green premaxilla in the male and the pink premaxilla in the female 52

Figure 2.11. Temporal distribution of catch-per-angler-minute at 8 of the 9 standard sites 53

Figure 3.1. Locations and depths of the nine standard red porgy collection sites. Depth contours are 5m isobars.....84

Figure 3.2. Overall length frequency distributions of red porgy at the standard sites. Distributions with like letters near the y axis were not significantly different 85

Figure 3.3. Overall length frequency distributions of hook and line-caught red porgy by depth interval. Distributions with like letters near the y axis were not significantly different 86

Figure 3.4. Length frequency distributions by collection for the Good Bottom and Ivy's Reef sites 87

Figure 3.5. Overall age frequency distributions of red porgy at the standard sites. Distributions with like letters near the y axis were not significantly different 88

Figure 3.6. Age composition in 2000 and 2001 at Good Bottom, Ivy's Reef, Ridge, and Benny Allen. The gray bar indicates the modal age.....89

Figure 3.7. Mean sizes at age and 95% C.L.'s of red porgy ages 2-7. GB = Good Bottom, IR = Ivy's Reef, 3x5 = 3 x 5's, RDG = Ridge, SIG = Sig1_2, BA = Benny Allen, WG = Whoopi Grounds, ER = Elbo Reef, J248 = John's 248 90

Figure 3.8. Mean observed sizes at age of red porgy among studies from the southeastern U.S.....91

Figure 4.1. Percentages of female red porgies in transition by site, Mar- Nov, and depth of site. Numbers above each box indicate the number of collections for that site. Only collections with >5 fish were included in analysis.....111

Figure 4.2. Percent frequency size distributions of female red porgies in transition, Mar-Nov only, and males, all months. Numbers above black bars indicate total number of females plus transitionals in that length interval. Numbers above gray bars indicate total number of all fish in that length interval 112

Figure 4.3. Percent frequency age distributions of female red porgies in transition, Mar-Nov only, and males, all months. Numbers above black bars indicate total number of females plus transitionals in that age interval. Numbers above gray bars indicate total number of all fish in that age interval.....113

Figure 4.4. Percentages of male red porgies by site, all months. Numbers above each box indicate the number of collections for that site. Only collections with >4 fish were included in analysis 114

Figure 4.5. Percentages of mature female red porgy (as indicated by the presence of POF's) by size during Dec-Feb for six of the standard sites. Numbers adjacent to data points are total number of mature + immature females at each site. 115

Figure 4.6. Regression of mean size at transition at the nine sites on mean annual growth rate for ages 2-4. Growth rate was calculated as the average of the mean size at age/age for ages 2, 3, and 4. 116

Figure A.1. A. Depth distributions of all hook and line samples of red porgy. B. Monthly distribution of all red porgy hook and line collections 123

Figure A.2. Monthly percent frequency distribution of female red porgies with post-ovulatory follicles. Numbers at top of bars are sample sizes 124

Figure A.3. Monthly percentages of female red porgies with high rates of atresia (i.e. >50% of the vitellogenic oocytes are atretic). Numbers above each box indicate the number of collections for that month.....125

Figure A.4. Percentages of female red porgies with early and late FOM stage ovaries and with POF's by depth interval during Dec-Feb. Numbers at top of bars are sample sizes.....126

Figure A.5. Temporal percent frequency distributions of premaxilla color of red porgy identified as males by macroscopic (most) or histological (few) examination of gonads 127

Figure A.6. Seasonal mean standardized catch per angler minute and 95% C.L. for the standard sites. All collections within a site were standardized by dividing by the highest catch-per-angler- minute for that site. Numbers above each point represent sample sizes, i.e., number of collections 128

Figure A.7. Percent males by collection and month for Benny Allen, Good Bottom, and Ivy's Reef. .Only collections with >4 fish were included in analysis.....129

Figure A.8. A. Whole sagittal otolith of a red porgy showing 3 annuli (black dots). C = core. B. Broken and burned sagitta of a red porgy showing 6 annuli.....130

Figure A.9. Length frequency distributions by collection for the Benny Allen, Ridge, Sig1_2, and 3x5's sites 131

Figure A.10. Seasonal length frequency distributions for the Benny Allen, Good Bottom, Ivy's Reef, and Ridge sites. The Dec-Feb panels represent the spawning season. Distributions with like letters near the y axis (right margin for Ridge) were not significantly different 132

Figure A.11. Proportions of young (≤ age 2) and older (≥ age 6) red porgy at the standard sites. Numbers at top of bars are sample sizes for that site 133

Figure A.12. Overall age frequency distributions of hook and line-caught red porgy by depth interval. Distributions with like letters near the y axis were not significantly different 134

Figure A.13. Proportions of younger (≤age 2) and older (≥ age 6) red porgy by depth interval. Numbers at top of bars are sample sizes for that depth interval 135

Figure A.14. Von Bertalanffy growth curves for all hook and line-caught red porgy from the northeastern Gulf of Mexico and raw age length data 136

Figure A.15. Annual mean sizes at age and 95% C.L.'s of red porgy ages 2-7 for Good Bottom (GB) and Ridge during Jul 99 – Jun 00 and Jul 00 – Jul 01, and for GB and Ivy's Reef during Jun-Dec 2000 and Jan-Aug 2001 137

Figure A.16. Relationship between mean age and instantaneous fishing mortality rate 138

Figure A.17. Ln mean ± SE size (mm TL) at transition (upper panel) and age at transition (lower panel) of red porgy by site. Letters identify groups of sites which Tukey's HSD test indicated were not significantly different at α=0.05. John's 248 and Elbo Reef were excluded from the size at transition analyses because of their small sample sizes 139

Figure A.18. Percent males by depth for Benny Allen, Ivy's Reef, and all other collections, including non-standard sites. Only collections with >4 fish were included in analysis 140

Figure A.19. Percentages of mature female red porgy (as indicated by the presence of POF's) by age during Dec-Feb for seven of the standard sites. Numbers adjacent to data points are total number of mature + immature females at each site 141

ABSTRACT

Protogynous fishes are often assumed to be more sensitive than gonochorists to exploitation, primarily because of potential sperm limitation and/or social disruption of mating if larger, mostly male individuals are selected for. Overall goals of this research were to study the reproductive ecology of the red porgy *Pagrus pagrus* (Sparidae) in the NE Gulf of Mexico to learn how fishing might affect this and other protogynous species; and to examine the temporal, bathymetric, and small scale (10's of kilometers) spatial variability of its life history traits and demographics to gain insight on population structure and shed light on the apparent sensitivity to exploitation of the stock(s) in the U.S. South Atlantic Bight (SAB).

Almost 4000 red porgy were collected year-round, Mar 1998-Sep 2001, in the NE Gulf, primarily using standardized hook and line gear in depths of 22-92 m. Most (n=2,586) were collected at 9 sites off NW Florida in 30-68 m sampled repeatedly. Fish were aged using whole and broken and burned sagittae, and sexed and staged histologically (females and transitionals) or macroscopically (males). An early objective was to determine if the behaviorally-related size and/or sex selectivity observed in other protogynous species occurred in red porgy, i.e., were larger individuals or males at a site more aggressive and more likely to bite a hook and be caught before smaller ones or females? Non-parametric runs tests of ordered size and sex data showed no evidence of such selectivity, indicating that hook-and-line gear is a fair way to sample red porgy. More importantly, any evidence of truncation in size structure or skewing of sex ratios in exploited populations should not be attributed to greater aggression or "hook attraction" in males but can be easily explained as the results of simple size-selective harvesting.

Histological evidence indicated that red porgy in depths of 20 – 78 m in the NE Gulf spawn wherever they occur, primarily Dec – Feb. Estimated size and age at 50% maturity for females was 211 - 216 mm TL and <2 yr. Sex change occurred wherever they were found, almost exclusively Mar-Nov, and across a wide range of sizes (206-417 mm TL) and ages (2-9 yr), strong evidence it is socially controlled. Red porgy are permanently sexually dichromatic. The premaxilla is green or bluish-green in males and pink or reddish in females. Observations of captive fish suggest they pair spawn. Seasonal patterns in catch rates and sex ratios, and wide-spread occurrence of spawning females, indicated that red porgy do not form large, predictable spawning aggregations. I found no evidence that protogyny or their reproductive ecology might

1) explain the apparent crash of the red porgy stock(s) in the SAB or 2) make the species more sensitive to exploitation than gonochorists - in fact they are probably less sensitive in some cases. Many aspects of their biology and behavior, including widespread spawning grounds, no tendency to form spawning aggregations, absence of behaviorally-related size or sex selectivity, socially controlled sex change, co-occurrence of sexes year-round, and an extended period of transition, should stabilize or enable rapid compensation of sex ratios (preventing sperm limitation or disruption of mating). Socially controlled sex change also enables size and age of transition to slide downward as fishing truncates the size structure, similar to the declines in size and age at maturity seen in many gonochorists.

Several population traits differed significantly among the 9 regular sites (which ranged from 1.3 to 58.4 km ($\bar{x}$ = 28.7) apart), including size and age composition (K-S 2 sample test); means ranged from 261 to 309 mm TL and 2.7 to 4.1 yr. Size at age varied considerably, primarily because of significant differences among sites. The relationships of mean size at age among sites were consistent across ages and temporally stable. Robson-Chapman maximum likelihood estimates of annual survival ranged from 38 to 65 % among sites, and 95% CI's did not overlap for 6 of the 8 sites with estimates. Logistic regression indicated that the proportion of females changing sex differed significantly among sites (medians: 12 - 33%) and depths. Sizes and ages at transition also varied spatially, with site-specific means of 266 - 313 mm and 3.1 - 4.6 yr. Sex ratio was yet another demographic that differed among sites: 28 of 36 pairwise comparisons were significant (log. regress.).

These persistent differences in population traits at such a small scale likely reflect phenotypic, not genetic, effects. Two factors - spatial heterogeneity of their environment and site fidelity - probably explain most of those differences. The live bottom habitat preferred by red porgy is widespread but very patchy. These patches, grossly similar, have variable hydrological, geological, biological, and ecological characteristics; and they range from unexploited to heavily exploited. Biological and ecological characteristics likely to vary among patches include density, predator and prey composition and density, and competition. Adult red porgy exhibit considerable site fidelity, so once recruited to a given patch of habitat, they are exposed to a unique suite of many factors which could affect growth, mortality, and reproduction.

The consistent, persistent, significant differences in size and age structure, growth,

mortality, transition rates, size and ages at transition, and sex ratios among sites separated by only 10's of kilometers strongly suggests that red porgy in the NE Gulf have a complex population structure composed of many local subpopulations. These subpopulations closely resemble Crowder et al.'s (2000) definition of sources and sinks – "areas of differing demographic rates dictated by underlying differences in habitat quality". This complex structure is not the classical metapopulation of Levins (1970), i.e., a "population of populations that go extinct and recolonize", and which are exposed to the same conditions in each habitat patch. It does, however, fit the broader definition of metapopulation espoused by Hastings and Harrison (1994), Hanski and Simberloff (1997), and Kritzer and Sale (2004), which relaxes the requirement for extinctions and recolonizations and does not require uniform conditions across patches.

Whether the population subunits are called local subpopulations, sources and sinks, or members of a metapopulation, the critical point is that many may have significantly different demographics and life history traits, which has potentially significant implications regarding stock assessment and management of red porgy. Data pooled from several subpopulations may yield skewed parameter estimates, which in turn could bias stock assessments and the models used to predict responses to exploitation. It could also introduce excessive variability to the parameter estimates. Such complexity could certainly frustrate and confound the efforts of those trying to assess the status of these stocks and predict the effects of fishing on them, as it requires examination of population biology at much smaller spatial scales than typically done and use of more complex, spatially-explicit population models. It is likely that small scale population complexity has played some part in the failure of some southeastern U.S. reef fish fisheries to respond to management measures in recent years.

INTRODUCTION

In recent years increasing numbers of modeling and empirical studies have concluded that, under certain circumstances, protogynous fishes are more sensitive to the effects of fishing than are gonochorists (Smith 1982, Bannerot et al. 1987, Shapiro 1987, Buxton 1993, Shepard and Idoine 1993, Huntsman and Schaaf 1994, Coleman et al.1996, Adams et al. 2000, Armsworth 2001, Alonzo and Mangel 2004). Fishing that is size or sex selective is potentially most problematic. With protogynous species, in addition to growth overfishing and reduction in size and age at maturity effects common to both gonochorists and hermaphrodites, fishing which selectively removes larger, primarily male individuals could, if there is no compensatory mechanism, lead to sperm limitation, simply because of a lack of males or because sex ratios become so skewed that mating is socially disrupted (Smith 1982; Bannerot et al. 1987; Shapiro 1987; Buxton 1992; Shepherd and Idoine 1993; Huntsman and Schaaf 1994; Coleman et al. 1996; Koenig et al. 1996; Coleman et al. 1999; Adams et al. 2000; Koenig et al. 2000; Armsworth 2001; Alonzo and Mangel 2004). Another potential effect of size-selective fishing unique to protogynous species, if there is a compensatory drop in size at sex change, is a decrease in population fecundity, as this would essentially equate to increased mortality on the largest, most fecund females (Smith 1982; Shepard and Idoine 1993).

Many protogynous species are found in the families Labridae, Scaridae, Serranidae, and Sparidae, families dominated by species usually associated with rocky or coral reef habitats (Shapiro 1987, Buxton and Garratt 1990). Sale (1998) noted that the obvious patchy nature of these sorts of environments forces certain spatial scales on reef fish populations, scales ranging from 10's of meters to 100's of kilometers; and reef fish, upon settlement, tend to strongly prefer a particular reef habitat. Levin (1992) argued that scale is the central problem in ecology, and concluded that “the development and maintenance of spatial and temporal pattern, and the consequences of that pattern for the dynamics of populations and ecosystems” were fundamental, closely connected themes. Jones (1991) stressed the need to determine the spatial scales at which various demographic parameters operate in order to best understand reef fish dynamics. Sale (1998) also pointed out that the spatial scale of a study determines which processes and patterns will be discovered and which will be missed, and he warned that one cannot infer population structure or dynamics at a smaller scale by extrapolating downward from the results

of a larger scale study. Camus and Lima (2002) highlighted the need for those dealing with the problems of population management and conservation to explicitly consider the spatial scales of the processes of those populations - a scale determined by the mobility of the organism and its spatial requirements. Robertson et al. (2005) stressed the need, when trying to assess the effects of exploitation, to consider habitat effects on size, growth, and abundance because of their ability to confound or overpower effects due to fishing, especially when making the typical large-scale regional comparisons. Striking intraspecific differences in social systems of reef fishes have been found within and among reefs, differences attributable in part to 1) the complex, variable distribution of resources within and among reefs, 2) the ability of many species to occupy a variety of microhabitats because of their generalist feeding strategies, and 3) recruitment which varies in rate, space, and time (Shapiro 1991).

In recent years, there has been increasing focus on spatial variability in population processes and life history traits of reef fishes at smaller scales (10's of m to 10's of km), and in some cases, multiple scales. Many of the studies dealt with small-bodied families such as labrids (Warner and Hoffman 1980), pomacentrids (Aldehoven 1986, Meekan et al. 2001), and acanthurids (Hart and Russ 1996), which tend to be logistically easier to study as they typically have small home ranges (1's - 100's of meters) (Gust 2004). More recently, there has been more focus on smaller scale patterns in larger, usually exploited species, including scarids (Dudgeon et al. 2000, Gust et al. 2001, 2002, Gust 2004), lutjanids (Newman et al. 1996, Kritzer 2002), serranids (Ferreira and Russ 1995, Adams et al. 2000), and lethrinids (Williams et al. 2003). Small scale spatial variability in population biology has been examined in only two exploited reef fishes off the eastern United States - the gray triggerfish, *Balistes capriscus* (Ingram 2001) and the white grunt, *Haemulon plumieri* (Murie and Parkyn 2005).

The red porgy *Pagrus pagrus* (Sparidae) is a protogynous species, the adults of which are typically associated with low-profile hard (live) bottom, rocky, or gravel habitats (Manooch and Hassler 1978, Grimes et al. 1982). This sparid occurs in warm temperate to subtropical waters on both sides of the N Atlantic, including the northern Gulf of Mexico (Gulf) and Mediterranean Sea, and in the SW Atlantic from Venezuela to Argentina (Manooch and Hassler 1978, Bauchot and Hureau 1990). It is one of the most abundant, exploited reef fishes in the NE Gulf. In an annual video survey of reef fish in that area, it is one of the most frequently observed species (C. Gledhill, NMFS Pascagoula Lab., personal. communication, 2000.).

Red porgy are only lightly exploited in the Gulf, where they are often taken as bycatch by fishermen targeting more desirable reef fishes. Commercial and estimated recreational landings from Florida Gulf waters during 1998-2002 ranged from 23.2 to 38.2 and 19.7 to 28.9 mt, respectively (National Marine Fisheries Service, Fisheries Statistics and Economics Division, personal. communication, 2003). These data show no evidence of the kind of steep decline in numbers of red porgy observed in the South Atlantic Bight (SAB) off the southeastern U.S. during the 1980's and 90's, a decline so steep (89% drop in spawning stock biomass 1979-1997, 2 orders of magnitude drop in recruitment to age 1, 1988-1997) that in 1999 a 1 year moratorium was placed on their harvest and possession (Vaughan and Prager 2002). This population crash was blamed on overexploitation, which is also thought to be the cause of significant reductions in size-at-age and growth, and in size-at-maturity and at transition (Harris and McGovern 1997).

Only recently Hood and Johnson (2000) provided the first information on the biology and fisheries for red porgy in the NE Gulf. Their findings were somewhat limited in scope, however, as all sampling, which only lasted one year, was fishery dependent, and data were not site specific. The only other information on red porgy in the Gulf was based on 161 fish collected off Texas, where the species is uncommon (Nelson 1988).

This study had two overall goals, one being to collect information on the reproduction and reproductive ecology of red porgy in the NE Gulf. Such information, nonexistent until recently, could serve several purposes. First of all, it could help validate and advance current theory on how fishing affects protogynous species, and provide more insight on the variability of their life history patterns and how or whether those patterns affect their sensitivity to exploitation. Additionally, data on reproduction and reproductive ecology will be invaluable to those involved in assessing and managing red porgy stock(s) in the Gulf and elsewhere, and may be of use to those working with other sparids, many of which are hermaphroditic and exploited to varying degrees. Red porgy will likely be one of the next reef species targeted commercially in the Gulf, given that 1) most of the common, more valuable reef fishes are already fully- or overexploited, and 2) fishermen usually switch to more abundant, less valuable, less managed species in the face of decreased abundance and increasingly restrictive management of more valuable species. Last of all, I hoped that detailed information on reproductive biology (and other life history traits and demographics) would shed some light on why the SAB stock(s) appeared to be so sensitive to exploitation and whether protogyny played any role in that sensitivity, and would help fishery

managers prevent similar population crashes in the future.

The second overall goal of this study was to examine the temporal, bathymetric, and small scale (10's of kilometers) spatial variability in life history traits and demographics of red porgy. Such information should indicate the phenotypic heterogeneity of population traits and the persistence and consistency of those patterns among red porgy living on isolated pieces of suitable habitat separated by no more than 10's of km. This sort of information could be invaluable to those designing sampling programs for monitoring red porgy population trends, for those modeling their population dynamics and trying to predict their responses to fishing, and for those attempting to manage this species. Information on temporal variability should provide insight on seasonal or spawning movements or behavior (i.e., aggregations), and will certainly indicate how persistent and consistent the spatial patterns are. Data on spatial patterns in the population biology of red porgy may also help explain observed patterns in other reef fishes and their responses to exploitation, as well as stimulate new research on the scale of variability of population traits. Last of all, I hoped that this information, like that on reproduction and reproductive ecology, would provide some insight on the apparent sensitivity of the SAB population to exploitation.

One important question that needed to be addressed early in the study because of its significant implications, not only from a population dynamics perspective but also from a sampling standpoint, was whether the size and/or sex selectivity observed in a few other protogynous species occurred in hook and line catches of red porgy, i.e., were the larger individuals or males at a site more aggressive and more likely to be caught before smaller ones or females? If such selectivity occurred, it could lead to very biased conclusions about all aspects of red porgy population biology.

Some of the more significant findings on red porgy in the NE Gulf for which I present evidence include: 1) there was no evidence of behaviorally-related size or sex selectivity with hook and line gear, 2) they are pair spawners, spawning wherever they are found and not in large aggregations, 3) they change sex over a wide range of sizes and ages, indicating the process is socially (exogenously) controlled, 4) they are sexually dichromatic, and 5) size and age structure, growth, mortality rates, sex ratios, transition rates, and size and age at transition vary significantly at a spatial scale of 10's of kilometers.

CHAPTER 1

SIZE AND SEX SELECTIVITY IN HOOK AND LINE SAMPLING FOR RED PORGY

Introduction

Currently, there is considerable concern over the impact of fishing on protogynous species, i.e., sequential hermaphrodites which begin life as females, and then some or all later change sex to males, especially if the fishing is size or sex selective. In one way, size-selective fishing affects gonochoristic (sexes separate) and protogynous species similarly. It not only reduces numbers, but also truncates size distributions, which in turn, either by plasticity or selection, has been shown to result in earlier maturation at smaller sizes and hence, at the very least, a reduction in individual fecundity. With protogynous species, however, because there is a "second" maturation, i.e., when sex change occurs, size-selective fishing could impact the population in at least two other ways. As exploitation removes the larger and primarily male members of the population, without some compensatory response, sperm limitation and decreased fertilization rates could occur, either by reduction in the number of males or social disruption of mating related to skewed sex ratios (Smith 1982; Bannerot et al. 1987; Shapiro 1987; Buxton 1992; Shepherd and Idoine 1993; Huntsman and Schaaf 1994; Coleman et al. 1996; Koenig et al. 1996; Coleman et al. 1999; Adams et al. 2000; Koenig et al. 2000; Armsworth 2001; Alonzo and Mangel 2004). Naturally low sex ratios have been shown to decline precipitously in some heavily fished protogynous species, especially those which form spawning aggregations (Coleman et al. 1996). The other potential impact of size-selective fishing unique to protogynous species is a decrease in population fecundity which could accompany a compensatory drop in size at transition, as this would essentially equate to increased mortality on the largest, most fecund females (Smith 1982; Shepard and Idoine 1993).

The red porgy *Pagrus pagrus*, a protogynous sparid, is one of the most abundant, exploited reef fishes in the northeastern Gulf of Mexico (Gulf). Although lightly exploited in the Gulf, the population(s) in the south Atlantic Bight (SAB) off the southeastern U.S. declined so steeply

during the 1980's and 1990's that in 1999 the South Atlantic Fisheries Management Council placed a 1 year moratorium on their harvest and possession (Vaughan et al. 1992; Vaughan and Prager 2002). In an attempt to determine why the SAB stock(s) appeared to be so sensitive to exploitation, and in particular if it was related to their hermaphroditism, I began a study of their reproductive ecology, demographics, and life history in the northeastern Gulf, emphasizing small-scale spatial variability (Chapters 2-4). One important question that needed to be addressed was whether the size and/or sex selectivity observed in a few other protogynous species occurred in hook and line catches of red porgy, i.e., were the larger individuals or males at a site more aggressive and more likely to be caught before smaller ones or females? This question was important not only from a population dynamics perspective but also from a sampling standpoint - if either size or sex selectivity occurred, it could lead to very biased conclusions about such demographics as size and age structure and sex ratios.

To answer this selectivity question I used nonparametric tests to look for trends and randomness in series of size and sex data from individual collections, in the order they were caught, from several locations. These analyses showed no evidence of either size or sex selectivity related to catch order. The absence of selectivity strongly suggests that exploitation is unlikely to cause rapid, significant shifts in sex ratios, specifically declines in the proportion of males, and the sperm limitation that might cause. These results also suggest that data I collected on red porgy in the northeastern Gulf are reasonably unbiased and accurately describe their demographics.

Methods

Red porgy were collected using standardized hook and line gear during Feb-Nov 2000 at seven sites in depths from 41 to 67 m off Panama City, FL. The sites were the seven deepest of nine sites sampled regularly for a study on small-scale spatial and temporal variability in life history traits and demographics of red porgy in the northeastern Gulf of Mexico (Figure 1 in Chapter 3). Standardized gear consisted of one or two size 1 Mustad j-style hooks attached to short (~5-10 cm) droppers on a 27 kg test monofilament leader with a terminal lead sinker of varying weight, depending on current and wind conditions. I used pieces of squid, and

occasionally cut fish, for bait. All fishing was done during daytime from an anchored boat by two to four anglers with varying levels of experience.

Each time a site was fished, I attempted to catch 25-30 red porgies. If it became apparent that it would take several hours to reach that goal, I would stop sampling and move to a new location. For each collection, each fish was labeled with its capture order as it was caught, i.e. the first fish caught at a site was labeled number 1, the second number 2, etc. All fish were separated by collection site, placed on ice, and returned to the laboratory for processing the next day. In the lab all fish were measured to the nearest mm total length (TL) and sexed macroscopically, after which histological samples were taken from the gonads of any identified as female or transitional. Final determination of sex was based on histological findings if available.

I used two types of nonparametric runs tests - "above and below the median" and "up and down" - to determine if size selectivity occurred in any of the collections (Sokal and Rohlf 1969, Zar 1999). The former tests whether the order of a series of observations is random, i.e., if each observation is independent of its predecessor. The latter is particularly designed for trend data, such as steadily decreasing or increasing fish sizes with catch order. To determine if the order in which sexes were captured for a given collection was random, I used a runs test for dichotomized data (Sokal and Rohlf 1969, Zar 1999). Because I did not know if transitional fish would behave more like males or females, I ran two analyses - one in which transitionals were considered males and another in which they were considered females. Coleman et al. (1996) suggested that transitional gag *Mycteroperca mircolepis* and scamp *M. phenax*, if they adopt male behaviors before completing sex change, may be as susceptible as fully transformed males to sex selectivity. *Pseudanthias squamipinnis* exhibits such a change in behavior before any visible morphological changes (Shapiro 1987). For all of the runs tests I only used collections with at least 10 fish, and 21 of the 27 tested had between 22 and 31.

Results

I found no evidence of size or sex selectivity in 27 hook and line collections of red porgy: 11 at Good Bottom, 4 each at Benny Allen, Ivy's Reef, and Sig1_2; 2 at Whoopi Grounds; and 1 at both 3 x 5's and Ridge. Five of the collections occurred in Feb, the final month of the three month spawning season, two were in Mar when many fish with spent or atretic gonads were

collected, and the remainder were made outside the spawning season; and the results were the same in all cases. Plots of fish size by capture order showed what appeared to be random variation, with no indication that larger fish were the first to be caught (Figure 1.1). With both the "above and below the median" and "up and down" runs tests, the hypothesis that the sequence of lengths was random could not be rejected at =0.05 for any of the collections (Table 1.1). Plots of fish sex by capture order offered no evidence that males were more likely to be caught before females in a given collection, i.e., that the pattern was not random (Figure 1.2). The runs tests for dichotomized data, whether transitionals were considered males or females, indicated that the hypothesis that the order in which sexes were caught was random could not be rejected at =0.05 in all but 4 instances (Table 1.2). In those 4 cases only one male was caught and the test values fell outside the limits of the table used.

These conclusions do assume that the site-specific size structure of my hook and line samples were the same as or very similar to the true size structure at each site. If in fact there were much greater proportions of small fish at these sites than suggested by my hook and line sampling, then it would be possible for behaviorally-related selectivity for larger fish to occur undetected. Size data collected in the eastern Gulf during annual NOAA Fisheries reef fish surveys using stationary cameras outfitted with parallel lasers, however, showed no evidence that the true size structure of red porgy was noticeably different from that derived from hook and line samples (Figure 1.3). In fact, the video survey results show a distribution shifted slightly to the right compared to the hook and line distribution. Thus, if anything, the hook and line distribution is biased downwards, not upwards, which means that any truncated size distributions with larger fish removed must be due to size-selective harvesting and not size-bias toward the hook. Video sampling should have minimal, if any, selectivity problems. Given that the size structure of hook and line samples appears to accurately reflect the true size distribution, it seems very unlikely that the sex ratios of the former would be significantly different from the true values, and therefore that my finding of no evidence of sex selectivity is valid.

Discussion

The overall finding of this study, that hook and line samples of red porgy showed no size or sex selectivity, i.e., that the gear is not biased by size or gender, indicates not only that it is a fair

way to sample the species, but much more importantly, that any evidence of truncation in size structure or skewing of sex ratios in exploited red porgy populations should not be attributed to greater aggression or "hook attraction" in males but can be easily explained as the results of simple size-selective harvesting, a common phenomenon not unique to protogynous fishes.

Even with size-selective fishing, the rapid, uncompensated decline in male numbers and accompanying sperm limitation hypothesized to occur in some protogynous serranids (see Introduction) is unlikely in exploited red porgy populations. Coleman et al. (1996) noted that sex ratios in a protogynous species can become more female-biased in at least two ways - selective harvest of males or overriding of the mechanisms regulating sex ratio. They predicted that fishing is unlikely to override sex ratio-regulating mechanisms which are temporally and spatially unrestricted and cited red grouper *Epinephelus morio* as an example. This species, which spawns in small polygynous groups and in which sexes co-occur year-round, has shown no marked changes in sex ratio or size structure in the eastern Gulf during the last 25 - 30 yr, despite heavy fishing. Red porgy, besides lacking behaviorally-related sex or size selectivity, and similar to red grouper, do not form large, predictable spawning aggregations, but have wide-spread spawning grounds, and are capable of changing sex much of the year (Chapter 2), traits which Coleman et al. (1996) concluded should help stabilize sex ratios.

Data from the South Atlantic Bight support the prediction of stable sex ratios in red porgy. During years of heavy fishing (late 1970's - early 1990's) in that region, there was no evidence of an increasingly female-biased sex ratio, and in fact, the proportion of males rose slightly from 15.75 to 20.42 % (Harris and McGovern 1997). During this time, there was however, evidence of size selection at the fishery level: mean weight dropped from ~1.2 to 0.7 kg in the commercial fishery (Vaughan and Prager 2002), and size at maturity of females, sizes-at-age, and theoretical mean maximum length (L_{∞}) decreased as well (Harris and McGovern 1997). This size-selective harvesting, a result of the targeting behavior of fishermen - not to be confused with selectivity resulting from fish behavior which was the focus of this study - may have skewed sex ratios temporarily by taking larger individuals more likely to be male, but this was apparently compensated for by decreases in the size at transition. This drop in size at sex change explains why virtually all of the increase in the proportion of males documented by Harris and McGovern (1997) was in the smaller size classes. Size-selective harvesting is likely in red porgy, as their size structure can vary significantly and consistently among sites separated by only 10's of

kilometers (Chapters 3 and 4), and fishermen quickly learn to exploit those locations which produce larger fish.

To date, behavior-related size or sex selectivity has been documented in only two protogynous fishes, both serranids in the genus *Mycteroperca* common in the eastern Gulf of Mexico. Gilmore and Jones (1992) reported a bias towards large males in hook-and-line collections of scamp *M. phenax*, and speculated, based on concurrent submersible observations, that it may have been related to the more aggressive behavior, greater movement, and higher positions in the water column of that sex. The authors did not, however, indicate how many, if any, females were caught, how many collections were made, or present any sex ratios. Coleman et al. (1996) cited significant declines in the proportion of males and the modal size of gag *M. microlepis* in the Gulf of Mexico over time as evidence of size and/or sex selectivity, and also cited a personal communication from Gilmore as having observed sex selective fishing on male gag. They reported a decline from 17% males (Hood and Schlieder 1992) during 1977-80 to 1.3-2.7% during 1991-93. Similarly, the proportion of male gag in catches off the U.S. Atlantic coast dropped from 19.6% during 1976 - 82 to 5.5% in 1995 (McGovern et al.1998).

The responses of protogynous species to fishing, however, are apparently quite variable (Coleman et al. 1996, Adams et al. 2000). Buxton (1993) did find significantly fewer male *Chrysoblephus cristiceps* and *C. laticeps*, both protogynous sparids, in open versus closed areas off South Africa, and attributed it to selective removal of larger size classes. He did not, however, look for evidence of behaviorally-related selectivity. In the case of *C. laticeps*, these findings are somewhat surprising, as this is a non-aggregating pair spawner that changes sex year round, traits that Coleman et al. (1996) predicted should produce stable sex ratios. In contrast, another study comparing demographics of a protogynous species (*Plectropomus leopardus* : Serranidae) in areas open and closed to fishing found that the average size/age of males was not consistently smaller nor was the sex ratio always more highly female-biased in the open areas (Adams et al. 2000).

Rapid skewing of sex ratios in protogynous fishes caused by behavior-related size or sex selectivity may be more an exception than the rule, but until more simple studies like this one are conducted on other species, the prevalence of this phenomenon will remain unknown. In the two species reported to have behavior-related size or sex selectivity, scamp and gag (Gilmore and Jones 1992, Coleman et al 1996), the evidence is primarily circumstantial and/or observational

with no controls or statistics. Although the case for gag is fairly convincing, more statistically rigorous direct testing of the hypothesis would certainly strengthen these conclusions.

Table 1.1. Results of two different runs tests for size selectivity in hook and line collections of red porgy (Sokal and Rohlf 1969, Zar 1999). $\alpha = 0.05$. ns = not significant.

		Above and Below the Median				Up and Down		
Location	Date	Runs	n_1[1]	n_2[1]	Prob	Runs	n[2]	Prob
Whoopi Grounds	7/25/2000	11	9	9	ns	13	18	ns
Whoopi Grounds	8/28/2000	6	5	5	ns	6	9	ns
3 x 5's	5/3/2000	11	15	15	ns	17	29	ns
Benny Allen	2/8/2000	12	15	15	ns	19	29	ns
Benny Allen	4/6/2000	12	13	13	ns	19	29	ns
Benny Allen	5/4/2000	11	8	8	ns	12	16	ns
Benny Allen	7/25/2000	8	11	11	ns	13	21	ns
Good Bottom	2/8/2000	19	15	15	ns	20	29	ns
Good Bottom	3/1/2000	16	15	15	ns	19	30	ns
Good Bottom	3/21/2000	11	14	15	ns	22	30	ns
Good Bottom	4/13/2000	14	15	15	ns	18	29	ns
Good Bottom	5/3/2000	16	13	13	ns	15	26	ns
Good Bottom	6/14/2000	15	15	15	ns	18	29	ns
Good Bottom	7/25/2000	11	14	14	ns	20	27	ns
Good Bottom	8/28/2000	17	12	12	ns	18	23	ns
Good Bottom	10/5/2000	14	12	12	ns	17	25	ns
Good Bottom	10/30/2000	11	11	12	ns	14	24	ns
Good Bottom	11/28/2000	15	12	12	ns	16	24	ns
Ivy's Reef	8/28/2000	12	12	12	ns	19	24	ns
Ivy's Reef	10/5/2000	8	11	12	ns	17	24	ns
Ivy's Reef	10/30/2000	12	12	12	ns	14	24	ns
Ivy's Reef	11/28/2000	9	11	12	ns	16	24	ns
Ridge	2/17/2000	14	13	13	ns	16	26	ns
Sig1_2	2/17/2000	5	5	5	ns	9	10	ns
Sig1_2	9/14/2000	17	11	12	ns	18	24	ns
Sig1_2	2/17/2000	9	6	6	ns	8	11	ns
Sig1_2	4/27/2000	6	5	5	ns	6	9	ns

[1] n_1 and n_2 are sample sizes of individuals > and < the median size. Fish which equaled the median size were excluded.
[2] n = total number of fish collected - 1.

Table 1.2. Results of runs tests for sex selectivity in hook and line collections of red porgy (Sokal and Rohlf 1969, Zar 1999). The test for dichotomized data was used to examine sex selectivity in two ways - considering all transitionals as males and all as females.. = 0.05. ns = not significant.

		Transitionals = males				Transitionals = females			
Location	Date	Runs	n_1[1]	n_2[1]	Prob	Runs	n_1[1]	n_2[1]	Prob
Whoopi Grounds	7/25/2000	10	6	13	ns	10	6	13	ns
Whoopi Grounds	8/28/2000	3	4	6	ns	3	1	9	n/a
3 x 5's	5/3/2000	13	10	20	ns	8	8	22	ns
Benny Allen	2/8/2000	14	12	18	ns	15	16	14	ns
Benny Allen	4/6/2000	16	11	19	ns	18	15	15	ns
Benny Allen	5/4/2000	9	5	12	ns	9	7	10	ns
Benny Allen	7/25/2000	12	10	12	ns	10	9	13	ns
Good Bottom	2/8/2000	12	8	22	ns	12	8	22	ns
Good Bottom	3/1/2000	20	13	18	ns	13	10	21	ns
Good Bottom	3/21/2000	17	14	17	ns	9	8	23	ns
Good Bottom	4/13/2000	15	12	18	ns	9	6	24	ns
Good Bottom	5/3/2000	12	13	14	ns	12	8	19	ns
Good Bottom	6/14/2000	15	13	17	ns	11	8	22	ns
Good Bottom	7/25/2000	15	12	16	ns	11	6	22	ns
Good Bottom	8/28/2000	11	9	15	ns	11	6	18	ns
Good Bottom	10/5/2000	10	9	17	ns	10	5	21	ns
Good Bottom	10/30/2000	11	12	13	ns	9	12	13	ns
Good Bottom	11/28/2000	7	4	21	ns	5	3	22	ns
Ivy's Reef	8/28/2000	12	8	17	ns	16	14	11	ns
Ivy's Reef	10/5/2000	9	4	21	ns	12	16	7	ns
Ivy's Reef	10/30/2000	7	5	20	ns	10	15	10	ns
Ivy's Reef	11/28/2000	9	10	15	ns	9	14	11	ns
Ridge	2/17/2000	14	11	16	ns	14	11	16	ns
Sig1_2	2/17/2000	3	1	10	n/a	3	1	10	n/a
Sig1_2	9/14/2000	11	6	17	ns	3	1	24	n/a
Sig1_2	2/17/2000	5	3	9	ns	5	2	10	ns
Sig1_2	4/27/2000	6	5	5	ns	6	3	7	ns

[1] n_1 = sample size of the sex with fewer number of individuals and n_2 = sample size of the sex with greater number of individuals.

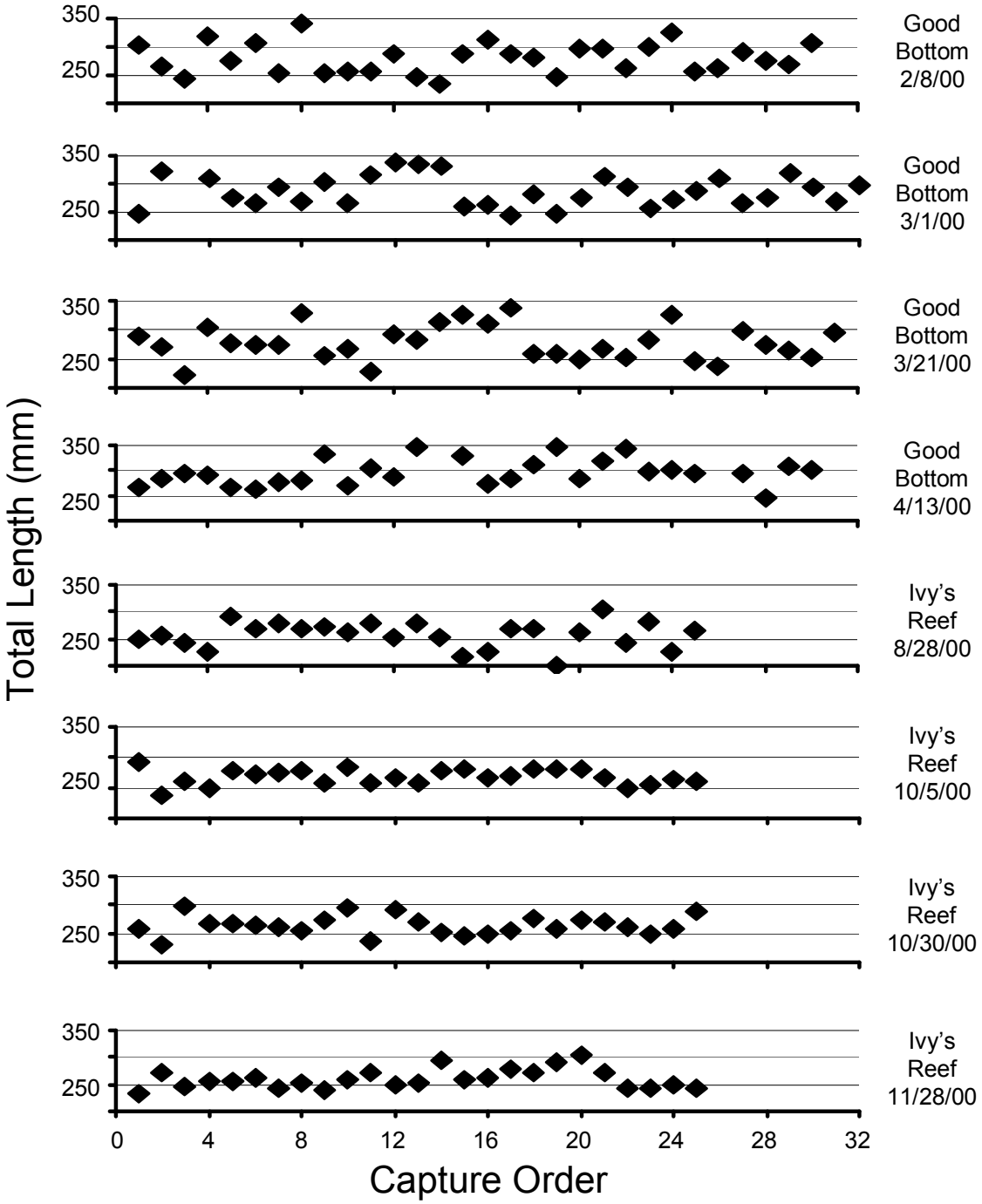

Figure 1.1. Plots of individual size (TL mm) versus capture order for selected collections from Good Bottom and Ivy's Reef

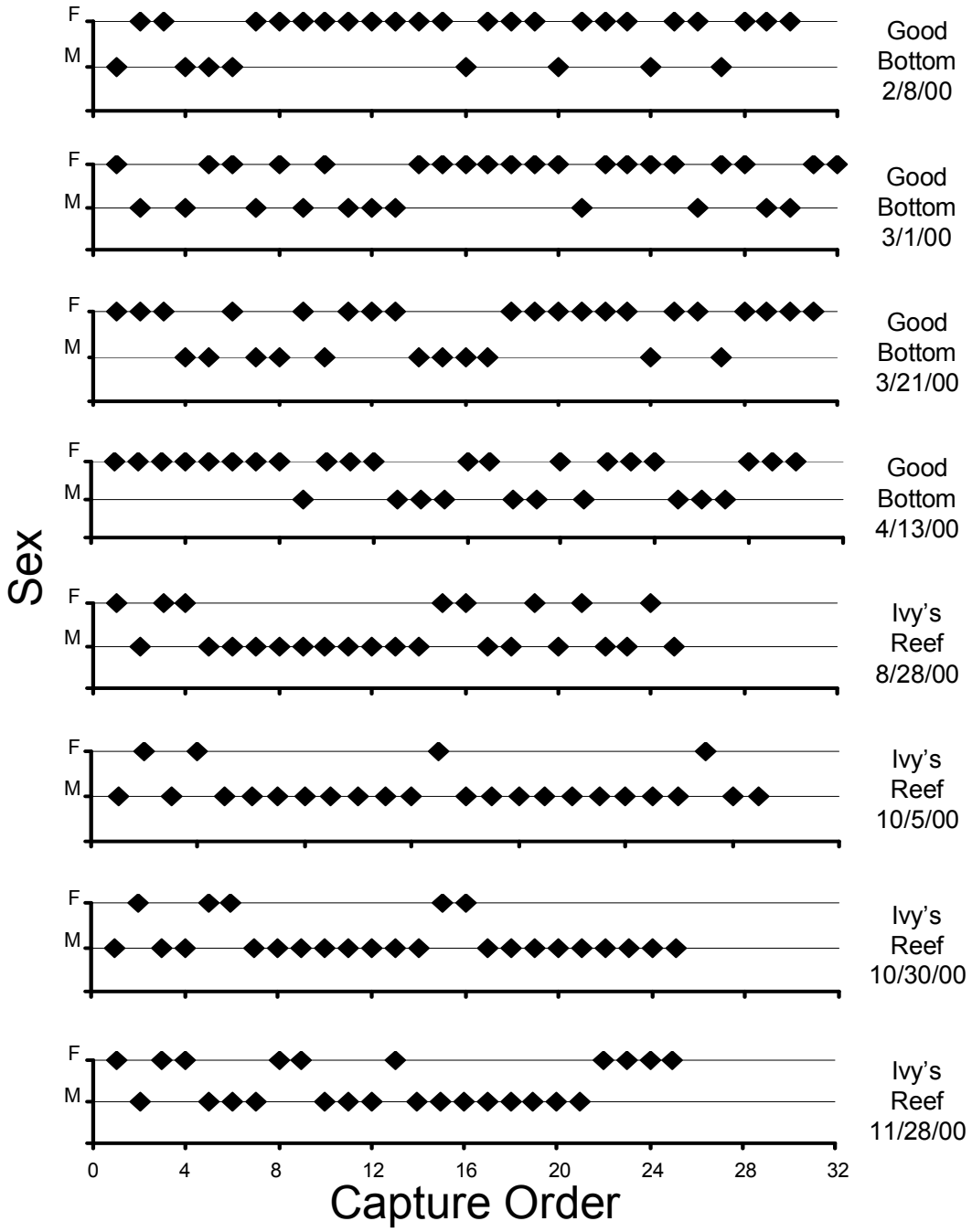

Figure 1.2. Plots of individual sex versus capture order for selected collections from Good Bottom and Ivy's Reef. Transitionals were considered males.

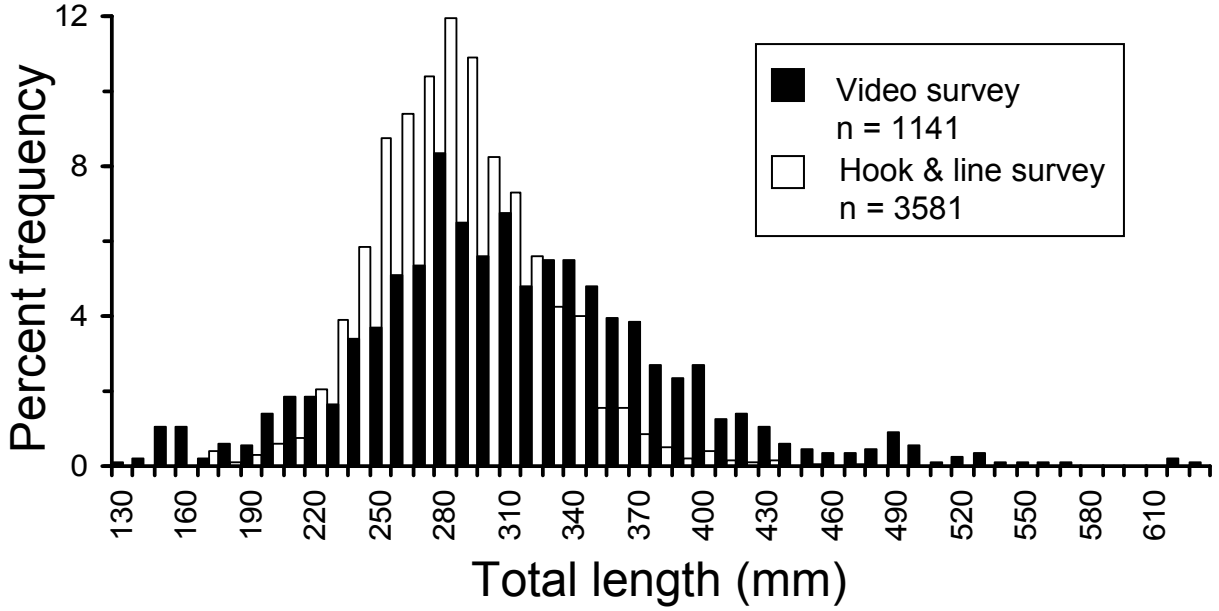

Figure 1.3. Overall length frequency distributions of red porgy from NMFS stationary video surveys since 1996 and from all hook and line collections in this study.

CHAPTER 2

ASPECTS OF REPRODUCTION IN RED PORGY IN THE NORTHEASTERN GULF OF MEXICO

Introduction

In recent years scientists have increasingly warned that protogynous fishes may be more sensitive than gonochorists to the effects of fishing, especially if size-selective fishing on the larger, mostly male individuals results in sperm limitation and/or social disruption of mating (Smith 1982, Shapiro 1984 cited in Bannerot et al. 1987, Bannerot et al. 1987, Shapiro 1987, Buxton 1993, Shepard and Idoine 1993, Huntsman and Schaaf 1994, Coleman et al.1996, Adams et al. 2000, Armsworth 2001, Alonzo and Mangel 2004). However, simulation modeling predicted that stable sex ratios reduce the impact of fishing on a protogynous species and those able to compensate for loss of males were no more sensitive to fishing than gonochorists (Huntsman and Schaaf 1994); and in the absence of sperm limitation, protogynous species would be reproductively superior to gonochorists (Bannerot et al. 1987). The likelihood of harvest-induced sperm limitation depends on such factors as whether the species aggregates to spawn at predictable locations and times (Coleman et al. 1996), as well as the timing and proximal mechanism of sex change, the degree of sex selectivity in the fishery, and the ability of males to fertilize more females than typical (Petersen and Warner 2002).

There are many protogynous species in the widespread, economically valuable family Sparidae, (Buxton and Garratt 1990), including the red porgy, *Pagrus pagrus.* Overexploitation was blamed for a steep decline in red porgy numbers (89% drop in spawning stock biomass and a two orders of magnitude drop in recruitment to age 1) in the south Atlantic Bight (SAB) off the southeastern U.S. during the 1980's and 1990's (Vaughan et al. 1992; Vaughan and Prager 2002). The situation was so severe that in 1999 all fishing was halted for one year. This same overexploitation is also thought to have caused significant reductions in size-at-age and growth, and in size-at-maturity and at transition, which of course resulted in much higher proportions of males at smaller sizes, and truncation of the size structure (Harris and McGovern 1997).

In contrast, red porgy in the NE Gulf of Mexico (Gulf), despite being very abundant, have

been only lightly exploited, and their numbers have shown no evidence of a steep decline. Commercial and estimated recreational landings from Florida Gulf waters during 1998-2002 ranged from 23.2 to 38.2 and 19.7 to 28.9 mt, respectively (79-100 and 83-96 % of the total Gulf take) (National Marine Fisheries Service, Fisheries Statistics and Economics Division, personal communication, 2003). In contrast, estimated recreational landings of the more heavily exploited gag *Mycteroperca microlepis*, red grouper *Epinephelus morio*, and red snapper *Lutjanus campechanus* from the same area and years were all, except for red grouper in 1998, two orders of magnitude higher (National Marine Fisheries Service, Fisheries Statistics and Economics Division, personal communication, 2003).

Besides occurring in the SAB and Gulf of Mexico, this warm temperate to subtropical species is found in the NE Atlantic from the British Isles to Angola (including the various oceanic islands off W. Africa and the Adriatic and Mediterranean Seas) and in the SW Atlantic from Venezuela to Argentina (Manooch and Hassler 1978, Bauchot and Hureau 1990). Adults are typically associated with low-profile hard (live) bottom, rocky, or gravel habitats (Manooch and Hassler 1978, Grimes et al. 1982). Red porgy is one of the most abundant, exploited reef fishes in the NE Gulf, where the population appears to be centered. One of the most frequently observed species in an annual video survey of reef fish in that area (C. Gledhill, NMFS Pascagoula Lab., personal communication, 2000.), it is also one of the most commonly caught species in the Florida Middle Grounds, the northernmost coral reef on the West Florida shelf (Manooch and Hassler 1978). In the headboat fishery, an estimated 150,500 red porgies were landed in NW Florida in 1995, compared to ~ 7500 in west and SW Florida, and virtually none west of Alabama (R. Dixon, NOAA Fisheries, Beaufort, NC, personal communication, 2000).

Until recently, little was known about the biology or fisheries for red porgy in the Gulf of Mexico. The only life history data from the NE Gulf came from a recent one year study (Hood and Johnson 2000), however, because of its short duration and heavy reliance on fishery dependent sampling (68% from headboats fishing the Florida Middle Grounds), their findings should be considered limited and preliminary. The only other life history data from the Gulf came from a very limited study (n=161 fish) off east Texas (Nelson 1988). All other information on red porgy is based on studies conducted in the U.S. South Atlantic Bight (Manooch 1976, Manooch 1977, Manooch and Huntsman 1977, Grimes et al. 1982, Collins and Sedberry 1991, Vaughan et al. 1992, Collins et al. 1996, Harris and McGovern 1997; the eastern Atlantic

(Alekseev 1982, Alekseev 1983, Serafim and Krug 1995, Pajuelo and Lorenzo 1996); the Mediterranean Sea (Vassilopoulou and Papaconstantinou 1992, Labropoulou et al. 1999, Kokokiris et al. 1999); and the southern Atlantic (Ciechomski and Weiss 1973, Ciechomski and Cassia 1974, Cotrina 1986, Cotrina and Christiansen 1994, Cotrina and Raimondo 1997).

My primary objective was to collect information on the reproduction and reproductive ecology of red porgy in the NE Gulf - information, nonexistent until recently, that is essential for effectively managing this important resource and hopefully preventing the kind of disastrous population crash that appears to have occurred in the SAB. Fishery managers need to know such things as the time required for sex change and the size range over which it occurs, and information on spawning behavior (Bannerot et al. 1987). Little is known about the reproductive ecology of larger reef fishes compared to the much more easily studied small species, and trying to generalize findings from those small species to the larger, exploited ones can cause problems for managers (Petersen and Warner 2002). Red porgy will likely be one of the next reef species targeted commercially in the Gulf, given that 1) most of the common, more valuable reef fishes are already fully- or overexploited, and 2) fishermen usually switch to more abundant, less valuable, less managed species in the face of decreased abundance and increasingly restrictive management of more valuable species. A secondary objective was to gain insight on how fishing might affect protogynous species, and in particular, why red porgy in the SAB seemed so sensitive to exploitation and whether protogyny played any role in that sensitivity.

I present evidence that red porgy in the NE Gulf: 1) spawn primarily during December-February with a peak in January, 2) spawn wherever and at whatever depths they are found, 3) mature at ~210-215 mm TL and by age 2 (females), 4) change sex almost exclusively during months outside the spawning season over a wide range of sizes and ages, 5) are sexually dichromatic, 6) spawn primarily during morning hours, 7) are pair spawners, and 8) do not aggregate to spawn.

Methods

Field Study

Red porgy were collected in the northeastern Gulf of Mexico between 83.66 and 88.34°W and

25.85 and 30.24°N, although 83% were collected southwest of Panama City, Florida between 84.75 and 86.50°W and 29.26 and 30.25°N (Figure 2.1). Most were collected using standardized hook and line gear (one or two size 1 Mustad j-style hooks) baited with squid, but some were also collected with fish traps. Fish were collected in depths from 22 to 92 m; most (91%) hook and line samples were taken between 30 and 68 m, while trap collections ranged from 52 to 92 m (Figure A.1). About 71% (n=2586) of the red porgy were collected at nine study sites, hereafter referred to as standard sites (Figure 3.1 and Table 3.1). Fish were collected all months of the year (Figure A.1), Mar 1998 - Sep 2001 (plus one collection in 1994 and a few in 1997). Most hook and line sampling was done from outboard boats during daylight hours, usually while anchored, by two to four anglers with varying levels of experience. Various types of fish traps were used, although the most common was a chevron trap (Collins 1990).

On all trips using outboard boats, I would attempt to catch 25-30 red porgies at each site each time it was fished, but would move to a new site if it was obvious that goal would not be met that day in a reasonable amount of time. At each site, I would record beginning and ending time of fishing (to calculate catch/effort), depth range fished, and bottom temperature (estimated from core temperature of a freshly caught fish). Fish were placed on ice and processed in the laboratory the next day. Processing included measuring to the nearest mm (total (TL), fork, and standard length), weighing to the nearest gram, and sexing and staging macroscopically. Sagittae were stored dry after being washed in tap water. Gonads were weighed to the nearest 0.1 gm and then preserved in 10% histological grade buffered formalin. Beginning in Jan 2000, after noticing two subtle color patterns on the premaxilla and snout (pink, green, or intermediate), the color of the premaxilla was also recorded. On multiple day cruises specimens were processed onboard within 12 hr of capture, but fish were weighed to the nearest 10 instead of 1 gm and gonads, preserved in formalin, were not weighed until returned to the lab. Preserved gonad weights were converted to fresh weights using: fresh weight = 0.0087 + 0.9618 * preserved weight ($r^2 = 0.994$, n = 2140).

Females and immature fish were staged macroscopically using a modification of Kesteven's system (Table 2.1) (Bagenal and Braum 1971). Fish were classified as transitional if a band of whitish, testicular tissue was visible along the ventral side of each lobe of the ovary, beginning at the posterior end. Although macro stages were assigned to males (immature/resting, early developing, developing, late developing, and spent), because of the difficulty in accurately

distinguishing these stages, the data were not used.

The ovaries of all macroscopically identified females and transitionals were also sexed and staged histologically. Transverse sections were taken ~1/3 the distance from the posterior end of the ovary and stained with hematoxylin and eosin . Ovaries < ~1 gm were processed whole, so the final section was not necessarily transverse. Stages were assigned using criteria derived from Wallace and Selman (1981), Brown-Peterson et al.(1988), and Harris and McGovern (1997) (Table 2.1). Transitionals were identified using the criteria of Sadovy and Shapiro (1987) and Harris and McGovern (1997); i.e., 1) spermatocytes, spermatozoa, or spermatids present along outer wall of ovary, 2) ovary almost always resting or spent, 3) at least some atresia (usually α or β) present, and 4) postovulatory follicles (POF's) rarely present. Final determination of sex and maturity stage was based on histological findings if available.

I determined the age of the majority of fish using whole otoliths following the MARMAP program methods (Harris and McGovern 1997). To improve the accuracy and precision of the ageing, I aged one set of 500 fish twice before actually assigning the ages used in these analyses. Both sagittae were placed in a black-bottomed watch glass containing water and examined with a dissecting microscope at 6-25x under reflected light provided by two fiber optic lights. Annuli appeared as white opaque bands of varying density (Figure A.8). Otoliths were examined without knowledge of size, sex, location, or date of collection. Older fish have larger, thicker, opaque sagittae for which the MARMAP method was not effective. I re-examined these otoliths with a break and burn technique (Christensen 1964). The left sagitta, if available, was scored through the core along the dorsal-ventral axis with a diamond pencil, then broken or cut with a low-speed saw. The broken or sawn edge of both halves was then held over an alcohol flame until it turned uniformly light brown. Both halves were then embedded with the cut or broken edge up in a small piece of black plasticine, the edges were coated with vegetable oil, and then examined with a dissecting microscope under reflected light at 6-25x. In some cases, readability was improved by polishing the broken edge using 400 and 600 grit wet-dry sandpaper.

The number of visible annuli and an estimate of marginal increment size relative to the previous annual increment (none, <1/3 as large, 1/3-2/3, >2/3) were recorded. Ages, to the nearest whole year, were assigned solely on the basis of number of visible annuli for fish collected 16 Jul - 31 Dec. Fish collected 1 Jan - 15 Jul had one year added to their age if the marginal increment was estimated to be ~1/3 the width of the previous increment. This

adjustment was necessary to assign individuals to the correct year class, as annuli typically form sometime during the spring to early summer (Hood and Johnson 2000) but are often difficult to distinguish until there has been at least some growth beyond the newest annulus.

Spawning season was identified by examining temporal patterns in the gonadosomatic index (GSI), maturity stages of females, occurrence of POF's (ephemeral structures indicative of recent spawning), and egg production in spontaneously spawning captive fish. GSI was calculated as (gonad weight/total weight) x 100. Spawning grounds were identified by examining spatial patterns of early or late final oocyte maturation (FOM) stage females and females having POF's.

To determine size and age at maturity of females, I examined the proportions of 1) mature females (vitellogenic through spent or stages 3-6) during the primary spawning months Dec-Feb (to eliminate the difficulty of distinguishing immature from resting fish during non-spawning months), and 2) females with POF's during Dec-Feb. I assumed all females above some minimum size would be vitellogenic and have POF's during Dec-Feb, and that the spawning season did not vary with size or age. I also estimated size at maturity by examining the lower limb of the size distributions of vitellogenic, early FOM, and late FOM (stages 3-5) females. Size at 50% maturity was estimated using LOESS regression after initially trying logistic regression. Perhaps because there were very few small, immature fish, and the size at maturity relationship was almost knife-edged, the predicted logistic curve fit the observed data poorly, suggesting a much more gradual increase in the proportion mature with size than indicated by the plotted data.

Based on my finding that very little sex change occurs during the main spawning season, only Mar-Nov data were used to examine relationships between transition rates and size and age.

After noticing two apparent color patterns on the premaxilla and snout of red porgy, I began examining the relationship between those patterns and the sex of the individual to determine if the species was sexually dimorphic. I also examined the seasonality of these color patterns to determine if they were a permanent trait or only present during the spawning season.

To determine if red porgy aggregate to spawn, I examined seasonal patterns in catch rates and sex ratios at the standard sites. I hypothesized that if red porgy did aggregate to spawn at a site, catch rates might increase there during the spawning season (or at least change from what they were outside the spawning season), and that the sex ratio at an aggregation site would change noticeably between the non-spawning and spawning seasons. Site-specific catch per unit effort

(CPUE) in fish per angler minute was calculated for each sampling date by dividing the total number of red porgy caught that day by the product of the number of anglers and the total number of minutes the site was fished. Besides examining seasonal patterns of CPUE within sites, I also used ANOVA to compare pooled mean standardized CPUE among quarters, with one of the quarters being Dec-Feb (the spawning season). All CPUE's from a site were standardized by dividing each one by the largest CPUE from that site, e.g., the sample with the highest CPUE for a given location would have a standardized CPUE of 1. This was done because average CPUE's varied considerably among sites.

Lab Study

Information on spawning behavior, as well as diel periodicity and seasonality of spawning, was obtained by observing fish held in captivity at the National Marine Fisheries Service laboratory in Panama City, Florida. The fish used for these observations were captured by hook and line off Panama City in depths from 30 to 62 m and brought to the lab within a few hours of capture. Fish with an over-pressurized swim bladder were immediately degassed at sea using a large gauge hypodermic needle. Fish were collected during late fall through spring when temperature differences between surface and bottom were minimal. Short-term survival rates usually exceeded 90% during that time of year compared to about 10% or less during summer or early fall. The mean fork length and 95% CI of female red porgies stocked in the tanks was 238±5 mm (range: 174-300 mm); the mean for males was 263±7 mm (range: 210-316 mm).

Fish were held in 4.6 m diameter, ~16,000 l circular fiberglass tanks ~0.9 m deep, or in 2.25 m diameter, ~3,000 l circular polyethylene tanks 0.9 m deep. The large tanks had individual recirculating biological filtration systems, while each pair of the four smaller tanks shared a biological filter. The tanks were housed in a tent-like building covered with a heavy duty, translucent, vinyl-coated fabric so that fish were exposed to natural photoperiods and light levels similar to what they would typically encounter at the depths from which they were collected. Water for the tanks was obtained from St. Andrew Bay and salinities were maintained between about 30 and 37 ppt. A freshwater heat exchange system in the filter system kept water temperatures from dropping below 14°C during winter months or exceeding 26°C during summer. On occasion, as evaporation raised salinities to >36 ppt, and to prevent excess buildup of nitrogenous waste products, about 1/3 to ½ of the water in a tank was drained and replaced

with new water from the bay. Fish were fed to satiation every other day with dead squid.

Newly-caught fish were placed in fresh water (0 ppt) for 1 min before being introduced to a tank for the first time to kill external parasites and disease organisms. When stocking an empty large tank, I would try to place 10-16 individuals in it in a ratio of between 2:1 and 3:1 females:males, the range I observed most often in my hook and line collections off Panama City. I determined sex using color of the premaxilla (see Results section on sexual dimorphism). Although not foolproof, this method was very accurate on dead fish; it was slightly more difficult to distinguish color differences with live fish, and of course there was no way to confirm these classifications without sacrificing the individuals. There was no way to confidently identify transitional individuals at the time of stocking. Total numbers and sex ratios fluctuated slightly as new fish were added to replace ones that had died or to simply augment the number already in the tanks.

During the 2000-2001 spawning season I stocked each small tank with a single pair in an attempt to obtain estimates of batch fecundity and spawning frequency. Because none of those pairs spawned that first year, the next spawning season I stocked 6 to 8 fish in each in ratios ranging from 4:1 to 1:1 females:males, depending on availability of each sex.

Spawning diel periodicity and seasonality were determined by monitoring fine mesh egg collectors placed in the outflow between the tanks and the filters for presence and development stage of fertilized eggs. During the 2000-2001 and 2001-2002 spawning seasons I attempted to check egg collectors in the morning, at midday, and late afternoon 3-5 days each week and at least once during the late afternoon most other days. All tanks were monitored for 2-3 wk past the last date eggs were found in any of the tanks. During the 2000-2001 spawning season, if eggs were present in the collector, the volume was estimated as trace (1-2 ml), few (3-5 ml), some (6-20 ml), or many (>20 ml). The next season volume was measured using a graduated cylinder. When eggs were found, a sample was staged microscopically and the predominant stage(s) was noted. Stages and estimated age in hours of each followed those of Hussain et al. (1981) for another winter-spawning sparid: *Acanthopagrus cuvieri*. They incubated eggs at 21°C, close to the upper limit of my tanks during the spawning season.

To determine spawning behavior, I observed fish activity in one of the large tanks for 1.5 - 4 hr on three occasions in 2001 (31 Jan - 15 Feb) and seven times in 2002 (31 Jan - 21 Feb). Observations began between 0415 and 0555 and ended between 0715 and 0850 CST except one

time in 2002 when fish were observed from 1450 to 1620 CST. Egg collection and egg development data suggested that spawning activity was greatest during these early morning hours. Observations were made from a position 4-5 m above the tank. By illuminating each tank with a single 60 watt red incandescent bulb installed ~5 m above the tank, I was able to use a pair of night vision binoculars to observe fish before daylight. During some of the 2002 observations, I used a hand-held video camera to document fish behavior, with the hope of recording an actual spawning event.

Results

Spawning Season

Red porgy in the northeastern Gulf spawn primarily during the winter months of December - February. GSI's for both sexes peaked in January during the winters of 1998-99 and 1999-2000 and in December the following winter (Figure 2.2). GSI's began rising in November and by April had fallen close to non-spawning season levels. Histological data from females confirmed the GSI results. Early and late final oocyte maturation (FOM) stages (stages 4 and 5) were present November - March (trace in April), with peak occurrence in January, and to a slightly lesser extent, in February (Figure 2.3). Resting and immature females dominated during April-October, and composed at least 91 % each month May-September. The temporal distribution of fish with post ovulatory follicles (POF's), evidence of recent spawning, further confirmed the timing of spawning. POF's were found November - March (trace in April), but were abundant only November-February with a peak in January (Figure A.2).

The seasonality of atresia rates also supported a Dec-Feb spawning season. The median proportion of females with high rates of atresia (>50 % vitellogenic oocytes atretic) clearly peaked at 10.4 and 5.9 % during March and April, the two months following the spawning season (Figure A.3). No highly atretic females were collected May-Nov, except one in October in a collection of only two fish. During the spawning season, although as many as 47 % of the females in an individual collection were highly atretic (Feb), median rates were very low, 0-2.4 %.

Mean bottom temperatures at the standard stations during the spawning months were

23.1±1.8°C (95% CL) in Nov, 21.1±1.9°C in Dec, 18.4±1.1°C in Jan, 18.5±0.7°C in Feb, and 19.0±0.9°C in Mar.

Seasonality of spawning by captive fish was consistent with field results. The first season captive fish were monitored (winter 2000-2001), egg collectors were not installed until Jan 4 and eggs were first collected Jan 8 in two of the tanks; in the third tank, stocked Jan 7, eggs were first collected Jan 14. Spawning continued almost daily in all three tanks until Feb 23-27. The following winter (2001-2002) fish spawned consistently in only one of the large tanks. Initially stocked Nov 7, the egg collector was installed Dec 4 and eggs were first collected Dec 6. The fish in this tank spawned almost daily until Feb 21. Spawning occurred in two of the smaller tanks for the first time that same season, beginning on Dec 23 and 28. Spawning in the former ceased on Jan 23 after one male died and a second jumped out of the tank, although it survived the incident. In the tank where spawning began on Dec 28, it continued intermittently until Feb 13. During the winter of 2002-2003, in the only large tank monitored, eggs were collected Dec 2 - Mar 4. Monitoring for eggs on a second large tank was dropped in late Dec after no eggs were found for several weeks after eggs were found in the other tank. During winter 00-01, water temperature in the large tanks during the period when spawning occurred averaged 18±0.5°C (95% CL) and ranged from about 16 to 21°C. The following spawning season (01-02) they again averaged 18±0.8°C.

Spawning Grounds

Evidence suggests that red porgy in the northeastern Gulf spawn wherever mature fish occur. During Dec-Feb, early and late FOM stage fish were found at all the standard sites except Whoopi Grounds, but only two fish were collected at that site those months (Figure 2.4a). There was no obvious relationship between the percent of early and late FOM stage fish and the depth of the site. Females with POF's were also found at all standard sites except Whoopi Grounds during Dec – Feb, consistent with the maturity stage findings. POF's were present in 84 to 97 % of females at John's 248, Elbo Reef, 3 x 5's, Good Bottom, Ridge, and Benny Allen, while at Sig1_2 and Ivy's Reef, 31 and 67 % had POF's (Figure 2.4b). The occurrence of early and late FOM stage fish and fish with POF's in every depth interval from 20-26 m to 65-78 m confirmed the occurrence of widespread spawning. Among females collected Dec - Feb in depth intervals from 20-26 m to 65-78 m, 31.7-62.5 % were early FOM stage, 8.6-23.0% were late FOM stage,

and 51.9-94.7% had POF's present (Figure A.4).

Size and Age at Maturity

Defining maturity as the presence of vitellogenic (≥stage 3) oocytes or POF's, LOESS regression models predicted that 50% of female red porgy in the Gulf mature at 211 or 216 mm, respectively. LOESS regressions fit the steep, almost knife-edge maturity functions much more closely and with much narrower confidence limits than logistic regressions (Figure 2.5). The smallest vitellogenic, early FOM, and late FOM (stages 3-5) females collected were 194, 203, and 217 mm TL, respectively. The smallest female with POF's was 197 mm.

Virtually all female red porgy in the northeastern Gulf apparently mature by age 2. Of all females ages 2-6 collected during Dec-Feb, 93-98 % had vitellogenic or more advanced oocytes, and POF's were present in 83-90 % (Figure 2.6). Histological samples were collected from only 3 age 0 and 3 age 1 females during the spawning season, and none of those were mature, but sample sizes were too small to estimate with any confidence what proportions, if any, mature at those ages. One mature age one fish with vitellogenic oocytes and POF's was collected in early March. Given the virtual knife-edge age at maturity function between ages one and two, I did not attempt to fit either a LOESS or logistic regression model to that data.

Sex Change

Sex change, or transition, occurred wherever adult red porgy were found and almost exclusively during months outside the spawning season (Mar-Nov). Transitionals were collected across the entire depth range sampled ~22 to 92 m. The median number of females in transition from collections with ≥ 6 fish ranged between 20 and 33 % Mar-Sep, then dropped to 14 % in Oct and 7 % in Nov; during the main spawning months (Dec-Feb) the median was 0 % (Figure 2.7). There was some suggestion of an increasing trend during the Mar - Sep period, but the data and sample sizes were quite variable.

Sex change occurred across a wide range of sizes and ages. Transitional fish ranged from 206 to 417 mm, with no obvious mode, while the smallest male I found was 222 mm (Figure 2.8). The rate of transition increased with size up to at least 320 mm (Mar-Nov data only), after which it appeared to reach an asymptote around 30-35 %, although interpreting the pattern at the largest sizes was problematic because of small sample sizes (Figure 2.9a). Transitionals ranged from

age 2 to 9, with a mode of age 4 for all hook and line caught fish (Figure 2.8). The youngest male I collected was also age 2. Not surprisingly, transition rates, Mar-Nov only, also increased with age, reaching an asymptote of about 30-35 % at age 4 (Figure 2.9b).

Sexual Dichromatism

Red porgies were found to be sexually dichromatic, differing in the color of the premaxilla (upper lip), and to a lesser extent, the snout and forehead. The premaxilla of males is green or bluish-green, while that of females is pink or reddish (Figure 2.10). Both sexes have an area of blue between and anterior to the eyes and along the sides of the snout, but the color tends to be more intense in males. In males, the areas both below and above the blue region between the eyes (the snout and forehead) are usually similar in color to the premaxilla, i.e., green or bluish-green. In females these areas are typically reddish, bluish-red, or greenish-red. The males also sometimes have a greenish tint along their backs beneath the first dorsal fin and above the lateral line, while females are uniformly pink or reddish; however, this difference is much more subtle than the others and often is not apparent at all. These color differences were most apparent in dead specimens that had been on ice for a few hours and in live specimens kept in shallow tanks. They were least discernible in freshly caught, still living fish.

The color differences were accurate predictors of a fish's sex and appeared to be permanent traits. They were observed in all months, not just during the spawning season, although the differences did seem more distinct then. Of the 609 red porgies identified as having a green premaxilla, 93.9% were males, 5.1 % were transitional, and only 1.0 % were females. Of the 1530 with a pink or red premaxilla, 81.7 % were females, 16.4 % were transitional, and only 1.9 % were males. The premaxilla of 82 fish was intermediate between pink and green, and of these, 61 % were males, 17.1 % were females, and 22.0 % were transitional. During Oct-Mar 94.3-100 % (mean = 97.4 %) of the fish identified as males had a green premaxilla (Figure A.5). May had the fewest males with a green premaxilla (59.2 %) and the highest percentage, by far, of fish with intermediate colors (28.6 %). The percentage of fish with an intermediate-colored premaxilla had an obvious mode Apr-Nov and none were found in Sep or Nov-Jan. In October, December, and January no fish positively identified as a male had a pink or red premaxilla, compared to 1.2-12.2 % during the other months.

Spawning Aggregations

I found no evidence that red porgy form large, predictable spawning aggregations typical of some larger serranids. Although monthly CPUE varied considerably for eight of the nine standard sites, there was no obvious pattern of decreased or increased catch rates during the Dec-Feb spawning season (Figure 2.11). ANOVA showed no differences in standardized CPUE among quarters, i.e., Dec-Feb (the spawning season), Mar-May, Jun-Aug, and Sep-Nov ($F=0.49$, $p=0.6901$) (Figure A.6).

The seasonal pattern of sex ratios within sites was also consistent with the hypothesis that red porgies do not aggregate to spawn. Plots of % males by collection by month for Good Bottom, Ivy's Reef, and Benny Allen (Figure A.7) showed no obvious seasonal patterns, only random variation. In logistic regressions of % males on month for these three sites, month was not significant (Wald χ^2, $p=0.9850$, 0.6250, and 0.9443, respectively).

The widespread occurrence of females with early and late FOM stage oocytes and POF's, mentioned previously, is consistent with the hypothesis that this species does not move from its home reef to form large, regional spawning aggregations. It does not, however, preclude the possibility of small localized aggregations on the home reefs.

Spawning Behavior

Analysis of the time of day eggs were collected from captive red porgies suggested that spawning peaked during early morning and little or none occurred during the night. In those instances where a tank was checked at least twice and usually three times throughout the day - morning (0600-1059 hr), mid-day (1100-1559), and evening (1600-1830)- eggs were found in 67.3 % (n=113) of morning, 59.0 % (n=105) of mid-day, and only 31.9 % (n=119) of evening collections. The eight times egg collectors were checked during 1800-1830 (4 different dates) no eggs were found; on one of these dates three of the tanks were checked again at 2200, and again no eggs were present. In all eight of these instances the tanks had been checked at mid-day and eggs were present in 7 of the 8. Eggs were found only 2 of the 19 times tanks were checked between 0400 and 0559 (on 7 different dates), at 0515 and 0550. In all of these 19 cases, fish had been regularly spawning in the tank for several days beforehand and the collecting nets had been checked and emptied the previous afternoon or evening. Not only was the frequency of occurrence of eggs lowest in the evening, but when they were present, the volume was also

usually much smaller. Only 3 of 38 (8 %) evening egg collections exceeded 20 ml, compared to 9 of 60 (15 %) at mid-day and 13 of 76 (17 %) from the morning. Similarly, 18 % of evening collections contained 6-20 ml of eggs compared to 33 % at mid-day and 29 % in the morning.

The temporal distribution of egg development stages was consistent with a morning spawning peak. The modal development stage of eggs indicated they were within one hour of hatching, i.e., they were undivided or at the 2 cell stage, in 38.6 % (27 of 70) of those collections with live eggs from before 1000 CST, in 20.6 % (13 of 63) of collections from 1000 to 1559, and only 14.8 % (4 of 27) of collections from after 1559. The modal age of eggs was within 2 hr of hatching, i.e. ≤16 cell stage, in 58.6 % of collections from before 1000, in 49.2 % of collections from 1000 to 1559, and in 44.4 % of collections from after 1559.

Probable pair spawning of red porgies was observed on 5 of the 9 days observations were made during early morning hours (a total of 7 instances). No presumed spawning was observed the one day observations were made during the afternoon. The seven presumed spawning events were all quite similar and lasted only a few seconds. In each case presumed spawning began with a single larger, darker fish (presumably a male) leisurely following, usually no more than one body length behind and often slightly below, a single, smaller, much lighter colored fish (presumably a female) for a few seconds at a time. The female would then suddenly accelerate, swimming very rapidly in a straight line near the surface and usually on her side. Simultaneously the male would increase speed to keep up with the female; and in every instance, 1-3 other larger, dark, presumed males would immediately join in chasing the female. Although I never saw the actual release of eggs or sperm, this sequence of events, observed several times, was certainly consistent with the hypothesis that it was spawning, and I always found very early stage eggs within 1-2 hr of observing this behavior. The leisurely following behavior did not always indicate that spawning was imminent; in fact, much more frequently the male would quickly appear to lose interest and veer off in a different direction.

Another frequently observed behavior was aggression by one of the presumed males towards all other males in the tank. The aggressive male, besides following females more often, seemed to consider the center of the tank, where there were several concrete blocks stacked on one another, as its territory, and frequently and aggressively chased off other approaching large, dark fish (presumed males). This behavior was easily distinguished from the leisurely, non-aggressive following of females, always involved only the presumed males, and seemed to only

be initiated by the one dominant fish. The frequency of both the following and aggressive behaviors seemed to peak during the first 1-2 hr of daylight, and then dropped off quickly.

Discussion

Spawning Season

Hood and Johnson's (2000) Jan-Apr spawning season in the NE Gulf was slightly later and longer than the Dec-Feb season I found, but we both found peak GSI's in January and highest numbers of fish with POF's during Dec-Feb. Nelson's (1988) reported Dec-Apr spawning season in the western Gulf was also a little longer. The shift in peak GSI for females from Jan in 2000 to Dec the following winter indicates that the spawning season can vary, probably in response to temperature variation. Mean bottom temperatures during late Nov 99 - Jan 00 were 3-4°C warmer than during late Nov 00 - Jan 01: 24.1±1.9 vs. 20.2±1.0°C in late Nov-Dec and 20.3±1.9 vs. 17.2±0.9°C in Jan. Although GSI's were somewhat elevated in March, the abundance of females with high rates of atresia and the scarcity of those with hydrated oocytes or POF's argues that most spawning was finished by then. The cessation of spawning by captive fish the last week of Feb - first week of Mar during 2001 - 2003 supports this conclusion.

The spawning season in the SAB is quite similar to that in the NE Gulf. The occurrence of late developing and hydrated oocytes peaked Jan - Feb, with high numbers in Dec as well (Roumillat and Waltz 1993). Manooch (1976) reported spawning Jan-Apr, with a Mar -Apr peak, but he found peak GSI's in Jan and highest proportions of ripe fish Jan-Mar and spawned (spent?) fish in Apr, all suggesting peak spawning occurred Jan-Mar. Red porgy in the eastern Atlantic spawn slightly later: Dec-May, peaking Feb-Mar, in the Canary Islands (Pajuelo and Lorenzo 1996), and Jan-Apr (peak GSI in Feb) off Spain (Cárdenas and Calvo 2003). In the eastern Mediterranean, spawning occurred spring to early summer, peaking Mar-Apr, (Vassilopoulou and Papaconstantinou1992); captive fish from that area spawned spontaneously from Feb or March to late Apr to early June (Stephanou et al. 1995; Kolios et al. 1997; Kokokiris et al. 1999, 2001; Mihelakakis et al. 2001.

Surprisingly, red porgy spawn Nov – Jan or Feb in the south Atlantic as well (Ciechomski and Weiss 1973, Costa et al. 1997, Cotrina and Christiansen 1994), meaning they are summer

spawners in the southern hemisphere but winter to early spring spawners in the north (Hood and Johnson 2000). GSI differences suggest that large fish finished spawning earlier than small ones in that region (Cotrina and Christiansen 1994). Water temperatures were 20-21°C off Argentina during Dec-Jan, well within the range I found during the spawning season in the NE Gulf (Ciechomski and Weiss 1973). Perhaps spawning is more tied to temperature than photoperiod, although Manooch (1976) concluded the opposite after comparing seasonal patterns in those two parameters versus GSI.

I found no evidence in red porgy of high rates of atresia during the spawning season, a phenomenon reported in white sucker (*Catostomus commersoni*) (Trippel and Harvey 1990) and gag (Coleman et al. 1996) which these authors hypothesized reflected reproductive failure in females caused by a shortage of males. The pattern I found in red porgy - low rates of atresia during the spawning season and high only during the two months immediately following it - supports the conclusion that sperm limitation is not a problem in this species, at least in the NE Gulf.

Spawning Grounds

My findings that mature red porgy seem to spawn wherever they occur, with no relationship to depth, are consistent with those of Manooch (1976), who found ripe fish in the SAB in depths from 21 to 100 m. In this respect, red porgy resemble the red grouper (*E. morio*), a protogynous serranid it typically co-occurs with in the Gulf, and which Coleman et al. (1996) found spawned throughout depths from 25 to 120 m.

Size and Age at Maturity

Female red porgy mature at smaller sizes in the NE Gulf than anywhere else they occur. My findings (50 % mature at 210-215 mm) were consistent with those of the only other NE Gulf study (Hood and Johnson 2000); they found 69 % of females 225-250 mm were mature. On average, female red porgy in the SAB mature at sizes ~ 50 mm larger than those of fish in the Gulf, even though size at 50 % maturity in the SAB dropped from 276-300 mm during 1979-81 to 251-275 mm in 1991-94 (Harris and McGovern 1997). An earlier study in the SAB (Manooch 1976) found no mature female <260 mm and estimated 50 % matured by 304 mm. In all but one study, estimated size at 50 % maturity for females in both the eastern and southern Atlantic

ranged from 225 to 250 mm (Cotrina and Christiansen 1994, Pajuelo and Lorenzo 1996, Costa et al. 1997, Cárdenas and Calvo 2003). The largest reported size at 50 % maturity for females - 365 mm - came from the Mediterranean, but that estimate was based on few fish (n=110) and macroscopic staging (Vassilopoulou and Papaconstantinou 1992).

Most female red porgy off the southeastern U.S. mature by age 2, and some as early as age 1. Over 90 % of 2 yr olds in the Gulf and >85% in the SAB were mature (this study, Roumillat and Waltz 1993, Hood and Johnson 2000). Roumillat and Waltz (1993) reported 19 % of age 1 females were mature, as were all 6 one year old females collected by Hood and Johnson (2000). Manooch (1976), in an earlier study in the SAB, estimated age at maturity was about one year older than that reported in Roumillat and Waltz (1993). This difference likely reflects the decline in size at maturity documented by Harris and McGovern (1997). In the south Atlantic both sexes were estimated to mature at age 3 (Cotrina and Christiansen 1994), while around the Canary Islands, females were reported to mature in their second year (age 2?) and males in their third year (Pajuelo and Lorenzo 1996). Evidence from reared fish suggests red porgy mature at older ages in the eastern Atlantic. Females caught as juveniles in the eastern Mediterranean and raised in captivity first matured at age 3 (only 11 %), but by age 4, 54 % were mature; males appeared to mature a little younger, with 77 % mature by age 3 (Kokokiris et al. 1999).

Sex Change

Like Hood and Johnson (2000), I found transitionals year round, but very few just before and during the spawning season. This finding is consistent with 1) the observation that seasonally, red porgy (and three other species of *Pagrus*) off W. Africa completed sex change before spawning began (Alekseev 1982), and 2) Shapiro's (1984) observation that sex change typically was most frequent after the spawning season ended. Unless the process occurred very quickly, any fish undergoing transition during a relatively short spawning season would likely reproduce less or not at all that year. Kokokiris et al. (1999), based on observations of captive red porgy, speculated that transition might be a slow process that could take longer than one reproductive cycle, although the rarity of transitionals during the spawning season in my collections does not support this conclusion. In other teleost families sex reversal lasts 2 wk to 9 mo (Sadovy and Shapiro 1987).

That I found transitional fish over a wide range of sizes (206-417 mm) and ages (2-9), as well

as large and old females to 472 mm and age 9 (Fig 2.8), strongly suggests that sex change in red porgy is controlled socially, as is the case for most sequential hermaphrodites that have been studied (Robertson 1972, Shapiro 1980, Warner 1984, Sadovy and Shapiro 1987). Obviously the minimum size and age at which sex change can occur has a genetic basis, but the asymptotic shape of the distributions of percent females in transition by size and age (Figure 2.9 a,b) suggests there is no endogenous control past those minimum limits. Although the percent of females in transition seems to level off in fish >300 mm, the overall proportion of females in the population steadily declines with size and age (Figure 2.9 a,b) simply because of the cumulative effects of sex change, which basically equates to female mortality.

That many studies of red porgy outside the Gulf of Mexico have also found wide size and age distributions of transitional fish, as well as very large and/or old females, strengthens the argument for social or exogenous control of sex change in this species (Roumillat and Waltz 1993, Cotrina and Christiansen 1994, Pajuelo and Lorenzo 1996, Costa et al. 1997, Cotrina and Raimondo 1997, Kokokiris et al. 1999, Hood and Johnson 2000). Alekseev (1982) concluded that sex change was not essential for all red porgy, again suggesting exogenous control, after finding rudimentary male tissue in the largest female he collected. Harris and McGovern (1997) cited the decline in size at transition in the SAB as evidence of socially or behaviorally stimulated sex change in red porgy; and Kokokiris et al. (1999), after finding red porgy ages 21-70 mo. with ovotestes in a captive rearing experiment, concluded that sex change was not related to a specific size or age, and might be stimulated by other factors.

The maximum monthly transition rates I observed in the NE Gulf (median of 33%) slightly exceeded the monthly frequencies of 10-20 % observed by Kokokiris et al. (1999) in their rearing experiment. Overall transition rates of 2 – 18 % have been reported for red porgy (Manooch 1976, Cotrina and Christiansen 1994, Pajuelo and Lorenzo 1996, Hood and Johnson 2000). However, the value and comparability of these overall estimates is very questionable, given how dependent they are on 1) the size, age, seasonal, and quite likely, spatial distributions of the samples and 2) the method used to identify transitional fish (macroscopic vs. histological). Missing fish in the early stages of sex change is certain if using macro-sexing. In this study, only 98 of 499 (19.6 %) fish classified as transitional histologically were also identified as such macroscopically. It was also difficult to distinguish late transitionals from resting males macroscopically - 36 of 144 (25.0 %) macro-classified transitionals were identified as males

histologically. Histological classification could also overestimate rates if some females have traces of male tissue but never actually change sex, as appears to be the case with red porgy (Alekseev 1982, Kokokiris et al. 1999). Differences between studies in the criteria used to identify a transitioning fish, e.g., how much ovarian degeneration is required, could also make comparisons meaningless.

Spawning Behavior

This is the first known report of pair spawning in red porgy, although it has been documented in other sparids, including *Pagrus* (*Chrysophrys) auratus* (Smith 1986), *Chrysoblephus laticeps* (Buxton 1990), *Cheimerius nufar* (Buxton and Garratt 1990), and *Rhabdosargus sarba* (Leu 1994). In each case except for *C. nufar*, the observations were made on captive fish. Consistent with my observations of pair spawning, male red porgy have relatively small testes, i.e., male GSI's are much smaller than females' during the spawning season. Males in pair spawning fishes typically have small testes, presumably because there is much less likelihood of sperm competition (Buxton 1990, Coleman et al. 1996). In contrast, many sparids are rudimentary hermaphrodites or gonochorists in which both sexes have gonads similar in size (Buxton 1990). My observation that captive red porgy spawned primarily in the early morning agrees with the findings of Stephanou et al. (1995).

Observations of captive red porgy during the spawning season suggest they are polygynous. One presumed male usually seemed to dominate the center of the tank, especially during the early morning hours when spawning activity peaked, repeatedly and aggressively driving off other presumed males. That apparently dominant male also appeared to be the primary participant in any spawning, although other males would always quickly attempt to join in, and it participated in pre-spawning behavior much more often than any of the other males. One of the requirements for polygamy is that individuals (in this case males) must be capable of defending multiple mates (Fischer and Petersen 1987, Buxton and Garratt 1990). Polygamy is most common among protogynous fishes; and virtually every protogynous species whose mating behavior has been studied displays some type of monopolization of mating by large males (Warner 1984). *C. laticeps*, a sparid found in S. Africa, is polygonous (Buxton 1990). Haremic mating systems are found more often in fishes typically found in the edge habitats between sand and reef, and among species characterized by site fidelity and moderate densities, where males

can defend several females (Petersen and Warner 2002); red porgy in the NE Gulf meet these criteria quite well.

That I saw no evidence of classical schooling behavior in red porgy in 10's of hours of in-situ video from many sites (pers. obs.), although they were often observed in very loose aggregations, is also consistent with the hypothesis of polygamy. Buxton and Garratt (1990) concluded that the potential for polygamy is reduced in schooling fishes "because schools are most often made up of individuals of similar size" and males in such species have relatively large testes.

The observation of a few other presumed males quickly joining in the spawning event of a single male and female was almost certainly what Warner (1984) described as "sneaking", a practice commonly observed in small males in protogynous labrids and scarids.

Sexual Dichromatism

Permanent sexual dichromatism has not been previously reported in red porgy, and seems to be rare among sparids. Two congeners are sexually dimorphic, one of which is also dichromatic; males of *P. ehrenbergii* are larger, more brightly colored, and have a more massive head (Stepkina 1973), and males of *P. auratus* develop a protuberant snout and a much more prominent hump on the top of their head than do females (Moran et al. 1998). *Petrus rupestris*, the largest sparid and a rudimentary hermaphrodite endemic to South Africa, is also permanently dichromatic. Females are uniformly copper colored, while males have a black back and premaxilla and black mottling on the operculum; and like red porgy, the male coloration is most obvious during the spawning season (Smale 1988). Males of *Spondyliosoma emarginatum* and *S. cantharus*, nest-building sparids, are seasonally dichromatic, developing black patterns during the spawning season (van Bruggen 1965, Potts 1984, Pajuelo and Lorenzo1999). Permanent sexual dichromatism is found in many other families, including labrids, blennids, scarids, clinids, balistids, ostraciids, chaenopsids, opistognathids, pomacanthids, serranids, and paralichthids (Thresher 1984, van der Heiden and Pérez 1992, Kodric-Brown 1998).

Permanent sexual dichromatism is very likely an adaptation related to the social mechanism controlling sex change in red porgy. Of the two social or exogenous mechanisms hypothesized to control sex change, sex ratio assessment (Shapiro and Lubbuck 1980) and size-ratio assessment (Ross et al. 1983, Lutnesky 1994), permanent dichromatism would most facilitate the former. Permanent sexual dichromatism and protogyny appear to be closely associated (many

references in Shapiro 1981); two primarily protogynous families, Labridae and Scaridae, have many spectacular examples (Roede 1972, Thresher 1984). Other permanently dichromatic protogynous fishes include the gag, a serranid (Gilmore and Jones 1992), and the pomacanthid *Centropyge potteri* (Lutnesky 1988).

Sexual dichromatism is also consistent with the hypothesis that red porgy have a haremic mating system. This trait is common in many other polygynous species, including many labrids and scarids (Randall and Randall 1963, Roede 1972). Color differences often serve not only to attract mates, but also to intimidate other males (Kodric-Brown 1998). Roede (1972) speculated that the bright colors and often striking dark spots or bars in labrids play a role not only in pair spawning, but in territorial defense as well. Dichromatism, however, would not seem to offer any selective advantage to group spawners. In the protogynous, dichromatic labrid *Thalassoma bifasciatum*, only some males change color, and only they are pair spawners; males that do not change color group spawn (Roede 1972). Red porgy, in contrast, probably only pair spawn, as virtually all males appear to develop the typical male coloration.

This dichromatism makes red porgy an ideal candidate for further investigation of the mechanism and timing of sex change, the mating system, and spawning behavior using captive fish. Being able to sex the fish without using some intrusive method requiring capture and handling eliminates a significant source of stress for captive fish. Because of the depth at which red porgy typically live, it is unlikely that these differences will be nearly as distinct when trying to make field observations, although that hypothesis could certainly be tested using a remotely operated vehicle to video caged fish of known sex held at depth.

Spawning Aggregations

My conclusion that red porgy in the NE Gulf do not form large temporally and spatially predictable spawning aggregations agrees with that of Harris and McGovern (1997) that they "probably do not aggregate to spawn" in the SAB. These authors also commented that red porgy "appear to be permanently schooled on the available areas of live bottom", although they did not define what they meant by "schooled" . Quite likely they were describing the loose aggregations commonly seen in the Gulf and previously discussed.

A congener, *P. auratus*, does form spawning aggregations during winter in Western Australia (Moran et al. 1998). *Acanthopagrus berda*, an estuarine-dependent sparid, aggregate to spawn at

the mouth of their home estuary (Garratt 1993, Sheaves et al. 1999). Spawning aggregations appear to be rare among sparids – none were mentioned in a review of tropical reef fish that aggregate to spawn (Domeier and Colin 1997).

Sensitivity to Exploitation

My findings strongly suggest that exploitation is unlikely to skew the sex ratios of red porgy enough to cause sperm limitation and/or disrupt mating, and in fact, they are probably no more, and in some cases, less sensitive than gonochoristic reef fishes to the effects of fishing. I found no evidence implicating either the protogynous mating system or the reproductive ecology of red porgy in the apparent sensitivity of the SAB population to exploitation. Several aspects of their biology and behavior should produce a stable sex ratio, or at least allow for relatively rapid compensation if the ratio were to become skewed, including: 1) spatially, bathymetrically widespread spawning grounds, 2) no apparent tendency to form large temporally and spatially predictable spawning aggregations, 3) absence of size or sex selectivity attributable to fish behavior in hook-and-line catches (see Chapter 1), 4) social control of sex change, 5) co-occurrence of sexes year- round, and 6) an extended period of transition.

That red porgy do not form large spawning aggregations, and additionally, spawn over widespread areas and depths, probably contribute most to stabilizing sex ratios and mitigating the effects of fishing by eliminating the focused, intense fishing experienced by species that do aggregate at specific times and places, and which could rapidly skew the sex ratio or socially disrupt mating. These same traits are thought to have helped prevent any noticeable change in the size- or sex-ratio of red grouper *E. morio* over the last 25-30 years, despite heavy exploitation (Coleman et al. 1996). Red grouper and red porgy typically co-occur in the NE Gulf and appear to have very similar mating systems.

The absence of size or sex selectivity related to male aggressiveness would certainly preclude the sort of rapid loss of males thought to occur when spawning aggregations of gag and scamp are fished (Gilmore and Jones 1992, Coleman et al. 1996, Chapter 1).

Social control of sex change also plays an important role in helping red porgy maintain stable sex ratios, enabling the affected fish to compensate for loss of males, even if fishing has truncated their size or age structure. That the sexes co-occur year-round and females can change sex at least nine months of the year further enhance the ability of red porgy to compensate if the

population becomes overly female biased. Sex ratios are likely to remain stable in the face of exploitation if the mechanism controlling sex change is temporally and spatially unrestricted; this phenomenon is thought to at least partially explain why red grouper sex ratios remained stable despite years of heavy fishing (Coleman et al. 1996). If transition only occurred during a few months and heavy fishing coincided with that period, then the probability of the sex ratio becoming skewed enough to cause sperm limitation would be much greater.

That the overall proportion of males in the SAB not only did not decrease during a period of high exploitation, but actually increased from 15.8 % during 1979-81 to 20.4 % during 1991-94 (Table 4 in Harris and McGovern 1997), supports my contention that fishing is unlikely to skew the sex ratios in red porgy enough to ever cause sperm limitation. Although fishing did truncate the size structure in the SAB, the loss of larger, presumably mostly male individuals was compensated for by decreases in sizes at maturity and transition, producing a large increase in males at small sizes.

Pair spawning is one trait which could increase red porgy's sensitivity to exploitation, although this is much more likely to be a problem for species that are aggregating pair spawners. Pair-spawning males tend to have smaller testes and produce less sperm than group spawners because there is much less sperm competition, potentially reducing their ability to increase spawning rate to compensate for an abnormally-female-biased sex ratio (Petersen and Warner 2002). In two haremic labrids, males had decreased fertilization rates when exposed to greatly increased mating success (Marconato et al. 1995; C.W. Petersen, R.R. Warner, and D.Y. Shapiro, unpubl. data, cited in Petersen and Warner 2002). Buxton (1993) did find that the sex ratios of two protogynous South African sparids, *Chrysoblephus laticeps* (a pair spawner) and *C. cristiceps* (unknown spawning method) were significantly more female-biased in exploited than in unfished areas.

That red porgy appear to be no more sensitive to fishing than most gonochorists was somewhat surprising, given the emphasis in recent years on the potentially greater sensitivity of protogynous fishes to exploitation (see Introduction). However, my findings support the conclusions of Coleman et al. (1996) that non-aggregating protogynous groupers with temporally unrestricted, exogenously controlled sex change, e.g. red grouper and graysby *Epinephelus cruentatus*, are most resilient to exploitation because they are able to maintain stable sex ratios and are less susceptible than aggregating species to local extinctions (see their Figure 6).

Although this study provided no great insights on why the SAB population crashed, its findings at least did not contradict the two, somewhat related hypotheses proposed as explanations. Harris and McGovern (1997) speculated that because smaller females are less fecund and may produce poorer quality eggs, the drop in sizes at maturity and transition they documented may have exacerbated the decline in recruitment. According to Vaughan and Prager (2002), the loss of mature female biomass resulting from a decrease in size at transition and an increase in transition rate may have produced a greater reduction in egg production than would have been expected, but less of a change in the sex ratio. Spawner-recruit relationships showed some evidence of depensation (Allee effect) at very low levels of spawners, although Vaughan and Prager (2002) noted that high retrospective error in recruitment estimates for recent years cast uncertainty on this hypothesis. Given my evidence on the likely stability of red porgy sex ratios, if there was an Allee effect, it is very unlikely it was caused by decreased fertilization rates because of a low density of males. Petersen and Warner (2002) concluded that such an effect was unlikely to occur in pair-spawning reef fishes based on their observations that females of non-aggregating species typically spawn with any courting male. One factor which may have contributed to recruitment failure in the SAB, and which was not accounted for in any stock assessments, was the potentially large unreported landings of red porgy used as bait in the snapper/grouper fishery (Patrick Harris, South Carolina Div. Mar. Resources, Charleston, SC, personal communication, 2000).

Detailed studies on the relationships between size/age of red porgy and fecundity, spawning frequency, and egg quality are needed to test the hypotheses of Vaughan and Prager (2002) and Harris and McGovern (1997) regarding population egg production and recruitment failure in the SAB. Vaughan and Prager (2002), citing a personal communication, said there was new evidence that older, larger female red porgy spawn more frequently and possibly over a longer period of time than do smaller, younger fish.

In conclusion, protogyny, in and of itself, does not make a species more sensitive to exploitation. Socially controlled sex change enables size and age of transition to slide downward as fishing truncates the size structure, an effect very similar to the declines in size and age at maturity seen in many gonochoristic fishes. Protogynous species most at risk are those 1) in which sex change initiation is temporally and spatially restricted, 2) which form temporally and spatially predictable spawning aggregations, and 3) in which males or larger fish are selectively

harvested (Coleman et al. 1996). It may be that gag, often cited as an example of how a protogynous species responds to fishing, and which has all of these traits, is more the exception than the rule. Before we can know what the rule is, many more detailed studies of the reproductive biology and reproductive ecology of other exploited protogynous species are needed.

Table 2.1. Macroscopic and histological gonad maturity stages assigned to female red porgy. Numbers in parentheses following histological stage names indicate stage number.

Macro Stage	Description	Histological Stage	Description
Immature/ Resting	Gonad very small, often threadlike, usually reddish pink	Immature/ Resting (1)	Only primary growth (PG) oocytes present, little or no atresia
Early Developing	Gonad small, reddish, individual eggs not discernable	Cortical alveolar (2)	PG and cortical alveolar (CA) oocytes present, little or no atresia
Developing	Ovaries orangish-yellow and occupy 25 to 50% of body cavity, individual eggs are discernable	Vitellogenic (3)	PG, CA, and vitellogenic oocytes (partially and fully yolked -PY & FY) present; up to 50% of vitellogenic oocytes atretic; POF's may be present
Late Developing	Ovaries yellowish and occupy 50% of body cavity, individual eggs are easily discernable	Early FOM (4)	PG, CA, PY, and FY oocytes present; lipid coalescence and often nuclear migration evident; up to 50% of vitellogenic oocytes may be atretic; POF's may be present
Hydrated	Ovary flesh colored with mottled, translucent appearance, eggs very large	Late FOM (5)	PG, CA, PY, and FY oocytes present; advanced yolk coalescence and breakdown of nuclear membrane (germinal vesicle) usually visible; hydation and/or POF's may be present; up to 50% of vitellogenic oocytes may be atretic
Spent	Ovaries brownish red, flaccid, partially or completely empty	Spent (6)	50% of vitellogenic oocytes atretic; all stages of oocytes may be present; POF's rarely present

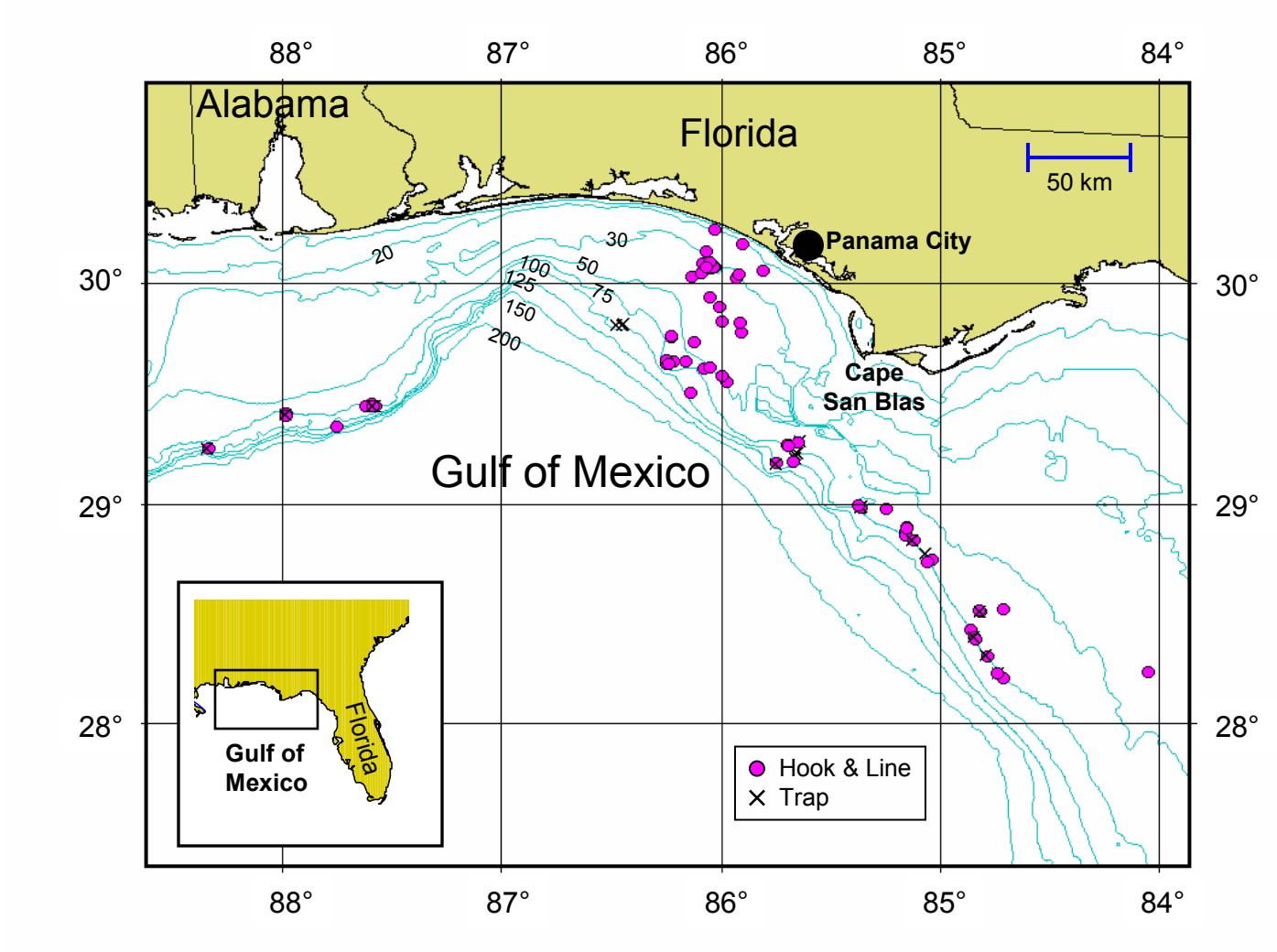

Figure 2.1. Locations of all red porgy collections by gear. Numbers associated with depth contours are depths in meters.

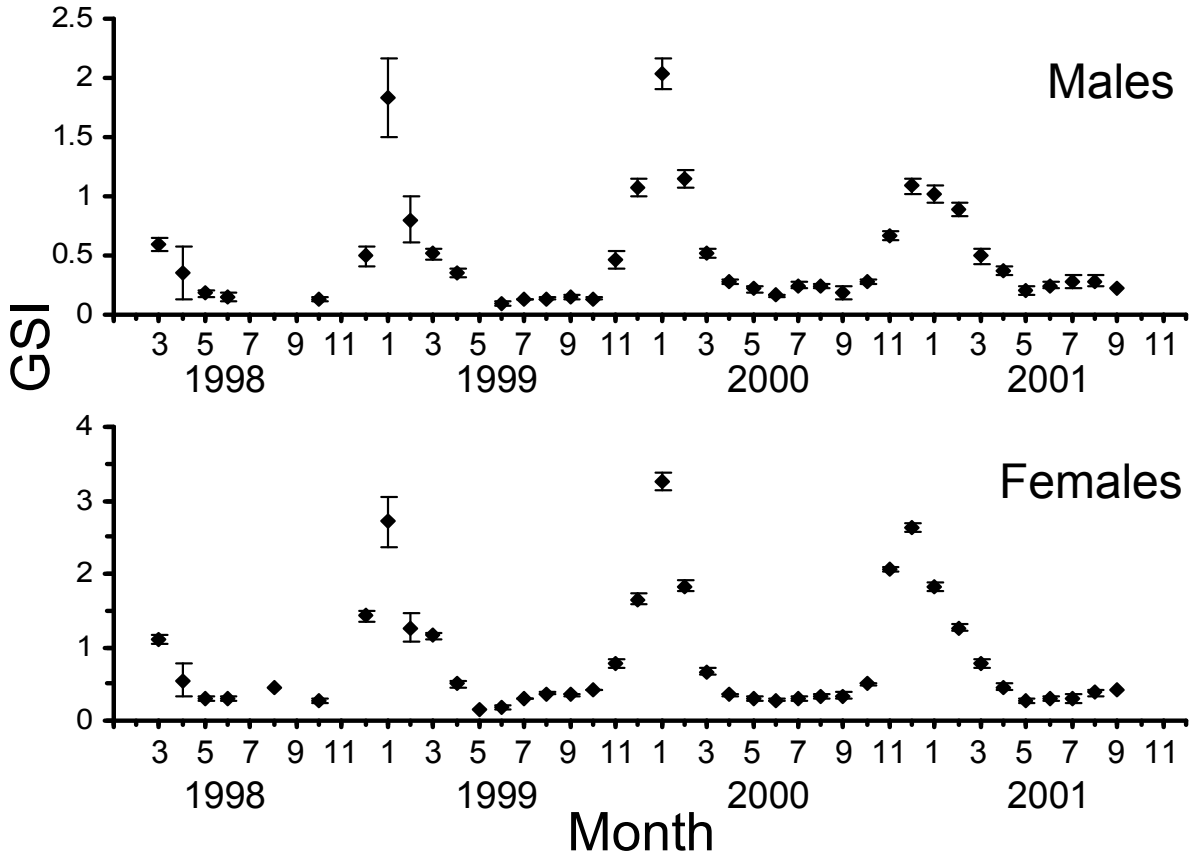

Figure 2.2. Gonadosomatic indices (GSI) for male and female red porgy from the northeastern Gulf of Mexico.

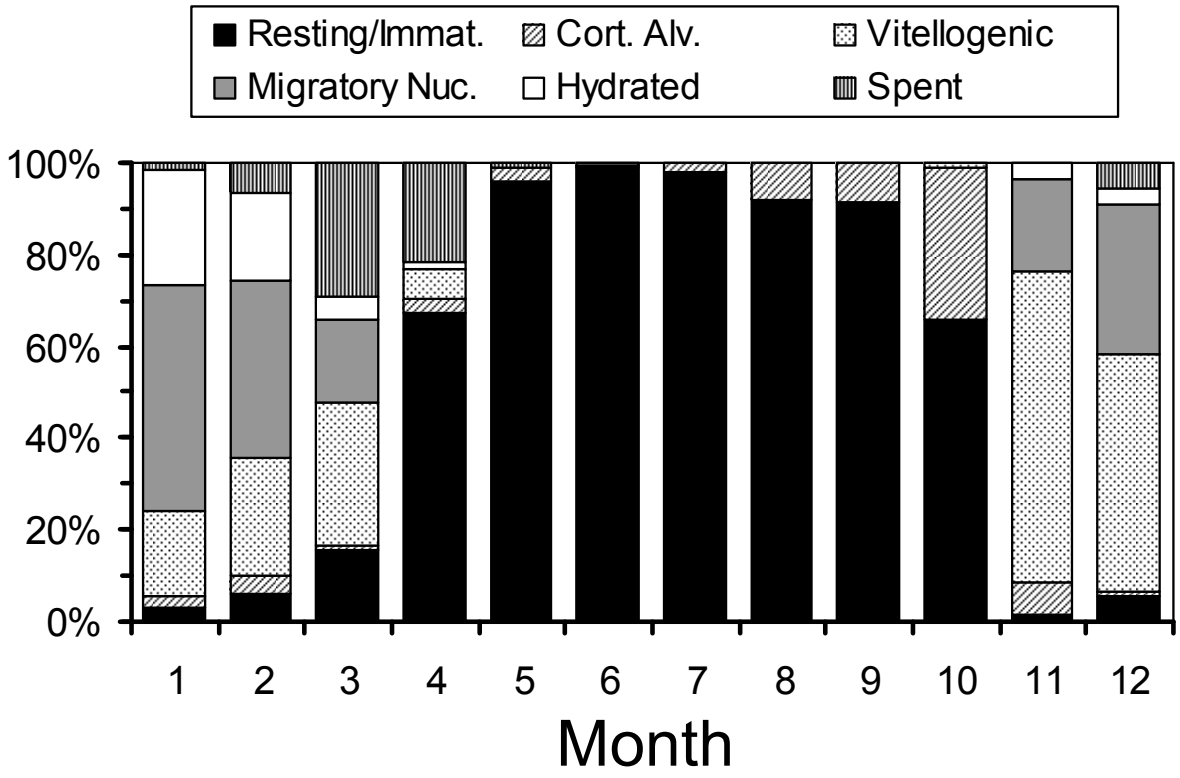

Figure 2.3. Monthly percent frequencies of reproductive stages in female red porgy. Cort. Alv. = cortical alveolar, Migratory Nuc. = migratory nucleus (= early FOM), Hydrated (= late FOM).

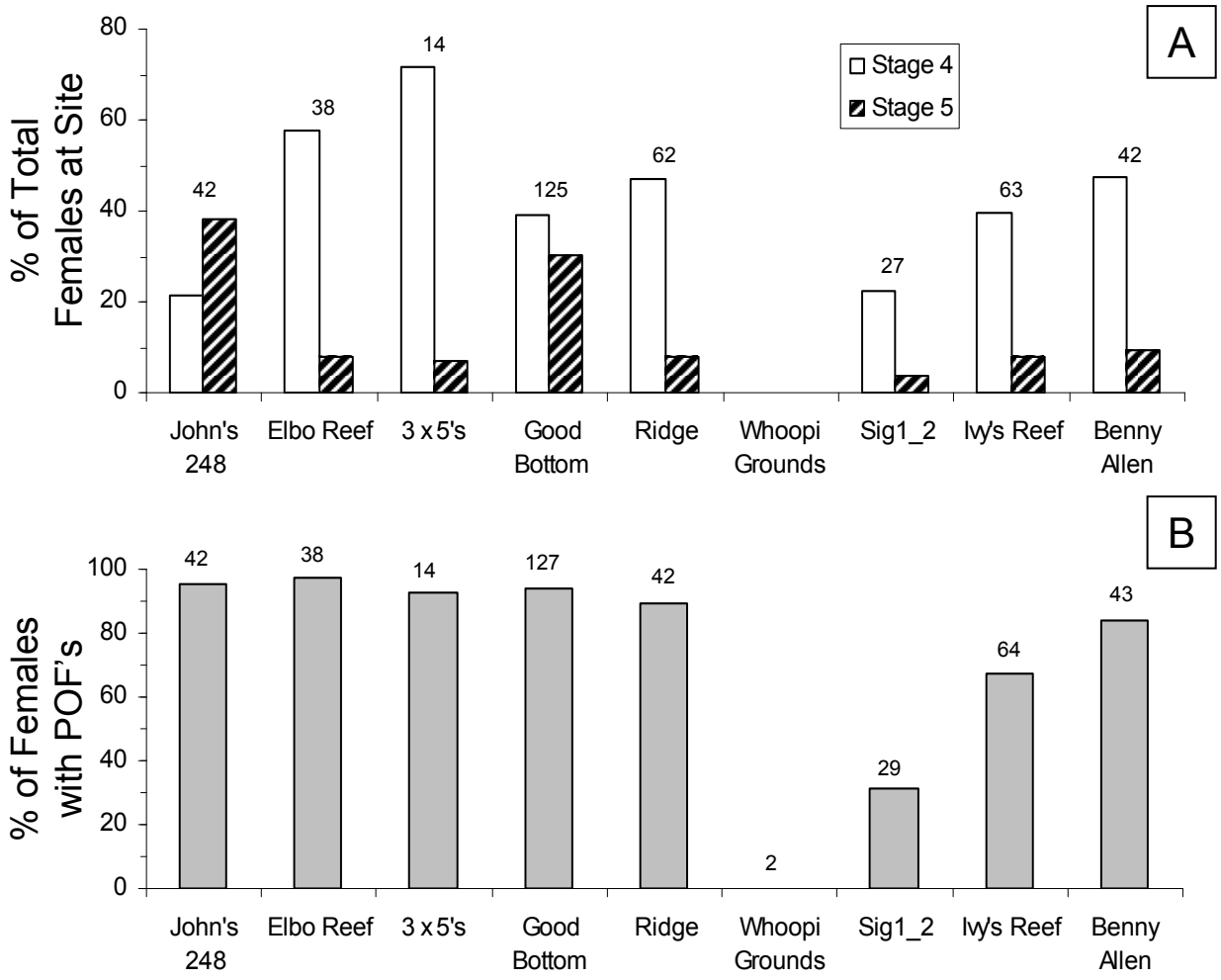

Figure 2.4. A. Percentages of stage 4 (early FOM) and stage 5 (late FOM) female red porgy by site for Dec - Feb only. B. Percentages of female red porgy with POF's by site during Dec-Feb. Numbers at top of bars are sample sizes.

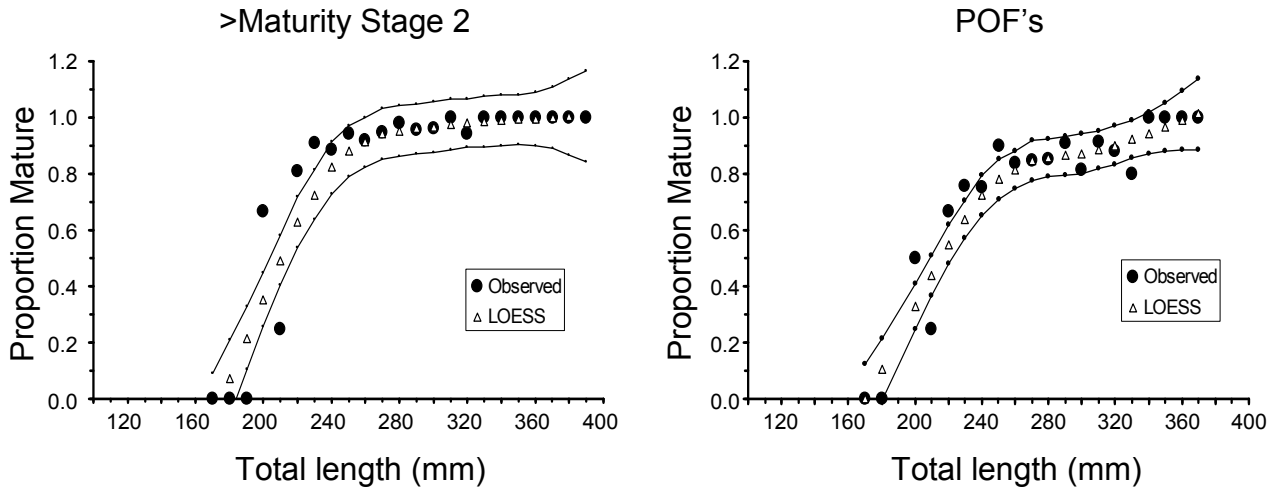

Figure 2.5. Size at maturity ogives and 95% C.L. using a LOESS regression model for female red porgy in the northeastern Gulf of Mexico. Mature fish were defined in two ways: the presence of vitellogenic oocytes (≥ maturity stage 3) or the presence of POF's. Only fish collected during the spawning season, Dec-Feb, were included in the analysis.

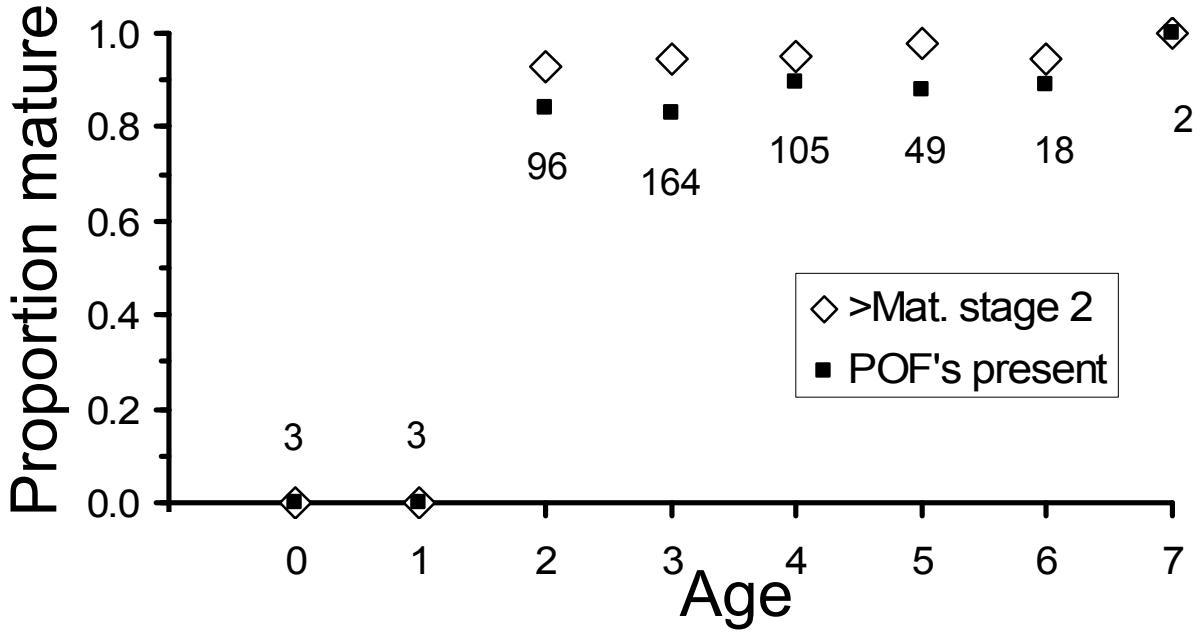

Figure 2.6. Proportions of mature female red porgy at age in the northeastern Gulf of Mexico. Maturity was defined as the presence of vitellogenic oocytes (≥ maturity stage 3) and the presence of POF's. Only fish collected during the spawning season, Dec-Feb, were included in the analysis.

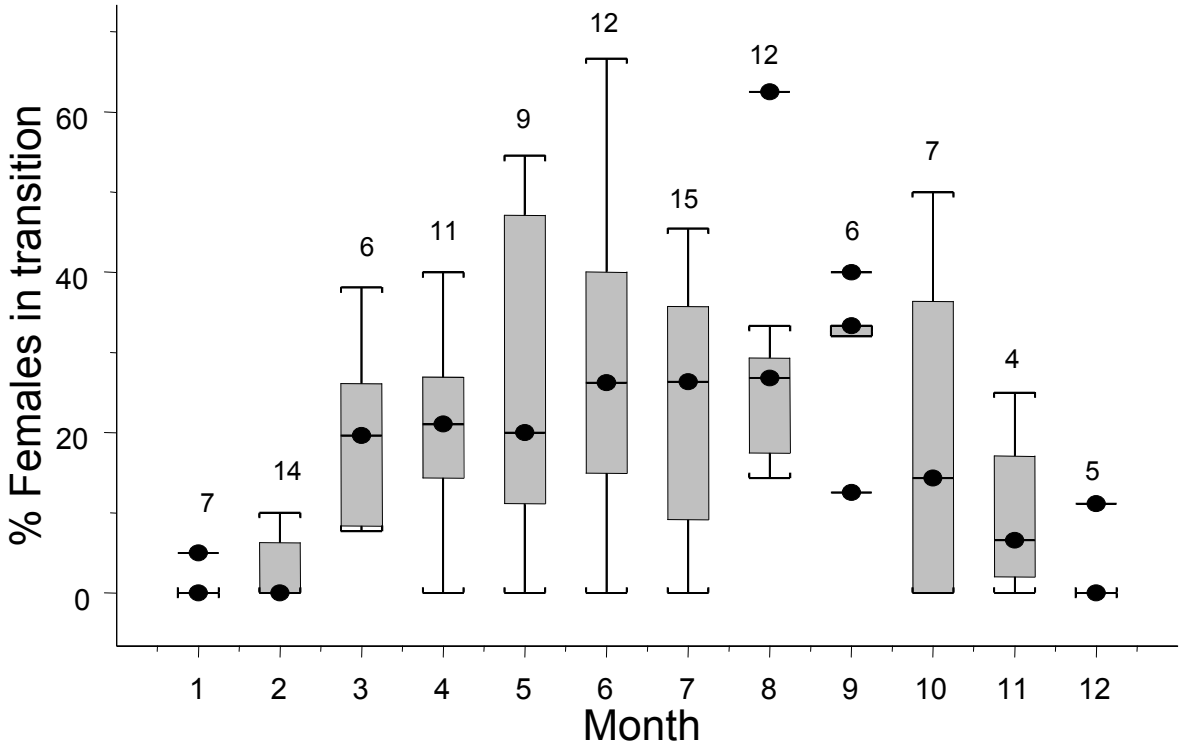

Figure 2.7. Monthly percentages of female red porgy in transition. Numbers above each box indicate the number of collections for that month. Only collections with >5 fish were included in analysis.

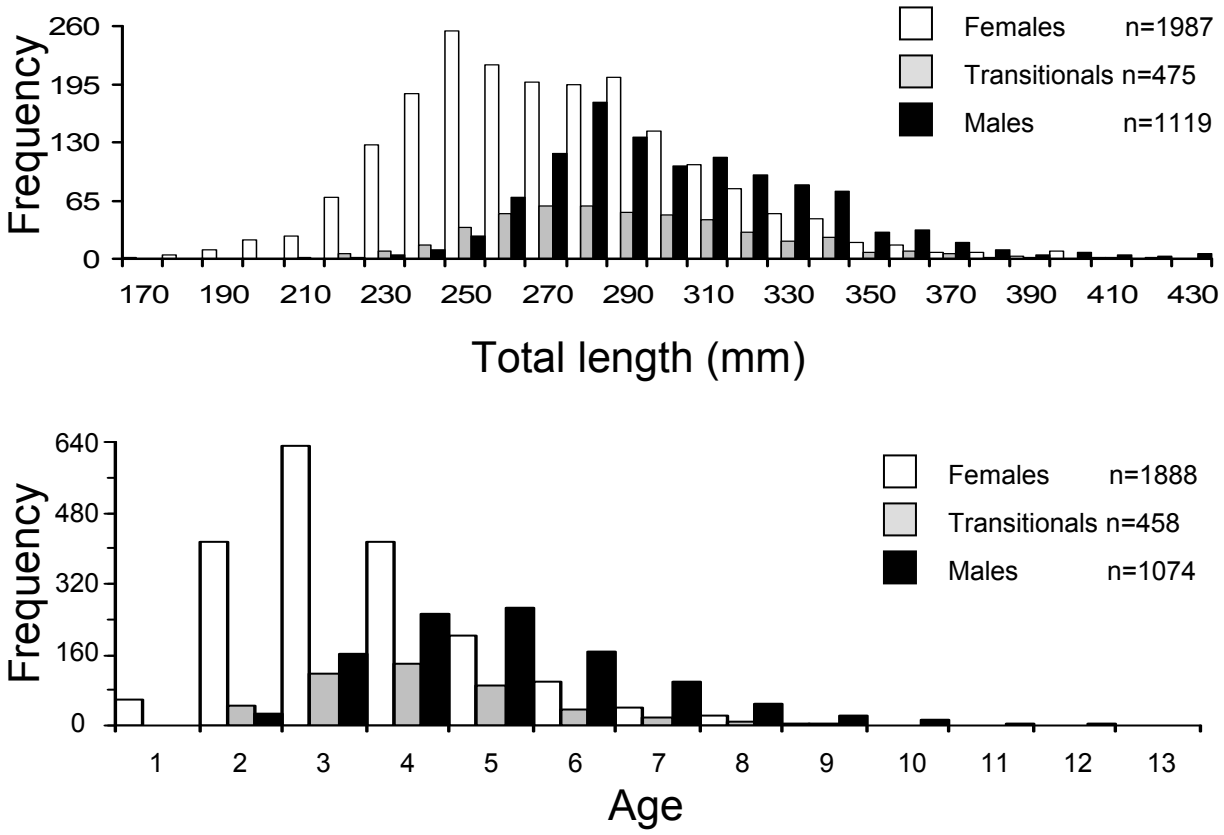

Figure 2.8. Overall length and age frequency distributions, by sex, of all red porgy collected by hook and line.

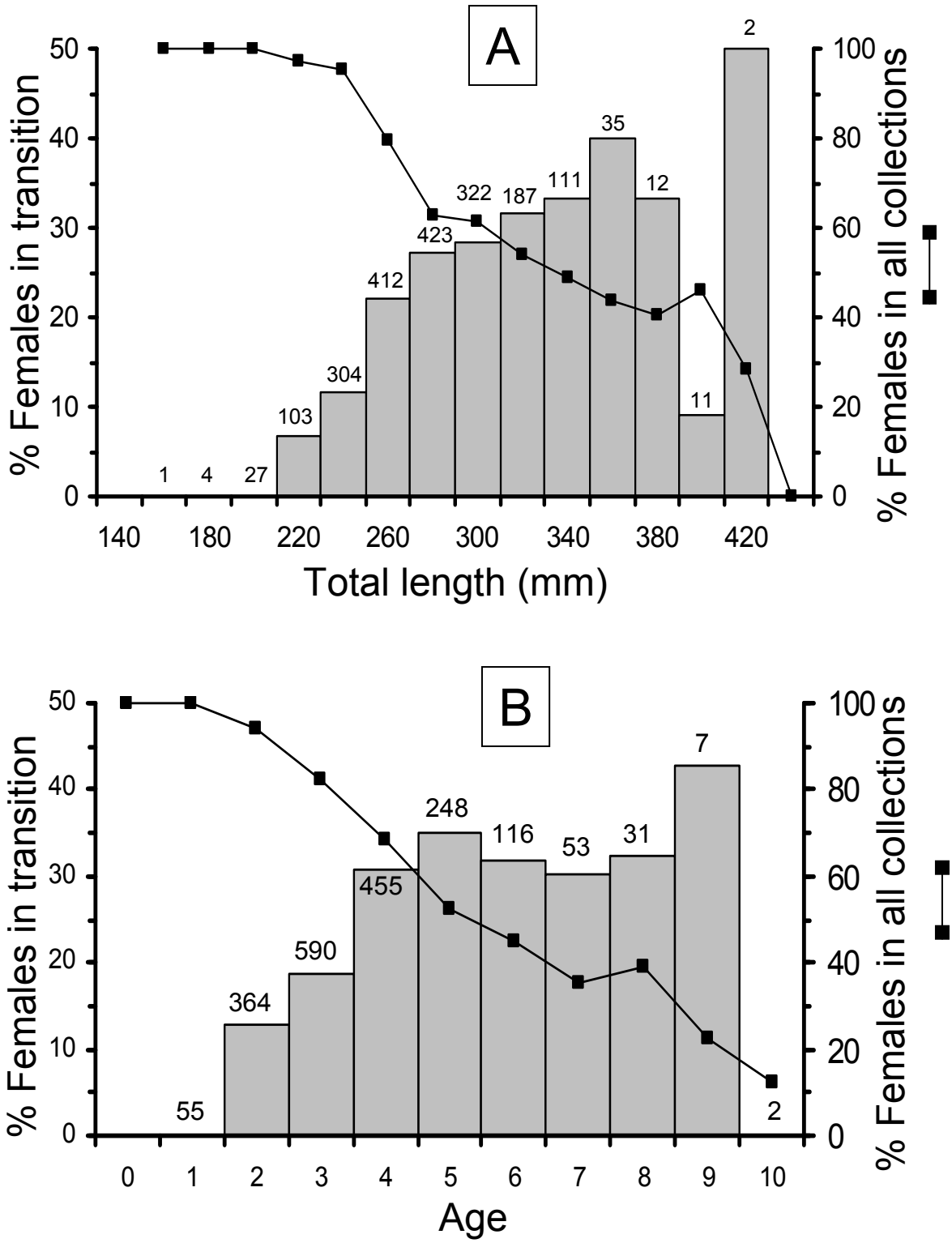

Figure 2.9. Overall percent frequency distribution of female red porgy in transition, Mar-Nov, by size (A) and by age (B). Numbers above bars indicate total number of females in that size or age interval.

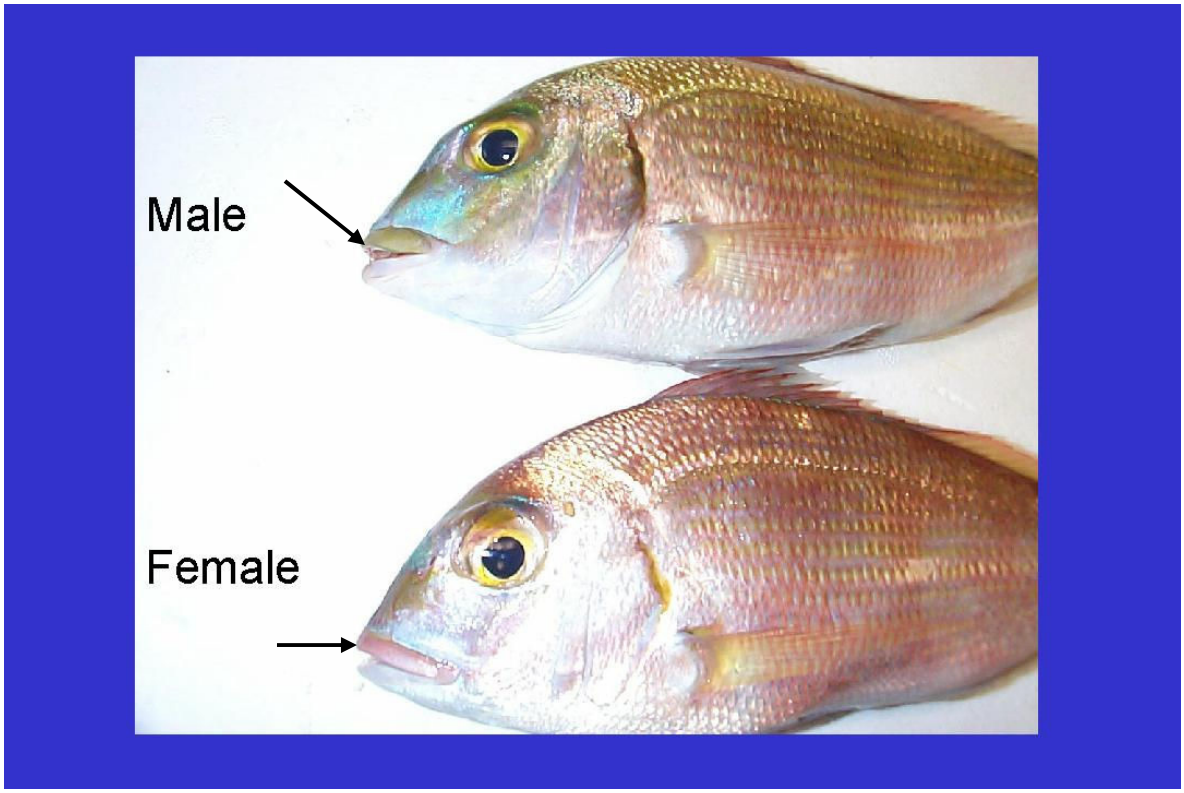

Figure 2.10. Color patterns of male and female adult red porgy. Note especially the green premaxilla in the male and the pink premaxilla in the female.

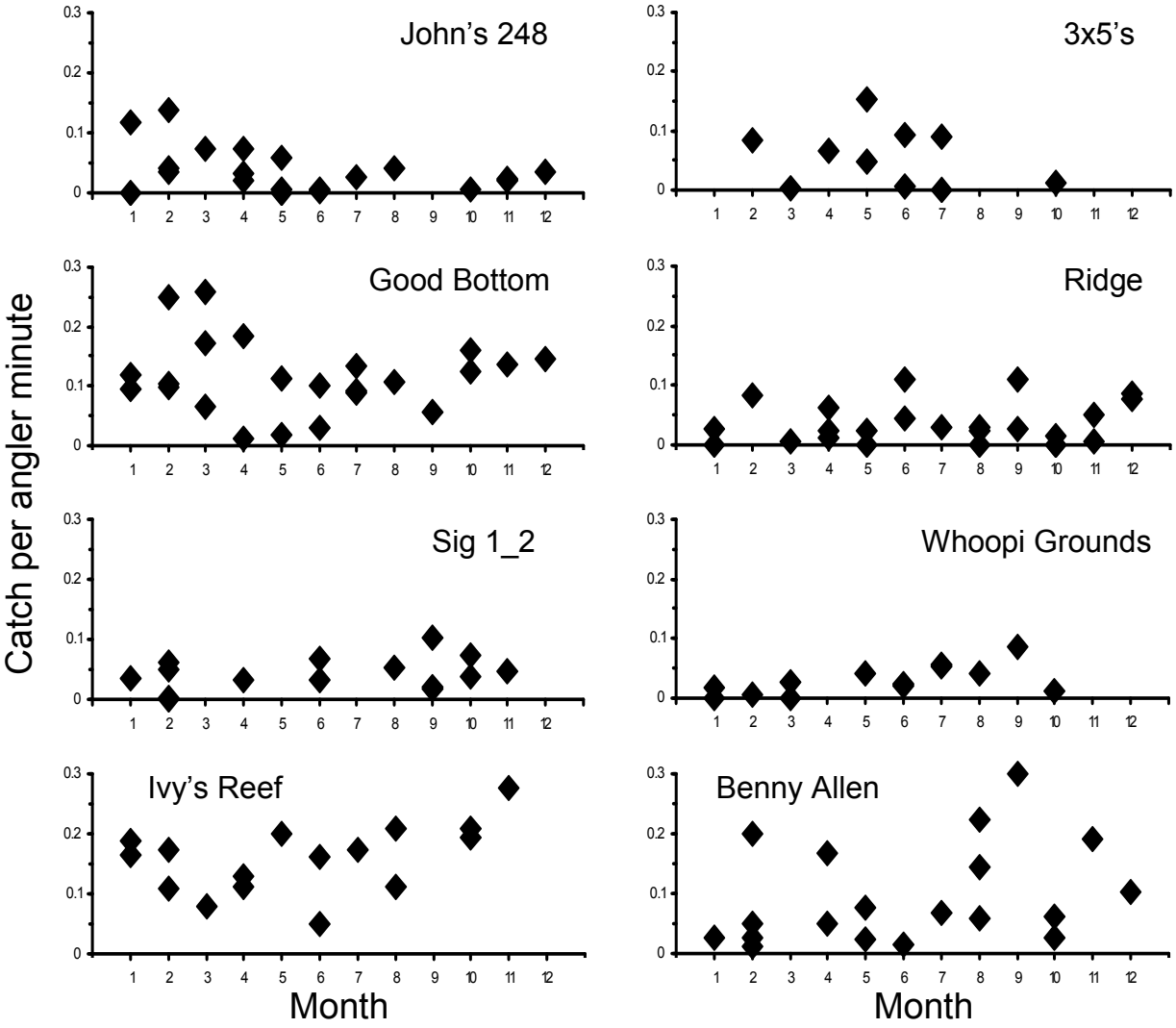

Figure 2.11. Temporal distribution of catch-per-angler-minute at 8 of the 9 standard sites.

CHAPTER 3

SMALL SCALE SPATIAL HETEROGENEITY IN LIFE HISTORY TRAITS AND DEMOGRAPHICS OF *Pagrus pagrus* (SPARIDAE), A PROTOGYNOUS REEF FISH IN THE NORTHEASTERN GULF OF MEXICO

Introduction

Levin (1992) argued that scale is the central problem in ecology; he suggested that understanding the "development and maintenance of spatial and temporal pattern, and the consequences of that pattern for the dynamics of populations and ecosystems• were among the most critical issues facing ecologists. This problem emerged not only in basic ecology but in a variety of applied contexts (Camus and Lima 2002). Jones (1991) and Sale (1998) emphasized the fact that the patchy nature of reef environments impose complicated dynamics upon reef fishes, with different processes unfolding across different spatial scales. The complexity introduced by patchiness and scale extends to behavioral problems because so many reef fishes have sophisticated social interactions; striking variation in social systems has been found among reefs, produced by a combination of the patchiness of resources, habitat preferences, and highly variable recruitment dynamics (Shapiro 1991).

In recent years, fisheries scientists and ecologists, particularly several working on the Great Barrier Reef (GBR), have focused increasing attention on spatial variability in population processes and life history traits at smaller scales (10's of m to 10's of km), and in some cases, multiple scales. These studies have uncovered substantial heterogeneity among locations produced by processes that vary over a variety of scales. Many of the studies dealt with small-bodied families such as labrids (Warner and Hoffman 1980), pomacentrids (Aldehoven 1986, Meekan et al. 2001), and acanthurids (Hart and Russ 1996). More recently, there has been more focus on smaller scale patterns in larger, usually exploited species, including scarids (Dudgeon et al. 2000, Gust et al. 2001, 2002, Gust 2004), lutjanids (Newman et al. 1996, Kritzer 2002), serranids (Ferreira and Russ 1995, Adams et al. 2000), and lethrinids (Williams et al. 2003). If these stocks are to be managed and conserved in the face of their exploitation, Levin's (1992)

comments about understanding scale and heterogeneity loom much larger as imperatives for understanding.

Yet despite the increasing awareness of spatial processes among ecologists (Hanski and Gaggiotti 2004), small scale spatial variability in demographics and life history traits has been examined in only two exploited temperate or tropical reef fishes off the eastern United States - the gray triggerfish, *Balistes capriscus* (Ingram 2001) and the white grunt, *Haemulon plumieri* (Murie and Parkyn 2005). The situation is no different on the Pacific coast of North America; only one study examined variation in size structure and growth on a fine spatial scale, Gunderson's (1972) scrutiny of aggregations of *Sebastes alutus* in Queen Charlotte Sound, B.C.

The red porgy *Pagrus pagrus* offers a promising opportunity to address this deficiency. The red porgy is a warm temperate to subtropical protogynous sparid found on both sides of the N Atlantic, including the northern Gulf of Mexico (Gulf) and Mediterranean Sea, and in the SW Atlantic from Venezuela to Argentina (Manooch and Hassler 1978, Bauchot and Hureau 1990). One of the most abundant, exploited reef fishes in the NE Gulf, adults are typically associated with low-profile hard (live) bottom, rocky, or gravel habitats (Manooch and Hassler 1978, Grimes et al. 1982). Red porgy are only lightly exploited in the Gulf, where they often are taken as bycatch by fishermen targeting more desirable reef fishes; but their numbers in the South Atlantic Bight (SAB) off the southeastern U.S. declined so steeply during the 1980's and 90's that in 1999 a 1 year moratorium was placed on their harvest and possession (Vaughan and Prager 2002) (see Chapter 2 for more details).

Hood and Johnson (2000) provided the first information on the biology and fisheries for red porgy in the NE Gulf. Their findings were limited in scope because sampling was fishery dependent; specific location and depth data were not collected, and the study only lasted one year. The only other study on red porgy in the Gulf was conducted off Texas, where the species is uncommon, and had a sample size of only 161 (Nelson 1988). There have been several other life history studies on red porgy outside the Gulf, throughout their range (many citations in Chapter 2).

The objectives of this study were to determine size and age structure, growth, and mortality of red porgy in the NE Gulf, and whether any of those demographics and life history traits varied temporally, bathymetrically, or spatially (at scales of no more than 10's of km). I present evidence that 1) size and age structure, growth, and mortality rates varied significantly at a

spatial scale of 10's of kilometers, and in some cases, bathymetrically, although with no consistent pattern, 2) size structure within sites varied temporally, but with no obvious seasonal pattern, and that variation was smaller than that among sites, 3) age structure varied annually and consistently within sites, and 4) males tended to be larger at age than females, at least at ages 3-5. These findings suggest that red porgy in the NE Gulf have a complex population structure composed of many local subpopulations and offer some insight into potential strategies for managing red porgy and why porgy stocks in the Atlantic Ocean off the southeastern U.S. suffered a precipitous population crash.

Methods

Red porgy (n=3658) were collected year round in the northeastern Gulf of Mexico, primarily southwest of Panama City, Florida, using standardized hook and line gear in depths from 22 to 92 m during 1998-2001, although a few were collected in March of 1994 and 1997 (Figure 2.1). A few fish (n=270) were also collected with fish traps. The seasonal and depth distributions of the samples are shown in Chapter 2, Figure A.1. A majority of the hook and line samples (n=2586, 71%) were taken at 9 productive locations (hereafter referred to as standard sites) ranging in depth from 29.8 to 66.8 m, most of which were repeatedly sampled at approximate monthly to bimonthly intervals from Jul 1999 through Aug 2001 (Figure 3.1, Table 3.1). Sampling frequency varied, however, depending on productivity of the site, weather, and logistics. One very productive site, Ivy's Reef, was not discovered until Jun 2000, so was only sampled for one year. Standardized hook and line gear consisted of one or two size 1 Mustad j-style hooks attached to a 27 kg test monofilament leader by short (~5-10 cm) pieces of the same strength line, with a terminal lead sinker of varying weight, depending on current and wind conditions. Fishing was done during daylight hours from outboard boats, usually while anchored, using squid for bait.

I would attempt to catch 25-30 red porgies at each site each time it was fished. If it became apparent that it would take several hours to reach that goal, I would stop sampling and move to a new location. Fish were immediately iced and processed in the laboratory the next day. They were measured to the nearest mm total (TL), fork, and standard length, weighed to the nearest

gram, and sexed and staged macroscopically. All fish identified macroscopically as female or transitional were also sexed and staged histologically, and final determination of sex was based on those findings. Both sagittae were removed, washed in tap water, air dried, and stored in coin envelopes. Additional details on the sampling and specimen processing are given in Chapter 2.

I determined the age of the majority of fish using whole otoliths following the MARMAP program methods (Harris and McGovern 1997). To improve the accuracy and precision of the ageing, I aged one set of 500 fish twice before actually assigning the ages used in these analyses. Both sagittae were placed in a black-bottomed watch glass containing water and examined with a dissecting microscope at 6-25x under reflected light provided by two fiber optic lights. Annuli appeared as white opaque bands of varying density (Figure A.8). Otoliths were examined without knowledge of size, sex, location, or date of collection. Older fish have larger, thicker, opaque sagittae for which the MARMAP method was not effective. I re-examined these otoliths with a break and burn technique (Christensen 1964). The left sagitta, if available, was scored through the core along the dorsal-ventral axis with a diamond pencil, then broken or cut with a low-speed saw. The broken or sawn edge of both halves was then held over an alcohol flame until it turned uniformly light brown. Both halves were then embedded with the cut or broken edge up in a small piece of black plasticine, the edges were coated with vegetable oil, and then examined with a dissecting microscope under reflected light at 6-25x. In some cases, readability was improved by polishing the broken edge using 400 and 600 grit wet-dry sandpaper.

The number of visible annuli and an estimate of marginal increment size relative to the previous annual increment (none, <1/3 as large, 1/3-2/3, >2/3) were recorded. Ages, to the nearest whole year, were assigned solely on the basis of number of visible annuli for fish collected 16 Jul - 31 Dec. Fish collected 1 Jan - 15 Jul had one year added to their age if the marginal increment was estimated to be ~1/3 the width of the previous increment. This adjustment was necessary to assign individuals to the correct year class, as annuli typically form sometime during the spring to early summer (Hood and Johnson 2000) but are often difficult to distinguish until there has been at least some growth beyond the newest annulus.

Size and age distributions were compared among sites and depths using Kolmogorov-Smirnov two-sample tests (Sokal and Rohlf 1969). Analysis of depth patterns included data from all hook and line collections, not just the standard sites (n=3420 vs. n=2493). Observations were assigned to one of seven roughly equal depth strata: 20-26, 27-36, 37-44, 45-54, 55-64, 65-78, and 79-92

m. These strata loosely followed natural breaks in the overall bathymetric distribution of the samples, and were also chosen to produce similar sample sizes in at least the five most heavily sampled intermediate strata.

Von Bertalanffy growth equations were fitted to quarterly observed lengths at age using Marquardt's nonlinear regression procedure. Overall growth equations, using all hook and line-caught fish aged (n=3489), sexes pooled, were calculated two ways – with t_0 constrained to equal 0, and with t_0 not constrained (the typical method). The former method was used in an attempt to deal with the problem of an upward bias in K and a downward bias in L_∞ which results when size selective sampling collects primarily the fastest growing of the young fish (Kritzer et al. 2001, Williams et al. 2003, Walters and Martell 2004). Site specific growth parameters, used to estimate natural mortality, were estimated in the same manner.

To compare growth among standard sites, I ran separate unbalanced, one way ANOVA's on size at age for ages 2-7, the most abundant age classes, sexes combined, followed by Tukey's HSD test (Kuehl 1994). Homogeneity of variance was checked by examining residual scores plots of TL by age. Normality was checked using the Shaprio-Wilk test and by examining normal scores plots of residuals of TL for each age. In an effort to reduce the heterogeneity of variances for ages 5-7, sites with small sample sizes (n<10) were excluded from the final ANOVA's. I did not use von Bertalanffy parameter estimates to compare growth among sites. Estimates of L_∞ and k are highly correlated and very sensitive to the range and distributions of the observations used in their calculation, and those ranges and distributions varied considerably among the groups being compared. Newman et al. (1996) found significant differences in von Bertalanffy growth functions (VBGF) among reefs in *Lutjanus quinquelineatus*, but no differences in mean size at age for ages 2-6, and attributed this contradiction to the effects on the VBGF of differences in the number of young fish available for capture at each reef.

To compare growth between sexes, I ran separate unbalanced, one way ANOVA's for each site on size at age for ages 3-5, the age classes in which both sexes were relatively abundant, followed by Tukey's HSD test. For this analysis, transitionals were considered females. To examine temporal stability in growth differences among sites, I compared mean sizes at age for ages 2-7 at Good Bottom and the Ridge sites during two time periods: Jul 99 – Jun 00 and Jul 00 – Jul 01. I also compared Good Bottom and Ivy's Reef during Jun-Dec 2000 and Jan-Aug 2001.

Instantaneous total mortality rates (Z) were estimated using least squares (LS) catch curve analysis (Ricker 1975) and the maximum likelihood (ML) method of Robson and Chapman (1961). The latter estimates annual survival (S), which was converted to Z using Z = -lnS. For both methods I used the total, sexes combined, age composition data (ln transformed for the least squares) from each site. To reduce bias in the estimates, I used only the first fully recruited age class and all older age classes with ≥6 individuals (Chapman and Robson 1960, Murphy 1997). ML estimates of S were compared by examining overlap in their 95% confidence intervals. Although not a true test of significance, this procedure did provide insight into spatial patterns. Spatial variability in mortality was also examined by making pairwise comparisons of the slopes of the catch curve regressions. This was done by checking for significant interaction terms (age x site) between all possible pairs of standard sites.

Instantaneous natural mortality rates (M) were estimated using Pauly's (1980) method; in all calculations, temperature was represented by 22.4°C, the mean of overall monthly mean bottom temperatures from all sites. Site-specific M's were estimated from von Bertalanffy parameters estimated with and without having t_0 constrained to equal zero.

Site-specific instantaneous fishing mortality rate (F) was estimated using the relationship F=Z-M. Values were calculated using both ML and LS estimates of Z. Three different estimates of M were used: an overall pooled value of 0.36 and site specific values derived from von Bertalannfy k and L_4 where 1) t_0 was constrained to 0, and 2) where t_0 was unconstrained. Annual exploitation rates (u) were estimated using the relationship u = FA/Z.

Results

Size Composition

The overall size compositions of female, male, and transitional red porgy were consistent with the pattern expected in a protogynous species: females smallest and males largest. Of all hook and line-caught fish, females ranged from 165 to 472 mm TL, transitionals from 210 to 417 mm, and males from 222 to 446 mm; respective modes were 260 mm, 280-290 mm, and 280-290 mm (Figure 2.8).

Among the standard stations, size composition varied significantly, but with no consistent relationship to depth (Figure 3.2). Of 36 possible paired comparisons (K-S 2 sample test) of size structure among the standard sites, 30 were significantly different, with p#0.01 in 26 of the 30 (Table 3.2). Mean sizes at the nine sites ranged from 261 to 309 mm, median sizes from 262 to 310 mm (Table B.1). The 3x5's site, the third shallowest (41m), had the greatest proportion of large fish (59% >305 mm), and the largest mean and median size; while Ivy's Reef, the second deepest site (62m), had the smallest median and second smallest mean size, and only 2% >305 mm (Figure 3.2, Table B.1).

Size structure differed considerably between two sites at the same depth (47m) - Good Bottom and Ridge; median size was 296 vs. 270 mm, 41 % vs. 7 % were >305 mm and 4 % vs. 17 % were <245 mm, respectively (Figure 3.2, Table B.1). The deepest site, Benny Allen (67m), had much fewer large fish (>305 mm) than 3x5's, Good Bottom, and Whoopi Grounds - 15% vs. 59, 41, and 41%, respectively.

Red porgy were clearly smallest in the shallowest stratum (20-26m), but there was no consistent trend in the remaining strata. All depth intervals differed significantly from each other ($p<0.001$ in all but 2 cases) except 55-64 and 79-92 m. In 20-26 m, 52% were <245 mm, compared to 23, 3, 8, 15, 15, and 24 % in the remaining respective strata; and the largest fish in the shallowest stratum was only 285 mm, while 6, 52, 31, 22, 28, and 27 % were >305 mm in the remaining strata (Figure 3.3). Fish were smallest in 20-26 m (mean±95% CI = 242±4.6 mm) and largest in 37-44 m (306±3.3 mm); medians were the same as means. A few very small fish (<200 mm) were collected in all depths, and in fact the smallest porgy collected, 165 mm, came from the deepest (79-92m) stratum. There was weak evidence that the abundance of the always rare (total n=28), very large individuals ≥400 mm increased with depth (Figure 3.3). Fish ≥400 mm composed 0.3% of the total in 37-44m, 0.2% in 45-54m, 0.9% in 55-64m, and 2.7% in 65-78m, with none in the shallowest two and the deepest strata.

Temporal Patterns

Although size structure certainly varied among collections within a site, the variability was lower within sites than between them, and there were no obvious seasonal patterns (Figures 3.4 and A.9). The mean within-site CV of median TL was 4.6% while the overall among-sites CV

of median TL was 6.1%. Site specific CV•s ranged from 2.7 to 8.4%; excluding the Sig1_2 data, the range dropped to 2.7-5.4% and the mean CV to 4.1%.

When pooled into 3-mo periods, size structure within sites did vary but showed no consistent pattern between the spawning season (Dec-Feb) and either the preceding or following period (Figure A.10). Between the quarter before spawning and the spawning season, size structure showed no change at Benny Allen and the Ridge, while it shifted left (fish were smaller) at Ivy's Reef and Good Bottom ($p<0.01$). The quarter after spawning, the size structure shifted right (fish were larger) at Ivy's Reef and the Ridge ($p<0.001$), shifted left at Benny Allen ($p<0.01$), and showed no change at Good Bottom.

Age Composition

Red porgy from the northeastern Gulf ranged from age 0 to 17. Females ranged from age 0 to 10 (mode = 3), transitionals were ages 2-9 (mode = 4), males were ages 2-17 (mode = 4-5) (Figure 2.8), and each of these distributions was significantly different from the others ($p<0.0001$). The distribution of ages was consistent with the pattern expected in a protogynous species. The few age 0 (n=2) and age 1 (n=58) fish were all females, and only 2.6% of all males were age 2 compared to 22% of all females. At the upper end of the age distributions, only 3.5 % of females were above age 6 compared to 18.5% of males.

Spatial Patterns

As with size, age composition varied significantly among the standard stations, and there was some evidence that red porgy in the shallowest sites move to deeper water with age (Figure 3.5). One year olds were found at every standard site but were very rare at all but John's 248, the shallowest. Modal ages were 3 and 4 at all sites except Elbo Reef and Ridge, where 2 and 3 yr olds predominated. Fish ≥age 8 were rare anywhere, composing 0 - 5.1 % at the standard sites, and <2% at 7 of those sites. Of 36 possible pairwise comparisons of age distributions between standard sites, 23 were significant ($p<0.01$ in 20 of the 23)(Table 3.2). Among standard sites, fish #age 2 composed 5.2 - 34.7 % of the samples, while older fish (≥age 6) made up 3.2 - 24.2 % of the age distributions (Figure A.11). Ivy's Reef (62 m) and Good Bottom (47 m) were not statistically different, and had, by far, the greatest proportions of fish ≥age 6 - 24.2 and 20.6 %, respectively (Figure A.11). These two sites also had the second and third lowest percentages of

young (#age 2) porgies. Elbo Reef, the second shallowest site at 31 m, had the smallest proportion of older individuals (3.2%) and the greatest proportion of young fish - 34.7%. The 3x5's site had the least number of young fish (5.2 %) but intermediate numbers of older fish (9.1 %).

Depth Patterns

Ages 2 and 3 predominated in the shallowest (20-26 m) depth interval, while 3 and 4 yr olds were most abundant at all other depths. Age distributions in the two shallowest strata, 20-26 and 27-36 m, where median age was 2 and 3, respectively, differed significantly from each other and from all other strata ($p<0.001$), but there were no differences between any of the other, deeper strata, each of which had a median age of 4. Among all hook and line collections, not just the standard stations (n=3420 vs. n=2493), 92.9 % of the fish from 20-26 m were ages 2 and 3, 94.6 % were ≤age 3, and none were >5 - a much more truncated age structure than in any deeper stratum (Figure A.12). The percentage of young fish (≤age 2) dropped from 55 % at 20-26 m to 29 % at 27-36 m to 9 % at 37-44 m, then fluctuated between 13 and 16 % in the remaining strata (Figure A.13). The proportion of older (≥age 6) fish also increased with depth. The percentage of fish ≥age 6 increased from 6% at 27-36 m to 28 % at 79-92 m, although the latter value was based on a small sample size. At both 55-64 m and 65-78 m, 22 % were ≥age 6.

Temporal Patterns

Age composition did vary annually, and in a consistent pattern, at the four sites with sample sizes large enough to make analysis worthwhile. At Good Bottom, Ridge, Ivy's Reef, and Benny Allen the modal age was 3 in 2000 and 4 in 2001 (Figure 3.6).

Growth

Growth of red porgy in the northeastern Gulf of Mexico was highly variable and quite rapid through age 3 or 4, when most fish attain a size of around 300 mm, after which growth is so slow that the trajectory is almost flat. (Figure A.14). Estimated parameters of the von Bertalanffy growth equation (t_0 not constrained) for all hook and line-caught fish aged (n=3489), sexes pooled, were: L_∞ = 343.2 mm, k = 0.28, and t_0 = -2.25 (95% CL were 335.2-351.3, 0.24-

0.32, and -2.73 to -1.78, respectively). When t_0 was constrained to equal 0, the remaining parameters were L_∞ = 312.4 mm (CL=310.3-314.4) and k = 0.65 (CL=0.63-0.67).

Overall, size at age varied considerably, and much of this variability can be attributed to significant differences in growth among sites. By age 3 the range in sizes at any given age was about 100-150 mm (Figure A.14). In separate ANOVA's by age for ages 1-7 of size at age, as well as for weight at age, site was highly significant ($p<0.0001$) in every case. Site specific estimates of k and L_∞ ranged from 0.14 to 0.44 and 296 to 388 mm when t_0 was not constrained and from 0.59 to 1.12 and 276 to 332 mm when t_0 was constrained to zero (Table B.2).

The relationships of both mean size and mean weight at age among sites were very consistent across ages. More importantly, they appeared to be temporally stable; i.e., differences in growth among sites were consistent throughout the lifetimes. For ages 2-7, mean size at age was always greatest at 3 x 5's and lowest at Ivy's Reef; the differences between these two sites (39-69 mm, mean = 52) were all significant (Tukey's HSD) (Figure 3.7, Table B.3). Whoopi Grounds and Good Bottom had the second and third highest mean sizes at age for all ages between 2 and 7, and the rankings of the other 5 sites varied little or none at all. In many cases the difference between a given pair or groups of sites was significant (Table B.3). As would be expected given the exponential relationship between weight and length, the differences in mean weight between pairs of stations increased much more rapidly with age than the differences in mean size. For example, mean size at age was 16.2% larger at 3x5's than at Ivy's Reef at age2 and 24.7% larger at age 7, a difference of 8.4% between the two ages; while mean weight at age was 54.1% larger at age 2 and 91.0% larger at age 7, an increase of 36.8 %. Evidence of the temporal stability of the growth differences among sites can be seen in Figure A.15. Mean sizes at age (±95% CI) for ages 2-7 at Good Bottom averaged 21±9 mm larger than those at the Ridge during Jul 99 – Jun 00 and 24±20 mm larger during Jul 00 – Jul 01. Mean sizes at age at Good Bottom averaged 43±10 mm larger than those at Ivy's Reef during Jun-Dec 2000 and 40±14 mm during Jan-Aug 2001.

Males tended to be slightly larger at age than females. Observed size at age was larger in males than females at ages 3-5 at all standard sites, significantly so in 16 of 27 cases (ANOVA). The average difference was 14.3 ± 5.2 mm for age 3, 14.8±4.4 mm for age 4, and 15.8±4.3 mm for age 5.

Mortality / Survival Rates

Maximum likelihood (ML) estimates of annual survival (S) of red porgy in the NE Gulf were quite variable among sites, ranging from 38 to 65 % (Z=0.98-0.43); least squares (LS) estimates ranged from 41 to 58 % (Z=0.90-0.54) (Table 3.3). Estimates of S from the two methods differed no more than 3 % at any site except Ivy's Reef, where the difference was 7 %. The 95 % CI's of the ML estimates of S for 6 of the 8 sites with estimates did not overlap. Although a comparison of confidence intervals is not a true significance test, this result suggests that at least some of these differences are real (Table 3.3). In contrast, comparison of catch curve Z's between sites, based on significance of the interaction terms (ageHsite), indicated that only the Ridge and Sig1_2 sites had significantly different total mortality rates (P=0.05). This test was probably quite insensitive, though, given the few age classes (independent variable) used in these regressions (3-5 for all but the Good Bottom site, which had 6).

There was no apparent relationship between annual survival rate and depth. Neither regression of ML or LS estimates of S on standard site depth was significant (ML: F=1.54, P=0.260 and LS: F=0.978, P=0.361). Given the significant variation in S among sites and the lack of a relationship between S and site depth, it did not seem prudent to examine the relationship between S and depth interval. Pooling of age structure data from different sites within a depth stratum would mask the true spatial complexity and yield estimates of S that would more likely reflect the spatial distribution of the age samples within each stratum than the true pattern in the population.

Pooling all hook and line age data, the overall estimates of instantaneous natural mortality rate (M) were 0.36 using k=0.28 and L_4=342.4 (t_0 unconstrained) and 0.64 using k=0.65 and L_∞=311.8 (t_0 constrained to 0). Site specific estimates of M derived using k and L_∞ from equations where t_0 was unconstrained ranged from 0.22 to 0.50 - these equate to annual natural mortality rates (n) of 20 - 39 % (Table 3.4). Estimates of M derived using von Bertalanffy parameters from equations in which t_0 was constrained to 0 were unrealistically high (0.59 - 0.94 ; n = 45- 61 %), in fact, they exceeded ML and LS estimates of Z by as much as 77% for three of the sites (Table 3.4). Because of these unrealistic results, I did not use them to calculate estimates of fishing mortality rates.

Given the spatial variability in Z and M, and that fishing mortality rate (F) was calculated as Z-M, it was no surprise that the latter also varied greatly among sites (Table 3.5). Using ML Z's

and a fixed M of 0.36, F ranged almost nine fold, 0.07 - 0.62; while those based on LS Z's ranged about threefold, from 0.18 to 0.49. The smaller range in the latter probably reflects that LS Z's were not significant for John's 248 and Sig1_2, and therefore F could not be calculated for those sites (Table 3.5). Using site specific M's and ML Z's, F ranged from 0.04 to 0.69; with LS Z's the range was 0.16 to 0.41. F was lowest at Ivy's Reef in every case and highest at John's 248 using ML Z's. With LS estimates of Z, F was highest at Whoopi Grounds using M=0.36, and at 3 x 5's using site specific M's. Assuming the red porgy fishery is a Type 2 fishery, that is, fishing and natural mortality operate concurrently (Ricker 1975), estimates of exploitation rate (u) ranged from 4 to 44 % (Table 3.5).

Discussion

Small Scale Variability – Review

The significant spatial variability I found in the size and age structure, growth, and mortality of red porgy at a scale of 10's of kilometers has not been previously reported for this species or for any sparid. In fact, such small scale variability in demographics and life history traits has been documented in only two other exploited reef fishes in the southeastern United States. Ingram (2001) found significant differences at this scale in growth, mortality, and gonadosomatic indices of gray triggerfish in the north central Gulf. Murie and Parkyn (2005) reported growth differences in white grunt *Haemulon plumieri* between two areas about 70 km apart in the NE Gulf.

Most of the ground-breaking work on this phenomenon has occurred on the Great Barrier Reef. Mortality rates of *Centropyge bicolor* differed by as much as an order of magnitude and life expectancies ranged from 1 to 13 yr among four reefs no more than 6 km apart (Aldehoven 1986). In one of the most comprehensive studies, Gust et al. (2002) found significant differences in growth, asymptotic size, mean age, longevity, and mortality in two, virtually unexploited scarids – *Chlorurus sordidus* and *Scarus frenatus* – between mid- and outer-shelf reefs separated by about 20 km. Hart and Russ (1996) reported significant differences in mean length, growth rates, and size at age in *Acanthurus nigrofuscus* on reefs as close as 3 km apart. Size structure, growth, and mortality of *Lutjanus carponotatus* differed among reefs no more than 20 km apart

(Kritzer 2002); age structure and total mortality varied significantly in *L. adetii* and L. *quinquelineatus* among reefs separated by no more than 10's of kilometers (Newman et al. 1996).

Small spatial scale differences in population biology are apparently not restricted to reef fishes. Berg and Pedersen (2001) found significant differences in growth and size at maturity in cod *Gadus morhua* in two connected fjords in Norway. Olsen et al. (2004) reported significant differences in size at age and mortality among local populations of *G. morhua* along the Norwegian Skagerrak coast.

Small Scale Variability – Causes

These observed, persistent differences in size and age structure, growth, and mortality among red porgy collected from sites ≤60 km apart most likely reflect phenotypic, not genetic, effects. Cultured pelagic larvae of this broadcast spawner transformed to juveniles at 23-32 d (Mihelakakis et al. 2001), and there are no obvious physical, oceanographic, or physiological barriers to prevent gene flow over such small distances. Mitochondrial DNA analysis indicated that red porgy from the northeastern, northwestern and southwestern Atlantic were genetically distinct, but within those populations diversity was low (Ball et al. 2003). That the four sites with the largest sample sizes all showed the same shift from a modal age of 3 in 2000 to 4 in 2001 suggests that recruitment is uniform among sites, i.e., the individual sites are probably not closed populations; and therefore, the demographic differences probably reflect post-recruitment effects. (Dudgeon et al. 2000) found no genetic evidence of population structuring in two scarids with significantly different life history traits and demographics at reefs ~20 km apart (Gust et al. 2002).

Two overriding factors - spatial heterogeneity of their environment and site fidelity - probably explain why the demographics and life history traits of red porgy are so variable at such a small spatial scale. The continental shelf in the NE Gulf off NW Florida is quite heterogeneous. The very low-relief (typically flat) live bottom habitat preferred by red porgy is widespread spatially and bathymetrically but very patchy, with patches varying greatly in size and usually separated from each other by large areas of sand bottom (Thompson et al. 1999, pers. obs.). These patches, although most are grossly similar, have variable hydrological, geological, biological, and ecological characteristics; and although overall the species is lightly fished, range from

unexploited to heavily exploited. Exploitation is probably one of the more variable and potentially influential factors affecting red porgy demographics, at the very least truncating size and age structure, i.e., growth overfishing (Law 2000); and likely explains why, on average, red porgy at the two shallowest sites, which were also closest, by far, to the nearest port, were youngest, among the smallest, and had the highest mortality rate. This was further confirmed by a significant negative relationship between mean age and instantaneous fishing mortality rate (Figure A.16).

Biological and ecological characteristics likely to vary among patches include density, predator and prey composition and density, as well as inter- and intra-specific competition. Diets of red porgy - opportunistic browsers with extremely diverse food habits (Manooch 1977) – must vary qualitatively and quantitatively among habitat patches, almost certainly resulting in variable growth, which in turn could impact many other population traits. Predator density and species composition could impact size and age structure and mortality, and potentially, assuming socially mediated sex change, size and age at transition and sex ratio. Rodd and Reznick (1997) found an association between demography and predators in wild guppy populations. Competition, both inter- and intraspecific, if for food resources, could impact growth; and if for space, because of their complex social and mating system, could affect sex ratio and size and age at transition. Jones (1987) demonstrated that the presence of adult *Pomacentrus amboinensis* had a significant effect on the growth and mortality of one year old fish.

What little tagging data there is indicates that adult red porgy exhibit considerable site fidelity, making only limited movements (Grimes et al. 1982, Beaumariage 1969, Collins et al. 1996). Because of that site fidelity, once red porgy recruit to a given patch of habitat, they are exposed to a unique suite of the various factors discussed above which act in concert to yield phenotypic changes unique to that group of fish. Site fidelity characterizes most, if not all, of the species whose population biology has been shown to vary significantly at small spatial scales, including *B. capriscus* (Ingram 2001), *H. plumieri* (Murie and Parkyn 2005), *P. leopardus* (Davies 1995), *C. sordidus* and *S. frenatus* (Gust et al. 2001), and *C. bicolor* (Aldenhoven 1986). There is good evidence that *P. auratus*, a congener of red porgy, are quite site fidelic (Willis et al. 2001, Moran et al. 2003), as are other reef sparids (Negpen 1977 cited in Buxton and Allen 1989, Buxton and Allen 1989, Griffiths and Wilke 2002).

Previous studies, most of which have focused on unfished or very lightly fished species or populations, have attributed small scale variability in demographics and life history traits to variation in predation, food availability, environmental parameters, density, and recruitment. Gust et al. (2002) concluded that growth differences at a scale of 20 km in two unexploited scarids was a density dependent effect, i.e., the combination of large differences in food levels and numbers of individuals. These authors speculated that differences in mortality rates reflected differences in predation rates, possibly related to differences in predator numbers, size structure of the scarids (higher rates on reefs with smaller fish), and habitat complexity (higher rates with reduced complexity). An earlier study on a Caribbean parrotfish attributed major changes in growth between reefs only 3 km apart to seasonal differences between the reefs in the availability of the algae they fed upon (Clifton 1995). Hart and Russ (1996) found significant differences in growth rates, mean size, and sizes-at-age in *Acanthurus nigrofuscus* among reefs separated by only 10's of kilometers; they concluded their findings were consistent with the hypothesis that growth would be higher on reefs impacted by crown-of-thorns starfish because more food was available there. Kritzer (2002) reported differences in growth, size structure, and mortality in *Lutjanus carponotatus* among four islands separated by ≤15 km and speculated the former may reflect density dependence or terrigenous influences (physiological stress from turbidity), while recruitment variation may have affected mortality. Newman et al. (1996) found significant differences in growth, age structure, and mortality in *L. adetii* and *L. quinquelineatus* among four reefs separated by ≤40 km; they hypothesized that spatially variable recruitment and persistence of strong cohorts contributed to the variability of the latter two traits. Abundance patterns of adult *Tautogolabrus adspersus*, a temperate reef fish, were thought to reflect differential mortality among habitats with different patch structure (Levin 1993). Berg and Pedersen (2001) hypothesized that a large difference in growth rate of cod between two connected fjords was caused by differences in diet, food intake rates, and possibly water temperature.

Size Composition

The red porgy I collected off northwest Florida were generally smaller, in some cases considerably so, than those collected in other studies in the southeastern U.S., all of which pooled data from large areas. Hood and Johnson's (2000) larger sizes likely reflect their use of

data pooled from many locations, and even more importantly, their use of fishery dependent data, which is often quite selective (Potts and Manooch 2002). Commercial and at least some headboat fishermen likely use larger hooks than I used, which would exclude small fish. Also, experienced captains would target places, such as my 3x5's site, known to hold larger fish, and avoid those, such as Ivy's Reef, which usually produce small fish. Most of Hood and Johnson's specimens came from the Florida Middle Ground, where depths are 26- 48 m (Smith et al. 1975), so the size differences between our two studies cannot be attributed to differences in sampling depths, nor does it appear to reflect regional differences in size structure. The mean size of a few collections I made in that area (311 mm, n=309) was only 2 mm larger than the mean at 3 x 5's, although the range was slightly larger (194- 472 mm vs. 221-400).

In the SAB, red porgy from the recreational headboat fishery in the early 1970's were much larger than those I collected, averaging 388 mm in depths <50 m and 437 mm in depths >50 m (Manooch 1975). There is no way to determine whether or how much these values reflect actual differences between the Atlantic and Gulf because, like Hood and Johnson's (2000) study, his findings were based on fishery dependent data, with its inherent selectivity. During 1988-94, Harris and McGovern (1997) collected red porgy averaging 300 mm (mode ~280 mm) in a fishery independent survey using traps (75%) and hook and line (25%) off the Carolinas. These sizes were very similar to what I found at the Good Bottom site and slightly smaller than those at the 3x5's, although they did have higher proportions of large fish and maximum sizes about 50 mm larger, suggesting that the Atlantic fish may typically grow slightly larger than those in the northeastern Gulf. The large difference in sizes between these two SAB studies probably reflects a real decrease as well as a selectivity effects because of gear differences and fishery dependent vs. independent sampling. Vaughan and Prager (2002) documented significant declines in mean weight of red porgy in both headboat and commercial catches from about 1978 to 1991, as well as sharp declines in catch per effort in the headboat fishery and the MARMAP fishery independent survey.

The weak evidence I found of a positive relationship between size and depth is consistent with the findings of most studies. As mentioned above, Manooch (1975) reported mean sizes of 388 mm in depths <50 m and 437 mm in depths >50 m from the headboat fishery in the SAB. Harris and McGovern (1997) found larger, older individuals ($P<0.05$) in deeper areas (46-90 m) in the SAB, but did not indicate how large those differences were. In addition, very large red porgy

400-550 mm are regularly caught in the deepwater grouper longline fishery off southwest Florida in depths of 128-183 m (70-100 fm)(Lew Bullock, Florida Fish and Wildlife Research Institute, St. Petersburg, FL, personal communication, 1999). Harris and McGovern (1997) speculated that the differences reflected lower fishing mortality rates in the deeper waters or an ontogenetic shift. The former explanation seems more likely, given that all evidence indicates adults move little (Grimes et al. 1982), and small individuals seem to occur at all depths. The lower end of the size and age distributions were the same inshore and offshore in Manooch's (1975) study. Labropoulou et al. (1999) caught juvenile red porgy <186 mm FL as deep as 250 m in trawls off Crete, although they were most abundant at 25- 50 m. I also collected small and young fish throughout the depth range sampled (Figures 3.3 and A.12). Conversely, Roumillat and Waltz (1993) found no differences in size or age structure in the SAB in 10 strata from 20 to 69 m during 1979-87.

Age Composition

The only other study of red porgy in the NE Gulf (Hood and Johnson 2000) reported the same maximum ages I found (♀:10, ♂:17), and similar low numbers of males < age 3 (1.8% vs. my 2.6%). Their modal ages for both sexes were one year older than mine, possibly reflecting lower fishing mortality rates in their sampling area because of its great distance from shore, although it could also reflect some selectivity effects as well. The age structure and modal age of a pooled sample (n = 307) from several fishery independent collections I made in the same general area (Florida Middle Grounds) was very similar to their findings. The slightly younger maximum and modal ages (♀:9 and 2, ♂:14and 3) found by Roumillat and Waltz (1993) in a fishery independent survey in the SAB, 1979-87, possibly reflect the truncating effects of overexploitation (Harris and McGovern 1997). Other SAB studies found red porgy to age 15 using scales for ageing (Manooch and Huntsman 1977) and 18 using sectioned otoliths (Potts and Manooch 2002). Similar maxima, 13-16 yr, have been reported from the eastern and southern Atlantic (Vassilopoulou and Papaconstantinou 1992, Serafim and Krug 1995, Pajuelo and Lorenzo 1996; Cotrina and Raimondo 1997). Although they may live 18 yr, very few exceed 12 yr. In the Gulf I found only 4 of 3442 (0.1%) and Hood and Johnson (2000) reported 5 of 854 (0.6%) older than 12 yr; similarly, only 0.1-0.4% were that old in the SAB (Manooch and Huntsman 1977, Harris and McGovern 1997, Potts and Manooch 2002).

Growth

At least three pieces of evidence support my conclusion that growth of red porgy in the NE Gulf varies at a scale of only 10's of kilometers and this variability is a permanent feature of their population ecology. First, variability in size at age as indicated by mean CV at age was less within sites than for all sites pooled (7.3±0.9 vs. 9.8±0.8). Secondly, the relationships of size at age among sites, i.e., their rankings with respect to each other, were very consistent at each age for ages 2 - 7. For example, 3.5's was always highest, Good Bottom was always third highest, and Ivy's Reef was always lowest. Lastly, that the growth differences were temporally stable over two years argues most strongly that this is a permanent phenomenon (Figure A.15). These spatial differences in growth do not appear to be depth-related, as the 3x5's, with the highest growth rate, was the third (of 9) shallowest site (41 m), while Ivy's Reef, with the lowest growth rate, was the second deepest (62 m). This is consistent with Harris and McGovern's (1997) finding no differences in size at age between fish from 0 to 45 m and 46 to 90 m using spatially pooled samples.

The considerable growth differences among sites, especially weight at age, could have significant implications regarding fecundity, and hence, population dynamics. Assuming that weight and fecundity are directly proportional to body volume, and given that weights at ages 2-4 were 54-71% larger at 3x5's than at Ivy's Reef, it is quite likely there are similar age-specific differences in fecundity between those sites. Depending on the age composition and overall population size at each site, such differences could have measurable effects on regional population dynamics, although admittedly, these two sites represented the extremes. Schultz and Warner (1991) found a significant correlation between growth and fecundity in *Thalassoma bifasciatum* on three reefs in close proximity to each other.

These spatial differences in size and weight at age could also affect mortality rates – both natural and fishing. Certainly predator suites and predation rate are bound to vary with fish size, and combined with spatially varying size at age, natural mortality would likely follow suite. If the growth differences result in noticeable differences size structures among areas, then, assuming other factors (e.g., distance from port) are equal, exploitation rates are likely to be higher in areas with larger fish than in those with smaller individuals.

Although no other studies have examined variability in growth of red porgy at a scale of 10's of km, comparisons of my results with those of past studies certainly has some merit. In the NE Gulf, Hood and Johnson's (2000) estimates of mean observed size at age for ages 1-10 (n's of 7-189) averaged 41 mm larger (range: 22-55) than my pooled estimates, although the growth trajectories were basically parallel (Figure 3.8). Their estimates for ages 1-8 averaged 61 mm larger (range: 39-77) than those from Ivy's Reef, the site with the lowest growth rate (Figure 3.8). Their estimates were, however, close to those from the 3x5's site (which had the highest growth rate) for ages 2-6, averaging only 10 mm larger (range: -5 – 19); this similarity is certainly consistent with the hypothesis that many of the differences between our studies more likely reflect size selectivity effects of their fishery dependent sampling, not real regional differences.

Harris and McGovern's (1997) observed sizes at age (1994 data) indicate that red porgy in the SAB follow a growth trajectory very similar to that of Gulf fish, at least at ages 2-8, but appear to grow faster before then, so that they are consistently larger at ages 2 and older (Figure 3.8). SAB fish averaged 25±11 mm larger at age than those at 3x5's for ages 2-7 and 78±18 mm larger than fish at Ivy's Reef ages 2-8. The fishery independent origin of Harris and McGovern's (1997) estimates lends credence to the conclusion that these are real differences between the Gulf and SAB; and the fact that their estimates were derived from spatially pooled data would only tend to minimize the differences. Manooch and Huntsman (1977) and Potts and Manooch (2002) reported much larger observed sizes at age in the SAB for fish > age 2 or 3, and a much steeper growth trajectory, i.e. higher growth rate and larger maximum size (Figure 3.18). Although each SAB study used a different ageing method (M&H: scales, P&M: sectioned sagittae, H&M: whole sagittae), the most likely explanation for the difference between Harris and McGovern (1997) and the other two studies is the sampling design. The former used fishery independent data, while the latter two studies used only, or 80% in the case of Potts and Manooch, fishery dependent data, with its almost certain bias for larger, faster growing individuals.

That my overall estimate for L_∞ when t_0 was not constrained was 343 mm, and yet fish 400-550 are caught in deep (128-183 m) waters of the eastern Gulf, is somewhat troubling, although there is no information on the demographics or abundance of these very large fish or their importance to the population(s).

My finding that males were larger at age than females for ages 3-5 appears to be consistent with those of Roumillat and Waltz (1993) and Pajuelo and Lorenzo (1996), although the latter did not say which sex was larger. Hood and Johnson (2000) and Serafim and Krug (1995), however, found no difference is size at age between sexes.

Mortality / Survival Rates

Most of the large spatial variability I found in total mortality was very likely due to differences in fishing mortality, although natural mortality may certainly have played a role. The John's 248 site, which had the highest ML estimate of total mortality (0.98) and the highest fishing mortality rate (0.62 using pooled M or 0.69 using site specific M), probably receives much more fishing pressure than any of the other sites because it is 10-20 nm (19-37 km) closer to St. Andrew Bay Pass, the closest access point to the Gulf. It is also possible that there is some ontogenetic movement from this shallowest of standard sites (which would be indistinguishable from mortality), but this is purely speculative. Conversely, Ivy's Reef, with the lowest ML estimates of Z (0.43) and F (0.07 or 0.04), is most likely very lightly exploited. This site was the second farthest from St. Andrew Bay Pass (~38 nm or 71 km), consistently produced small fish, was not very close to any obvious, easily found bottom features that would attract anglers pursuing the much more sought after snappers and groupers, and I never observed any other boats fishing close to that location. The sites with the second, third, and fourth highest Z's – Sig1_2 (0.85), Whoopi Grounds (0.82), and 3x5's (0.75) – although all were also quite distant from the Pass (~35 nm or 65 km), were immediately adjacent to well known, easily located, high profile rocky ridges (5-6m relief) which run for kilometers, and therefore are much more likely to be fished than the other sites which were similar distances from port but which were not as close to such attractive fishing areas.

The variability in natural mortality rates among sites was not surprising, given that M is a function of the von Bertalanffy parameters k and L_∞ in the Pauly equation and there were significant differences in growth among sites. The rankings of sites with respect to M differed greatly from the rankings by Z. The John's 248 and Sig1_2 sites had the highest and second highest total mortality rates (ML method) but the second lowest and lowest natural mortality rates (Tables 3.3 and 3.4). Given that Z = M+F, these differences in rankings are further evidence that there is considerable variability in fishing mortality (F) among sites. Although

natural mortality rates of red porgy, especially that due to predation, almost certainly vary spatially, the accuracy of these site specific estimates of M is questionable. Their biggest weakness is that they are a function of L_∞ and k, which, as previously mentioned, are highly correlated and extremely sensitive to the range and distributions of the observations used in their calculation. MacPherson et al. (2000) urged great caution in using indirect methods such as Pauly's (1980) to estimate M because they assume those values are constant for a species and independent of the potentially variable ecosystem which it inhabits. Given these likely problems with M, the accuracy of my site specific estimates of fishing mortality, derived from M and Z, are also questionable - the existence of spatial variability in F, however, is not. The patchiness of live bottom and reef habitat, as well as the logistical constraints and differences in numbers of small versus larger boats, strongly argue that it is certain, a conclusion supported by extensive personal observations and local knowledge. Ingram (2001) found that fishing mortality in gray triggerfish decreased with distance from shore.

My site-specific, fishery independent estimates of total mortality (ML: 0.43-0.98, LS: 0.54-0.90) bracketed Hood and Johnson's (2000) fishery dependent, pooled estimates from the NE Gulf for commercial, recreational, and headboat fisheries (0.54, 0.62, and 0.87, respectively). Manooch and Huntsman (1977), applying age-length keys to unaged fishery dependent samples collected from the headboat fishery in the SAB during 1972-1974, estimated Z's of 0.29-0.55 (overall mean: 0.44), depending on the area, year, and method used. Using a method based on age of the oldest fish observed, sample size, and age of recruitment to the sampling procedure (Hoenig 1983), Vaughan and Prager (2002) estimated Z=0.58 in the SAB, and considered that to be a likely upper bound of M. They also estimated F's for fully recruited ages (4+) in the SAB to be 0.11-0.20 during 1972-78, 0.28-0.43 during 1982-86, and 0.40-0.66 during 1992-96, depending on the catch matrix and value of M used (0.20-0.35). Total, natural, and fishing mortality for a lightly fished stock in the eastern Mediterranean Sea were estimated to be 0.34, 0.22, and 0.12, respectively (fishery independent data, n=151) (Vassilopoulou and Papaconstantinou 1992). Fishery dependent length samples (n=9129) from a heavily fished population in the Canary Islands, aged with a growth curve, yielded estimates of Z, M, and F of 0.56, 0.32, and 0.24 (Pajuelo and Lorenzo1996). Cotrina and Raimondo (1997) estimated M to be 0.182 for red porgy off Argentina in the southern Atlantic.

Population Structure

The consistent, persistent, significant differences in size and age structure, growth, and mortality at sites separated by only 10's of kilometers strongly suggests that red porgy in the NE Gulf are composed of a great many local subpopulations. It is possible that the fish on each significant patch (or closely adjacent patches) of suitable hard bottom habitat, with their unique suite of population traits, represent one of these subpopulations, although at this point that is speculation. With such a population structure, red porgy closely resemble Crowder et al.'s (2000) definition of sources and sinks – "areas of differing demographic rates dictated by underlying differences in habitat quality". Pulliam (1988) defined sources in a population at equilibrium as habitat patches in which birth rate exceeds death rate and immigration exceeds emigration, while sinks are patches where deaths exceed births and emigration exceeds immigration. Pulliam defined sources more generally for non-equilibrium situations as habitat patches with a net export of individuals but no net change in population size, while sinks are net importers. Crowder et al. (2000) attributed the rise of source-sink population dynamics theory to the observation that habitat quality varies, and likened it to metapopulation dynamics with the exception that demographics can differ among patches.

Red porgy population structure in the NE Gulf is not a classical metapopulation as defined by Levins (1970) i.e., a"population of populations that go extinct and recolonize", and which are exposed to the same conditions in each habitat patch. Smedbol et al. (2002), however, argued that it was necessary only that extinction was a possibility in at least one subpopulation for a system to be considered a metapopulation, but it was not essential that extinction and colonization events be documented. It is very likely that the low profile hard bottom habitat patches red porgies typically inhabit are occasionally completed buried by sediment during hurricanes. While such an event may not actually kill the individuals on that patch, it would essentially result in the extinction of the subpopulation by forcing it to emigrate to other unburied patches. A video survey in early 2006 in the Madison/Swanson MPA offshore of my study area documented the complete burial by sand of 2m high reefs in depths >65m, presumably caused by the almost 20m waves of Hurricane Katrina in 2005, and these were reefs observed one year earlier covered with large numbers of reef fish (Andrew David, NMFS Panama City Lab., personal communication, 2006).

The population structure in the NE Gulf is consistent with Kritzer and Sale's (2004) broader definition of metapopulation, i.e., "a system of discrete local populations, each of which determines its own internal dynamics to a large extent, but with a degree of identifiable and nontrivial demographic influence from other local populations through dispersal of individuals", a more inclusive view originally proposed by Hastings and Harrison (1994) and Hanski and Simberloff (1997), but not universally accepted (Smedbol et al. 2002, Grimm et al. 2003). Sale (1998) argued that the patchy nature of reef habitat, and the typically pelagic larval stages and sedentary adults of reef fishes, ensure they "exist as metapopulations". Only recently a few have used the term to describe population structure of marine fishes - *Clupea harengus (*McQuinn 1997), *Gadus morhua* (Smedbol and Wroblewski 2002), and some flatfishes (Bailey 1997); ironically, none are reef fishes. Man et al. (1995) used modeling to investigate the implications of using marine reserves to conserve and benefit species with a metapopulation structure.

Whether the groups of red porgy with their unique population traits are labeled local subpopulations, sources and sinks, or as members of a more broadly defined metapopulation (sensu Kritzer and Sale (2004)), the critical thing to remember is the significant implications regarding stock assessment and management of a species with such a complex population structure. Estimates of size and age structure, growth, and mortality will certainly be sensitive to the location and spatial weighting of the samples. Data pooled from a large area without regard for its spatial distribution will likely encompass multiple subpopulations, each with a potentially unique suite of population parameters. "Dynamics of neighboring sub-populations can be quite different from each other and from the global average" (Sale 1998). This pooled data may yield skewed parameter estimates, which in turn could bias stock assessments and the models used to predict responses to exploitation; it could also introduce excessive variability to the parameter estimates. Selectivity of fishery dependent data (Potts and Manooch 2002) is likely to be even more problematic for species with such a complex population structure. Besides the typical gear selectivity problems, fishing is likely to be focused on a limited number of sites (i.e., subpopulations) where the fish tend to be larger (e.g. my 3x5's site) (Law 2000). If those fish have significantly higher growth rates than surrounding unfished or lightly-fished subpopulations, as is the case at the 3x5's site, then growth estimates derived from that data will overestimate the potential yield from the overall population and its capacity to withstand the effects of fishing. Fishery independent sampling would greatly reduce the likelihood of this

problem, although it could still occur, depending on the spatial distribution and weighting of the samples. For example, if a subpopulation with a very low growth rate (e.g., Ivy's Reef) was over-sampled, it could result in an overly pessimistic stock assessment, and the capacity of the overall population to withstand fishing would be underestimated. Using minimum estimates of growth and natural mortality to predict the effects of fishing on the overall population, would however, be a very risk averse management option.

If more than one or two of the subpopulations sampled happen to be sinks, population-management decisions based on those data could lead to undesirable results (Pulliam 1988). This author also concluded that habitat-specific demographic rates may in many ways outweigh age-specific rates in their ecological importance, even though the latter have received much more attention in the literature. It is possible that the crash of the fishery in the SAB resulted from recruitment overfishing (possibly even an Allee effect) if the subpopulations targeted by the fisheries were mainly sources and not sinks; Vaughan and Prager (2002) found weak evidence of depensation in the spawner–recruit relationship during 1972-94.

Given the apparent complex population structure of red porgy in the NE Gulf, and the logistical difficulty of accurately identifying and assessing large numbers of subpopulations and then managing them, this species seems to be an ideal candidate for management by marine protected areas (MPA). Use of MPA's would greatly reduce, if not eliminate, the onerous recurring data needs of the standard method of managing fisheries in the southeastern U.S., i.e., stock-specific annual or periodic stock assessments resulting in estimates of allowable catch. Which subpopulations are protected will largely determine the success of the MPA. In MPA's with the goal of protecting or enhancing fisheries for red porgy, it will be important to identify and include those subpopulations which serve as sources to the overall population, not as sinks, (Pulliam 1988, Pulliam and Danielson 1991, Crowder et al. 2000, Tuck and Possingham 2000). In a modeling exercise examining the responses of a 2 subpopulation metapopulation to various protection and recruitment scenarios, Tuck and Possingham (2000) concluded that exploitation of a source population when the metapopulation structure is not recognized can lead to large reductions in harvest.

Conclusions

My finding that red porgy in the NE Gulf comprise many, phenotypically distinct local subpopulations, and that many other studies cited herein found different demographics and/or life history traits within species at locations separated by no more than 10's of kilometers, strongly suggests that the population or stock structure of many exploited reef fishes may be much more complex than what many have assumed. At least three other species in the Gulf of Mexico besides red porgy – gray triggerfish (Ingram 2001), white grunt (Murie and Parkyn 2005), and vermilion snapper *Rhomboplites aurorubens* (pers. comm., Robert Allman , NOAA Fisheries, Panama City, FL) - show some evidence of subpopulation structure. Such complexity could certainly frustrate and confound the efforts of those trying to assess the status of these stocks and predict the effects of fishing on them, as it requires examination of population biology at much smaller spatial scales than typically done and use of more complex, spatially-explicit population models. "The importance of individual spawning groups (or sub-units of a population in an area) to assessment and management has received little attention over the past 30 years as fisheries have been managed in units which were based on a combination of biological, political, and administrative boundaries• (Stephenson 1999). It is likely that small scale population complexity has played some part in the failure of some southeastern U.S. reef fish fisheries to respond to management measures in recent years. For that reason alone, there is a pressing need to examine the population structure of reef fishes in the region at much smaller spatial scales than has historically been done to determine which, if any, have a more complex subpopulation structure. For those species with such a structure, MPA's may be an effective, efficient way to conserve and manage them by eliminating the perpetual and logistically difficult stock assessment requirements.

Table 3.1. Depth, location, bottom temperature range, and sampling information for the nine standard sites.

Site	Depth (m)	Latitude/ Longitude	Bottom Temp. EC	Number of Nonzero Collections	Total Sample Size	Sampling Dates
John's 248	29.8	30.073E N 86.038E W	17.5-27.2	15	147	Aug 99-Jul 01
Elbo Reef	30.5	30.068E N 86.050E W	19.4-27	16	152	Oct 98-Sep 01
3 x 5's	40.8	29.551E N 85.975E W	17.5-27	10	234	Jun 98-Jul 01
Good Bottom	46.9	29.620E N 86.052E W	17.3-26.2	23	595	Jul 99-Jul 01
Ridge	47.5	29.733E N 86.127E W	17.8-29.6	21	314	Jul 99-Aug 01
Sig 1_2	59.0	29.757E N 86.232E W	16.8-26.8	13	178	Sep 99-Aug 01
Whoopi Grounds	59.7	29.612E N 86.081E W	16.5-26	14	152	Mar 99-Sep 01
Ivy's Reef	61.6	29.643E N 86.222E W	17.8-24.5	16	416	Jun 00-Aug 01
Benny Allen	66.8	29.630E N 86.251E W	17.3-26	18	398	Jul 99-Aug 01

Table 3.2. Results of Kolmogorov-Smirnov 2-sample tests of overall size and age distributions among nine standard sites. Numbers in bold indicate sites which were not significantly different.

	Size Distributions															
	Benny Allen		Ivy's Reef		Whoopi Grds		Sig1_2		Ridge		Good Bottom		3 X 5's		Elbo Reef	
	ks	p	ks	p	ks	p	ks	p	ks	p	ks	p	ks	p	ks	p
Ivy's Reef	0.181	0.000														
Whoopi Grounds	0.358	0.000	0.513	0.000												
Sig1_2	**0.085**	**0.312**	0.241	0.000	0.284	0.000										
Ridge	**0.076**	**0.242**	0.137	0.002	0.397	0.000	**0.118**	**0.072**								
Good Bottom	0.369	0.000	0.522	0.000	**0.050**	**0.896**	0.308	0.000	0.405	0.000						
3 X 5's	0.542	0.000	0.686	0.000	0.209	0.000	0.477	0.000	0.581	0.000	0.184	0.000				
Elbo Reef	0.165	0.004	**0.084**	**0.373**	0.513	0.000	0.239	0.000	0.130	0.054	0.529	0.000	0.702	0.000		
John's 248	0.168	0.004	0.132	0.039	0.491	0.000	0.213	0.001	**0.125**	**0.077**	0.473	0.000	0.637	0.000	0.179	0.013

	Age Distributions															
	Benny Allen		Ivy's Reef		Whoopi Grds		Sig1_2		Ridge		Good Bottom		3 X 5's		Elbo Reef	
	ks	p	ks	p	ks	p	ks	p	ks	p	ks	p	ks	p	ks	p
Ivy's Reef	0.153	0.000														
Whoopi Grounds	**0.045**	**0.969**	0.198	0.000												
Sig1_2	**0.094**	**0.207**	0.239	0.000	**0.099**	**0.356**										
Ridge	**0.079**	**0.201**	0.200	0.000	**0.084**	**0.429**	**0.091**	**0.272**								
Good Bottom	0.136	0.000	**0.036**	**0.903**	0.175	0.001	0.230	0.000	0.216	0.000						
3 X 5's	0.164	0.001	0.152	0.002	0.142	0.043	0.169	0.005	0.208	0.000	0.117	0.020				
Elbo Reef	0.167	0.009	0.320	0.000	**0.153**	**0.066**	0.178	0.015	**0.123**	**0.121**	0.297	0.000	0.295	0.000		
John's 248	0.129	0.051	0.282	0.000	**0.091**	**0.498**	**0.078**	**0.643**	**0.085**	**0.428**	0.259	0.000	0.166	0.011	**0.129**	**0.178**

Table 3.3. Least squares and Robson-Chapman estimates of annual survival (S) and instantaneous total mortality (Z) rates of red porgy for the standard sites. The least squares S was calculated as e^{-Z} and the Robson-Chapman Z was calculated as -lnS.

Site	Depth (m)	Ages Used	n	Least Squares S	Robson-Chapman S	Robson-Chapman 95% CL	Robson Chapman Z	Least Squares Catch Curve Z	Least Squares Catch Curve 95% CL
John's 248	29.8	4-6	62	0.41	0.38	0.359 - 0.395	0.98	0.90 [1]	2.927 - 1.135
3x5's	40.8	4-7	137	0.44	0.47	0.465 - 0.480	0.75	0.81	1.207 - 0.417
Good Bottom	46.9	4-9	365	0.54	0.58	0.580 - 0.585	0.54	0.62	0.786 - 0.463
Ridge	47.5	4-8	134	0.51	0.52	0.511 - 0.525	0.66	0.67	0.772 - 0.565
Sig 1_2	59.0	4-6	69	0.41	0.43	0.410 - 0.445	0.85	0.90 [1]	2.025 - 0.233
Whoopi Grounds	59.7	4-6	73	0.43	0.44	0.423 - 0.457	0.82	0.85	1.679 - 0.026
Ivy's Reef	61.6	4-8	239	0.58	0.65	0.649 - 0.658	0.43	0.54	0.898 - 0.187
Benny Allen	66.8	4-7	200	0.51	0.53	0.527 - 0.538	0.63	0.66	0.885 - 0.442

[1]Regression was not significant.

Table 3.4. Site specific estimates of instantaneous natural mortality (M) and conditional natural mortality (n, which = $1-e^{-M}$) rates calculated using Pauly's (1980) equation. For one set of estimates, the L_4 and k used in the Pauly equation were derived from a von Bertalanffy growth equation in which t_0 was not constrained, while for the second set of estimates, t_0 was constrained to 0. An overall pooled bottom water temperature of 22.4EC was used in all calculations.

	t_0 unconstrained				t_0 constrained to 0			
Site	k	L_4	M	n	k	L_4	M	n
John's 248	0.2	338.8	0.29	0.25	1.12	277.7	0.94	0.61
3x5's	0.34	354.8	0.40	0.33	0.69	332.4	0.65	0.48
Good Bottom	0.22	369.8	0.30	0.26	0.59	328.4	0.59	0.45
Ridge	0.44	301.4	0.50	0.39	0.84	287.5	0.77	0.54
Sig 1_2	0.14	388.4	0.22	0.20	0.7	301.4	0.68	0.49
Whoopi Grounds	0.44	336	0.48	0.38	0.68	323.2	0.65	0.48
Ivy's Reef	0.29	295.8	0.38	0.32	0.81	275.7	0.76	0.53
Benny Allen	0.27	337.5	0.35	0.30	0.63	304.2	0.63	0.47

Table 3.5. Site specific estimates of instantaneous fishing mortality (F) and exploitation (u) rates derived from both maximum likelihood and least square estimates of Z and 2 estimates of M - the overall pooled Pauly estimate of 0.36 and the site specific estimates based on von Bertalanffy k and L_4 where t_0 was unconstrained. A is the annual mortality rate and equals 1-S, where S = annual survival = e^{-Z} ; and u=FA/Z. Estimates of u assume a Type 2 fishery in which fishing and natural mortality operate concurrently. Symbols and formulae follow Ricker (1975).

	Maximum Likelihood Z						Least Squares Z					
	M=0.36			Site Specific M			M=0.36			Site Specific M		
Site	A	F	u	M	F	u	A	F	u	M	F	u
John's 248[1]	0.62	0.62	0.39	0.29	0.69	0.44				0.29		
3x5's	0.53	0.39	0.28	0.40	0.35	0.24	0.56	0.45	0.31	0.40	0.41	0.28
Good Bot.	0.42	0.18	0.14	0.30	0.24	0.19	0.46	0.26	0.20	0.30	0.32	0.24
Ridge	0.48	0.30	0.22	0.50	0.16	0.12	0.49	0.31	0.23	0.50	0.17	0.12
Sig 1_2[1]	0.57	0.49	0.33	0.22	0.63	0.42				0.22		
Whoopi Gr.	0.56	0.46	0.32	0.48	0.34	0.23	0.57	0.49	0.33	0.48	0.37	0.25
Ivy's Reef	0.35	0.07	0.05	0.38	0.04	0.04	0.42	0.18	0.14	0.38	0.16	0.12
Benny Allen	0.47	0.27	0.20	0.35	0.28	0.21	0.49	0.30	0.22	0.35	0.31	0.23

[1]Least square estimates of Z for John's 248 and Sig1_2 were not significant.

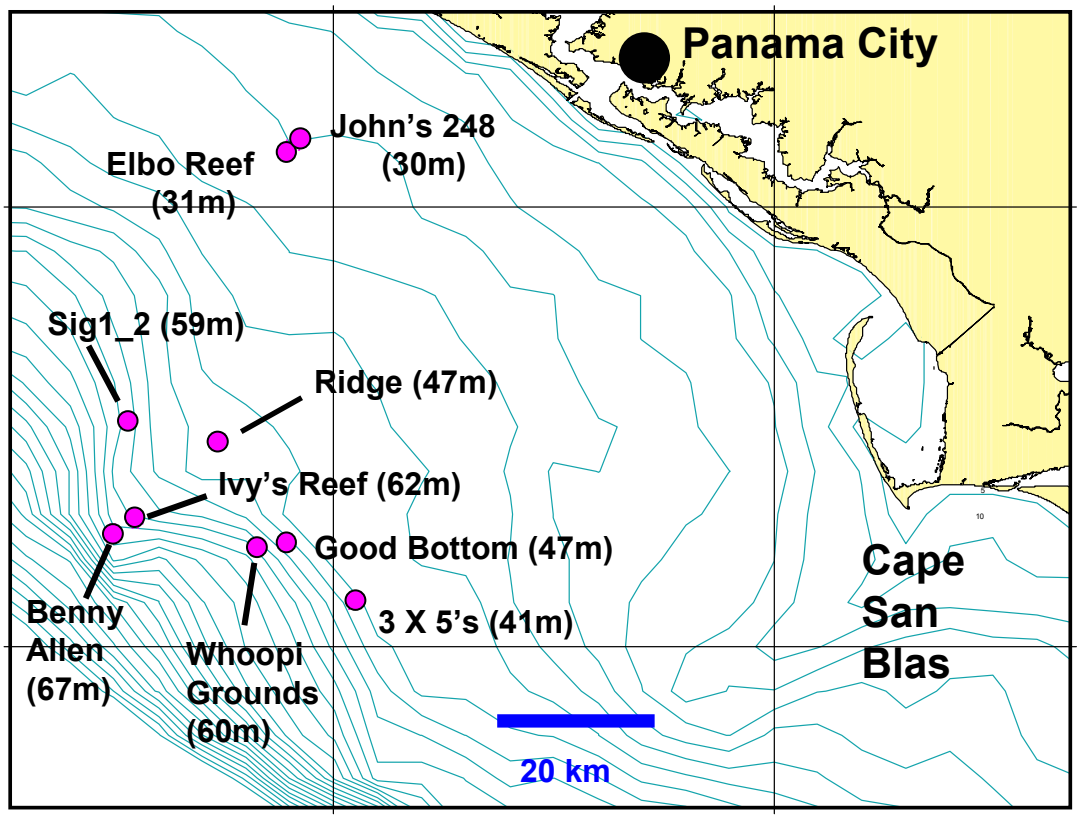

Figure 3.1. Locations and depths of the nine standard red porgy collection sites. Depth contours are 5m isobars.

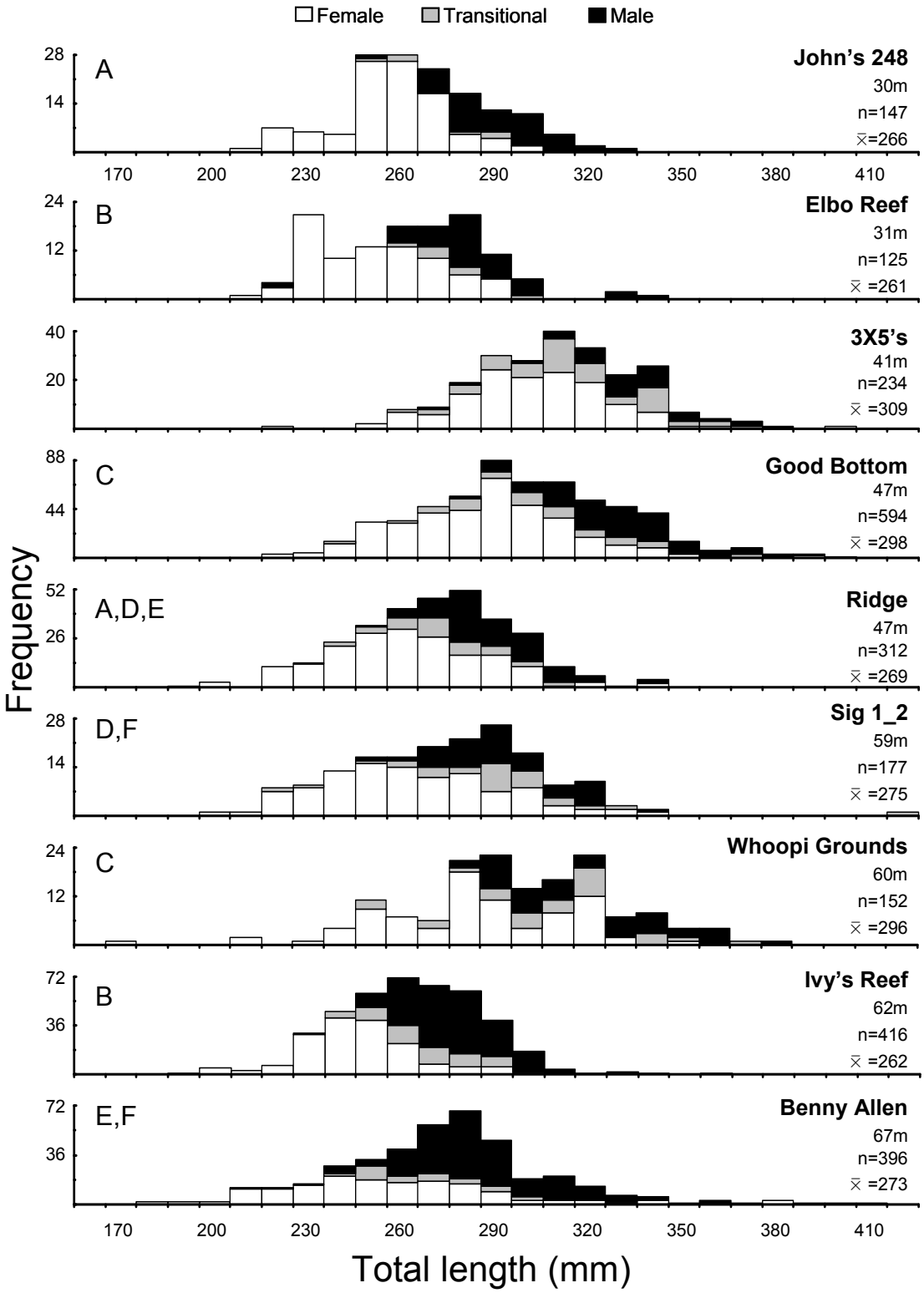

Figure 3.2. Overall length frequency distributions of red porgy at the standard sites. Distributions with like letters near the y axis were not significantly different.

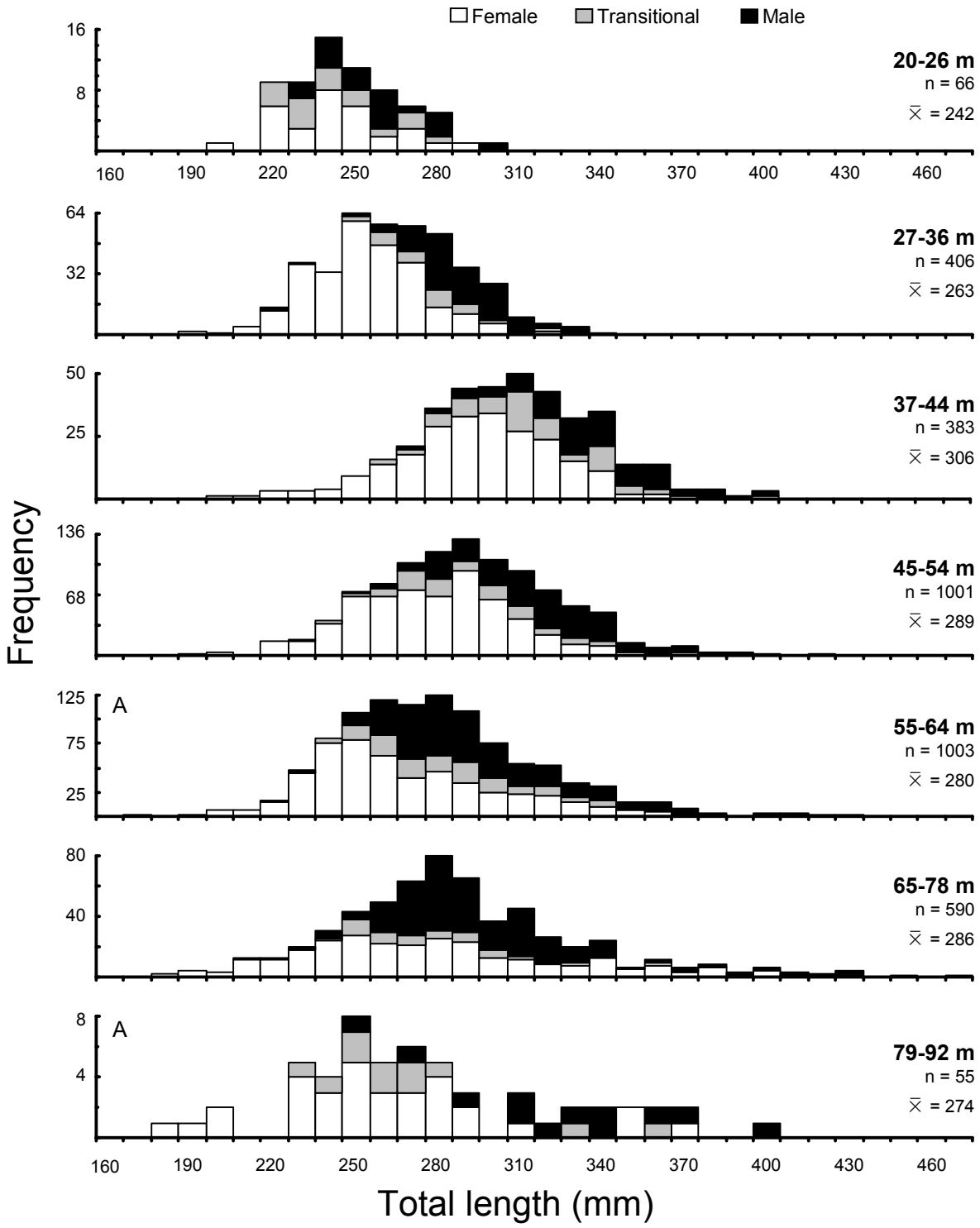

Figure 3.3. Overall length frequency distributions of hook and line-caught red porgy by depth interval. Distributions with like letters near the y axis were not significantly different.

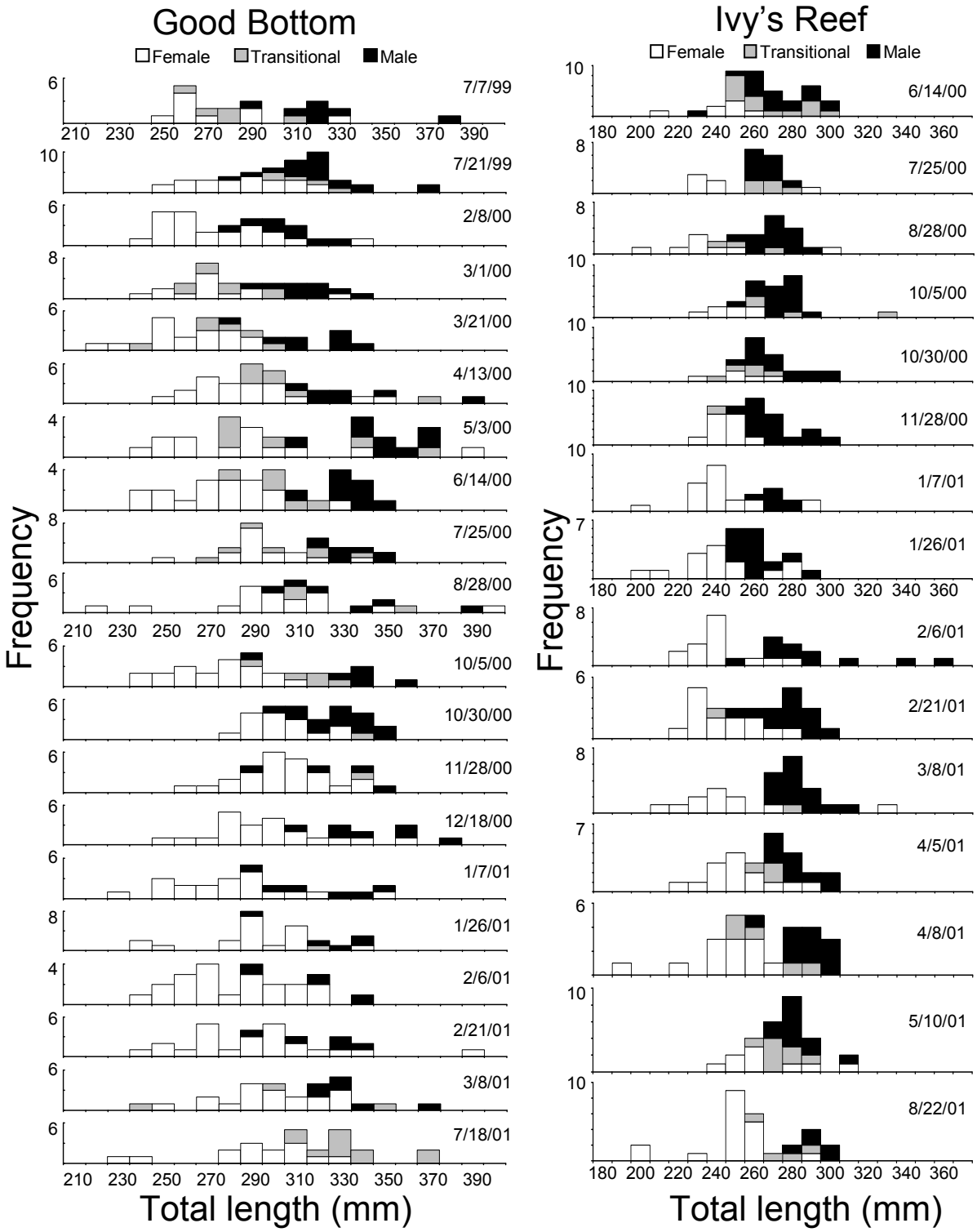

Figure 3.4. Length frequency distributions by collection for the Good Bottom and Ivy's Reef sites.

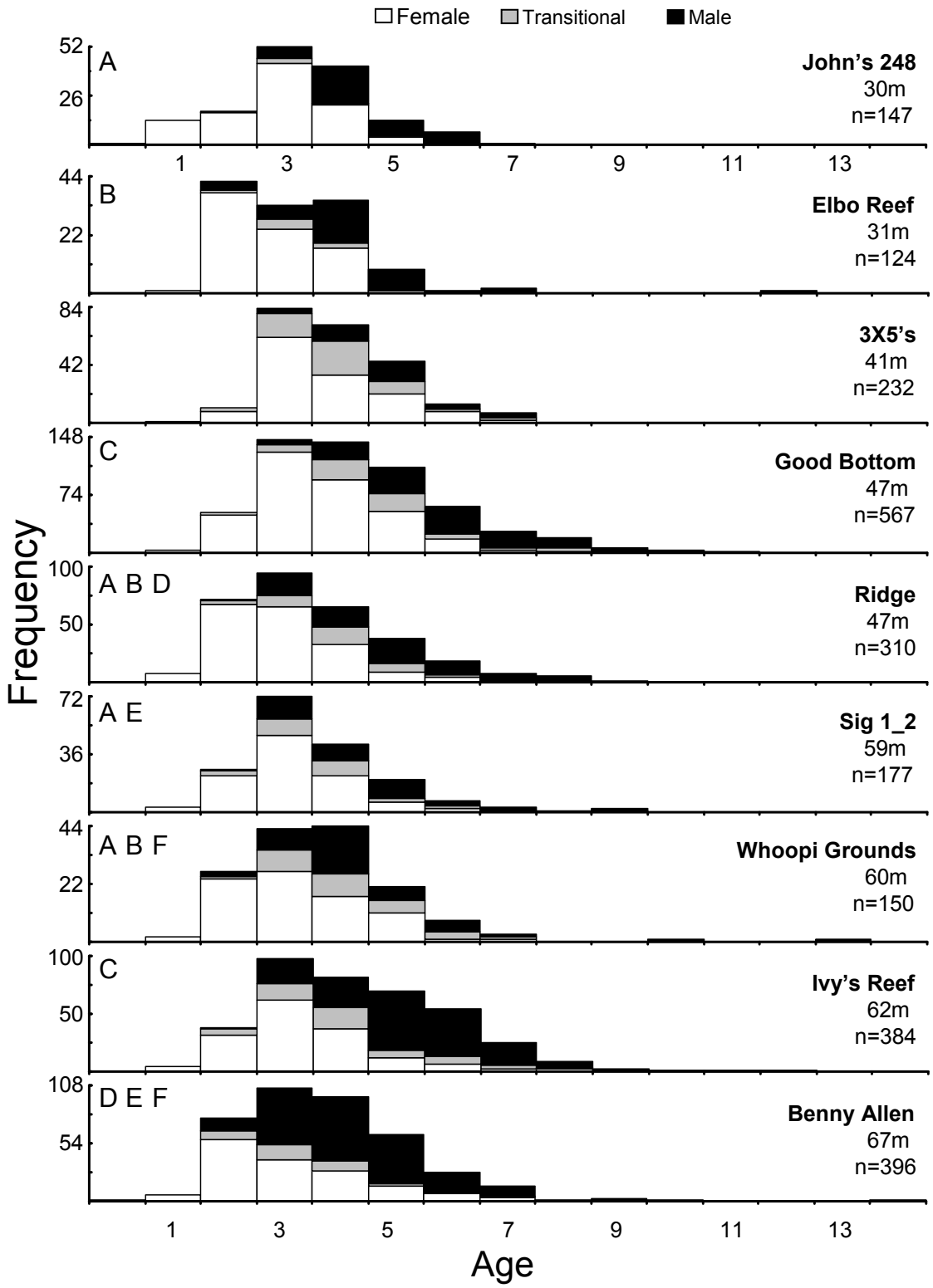

Figure 3.5. Overall age frequency distributions of red porgy at the standard sites. Distributions with like letters near the y axis were not significantly different.

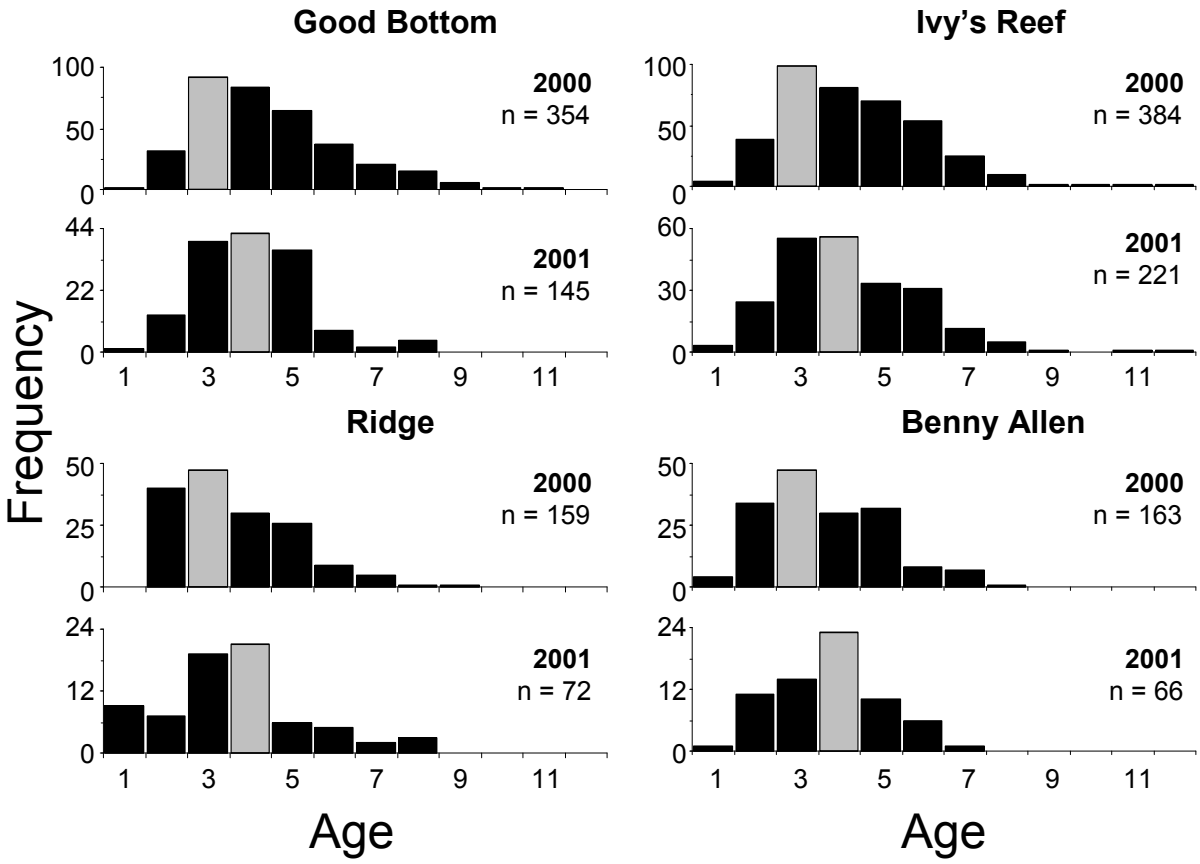

Figure 3.6. Age composition in 2000 and 2001 at Good Bottom, Ivy's Reef, Ridge, and Benny Allen. The gray bar indicates the modal age.

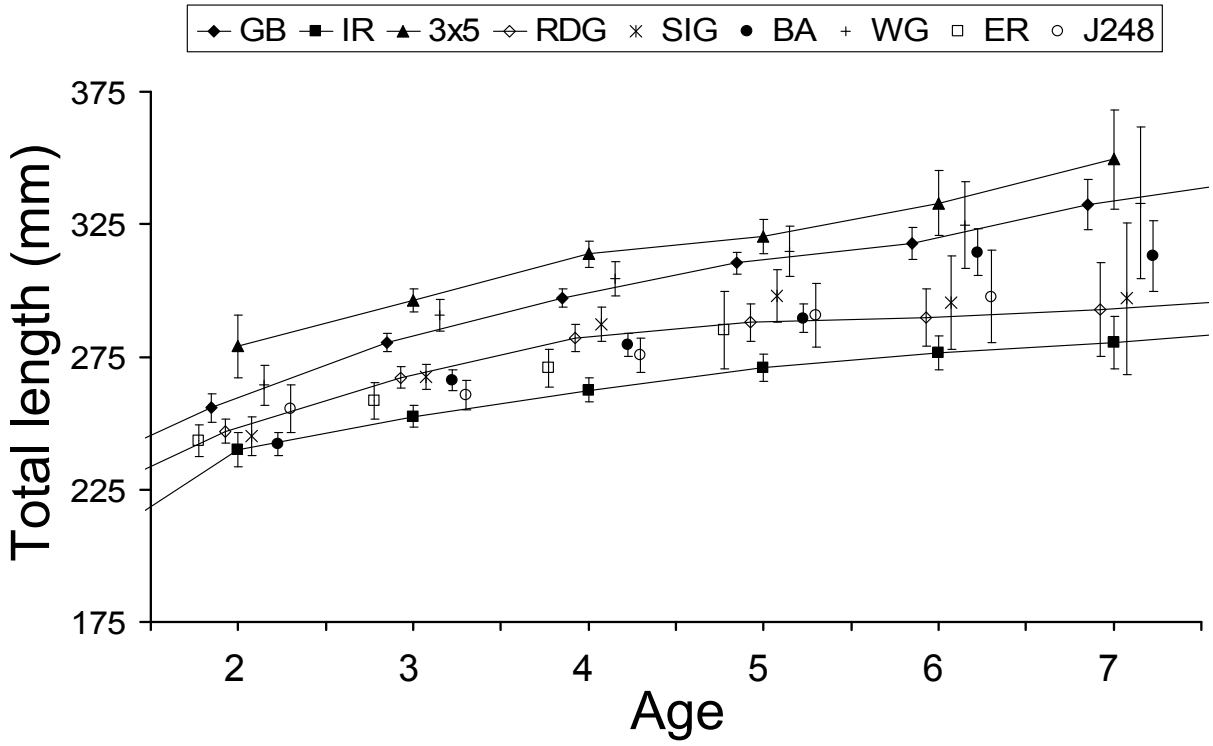

Figure 3.7. Mean sizes at age and 95% C.L.'s of red porgy ages 2-7. GB = Good Bottom, IR = Ivy's Reef, 3x5 = 3 x 5's, RDG = Ridge, SIG = Sig1_2, BA = Benny Allen, WG = Whoopi Grounds, ER = Elbo Reef, J248 = John's 248.

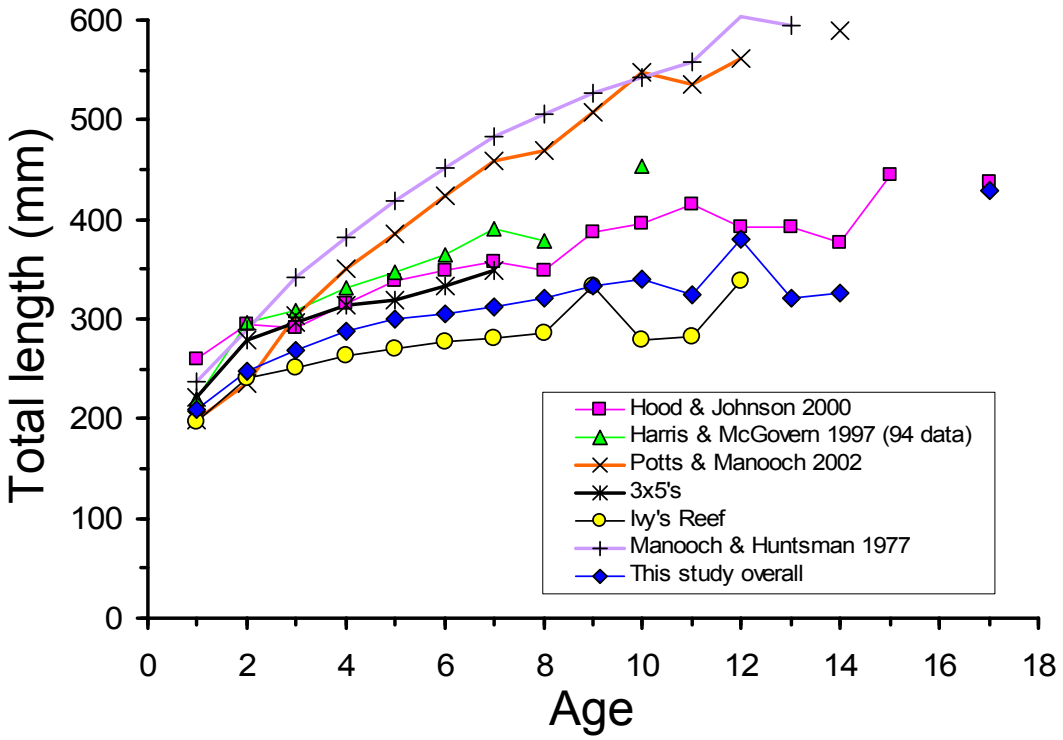

Figure 3.8. Mean observed sizes at age of red porgy among studies from the southeastern U.S.

CHAPTER 4

SPATIAL VARIABILITY IN MATURITY, RATES AND TIMING OF SEX CHANGE, AND SEX RATIOS OF *Pagrus pagrus* (SPARIDAE) IN THE NORTHEASTERN GULF OF MEXICO

Introduction

Beginning in the 1990's, there has been increasing focus on the importance of scale in the study of ecology, how the spatial extent of a study can greatly affect what patterns are observed and what conclusions are drawn regarding processes such as population dynamics or coexistence of species (Levin 1992, Camus and Lima 2002). Jones (1991) and Sale (1998) stressed the particular importance of considering scale when studying the dynamics and demographics of reef fish populations, in which different processes appear to unfold at different spatial scales. This issue looms large in the conservation and management of fishery stocks; Robertson et al. (2005) urged fishery scientists to consider carefully habitat effects on size, growth, and abundance because these factors can confound or overwhelm the effects of fishing, especially when making the typical large-scale regional comparisons.

Important spatial effects on reef fishes have been discovered by fisheries ecologists at smaller spatial scales ranging from dozens of meters to dozens of kilometers. Virtually all earlier studies have dealt with species that were easier to study, small-bodied taxa such as labrids (Jones 1980, Warner and Hoffman 1980, Cowen 1990), pomacentrids (Aldehoven 1986, Meekan et al. 2001, Kingsford and Hughes 2005), and acanthurids (Hart and Russ 1996). More recently, the focus of these studies has shifted to larger, usually exploited species, such as lutjanids; and much of the effort has focused on Australia's Great Barrier Reef (Newman et al. 1996, Kritzer 2002). These studies have examined a variety of taxa, some of which were protogynous, including serranids (Ferreira and Russ 1995, Adams et al. 2000), lethrinids (Williams et al. 2003), and scarids (van Rooij et al. 1996, Dudgeon et al. 2000, Gust et al. 2001, 2002, Gust 2004) One of the most provocative results of these studies is the discovery that in protogynous species there is substantial spatial heterogeneity in the timing of sex change.

Despite the substantial number of reef fish species that occupy the spatially patchy habitat off the coast of the eastern US, small scale spatial variability in demography and life history has been studied in only three gonochoristic reef species, all in the northeastern Gulf of Mexico. Small spatial scale variability has been reported in growth, mortality, and gonadosomatic indices of gray triggerfish *Balistes capriscus* (Ingram 2001), and in growth of white grunt *Haemulon plumieri* (Murie and Parkyn 2005) and vermilion snapper *Rhomboplites aurorubens* (Robert Allman , NMFS Lab., Panama City, FL, personal communication, 2005).

The red porgy *Pagrus pagrus* offers a promising opportunity to investigate the question of whether the patterns found in Australian taxa reflect general properties of reef systems or processes that emerge from the particular environmental characteristics of the Great Barrier Reef system. The red porgy is one of the most abundant, exploited reef fishes in the NE Gulf of Mexico (Gulf). A protogynous sparid found in warm temperate to subtropical waters on both sides of the N Atlantic and in the SW Atlantic (Manooch and Hassler 1978, Bauchot and Hureau 1990), adults typically occur on rocky or low-profile hard (live) bottom (Manooch and Hassler 1978, Grimes et al. 1982). Only lightly exploited in the Gulf where they are primarily taken as bycatch, red porgy are fairly heavily fished in most other areas where they are common. If fact, in 1999 a year-long total moratorium on fishing for red porgy in the Atlantic waters off the southeastern U.S. was enacted because their numbers had declined so steeply during the 1980's and 90's (Vaughan and Prager 2002) (see Chap. 2).

There have been many life history studies on red porgy outside the Gulf, throughout their range (many citations in Chap. 2), but only recently did Hood and Johnson (2000) provide the first information on the biology and fisheries for the species in the NE Gulf. Their one year study was not designed to investigate small scale spatial variability; they used fishery-dependent sampling and were unable to examine data as functions of particular locations and depths. The only other data on red porgy in the Gulf came from 161 individuals collected off Texas, where the species appears to be uncommon (Nelson 1988). Harris and McGovern (1997) compared size and age structure and size-at-age among latitudinal zones (N. of 33º N, 32-33 º N, and S. of 32 º N) off the southeastern U.S., but no study of red porgy has ever examined spatial patterns in their life history traits or demographics at a scale as small as 10's of km.

The specific objectives of this study were to determine if and how sex ratio, transition rates, size and age at transition, and size and age at maturity of red porgy in the NE Gulf varied

spatially (including bathymetrically) at scales of 10's of kilometers or less. The overall goal was to gain insight on the population structure and reproductive ecology of this protogynous species and hopefully shed some light on the apparent sensitivity of southeastern U.S. Atlantic stock(s) of red porgy to exploitation. Such information should not only be valuable to those trying to understand, assess, and manage red porgy populations, but hopefully will also prompt other researchers studying or managing other reef or hard bottom-associated species to investigate and consider the implications of small scale spatial variability in population biology.

I present evidence that 1) transition rate and sex ratios, both overall and, even more so, within size intervals, differed significantly among sites separated by no more than 10's of km; 2) transition rate and sex ratios varied bathymetrically, but the patterns were not linear; 3) size and age at transition varied spatially at the same small scale; 4) there were no apparent spatial patterns in size or age at maturity; and 5) spawning rate may vary at small spatial scales. These findings support the conclusion based on age, growth, and mortality data (see Chap. 3) that red porgy in the NE Gulf have a metapopulation structure.

Methods

Red porgy (n=2586) were collected monthly to bimonthly, primarily Jul 99 - Sep 01 (although some as early as Jun 1998), using standardized hook and line gear in a fishery independent survey in the northeastern Gulf of Mexico. Fish were collected at nine sites SW of Panama City, Florida in depths of 30 - 67 m (See Figure 3.1 and Table 3.1). Distances between sites ranged from 1.3 to 58.4 km, although in all but three cases, sites were separated by at least 10.5 km.

Each time I sampled a site, I attempted to catch 25-30 red porgies, although that goal was not always attained. Immediately after capture, fish were placed on ice. The next day, in the laboratory, they were measured to the nearest mm total length (TL), weighed to the nearest gram, and sexed and staged macroscopically using a modification of Kesteven's system (Table 2.1) (Bagenal and Braum 1971). Fish were classified as transitional if a band of whitish, testicular tissue was visible along the ventral side of each lobe of the ovary, beginning at the posterior end. All macroscopically identified females and transitionals were also sexed and staged histologically. Transverse sections were taken ~1/3 the distance from the posterior end of the ovary and stained using standard H and E techniques. Ovaries < ~1 gm were processed whole,

so the final section was not necessarily transverse. Stages were assigned using criteria derived from Wallace and Selman (1981), Brown-Peterson et al.(1988), and Harris and McGovern (1997) (Table 2.1). Transitionals were identified using the criteria of Sadovy and Shapiro (1987) and Harris and McGovern (1997); i.e., 1) spermatocytes, spermatozoa, or spermatids present along outer wall of ovary, 2) ovary almost always resting or spent, 3) at least some atresia (usually α or β) present, and 4) postovulatory follicles (POF) rarely present. Final determination of sex and maturity stage was based on histological findings if available. More detailed descriptions of sampling and processing procedures are given in Chapters 2 and 3.

Analyses of spatial patterns in size and age at maturity used maturity data based on the presence or absence of POF's in fish collected during the primary spawning months of Dec-Feb. Details on methods used to determine size and age at maturity are given in Chapter 2.

Spatial patterns in transition rates and sex ratios were examined using logistic regression (Trexler and Travis 1993, Wilson and Hardy 2002) to examine all pairwise comparisons of the nine sites using SAS Proc Logistic (SAS Institute 1999). For transition rates, the dependent variable, proportion of transitional fish, was calculated as (number of transitionals / (number of transitionals + females)). I ran two different models, one that included total length and location as main effects and a second model that included age and location as main effects. The covariance between total length and age made models with both variables intractable. In analyzing sex ratios, I used the proportion of males, calculated as (number of males)/(total number of males + females + transitionals) for the dependent variable. I ran the same two models for this measure. For these analyses, total length was rounded to the nearest 20 mm. In an attempt to minimize overdispersion, any interval at the upper end of the distribution with <5 individuals was excluded. For the same reason, in models including age, age classes at the upper end of the distribution with <5 observations were excluded. Length was examined as an effect because of the significant differences in size structure among locations and the fact that sex change does not occur before some minimum size and age, after which the proportion of females changing sex steadily increases until reaching an asymptote (see Chap. 2). The effect of age, highly correlated with length, was examined for the same basic reasons. Because very little sex change occurs during the spawning season (see Chap. 2), transition rates used in these analyses were calculated using only Mar-Nov data.

The sex ratios used in these analyses included data from all months and all individuals, so by strict definition, they were not operational sex ratios, i.e., mature females:mature males. Practically speaking, however, they could be considered as such. Size at 50% maturity was 211 mm based on oocyte stage data; the smallest vitellogenic fish was 194 mm; only 28 of 2586 (1.1%) fish were <211 mm; and only 10 (0.4%) were <200 mm. Assuming 25% of the fish <211 were mature, that would only leave 21 of 2586 (0.8%) immature, so for all practical purposes the sex ratios used herein can be considered as operational sex ratios.

For all logistic regression analyses, I first looked for evidence of overdispersion, a condition suggesting that the assumption of binomial variability may have been violated (assuming the model was correctly specified) and likely to result in underestimation of standard errors (SAS Institute 1999, Wilson and Hardy 2002). I assumed overdispersion was present if residual mean deviance (= residual deviance / residual df) was >1.25; if so, I would examine index plots of several different regression diagnostics provided by SAS Proc Logistic for the presence of overly-influential, outlying observations in the dataset, then rerun the model after removing them. If overdispersion was still present, I then reran the model using the Williams method, a scaling technique preferred when dealing with unequal sample sizes (SAS Institute 1999, Wilson and Hardy 2002).

Results

Transition Rates, Sizes, and Ages

Overall transition rate, i.e. the proportion of females changing sex, differed significantly among sites. Median % females in transition during Mar-Nov in collections with at least 3 females and/or transitionals ranged from 12 % at John's 248 to 33% at Ivy's Reef, an almost 2 fold difference (Figure 4.1). Transition rate did differ significantly among depth strata (Wald χ^2: p=0.028), however, the relationship was not straightforward. Median values were lowest at the two shallowest (~30 m) and the deepest (67 m) site – 12, 15, and 17%, respectively, while they fluctuated between 22 and 33 % at the intermediate depths. Ivy's Reef and Benny Allen, the two deepest sites and only 3.2 km apart, had the highest (33%) and third lowest (17%) median rates.

Logistic regression, in which location and total length were main effects, indicated that these differences among sites in the percent of females changing sex were significant in 16 of the 36 possible pairwise comparisons (Table 4.1). Total length was highly significant in all 36 of those comparisons ($p<0.0001$ in most cases). Ivy's Reef, which had the highest median percentage, was most unique. The percent of females in transition was significantly higher there than any other site ($p \leq 0.01$ and <0.0001 in four cases). Nearby Benny Allen was the second most unique – the percent of fish undergoing sex change there was significantly lower than at four other sites ($p \leq 0.024$ and $p=0.087$ at a fifth site). The only other site which differed from more than one or two of the others was Good Bottom; besides Ivy's Reef and Benny Allen, it differed significantly from Ridge and Sig1_2. When age, instead of length, was included as a main effect in the logistic regression model, location was significant in only 6 of 36 pairwise comparisons. Good Bottom differed from Ridge, Sig1_2, Whoopi Grounds, and Ivy's Reef; while John's 248 differed from Ivy's Reef and Benny Allen, and was close to significantly different from 3x5's ($p=0.08$) (Table 4.1). In these comparisons, age was significant in 29 of the 36 comparisons, and highly so in 24. Conclusions regarding the apparent low transition rates at the two shallowest sites – John's 248 and Elbo Reef – should, however, be considered preliminary, as there were only 5 collections during Mar-Nov at each site and 3 of those at Elbo Reef and 2 of those at John's 248 had few, i.e., n=2-7, total females (which included transitionals).

Besides spatial variation in transition rates, there were also significant spatial differences in the timing of sex change, as evidenced by the proportions of females in transition at a given size or age. For example, Ivy's Reef had considerably higher proportions of smaller and younger females changing sex than Good Bottom (Figures 4.2 and 4.3). In the 280 mm interval, on average 79.8±25.9 % (95% CL) of females were in transition in collections from Ivy's Reef vs. 17.0±11.5% at Good Bottom – a >4.5-fold difference; at 260 mm mean rates were 42.2±24.1% and 6.1±8.0%, respectively, an difference of almost 6 fold. These estimates were derived from Mar-Nov data, and only from collections with at least 3 females in the size interval. Logistic regression indicated these differences were highly significant (Wald χ^2: $p=0.004$ for 280 mm and $p=0.003$ for 260 mm). Similarly, the proportions of 3 yr olds changing sex at Ivy's Reef and Benny Allen (median values of 0.23 and 0.28) were significantly higher than at Good Bottom, where the median was 0.11 (Wald χ^2: $p=0.009$ and 0.010) and 3x5's , where the median was 0.14 (Wald χ^2: $p=0.023$ and 0.076). All other possible pairwise comparisons of transition rate of

age 3 fish among Good Bottom, Ivy's Reef, Benny Allen, 3x5's, and Ridge were not significant (p=0.094-0.888).

These large differences in size distributions of transitional fish among sites translated to significant differences in mean size at sex change. Location (site) was highly significant in a one way ANOVA on ln TL of transitional fish (F=21.7, p<0.0001). Tukey's HSD test indicated that transitionals were significantly larger at 3x5's, Good Bottom, and Whoopi Grounds (and not different from each other) than at all other sites (which also did not differ from each other) except Sig1_2, which was intermediate in size and fell in both groups (Figure A.17). Raw mean size of transitionals ranged from 266 mm at Ivy's Reef to 313 mm (18% larger) at 3x5's (Table B.1). In a reanalysis in which Elbo Reef and John's 248 were excluded - because they had much smaller sample sizes than the other sites and were the primary contributors to heteroscedasticity - site was again highly significant in an ANOVA of ln TL (F=27.4, p<0.0001). In this analysis Tukey's HSD test identified four groups: again 3x5's, Good Bottom, and Whoopi Grounds were largest; a second grouping of Good Bottom, Whoopi Grounds, and Sig1_2; a third of Sig1_2 and Ridge; and a fourth composed of Ridge, Ivy's Reef, and Benny Allen.

The average age of transitional individuals, measured on a log scale, also differed among sites (ANOVA, F=4.68, p<0.0001), although the differences were not as distinct as with size. Tukey's HSD test yielded two greatly overlapping groups, with only Good Bottom unique to the older group and Elbo Reef , John's 248, and Benny Allen unique to younger one (Figure A.17). Raw mean age of transitionals ranged from 3.1 yr at Elbo Reef to 4.6 yr at Good Bottom (Table B.4). Even if Elbo Reef and John's 248 are excluded because of their small sample sizes, the remaining minimum age – 3.4 yr at Benny Allen – was still >1 yr less than at Good Bottom. When the ANOVA was repeated excluding John's 248 and Elbo Reef, site was again highly significant (F=6.16, p<0.0001) and there were three very overlapping groups identified by Tukey's HSD test: Good Bottom, Ivy's Reef, 3x5's, and Ridge; Ivy's Reef, 3x5's, Ridge and Sig1_2; and lastly, 3x5's, Ridge, Sig1_2, and Benny Allen.

There were also significant spatial differences in mean size and age of males that closely mirrored those of transitionals. Site was highly significant in a one way ANOVA of male total length ($F_{8,816}$=89.8, p<0.0001). Four groups were identified by Tukey's HSD test: 1) 3x5's and Good Bottom, 2) Good Bottom and Whoopi Grounds, 3) Sig1_2, John's 248, Ridge, Benny Allen, and Elbo Reef, and 4) Benny Allen, Elbo Reef, and Ivy's Reef. On average, males were

13 mm larger than transitionals (range 2-21 mm) at a given site (Table B.1). In a linear regression, mean TL of males explained 93% of the variation in mean TL of transitionals ($p<0.0001$). In a one way ANOVA of male ln age, site was highly significant ($F_{8,792}=16.0$, $p<0.0001$). Tukey's HSD test identified three groups: 1) Good Bottom and Ivy's Reef, 2) all of the other seven sites, and 3) an overlapping group consisting of Ivy's Reef, 3x5's, Ridge, and John's 248. The relationship of age between males and transitionals was significant but not as close as with length. Mean age of males explained 64% of the variation in mean age of transitionals (linear reg., $p=0.01$), while ln mean age of males accounted for 57% of the variance in ln mean age of transitionals ($p=0.02$).

Sex Ratios

Sex ratio also varied significantly among sites. Although females typically outnumbered males by about 2 or 3 to 1 at 6 of the 9 sites, with median % males ranging from 22.2 to 33.3 (Figure 4.4), sex ratios were consistently and noticeably less female biased at Ivy's Reef and Benny Allen, where median % males was 46.9 and 48.2 – almost 1 to 1. In contrast, 3x5's was the most female biased, with a median of only 10% males. Logistic regression analyses in which location (site) and length were included as main effects in the model indicated that sex ratio was significantly different between sites in 28 of 36 pairwise comparisons ($p<0.0001$ in 20 cases), and 3 others had p values of 0.06-0.09 (Table 4.2). In the remaining 5 comparisons, 3 failed to converge, leaving only 2 pairs of sites with statistically equal sex ratios at $\alpha=0.1$: Elbo Reef and John's 248 ($p=0.35$) and Ivy's Reef and Benny Allen ($p=0.17$). Ivy's Reef and Benny Allen did differ from all other sites, with the possible exception of the latter and John's 248 ($p=0.089$). Whoopi Grounds also differed from all other sites except Sig1_2, and in that case the analyses failed to converge. In all 36 comparisons, length was highly significant ($p<0.0001$).

When I replaced length with age as a main effect in the logistic regression model, sex ratio differed significantly between sites in 22 of 36 comparisons ($p<0.0001$ in 13 cases), and in 4 others $p=0.06$-0.08 (Table 4.2). With this model, 3x5's differed from all other sites; Benny Allen differed from all but Elbo Reef (and p in that comparison was only 0.08); and Good Bottom differed from all but Whoopi Grounds - and again, p was only 0.08. Similar to the effect of length, age was very highly significant in all 36 comparisons ($p<0.0001$ in 35 cases).

As with transition rates, not only were there significant differences among sites in overall sex ratios, but there were even greater differences in ratios within size classes. In the 260, 280, and 300 mm size intervals the proportions of males varied 47-, 26-, and 28-fold among sites (Figure 4.2). These differences were persistent and consistent, as best evidenced by the fairly narrow 95% confidence limits around the mean % males per collection at Good Bottom and Ivy's Reef in the 260, 280, and 300 mm intervals: 0±0, 2.9±2.8, and 21.5±8.2 at the former and 47.0 ± 15.8,71.6 ±10.7, and 90 ±17.7 at the latter. These estimates were based on 12, 19, and 21 collections over 2 yr at Good Bottom and 14, 16, and 7 collections over 1 yr at Ivy's Reef. Overall, the two shallowest and two deepest sites (John's 248, Elbo Reef, Ivy's Reef, and Benny Allen) had high proportions of small males, while 3 x 5's, Good Bottom, and to a lesser extent, Whoopi Grounds, had much higher proportions of large males. In most cases the pattern of percent males reflected the proportion of females in transition (Figure 4.2).

Sex ratios within age classes varied less among sites than those within size intervals. Among 3, 4, and 5 yr olds, the proportion of males varied only 14-, 4-, and 4-fold compared to the 26-28 fold variation in the 260, 280, and 300 mm size intervals (Figure 4.3). Once again, as seen with sex ratio within sizes data, the pattern at Good Bottom and 3 x 5's stood out from the other sites. The proportions of males within age for ages 3-5 at those two sites were much lower than at all other sites but quite similar to each other (Figure 4.3). The 3 x 5's site was also unique in that the proportions of males remained low even among the older ages; only the Whoopi Grounds site had a similar pattern. The 3 x 5's site differed from every other site except Good Bottom. The latter site differed from John's 248, Elbo Reef, Ivy's Reef, and Benny Allen, and came close to differing from Ridge (Wald χ^2, p=0.06) and Sig1_2 (Wald χ^2, p=0.10). Benny Allen differed significantly not only from 3 x 5's and Good Bottom, but also from Ridge, Sig1_2, and Whoopi Grounds.

Although these results suggest that sex ratios become less female biased with depth, evidence from ancillary collections made at other, irregularly sampled sites in the NE Gulf does not support that conclusion. The proportion of males exceeded the median values at Ivy's Reef and Benny Allen at only one of 17 collections from other sites at equal or deeper depths, and that collection was very close to Benny Allen (Figure A.18). Males composed only 20 and 21 % of the only two collections made deeper than 80 m (90 and 92 m).

Size/Age at Maturity

Unlike the pattern for the transition between genders, the proportions of females during the spawning season with POFs did not exhibit any substantial spatial patterns in size or age at maturity. This suggests that the main distinction among sites is the timing of gender allocation and not the onset of any reproductive effort. However, there were few fish below the size and age at 50% maturity (~215 mm and <age 2, see Chap. 2) at each site, so these analyses were not powerful and would probably not have detected any effect other than an obvious, substantial one (Figures 4.5 and A.19).

Spawning Rate

What the site-specific data on females with POF's did suggest was that the proportion of active spawners was noticeably lower at Ivy's Reef than at other sites, or at the least, was much more variable. On average, 54% of females ≥ age 2 at Ivy's Reef were actively spawning, as evidenced by the presence of POF's, compared to 90-99% at John's 248, Elbo Reef, 3x5's, Good Bottom, Ridge, and Benny Allen (Figure A.19). The 95% confidence limits for Ivy's Reef were ±100% compared to 5-19% at the other sites, although admittedly, sample sizes were small – 3 collections for Ivy's Reef and 4-5 from each of the other sites.

Discussion

As I found with their size and age structure, growth, and mortality (see Chap. 3), this study revealed significant, persistent spatial variability in transition rates, mean sizes and ages at transition, overall sex ratios, and size- and age-specific sex ratios in red porgy in the NE Gulf of Mexico at a scale of 10's of kilometers. Such small scale spatial variability has not been previously reported for red porgy or any other sparid.

Transition Rates, Sizes, and Ages

Given the ample evidence that sex change in red porgy is socially mediated (see Chap. 2), it was not surprising that the proportion of females in transition varied at such a small spatial scale. Whether sex change is a function of size-ratio (Ross et al. 1983, Lutnesky 1994) or sex-ratio

(Shapiro and Lubbock 1980) assessment, or a combination of both (Cowen 1990), the significant variability I found in size and age structure (see Chap.3) and sex ratios at the same small spatial scale could certainly result in such variability in transition rates.

Findings from 3x5's and Benny Allen were consistent with predictions from sex allocation theory, which assumes sex-ratio assessment controls the rate of sex change, that transition rate should increase as the proportion of males declines, and vice versa (Charnov 1982, Coleman et al. 1996). The 3x5's had the lowest proportion of males and one of the higher median transition rates (4th highest): while conversely, Benny Allen had one of the highest proportions of males and the 3rd lowest median transition rate. In contrast, demographics at Ivy's Reef, very near Benny Allen, contradicted those predictions. Despite having a significantly higher proportion of males than any site except Benny Allen, it had the highest transition rate. If sex change is based on size-ratio rather than sex-ratio assessment, it may be that the high proportion of small fish at Ivy's Reef stimulated increased rates of transition despite the presence of a high proportion of males, albeit small ones. This explanation, however, is not very satisfying, as it does not explain the opposite results for Benny Allen and 3x5's. Harris and McGovern (1997) speculated that the increase in proportions of male red porgies which accompanied a considerable drop in average size during a period of heavy exploitation may have reflected the inability of smaller males to defend as large a territory as larger individuals, thus freeing up space for additional males. This hypothesis could also explain the high transition rate at Ivy's Reef, but again, it does not explain the opposite condition at Benny Allen, which had a similar size structure with a mean size only about 10 mm larger. It is very unlikely that either disruption of the social mechanism driving sex change or increased selectivity of transitioning individuals, as occur in some aggregating protogynous species such as *M. microlepis* and *M. phenax* (Coleman et al. 1996), explains the lower rates of transition at some sites (see Chap. 1 and 2).

The large - almost 7-fold in one case - differences among sites in the proportions of females in transition at a given size or age, and the related highly significant differences among locations in size at transition (0's = 266-313 mm) clearly demonstrate the considerable plasticity in the size at sex change in red porgy. Although the maximum mean length was only 18% larger than the minimum, this represents a 58% increase in weight, which could have significant implications regarding fecundities and total reproductive output of the females at the opposite ends of that size range.

The small scale spatial variability in mean size and/or age at transition has been reported in several other protogynous species, including labrids (Warner and Robertson 1978, Cowen 1990), serranids (Shapiro 1981, Adams et al. 2000), and scarids (Clavijo 1982, Gust 2004). Life history traits have been shown to vary among populations at very local levels in response to such factors as mortality, food availability, and recruitment rates (Stearns 1976, 1977 in Cowen 1990), so it is not surprising to find differences in the size/age of sex change among populations of a sequential hermaphrodite as a result of local environmental variation (Cowen 1990). Buxton (1993) noted that mean size at sex change in *Chrysoblephus laticeps*, a sparid, was significantly lower in exploited areas than in those open to fishing, and those exploited areas had significantly lower proportions of males.

The size at transition in red porgy was predicted very well by growth rate. Mean annual growth rate, calculated as the mean for ages 2-4 of the mean size at age divided by age, explained 84% of the variance in mean size at transition at the nine sites (lin. regress., $F_{1,7}$=37.9, p=0.0003) (Figure 4.6). This pattern is consistent with Warner's (1975) simulations of Ghiselin's (1969) size-advantage model of sex change, in which sex change is delayed (i.e., older age or larger size) in the presence of higher survival or an increased rate at which female fecundity changes with age (= faster growth). However, there was no relationship between mean size or age at transition and survival ($F_{1,6}$=0.32, p=0.59 and $F_{1,6}$=1.91, p=0.22), or between mean age at transition and growth ($F_{1,7}$=1.49, p=0.26). Excluding John's 248 and Elbo Reef, the two sites with much smaller sample sizes, had no effect on the analyses other than to increase P values. Jones (1980), Cowen (1990), and Gust (2004) each reported findings consistent with Warner's (1975) simulation predictions regarding both survival and age-specific fecundity; however, because of confounding, none were able to determine which of the effects had the stronger influence or whether they were additive or independent.

This close relationship between size at sex change and growth, coupled with the absence of a relationship between age at sex change and growth, strongly suggests that the timing of this critical event in red porgy is much more tied to size than age. Similarly, Jones (1980) concluded that life history traits in the protogynous labrid *Pseudolabrus celidotus* are much more size than age dependent. The key role of size is not surprising, given that age-specific fecundity was one of two factors predicted to affect timing of sex change (Warner 1975); and that fecundity, for purely physical reasons, is closely correlated with size (specifically body volume), certainly

much more than with age (Jones 1980). That differences in size can be much more easily discerned than differences in age lends support to the hypothesis that size is important to the timing of sex change in red porgy, especially if sex change is socially-mediated, as it appears to be (see Chap. 2), and particularly if the mechanism involves size-ratio assessment (Ross et al. 1983, Lutnesky 1994). Even though size and age are correlated, the wide variation in size at age (see Chap. 3) would tend to obscure any relationship between age at transition and growth.

Cowen (1990) proposed a model of social control of sex change involving both size and abundance of males which predicts variation in size at sex change and sex ratios consistent with my findings on red porgy. In this model the interaction of size and relative abundance of males within the group is the cue stimulating females to change or inhabiting them from changing sex. Cowen assumed at least some large females are likely to be in an area inhabited by a very large male, and conversely, females are likely to be small in areas where there are no large males. He hypothesized that a small number of large males may provide the same stimulus to females, i.e., inhibit transition, as a much larger number of small males. The interaction of these two cues would result in varying sizes or ages at transition and varying sex ratios – groups with larger males would be much more female biased and change sex at larger sizes and possibly older ages. The demographics at Ivy's Reef, Benny Allen, 3x5's, and Good Bottom are very consistent with the predictions of Cowen's (1990) model. Ivy's Reef and Benny Allen had the smallest and 3rd smallest mean sizes of males and transitionals and the highest proportions of males by far. In contrast, 3x5's and Good Bottom had the largest and 3rd largest sizes at transition and the largest and 2nd largest mean sizes of males; the former also had the lowest proportion of males and the latter an intermediate proportion.

Sex Ratios

The significant variability I found in sex ratios of red porgy – as much as 3-4 fold differences in median % males between sites separated by no more than 10's of km – has been reported in only a few other protogynous species, including two sparids, *Chrysoblemphus laticeps* and *C. cristiceps* (Buxton 1993). Sex ratios varied at small spatial scales by up to ~3 fold in the scarid *C. sordidus* (Gust 2004) and the serranid *P. leopardus* (Adams et al. 2000), and 1.5 fold in the labrid *S. pulcher* (Cowen 1990). Buxton (1993) noted that both *C. laticeps* and *C. cristiceps* had

more female biased sex ratios in exploited areas than in protected areas, although the scale of his comparisons ranged from 10's to low 100's of km.

Current theory on the effects of fishing on protogynous species does not consistently explain the significant small scale spatial variability in sex ratios of red porgy in the NE Gulf (Bannerot et al. 1987, Huntsman and Schaaf 1994). The wide range in sex ratios, from medians of 10% males at 3x5's to 47 and 48% males at Ivy's Reef and Benny Allen, cannot simply be considered as effects of varying exploitation rates. For one, there are no direct data on the exploitation rate of red porgy in these areas. For another, comparisons of several demographic and life history traits revealed conflicting evidence of exploitation history at several sites. High survival rates at Ivy's Reef and Benny Allen (highest and 3rd highest) are consistent with a history of low exploitation; but conversely, their truncated size structure and small sizes at transition suggest the opposite. Current theory would suggest that the highly female biased sex ratio (median % males = 10) at 3x5's was certainly consistent with the predicted effects of overfishing on some protogynous species; however, the site also had the largest mean sizes of males, females, and transitionals; the oldest mean age of females; and 4th oldest mean ages of males and transitionals – traits suggesting a history of low exploitation. Good Bottom resembled 3x5's with a relatively female biased sex ratio, suggesting high rates of fishing; but it had several traits suggesting low rates of fishing - the 2nd highest survival rate, the 2nd highest mean sizes of both sexes, 3rd highest size at transition, and oldest and 2nd oldest mean ages for males and females. The apparent social control of sex change (see Chap. 2) would preclude an absence of compensation, which one would expect with endogenous control, as a likely source of variable sex ratios in red porgy. As mentioned previously, skewing of sex ratios through disruption of the social mechanism controlling sex change or increased selectivity of transitionals (Coleman et al. 1996) is also very unlikely.

Ultimately, two overriding non-anthropogenic factors - spatial heterogeneity of their environment and philopatry – are probably most responsible for the small spatial scale variability in sex ratios and other aspects of the population biology of red porgy in the NE Gulf. Given the conflicting evidence on site-specific exploitation histories discussed above, and that overall red porgy are only lightly fished in the Gulf, the spatially highly variable exploitation (see Chap. 3) is probably not the major cause of this variability. Those red porgy that recruit to and remain at each heterogeneous piece of suitable habitat will be exposed to a unique suite of physical and

biological factors which act in concert to yield phenotypic changes unique to that location. Factors likely to shape population biology include predator and prey composition and density, inter- and intra-specific competition, habitat complexity, and oceanography (see Chap. 3 for much more detail). Any of these factors which produce variability in size or growth are especially likely to have significant effects on population traits related to reproduction. Because of the close, often causal relationship between size and timing of maturity and sex change, and the subsequent relationships between those reproductive milestones and sex ratios in protogynous fishes, any such factor is bound to secondarily create variability in those reproductive traits and demographics. Because of its complex social and mating system, the existing demography and density of red porgy on a given piece of habitat is also very likely to impart variability to those reproductive traits and demographics. This would be especially true if sex change is a function of the interaction of male size and relative abundance as proposed by Cowen (1990). Local population density has been identified as a likely cause of small scale variability in the social organization (e.g., sex ratios) of scarids (Gust 2004) and another sparid - *Sparisoma viride* (van Rooij et al. 1996).

Size/Age at Maturity

There is no way to know if the apparent lack of spatial variability in size or age at maturity I observed reflects reality, a selectivity problem with the sampling gear, a small sample size problem, or a combination of the latter two. Given that overall size at 50% maturity was 211 mm (see Chap. 2) and only 28 fish below that size (min.=173 mm) were collected, with only 12 of those from the spawning months of Dec-Feb, sample sizes were just too small to construct size at maturity ogives for the 9 sites. Although the hook size I used easily fit in the mouths of the smallest red porgies collected, it is possible that behavioral selection occurred, i.e., that smaller fish were outcompeted by more aggressive, larger individuals. I did not collect any observational data at the sites so I do not know at what size the juveniles recruit to these adult habitats. Given that changes in size at maturity have been documented in red porgy (Harris and McGovern 1997), and my finding of considerable small scale spatial variability in size at transition, it is certainly possible this trait also varies at the same small scale.

Spawning Rate

The hint of spatial variability in spawning rate of red porgy is very intriguing, and if real, would certainly have significant implications for stock assessment and yield prediction, as well as for siting of a marine protected area for the species. There is some evidence of variation in spawning rates in *Epinephelus morio*, a protogynous serranid that co-occurs with, and appears to have a social and mating system similar to, red porgy (see Chap. 2) in the NE Gulf (Gary Fitzhugh, NMFS Lab., Panama City, FL, personal communication, 2005). Answering this question will require considerably more replicate collections from throughout the spawning season.

Population Structure

My findings of persistent, significant variation in size and age at transition, transition rates, and sex ratios (both overall and within size intervals and ages) at a spatial scale of 1's to 10's of kilometers, is entirely consistent with my earlier conclusion - based on size and age structure, growth, and mortality data - that red porgy in the NE Gulf are composed of a great many local subpopulations (see Chap. 3). The existence of significant differences in transition rates with depth, but the absence of a straightforward relationship between them, i.e., lower rates at both the shallowest and deepest sites, is much more consistent with a complex subpopulation hypothesis than a hypothesis invoking some sort of ontogenetic movement. The overall similarity within sites of both size and age distributions of % males and % females in transition (Figures 4.2 and 4.3), and the related very high correlations between mean sizes of males and transitionals within sites (r^2=0.93), certainly supports the conclusion that these fish are philopatric. Sale (1998) noted that site fidelity almost ensures metapopulation formation, and red porgy population structure in the Gulf would be considered a metapopulation under the broader definition of Kritzer and Sale (2004). If, for example, males continuously and randomly moved among suitable habitat patches, one would expect to see much more uniformity in male size structure across sites and no relationship to size at transition. That the size and age distributions were so similar even though the sex data were derived using different methods (males- macroscopically, transitionals histologically), not only strengthens this conclusion; it also lends credence to my identification of transitioning females, which involves more subjectivity and are more difficult to identify than males.

Conclusions

This considerable small scale spatial variability in red porgy in both transition rates and timing of transition has important implications to stock assessment. Sex change in protogynous species essentially equates to female mortality, although it simultaneously reduces the apparent mortality in males (Shepard and Iodine 1993). If trying to model effects on spawning stock biomass, whether using fecundity as a proxy or actual number of females, the overall rate at which sex change occurs, how that rate varies with size, and how it varies spatially could each have a large impact on yield estimates. Yield predictions from a delay difference model developed to evaluate the effects of fishing on the protogynous serranid *Centropristis striata* were very sensitive to large changes in the transformation rate (Shepard and Iodine 1993). Obviously, both modelers and those collecting and providing the data for the models on species like red porgy should consider the potential existence and impacts of such variability for any species.

The considerable spatial variability at such a small scale in transition rates and size at transition strongly suggests that sex change is socially controlled in red porgy; and therefore, it is highly unlikely that the apparent crash of the fishery off the southeastern U.S. in the 1980's and 90's was the result of sperm limitation caused by an inability of the species to compensate for males lost to increased selectivity for larger fish. The obvious plasticity of transition rates and timing is further evidence that red porgy should be relatively insensitive to exploitation, or at least no more sensitive than a gonochoristic species (see Chap. 2 and 3 for further discussion). These findings also confirm the need expressed in Chapter 3 to determine which reef fishes in the region have a complex subpopulation structure, and then determine the spatial scale, distribution, and dynamics of their subpopulations. To accomplish this will require extensive sampling (Gust 2004).

Table 4.1. Results of two series of paired logistic regressions of proportions of females in transition on location. Two models were used - in one, total length was included, along with location, as a main effect; and in the second, age replaced length as a second main effect. Numbers in bold indicate significant differences. J248 = John's 248, E R = Elbo Reef, G B = Good Bottom, R D G = Ridge, SIG = Sig1_2, W G = Whoopi Grounds, and I R = Ivy's Reef.

Other Effect In Model	Site	Probability of a larger chi-square value in maximum likelihood analysis							
		Elbo Reef	3x5's	Good Bottom	Ridge	Sig1_2	Whoopi Grounds	Ivy's Reef	Benny Allen
Length	J248	0.2878	0.3798	0.5698	0.0690	0.3611	0.9971	**<0.0001**	0.1227
Age	J248	0.4426	0.0766	0.2066	0.1490	0.1128	0.2019	**0.0207**	**0.0297**
Length	E R		0.7239	0.4771	0.6003	0.6411	0.2031	**0.0022**	0.7565
Age	E R		0.3007	0.7027	0.5656	0.4617	0.6769	0.1299	0.2009
Length	3x5's			0.3790	0.1200	0.1103	0.9215	**0.0100**	**0.0215**
Age	3x5's			0.9107	0.4495	0.3307	0.8181	0.6165	0.8491
Length	G B				**0.0100**	**0.0257**	0.6446	**0.0003**	**0.0007**
Age	G B				**0.0046**	**0.0135**	**0.0240**	**<0.0001**	0.7111
Length	RDG					0.6117	**0.0334**	**<0.0001**	0.2203
Age	RDG					0.9712	0.7226	0.2038	0.2311
Length	SIG						**0.0337**	**<0.0001**	0.0865
Age	SIG						0.7630	0.2490	0.7485
Length	W G							**<0.0001**	**0.0038**
Age	W G							0.1396	0.5636
Length	I R								**0.0235**
Age	I R								0.3211

Table 4.2. Results of paired logistic regressions of proportions of males (i.e., sex ratio) on location. Two models were used - in one, total length was included, along with location, as a main effect; and in the second, age replaced length as a second main effect. Numbers in bold indicate significant differences. J248 = John's 248, E R = Elbo Reef, G B = Good Bottom, R D G = Ridge, SIG = Sig1_2, W G = Whoopi Grounds, and I R = Ivy's Reef. FTC = failed to converge.

Other Effect In Model	Site	Probability of a larger chi-square value in maximum likelihood analysis							
		Elbo Reef	3x5's	Good Bottom	Ridge	Sig1_2	Whoopi Grounds	Ivy's Reef	Benny Allen
Length	J248	0.3498	**<0.0001**	**<0.0001**	**0.0460**	FTC	**0.0001**	**0.0004**	0.0893
Age	J248	0.2637	**<0.0001**	**<0.0001**	**0.0277**	0.0611	0.7800	0.9525	**0.0237**
Length	E R		**<0.0001**	**<0.0001**	0.0553	0.0732	**<0.0001**	**<0.0001**	**0.0485**
Age	E R		**<0.0001**	**<0.0001**	**0.0065**	**0.0241**	0.5268	0.6987	0.0774
Length	3x5's			**0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**	**<0.0001**
Age	3x5's			**0.0492**	**<0.0001**	**0.0001**	**0.0002**	**<0.0001**	**<0.0001**
Length	G B				**<0.0001**	**0.0002**	**0.0296**	**<0.0001**	**<0.0001**
Age	G B				**0.0054**	**0.0104**	0.0844	**<0.0001**	**<0.0001**
Length	RDG					FTC	**<0.0001**	**<0.0001**	**<0.0001**
Age	RDG					0.9047	0.6968	0.0656	**<0.0001**
Length	SIG						FTC	**<0.0001**	**0.0010**
Age	SIG						0.2375	0.4460	**<0.0001**
Length	W G							**<0.0001**	**<0.0001**
Age	W G							0.2728	**<0.0001**
Length	I R								0.1698
Age	I R								**<0.0001**

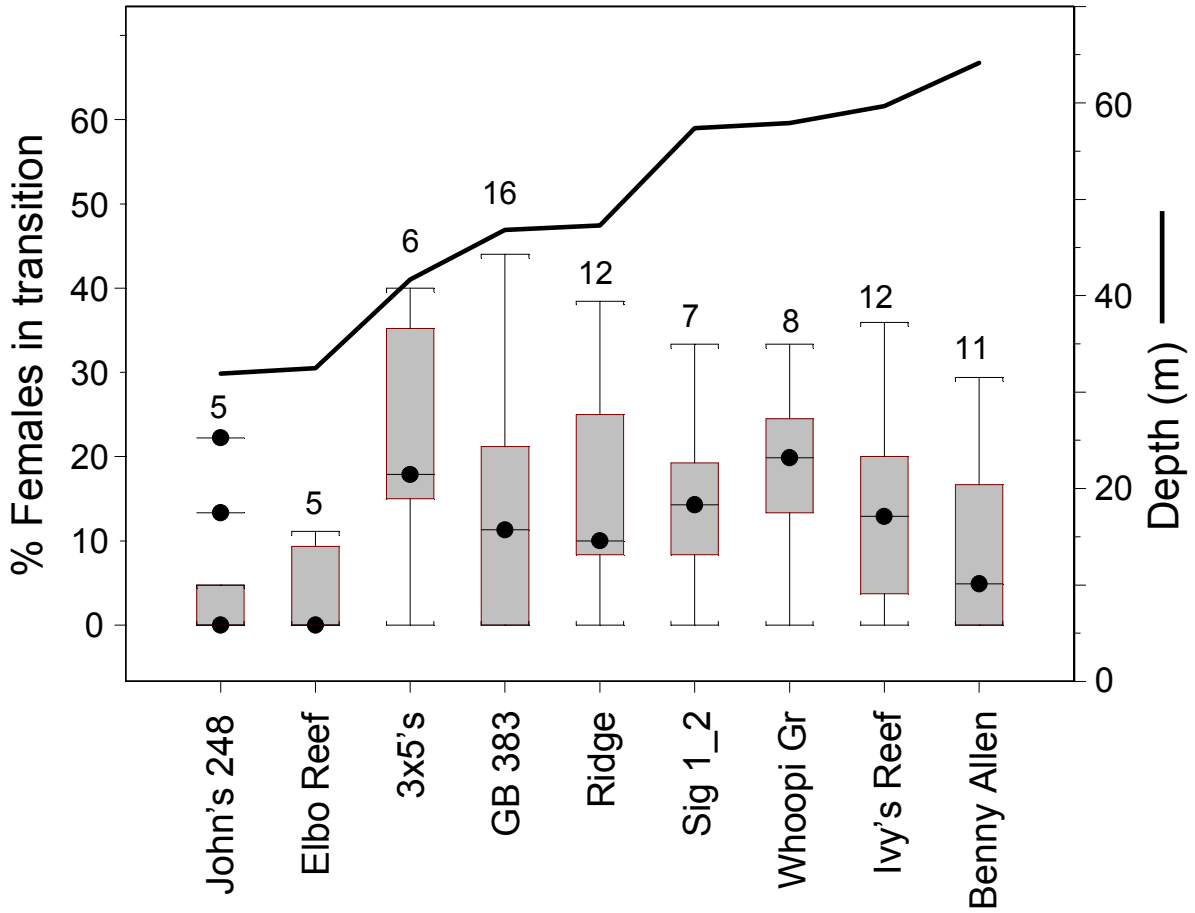

Figure 4.1. Percentages of female red porgies in transition by site, Mar- Nov, and depth of site. Numbers above each box indicate the number of collections for that site. Only collections with >5 fish were included in analysis.

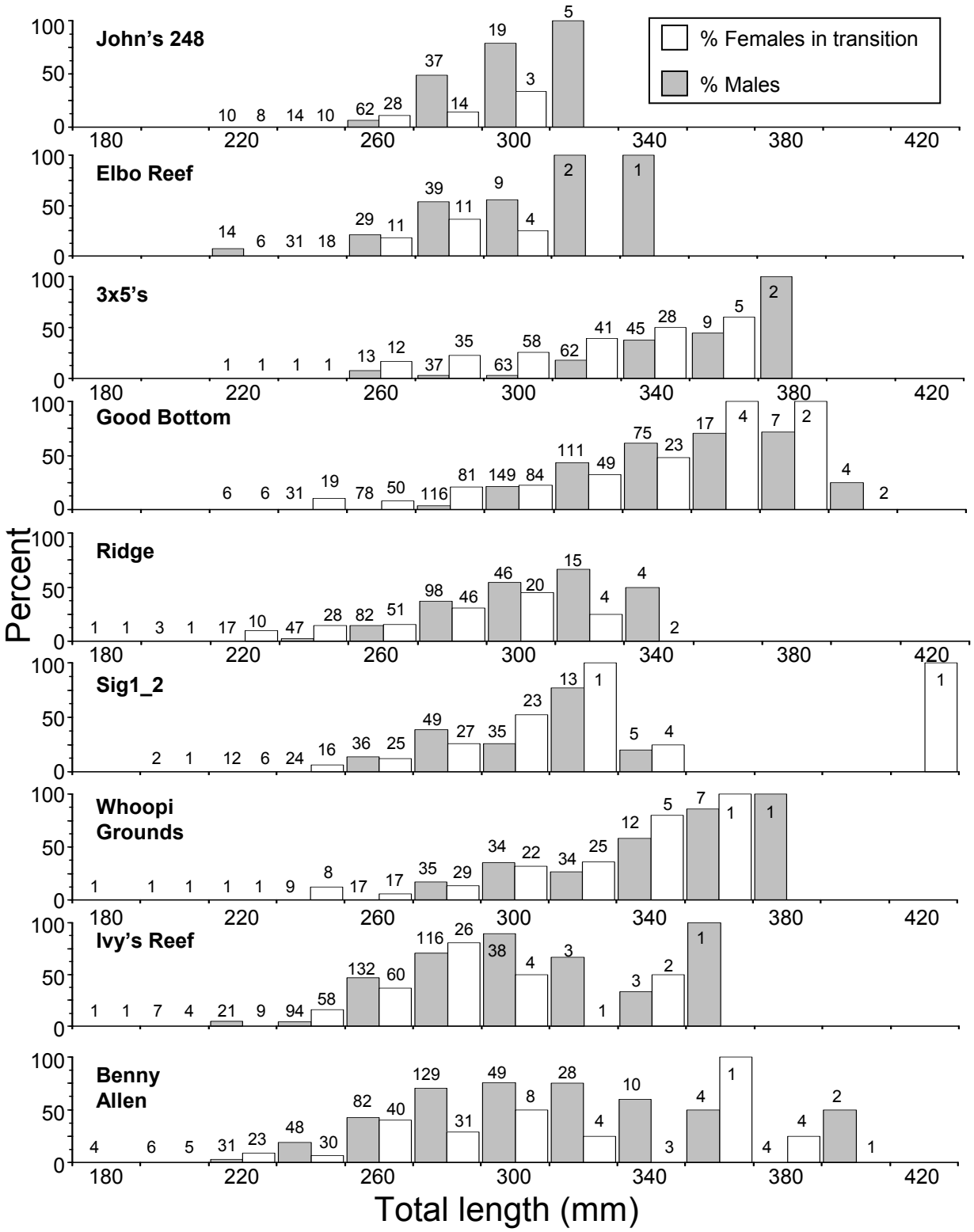

Figure 4.2. Percent frequency size distributions of female red porgies in transition, Mar-Nov only, and males, all months. Numbers above black bars indicate total number of females plus transitionals in that length interval. Numbers above gray bars indicate total number of all fish in that length interval.

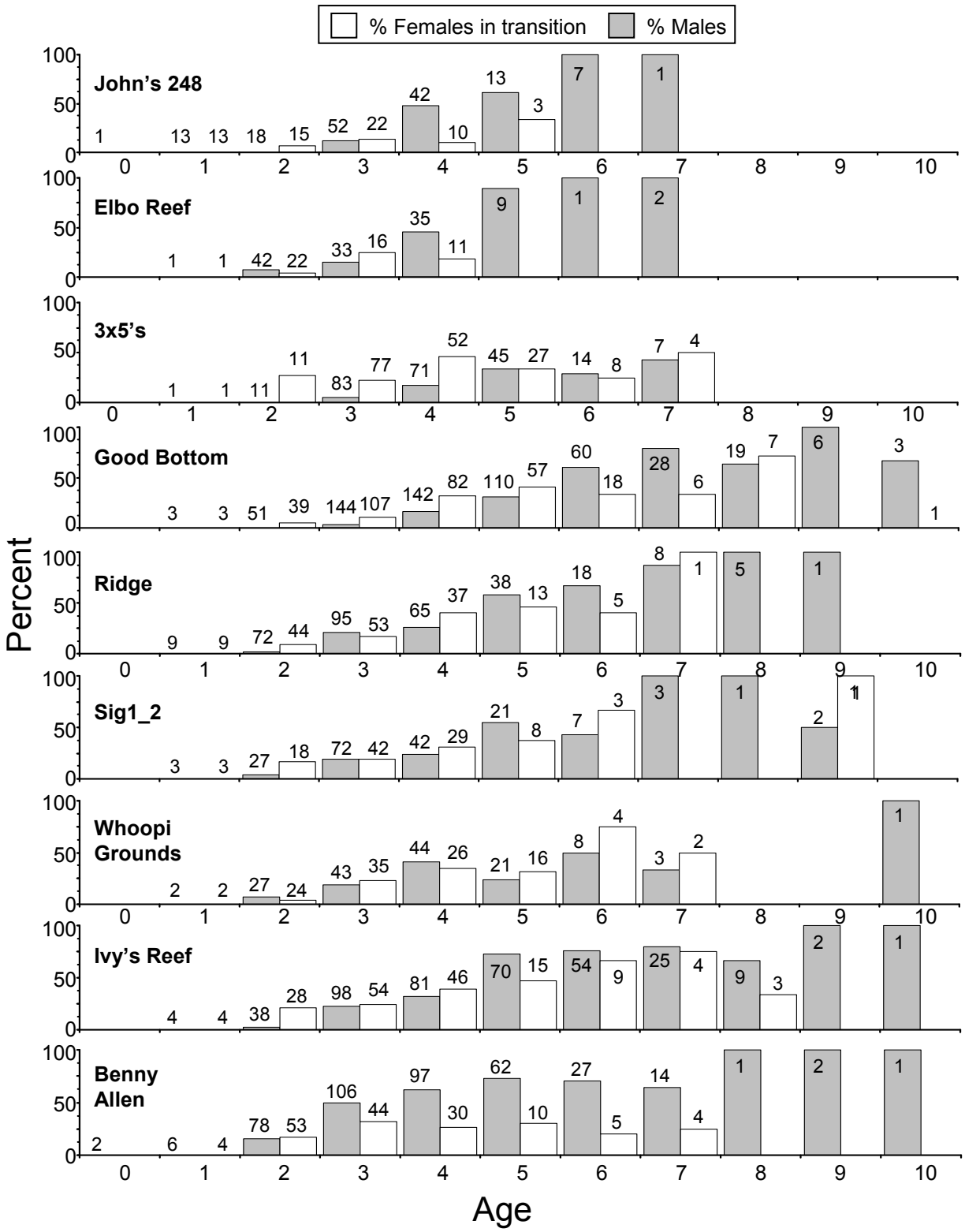

Figure 4.3. Percent frequency age distributions of female red porgies in transition, Mar-Nov only, and males, all months. Numbers above black bars indicate total number of females plus transitionals in that age interval. Numbers above gray bars indicate total number of all fish in that age interval.

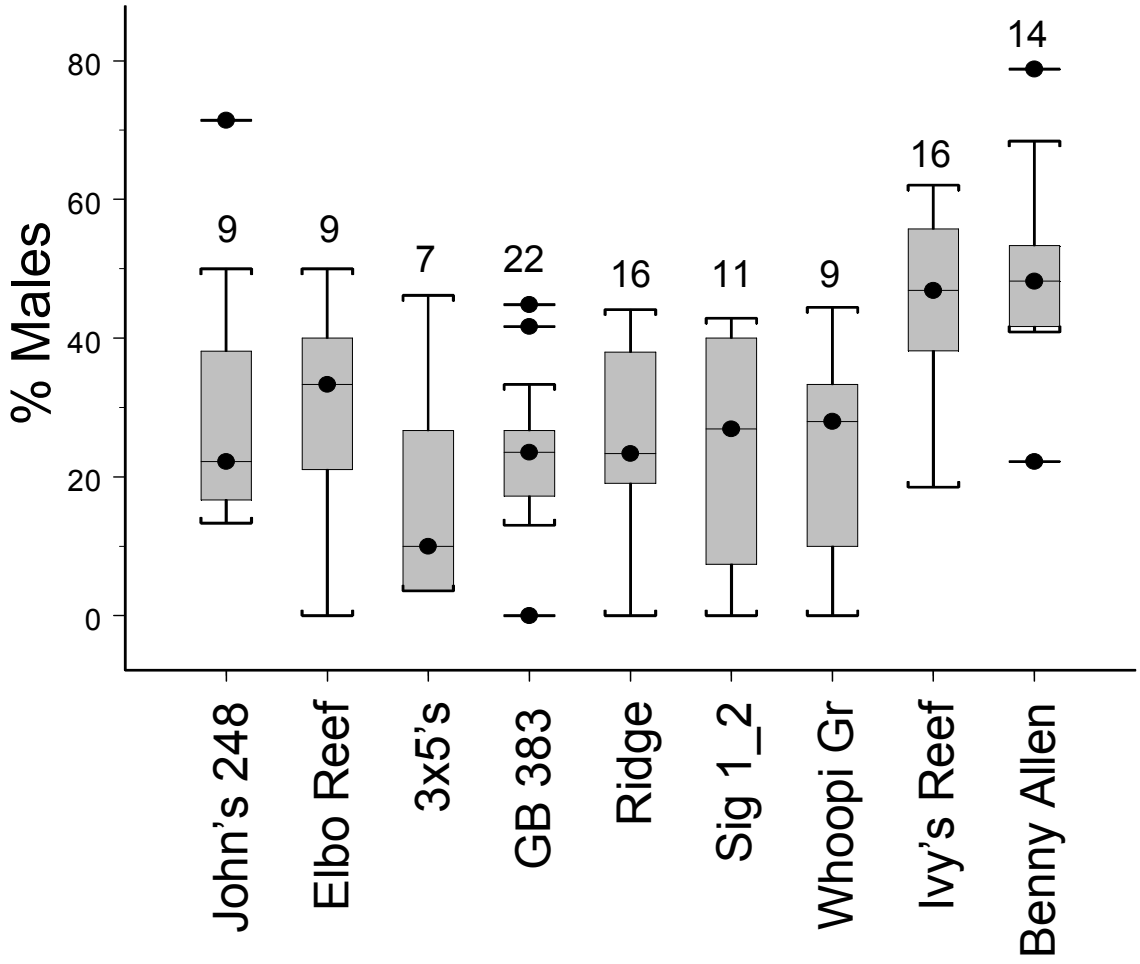

Figure 4.4. Percentages of male red porgies by site, all months. Numbers above each box indicate the number of collections for that site. Only collections with >4 fish were included in analysis.

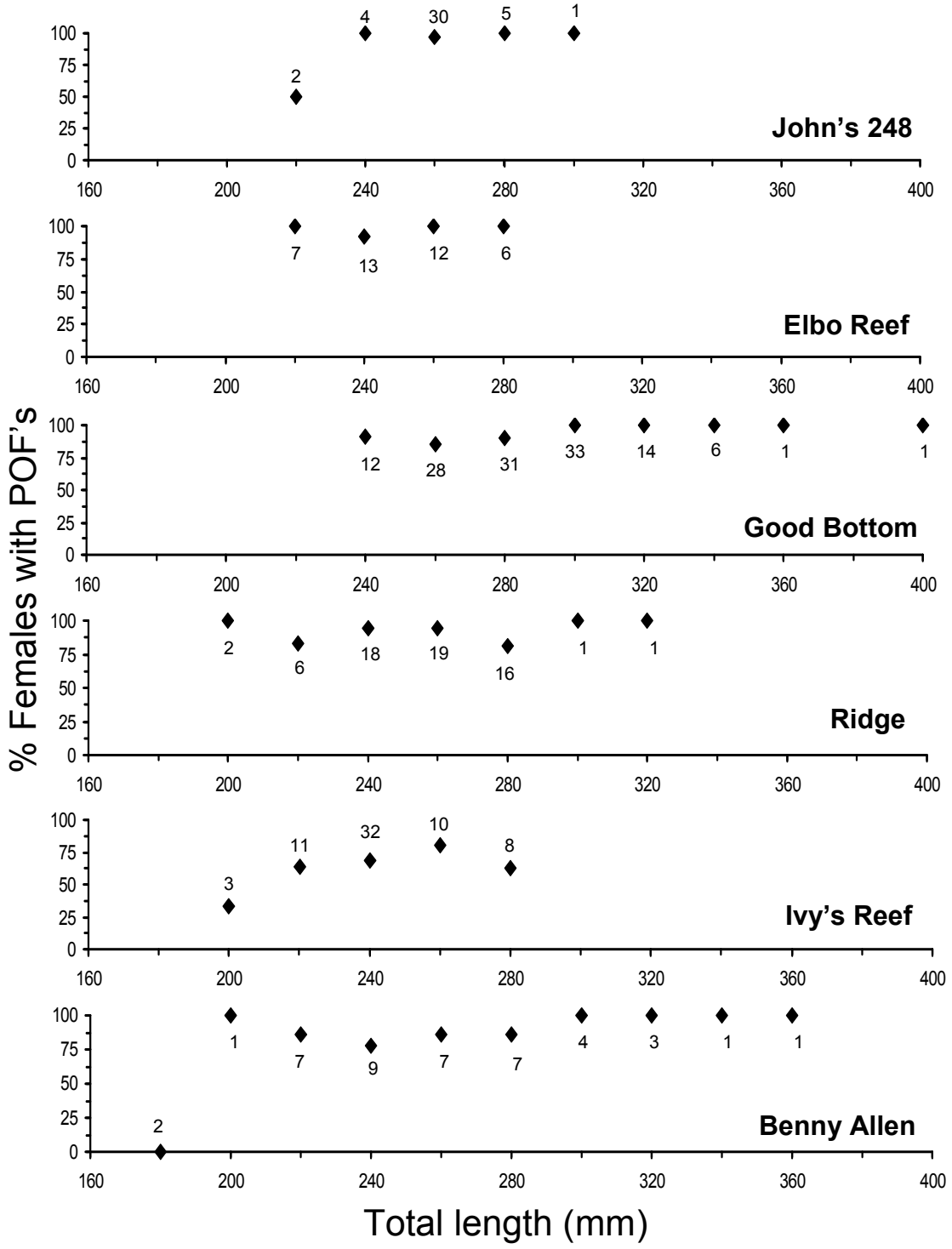

Figure 4.5. Percentages of mature female red porgy (as indicated by the presence of POF's) by size during Dec-Feb for six of the standard sites. Numbers adjacent to data points are total number of mature + immature females at each site.

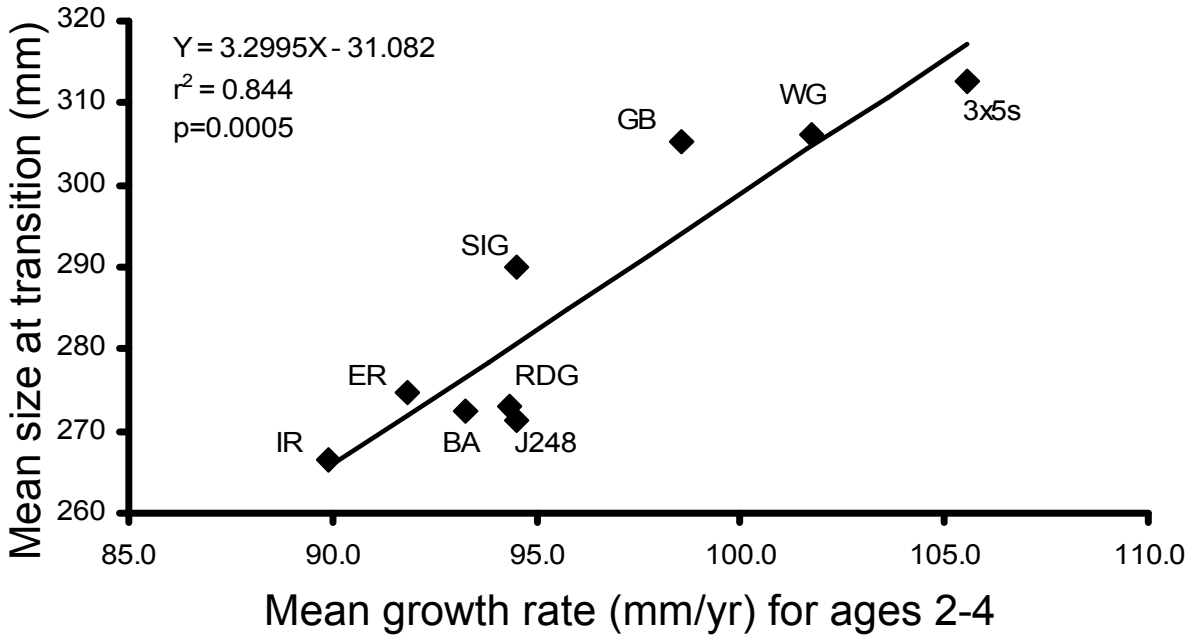

Figure 4.6. Regression of mean size at transition at the nine sites on mean annual growth rate for ages 2-4. Growth rate was calculated as the average of the mean size at age/age for ages 2, 3, and 4.

CONCLUSIONS

Hook and line samples of red porgy showed no evidence of behaviorally-related size or sex selectivity, i.e., the gear is not biased by size or gender. This indicated no only that it is an unbiased way to sample the species, but much more importantly, that any evidence of truncation in size structure or skewing of sex ratios in exploited red porgy populations should not be attributed to greater aggression or "hook attraction" in males but can be easily explained as the results of simple size-selective harvesting, a common phenomenon not unique to protogynous fishes. Rapid skewing of sex ratios in protogynous fishes caused by behavior-related size or sex selectivity may be more an exception than the rule, but until more simple studies like this one are conducted on other species, the prevalence of this phenomenon will remain unknown.

GSI and histological evidence, and observations of captive fish, indicated that red porgy in the NE Gulf spawn primarily during Dec – Feb wherever mature fish occur. Size at maturity functions in females were almost knife-edged, and LOESS regressions predicted that size at 50% maturity, as indicated by the presence of vitellogenic oocytes, was 211 mm TL, or, as indicated by the presence of POF's, 216 mm. Virtually all age 2 females were mature, but only 3 age 1 fish were collected during the spawning months, none mature, so no conclusions could be drawn about spawning rates for fish that age. Sex change occurred almost exclusively during months outside the spawning season (Mar-Nov) and wherever adults were found within the depth range of this study (22 to 92 m). Size and age at sex change were very plastic, ranging from 206 to 417 mm, with no obvious mode, and ages 2-9, with a mode at age 4. Such plasticity strongly suggests that sex change is under social or exogenous control. The rate of transition increased with size and age up to at least 320 mm and age 4, after which it appeared to reach an asymptote at around 30-35 %. Red porgy were found to be sexually dichromatic. In males the premaxilla (upper lip) is green or bluish-green, while in females it is pink or reddish. The color differences accurately predicted a fish's sex and were observed in all months, not just during the spawning season, although the differences did seem more distinct then. The absence of any temporal pattern in CPUE data or sex ratios suggested that red porgy do not form large, temporally and spatially discreet spawning aggregations, as some serranids and lutjanids do. Observations of captive red porgy indicated that they are pair spawners, although other males often joined in the spawning rush. Peak spawning in captive fish occurred during early morning hours. Captive

presumed males also were frequently observed acting aggressively towards other males, as if guarding a territory or harem.

I found no evidence that their protogyny or reproductive ecology might 1) explain the apparent crash of the red porgy stock(s) in the SAB or 2) make the species more sensitive to exploitation than gonochorists - in fact they are probably less sensitive in some cases. Many aspects of their biology and behavior, including widespread spawning grounds, no tendency to form spawning aggregations, absence of behaviorally-related size or sex selectivity, socially controlled sex change, co-occurrence of sexes year-round, and an extended period of transition, should stabilize or enable rapid compensation of sex ratios (preventing sperm limitation or disruption of mating). Socially controlled sex change also enables size and age of transition to slide downward as fishing truncates the size structure, similar to the declines in size and age at maturity seen in many gonochorists.

Protogynous species most at risk are those 1) in which sex change initiation is temporally and spatially restricted, 2) which form temporally and spatially predictable spawning aggregations, and 3) in which males or larger fish are selectively harvested (Coleman et al. 1996). It may be that gag, often cited as an example of how a protogynous species responds to fishing, and which has all of these traits, is more the exception than the rule.

Several population traits differed significantly among 9 regular sites (which ranged from 1.3 to 58.4 km apart), including size and age composition growth, mortality, transition rates, size and ages at transition, and sex ratios. These persistent differences at such a small spatial scale likely reflect phenotypic, not genetic, effects; and two factors - spatial heterogeneity of their environment and site fidelity - probably ultimately explain most of them. The live bottom habitat preferred by red porgy is widespread but very patchy. These patches, grossly similar, have variable hydrological, geological, biological, and ecological characteristics; and they range from unexploited to heavily exploited. Biological and ecological characteristics likely to vary among patches include density, predator and prey composition and density, and competition. Adult red porgy exhibit considerable site fidelity, so once recruited to a given patch of habitat, they are exposed to a unique suite of many factors which could affect growth, mortality, and reproduction.

The consistent, persistent, significant differences in so many life history traits and demographics among sites separated by only 10's of kilometers strongly suggest that red porgy

in the NE Gulf have a complex population structure, with many local subpopulations. It is possible that the fish inhabiting each significant patch (or closely adjacent patches) of suitable hard bottom habitat, with a unique suite of population traits, comprise such a subpopulation.

These subpopulations closely resemble Crowder et al.'s (2000) definition of sources and sinks – "areas of differing demographic rates dictated by underlying differences in habitat quality". Red porgy in the NE Gulf are not a classical metapopulation as originally defined by Levins (1970), i.e., a "population of populations that go extinct and recolonize", and which are exposed to the same conditions in each habitat patch. They can, however, be considered a metapopulation if using the broader definition espoused by Hastings and Harrison (1994), Hanski and Simberloff (1997), and Kritzer and Sale (2004), which relaxes the requirement for extinctions and recolonizations and does not require uniform conditions across patches. Specifically, the latter authors defined a metapopulation as "a system of discrete local populations, each of which determines its own internal dynamics to a large extent, but with a degree of identifiable and nontrivial demographic influence from other local populations through dispersal of individuals".

The existence of many local subpopulations has significant implications for stock assessment and management of red porgy. Estimates of most demographics and life history traits will be very sensitive to the location and spatial weighting of the samples used to derive them. Data pooled from a large area without regard for its spatial distribution, because it will probably encompass many subpopulations, each with a unique suite of population parameters, is likely to yield skewed estimates of those parameters. Selectivity problems with fishery dependent data (Potts and Manooch 2002) are likely to be exacerbated if fishing is focused on subpopulations where the fish tend to be larger (a likely scenario) and those fish also happen to have significantly higher growth rates than surrounding unfished or lightly-fished subpopulations. Growth estimates derived from such data would overestimate potential yields and underestimate sensitivity to exploitation. Yield predictions from spawning stock biomass models, whether using fecundity as a proxy or actual number of females, are certain to be sensitive to spatial variability in transition rates and sizes, as protogynous sex change essentially equates to female mortality (Shepard and Iodine 1993).

To accurately characterize such a complex population structure, fishery independent sampling coupled with complete knowledge of the areal extent of the subpopulations and the spatial

distribution of the fishery would be necessary. Realistically, that is probably not logistically feasible. A very risk averse management option would be to use minimum estimates of growth, natural mortality, and size and age at transition to predict the effects of fishing, however, this could certainly result in unnecessary loss of yield. A compromise might be to estimate population parameters for several subpopulations, and then use modal or mean values to predict the overall response to fishing.

It appears that red porgy in the NE Gulf, given their complex population structure and the resulting logistical difficulty of accurately assessing and managing them, are an ideal candidate for management by marine protected areas (MPA). Their use would eliminate the onerous recurring data needs of the standard stock-specific annual or periodic stock assessments and estimation of allowable catch. A key factor with this strategy, if the goal is to protect or enhance the fisheries for red porgy, would be to identify and include subpopulations which serve as sources, not as sinks, in the MPA's (Pulliam 1988, Crowder et al 2000, Tuck and Possingham 2000).

Whether complex population structure played a role in the crash of the fishery for red porgy in the SAB is unknown. Even though much of the data used to assess their status was fishery independent, the problems inherent in sampling and predicting effects of fishing in a species with such a complex population structure may have biased the assessments and painted an overly pessimistic picture. However, both fishery independent and dependent data showed a steady, significant decline in CPUE and mean size, suggesting that the crash was real (Vaughan and Prager 2002). If the fisheries in the SAB targeted mainly source subpopulations and not sinks, it is possible that recruitment overfishing occurred, and possibly even an Allee effect if exploitation was severe enough.

That the red porgy population in the NE Gulf appears to be composed of many small subpopulations, along with findings by many studies cited herein of significant variability in life history traits and/or demographics within reef fishes on Australia's Great Barrier Reef at scales of no more than 10's of km, strongly suggests that the population or stock structure of many exploited reef fishes may be much more complex than assumed. At least three other species in the Gulf of Mexico besides red porgy – gray triggerfish (Ingram 2001), white grunt (Murie and Parkyn 2005), and vermilion snapper *Rhomboplites aurorubens* (Robert Allman , NOAA Fisheries, Panama City, FL, personal communication, 2005) - show some evidence of

subpopulation structure. Such complexity requires examination of population biology at much smaller spatial scales than typically done, use of more complex, spatially-explicit population models, and may have played a part in the failure of some southeastern U.S. reef fish fisheries to respond to management measures in recent years. Obviously, there is a pressing need to determine the population structure of all exploited reef fishes in the region, including the spatial scales, distributions, and dynamics of subpopulations for those species that have them.

APPENDIX A

SUPPLEMENTARY FIGURES

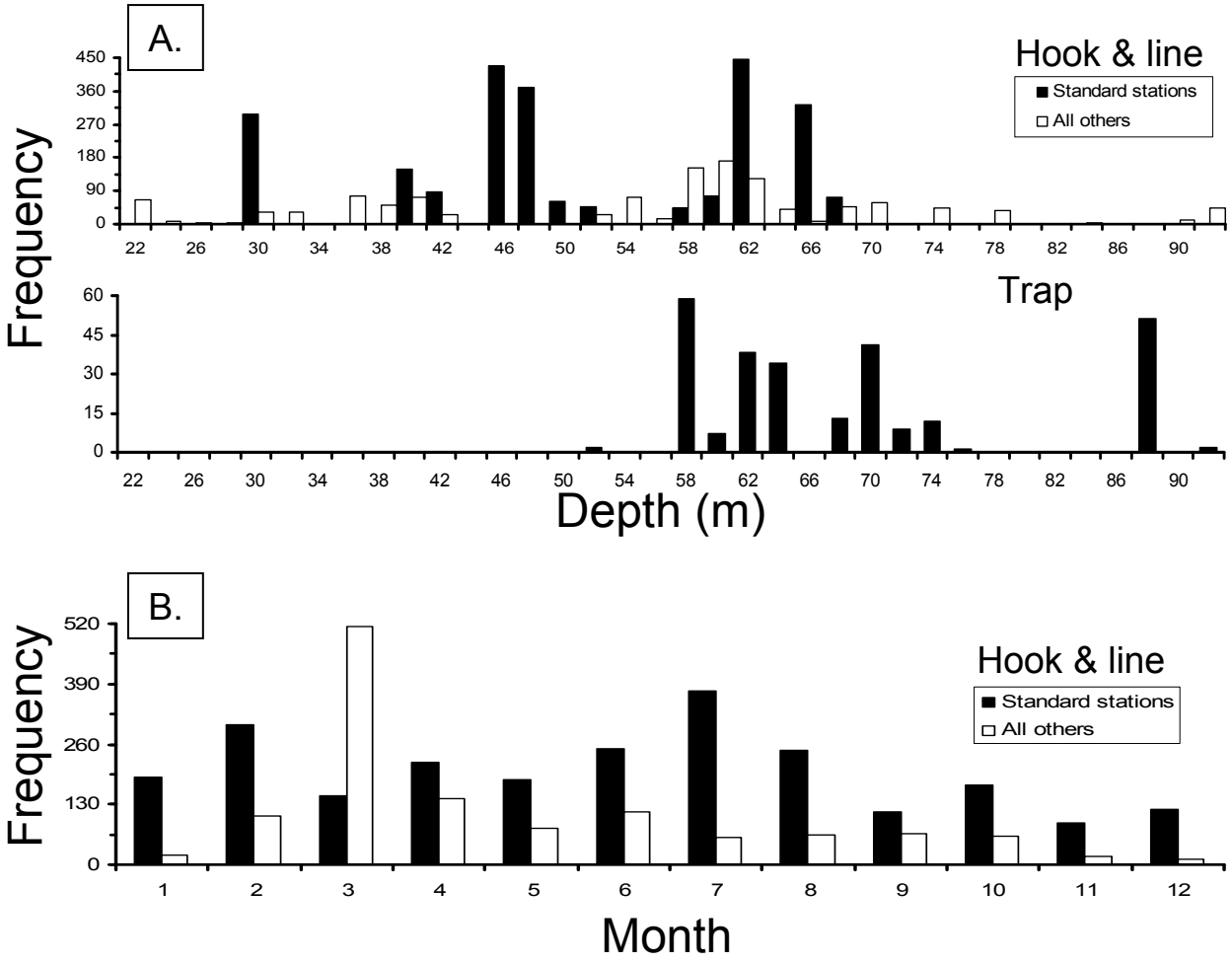

Figure A.1. A. Depth distributions of all hook and line samples of red porgy. B. Monthly distribution of all red porgy hook and line collections.

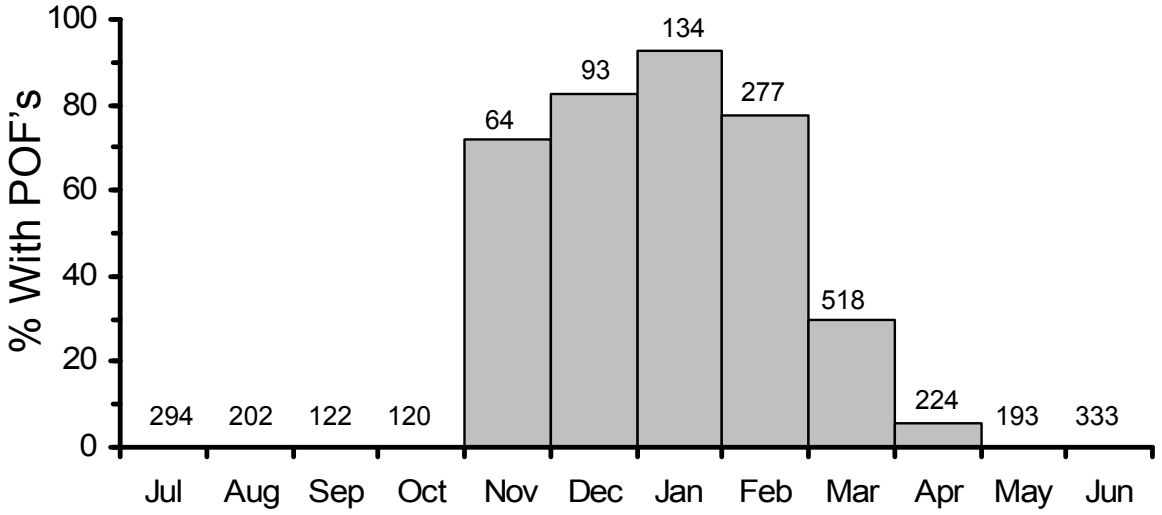

Figure A.2. Monthly percent frequency distribution of female red porgy with post-ovulatory follicles. Numbers at top of bars are sample sizes.

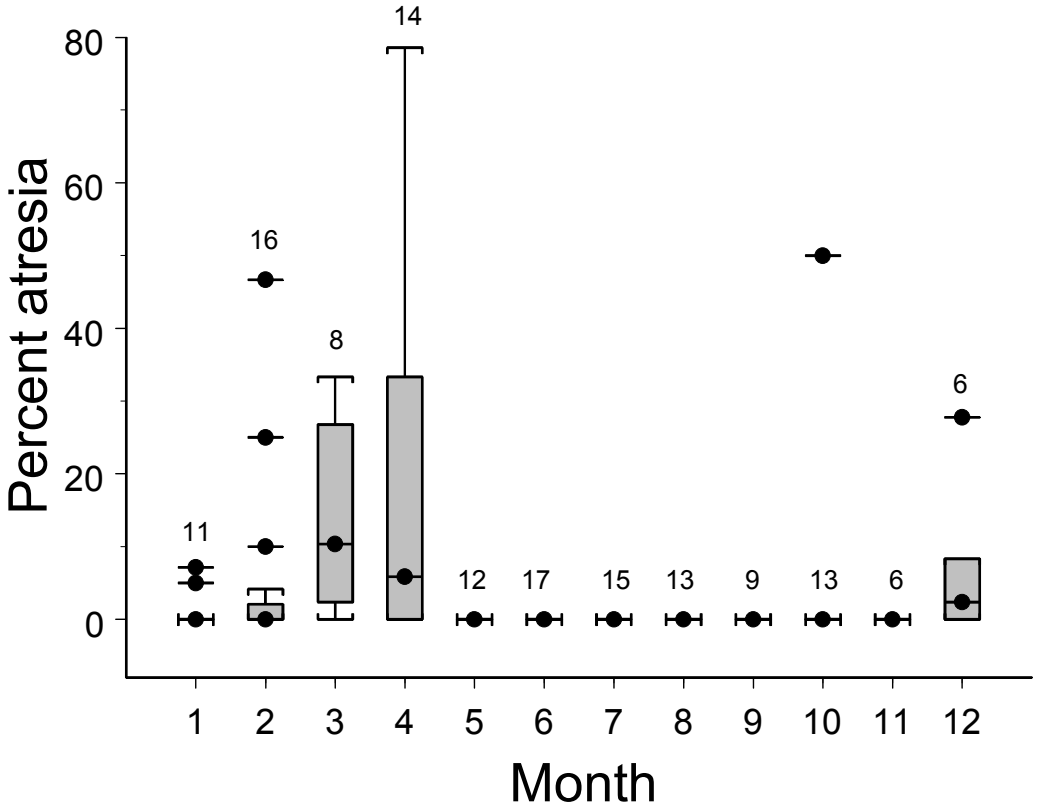

Figure A.3. Monthly percentages of female red porgy with high rates of atresia (>50% of vitellogenic oocytes atretic). Numbers above each box indicate the number of collections for that month.

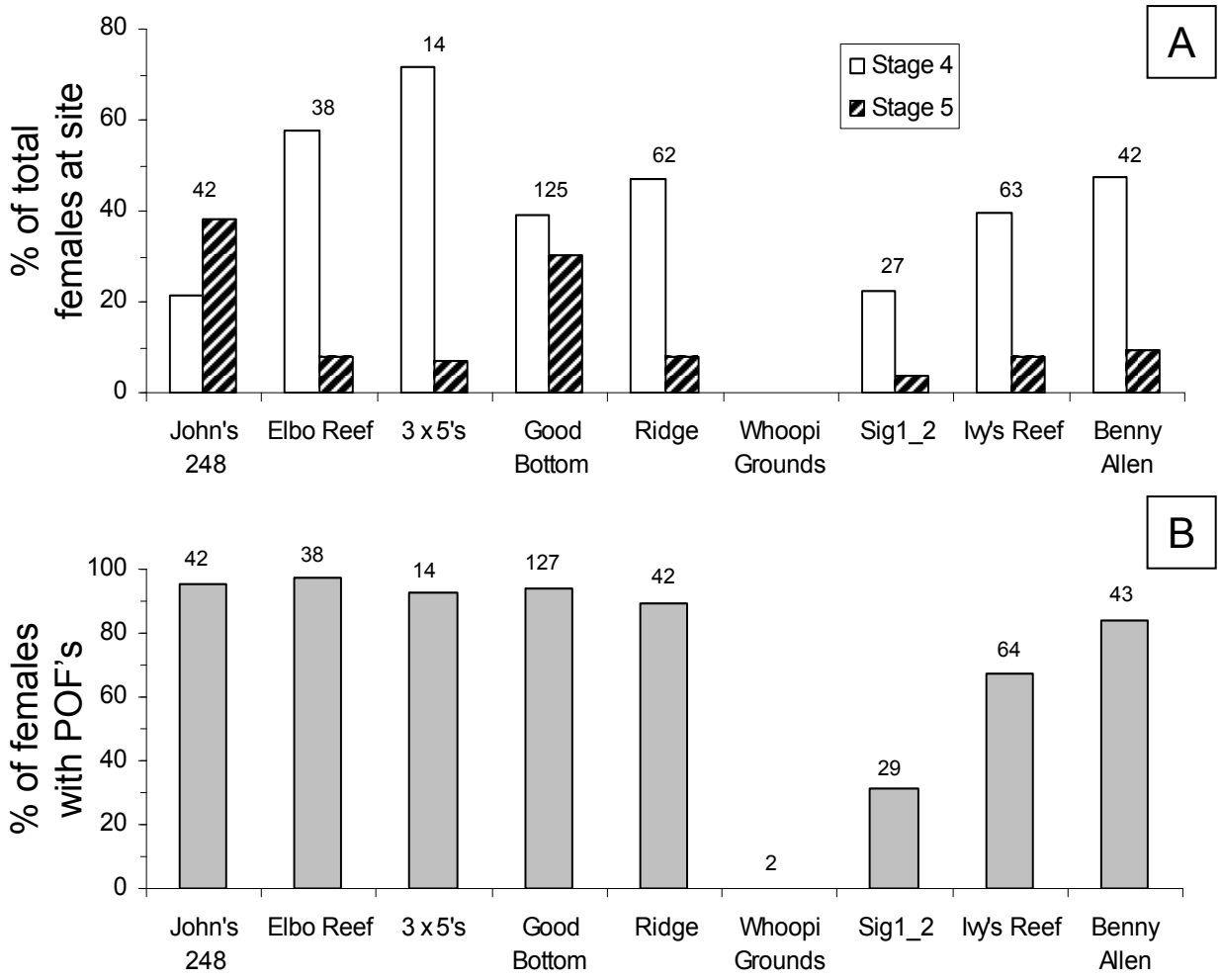

Figure A.4. Percentages of female red porgy with early and late FOM stage ovaries and with POF's by depth interval during Dec-Feb. Numbers at top of bars are sample sizes.

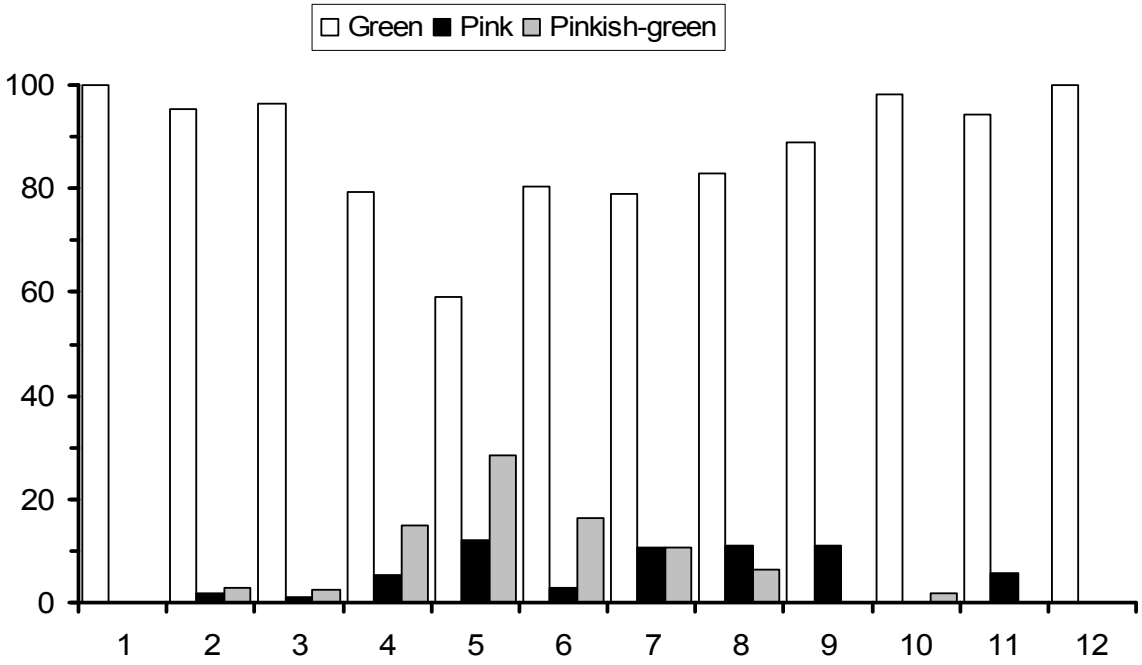

Figure A.5. Temporal percent frequency distributions of premaxilla color of red porgy identified as males by macroscopic (most) or histological (few) examination of gonads.

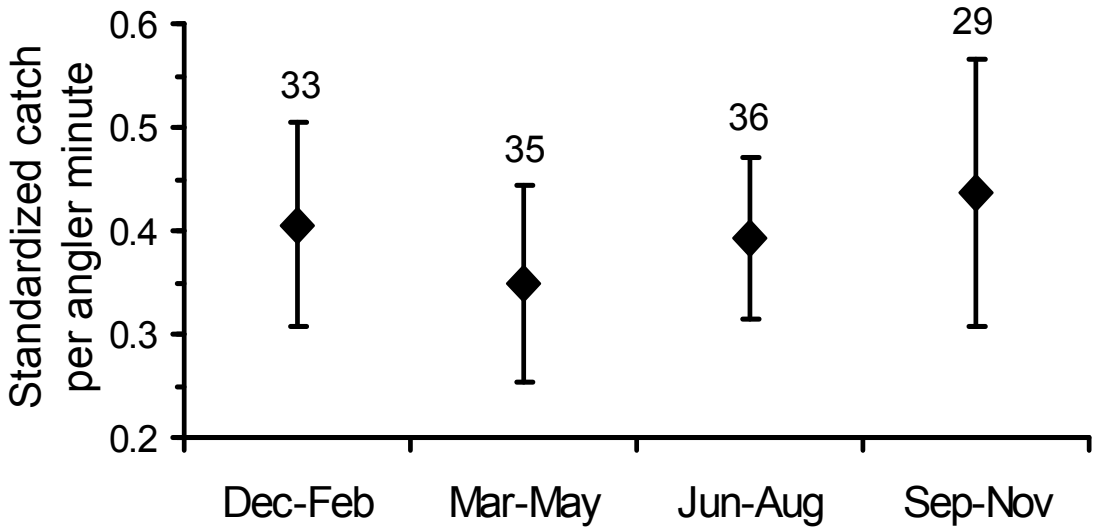

Figure A.6. Seasonal mean standardized catch per angler minute and 95% C.L. for the standard sites. All collections within a site were standardized by dividing by the highest catch-per-angler- minute for that site. Numbers above each point represent sample sizes, i.e., number of collections.

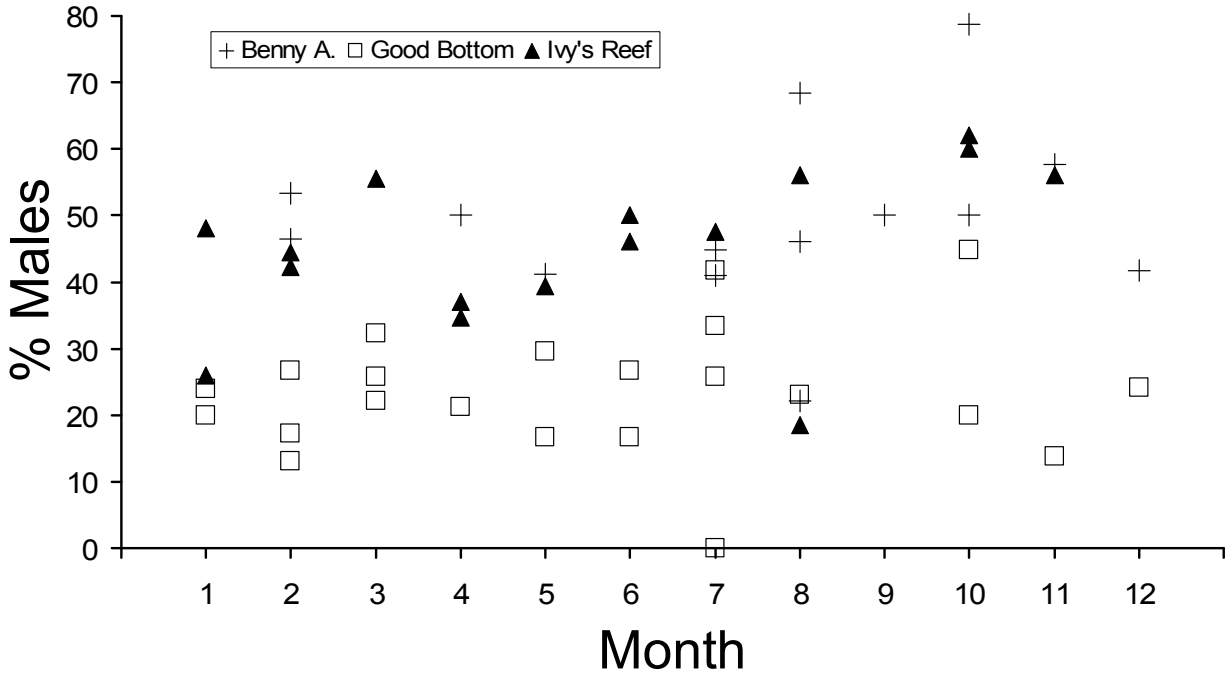

Figure A.7. Percent males by collection and month for Benny Allen, Good Bottom, and Ivy's Reef. Only collections with >4 fish were included in analysis.

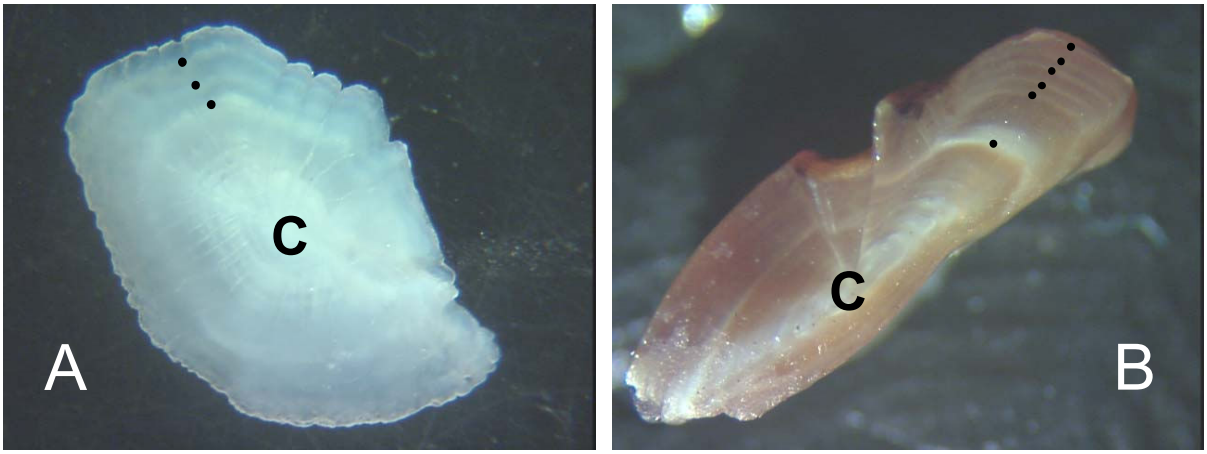

Figure A.8. A. Whole sagittal otolith of a red porgy showing 3 annuli (black dots). C = core. B. Broken and burned sagitta of a red porgy showing 6 annuli.

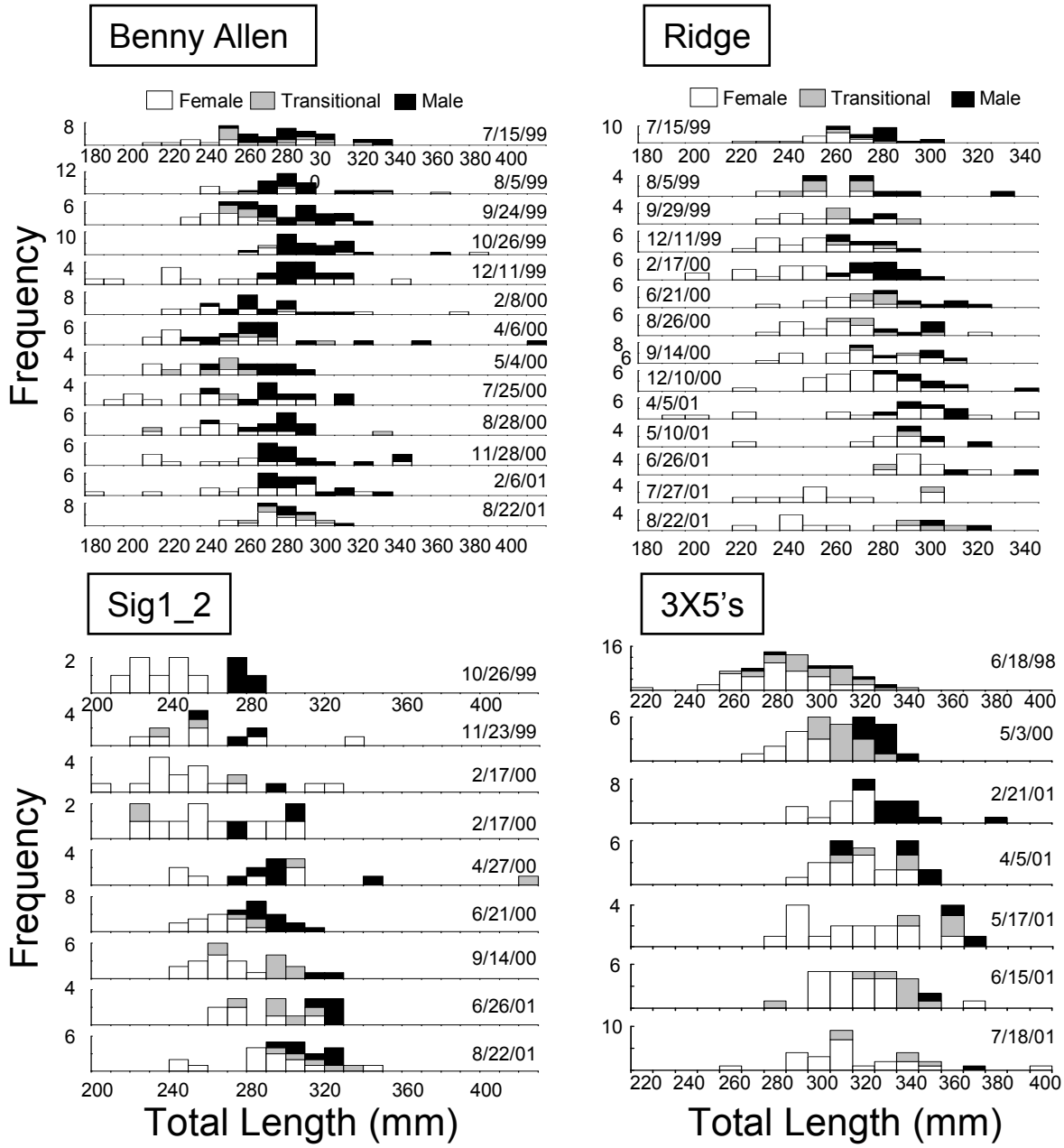

Figure A.9. Length frequency distributions by collection for the Benny Allen, Ridge, Sig1_2, and 3x5's sites.

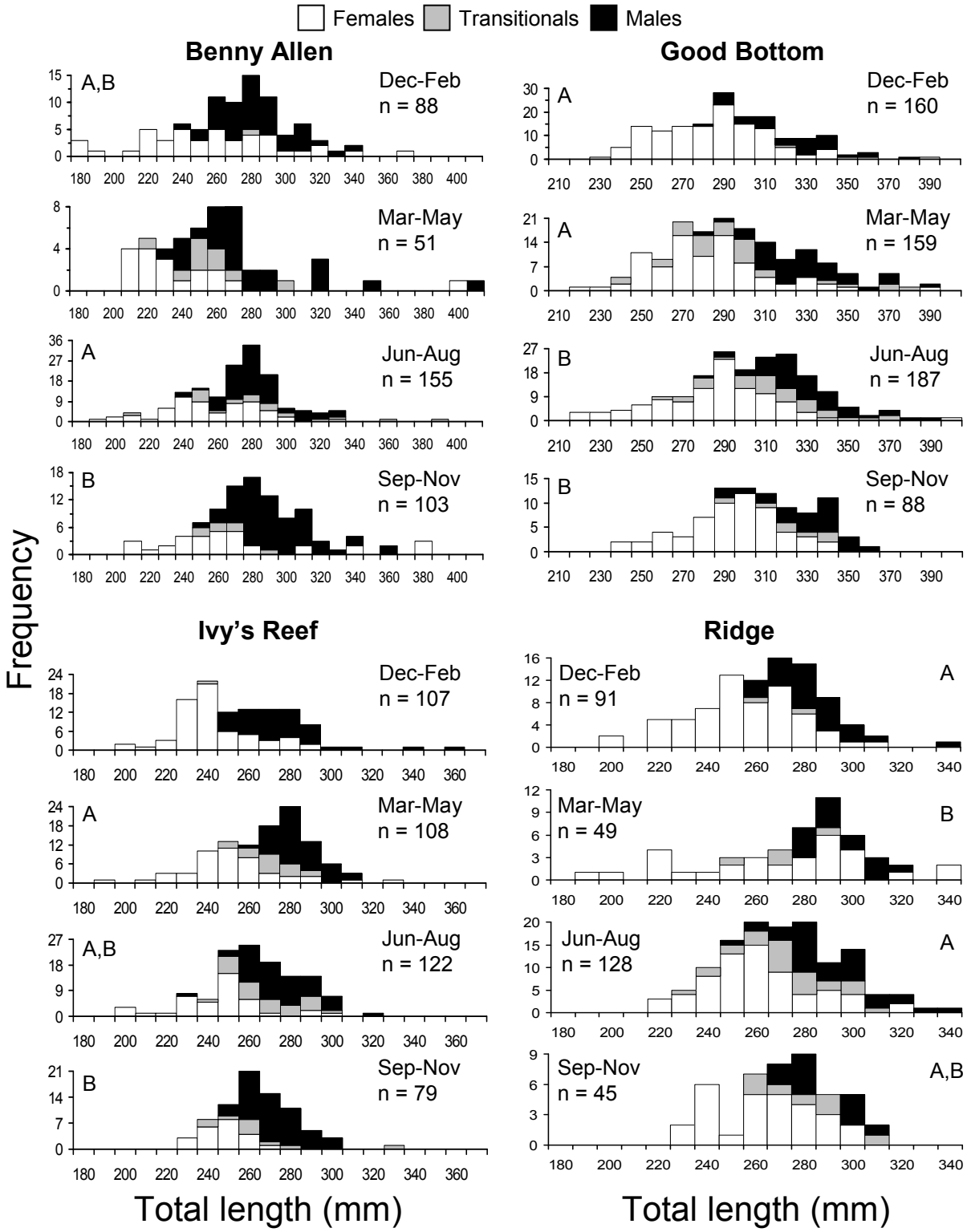

Figure A.10. Seasonal length frequency distributions for the Benny Allen, Good Bottom, Ivy's Reef, and Ridge sites. Distributions with like letters near the y axis (right margin for Ridge) were not significantly different.

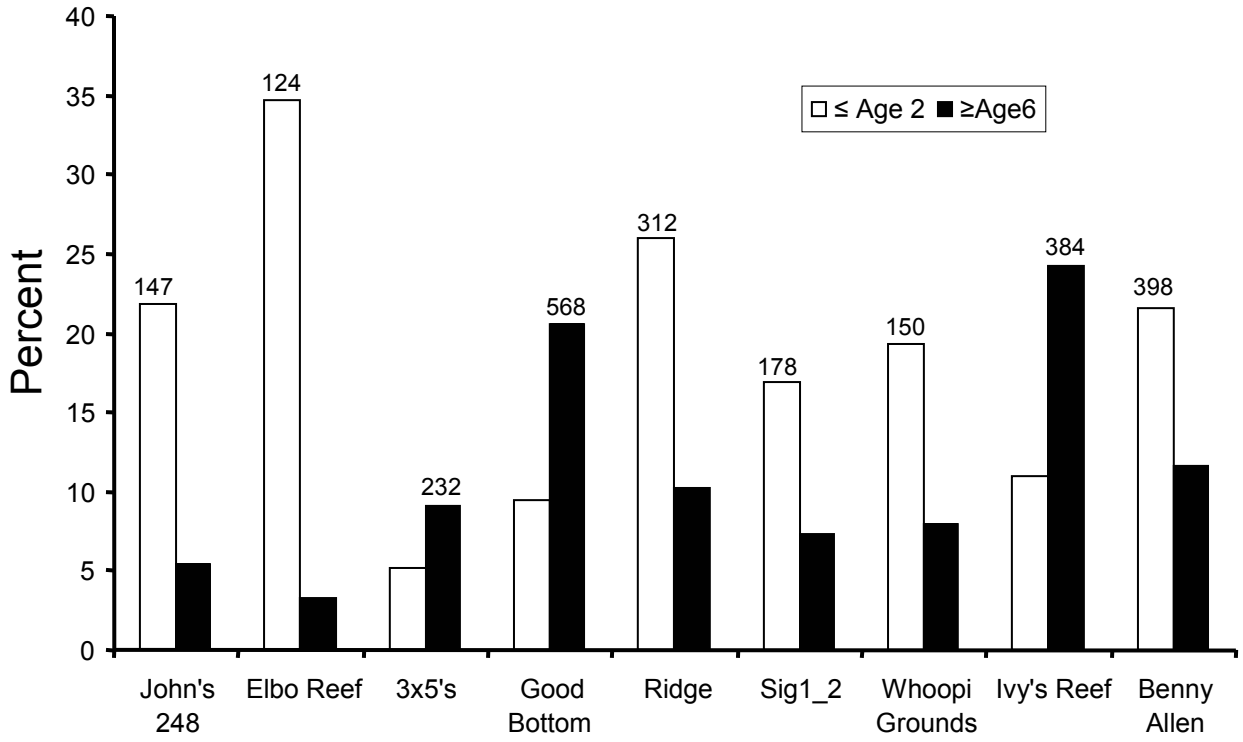

Figure A.11. Proportions of young (≤ age 2) and older (≥ age 6) red porgy at the standard sites.

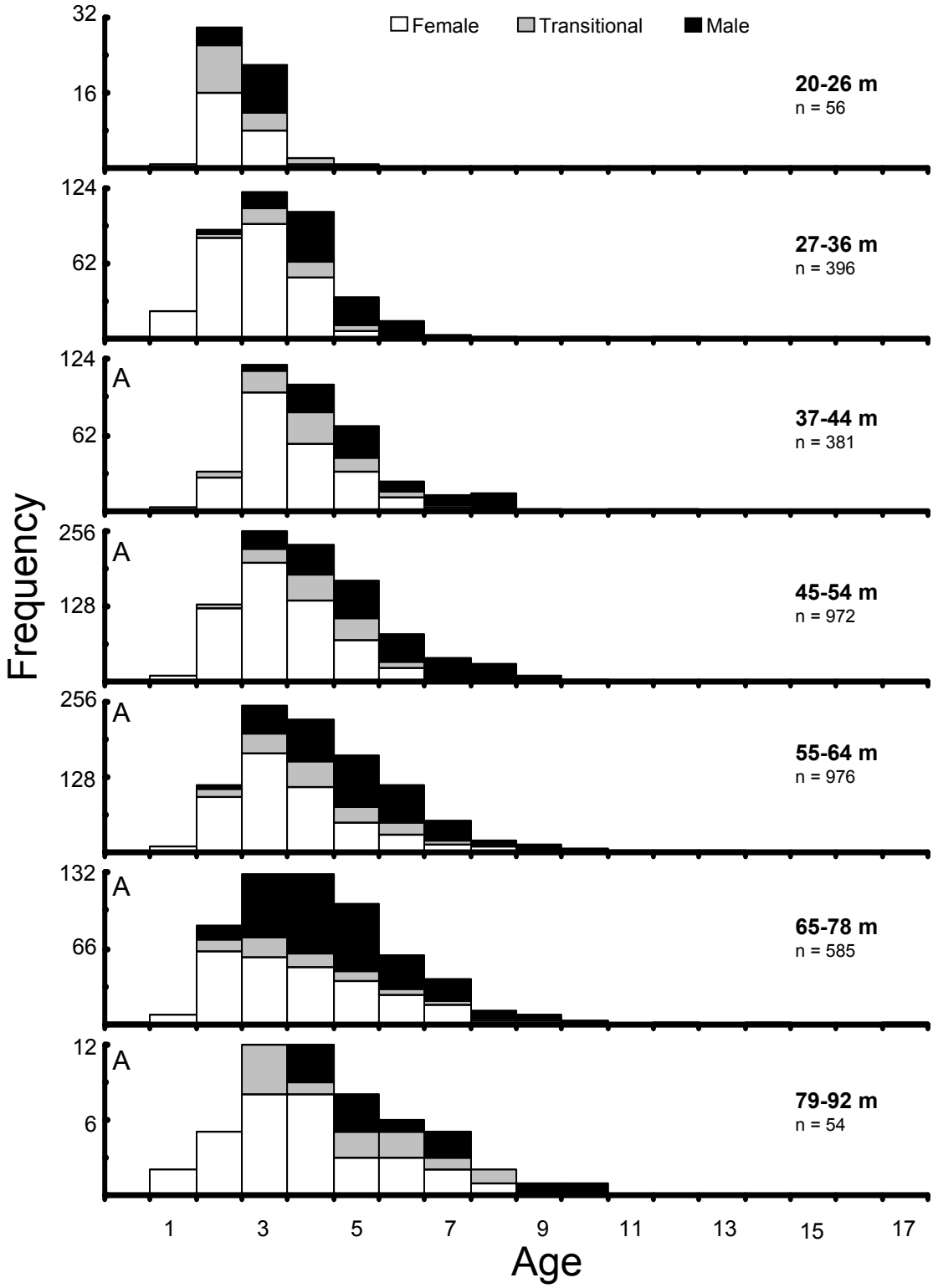

Figure A.12. Overall age frequency distributions of hook and line-caught red porgy by depth interval. Distributions with like letters near the y axis were not significantly different.

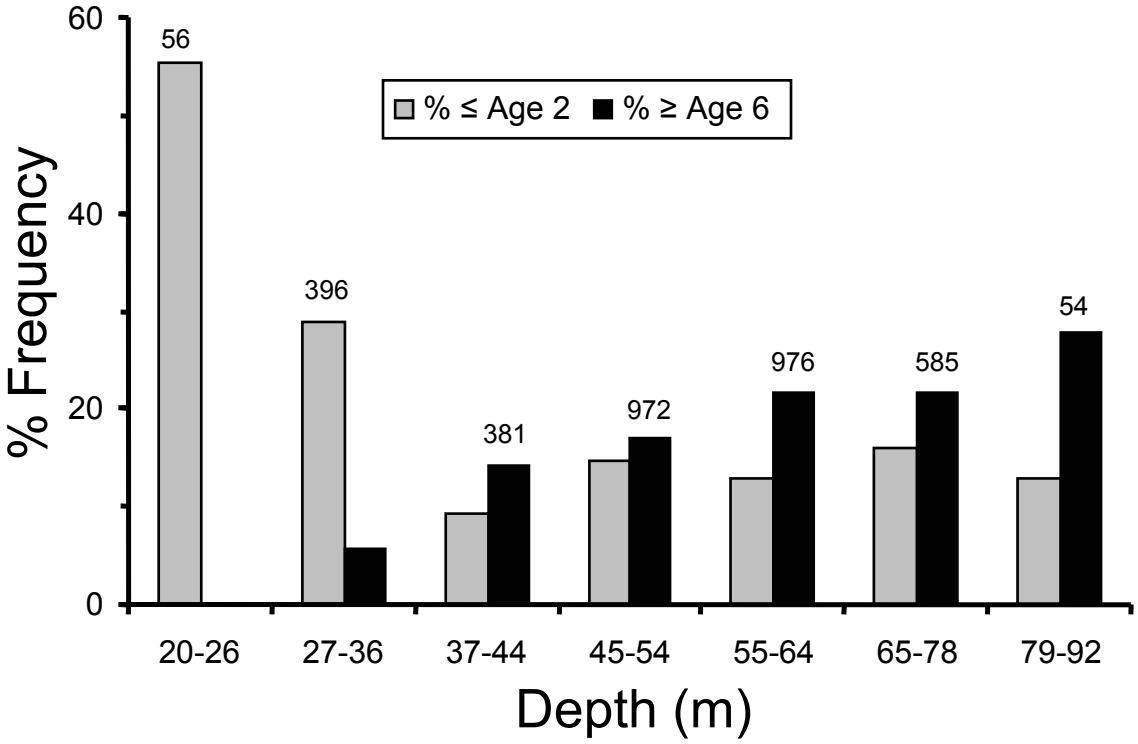

Figure A.13. Proportions of younger (≤ age 2) and older (≥ age 6) red porgy by depth interval. Numbers at top of bars are sample sizes for that depth interval.

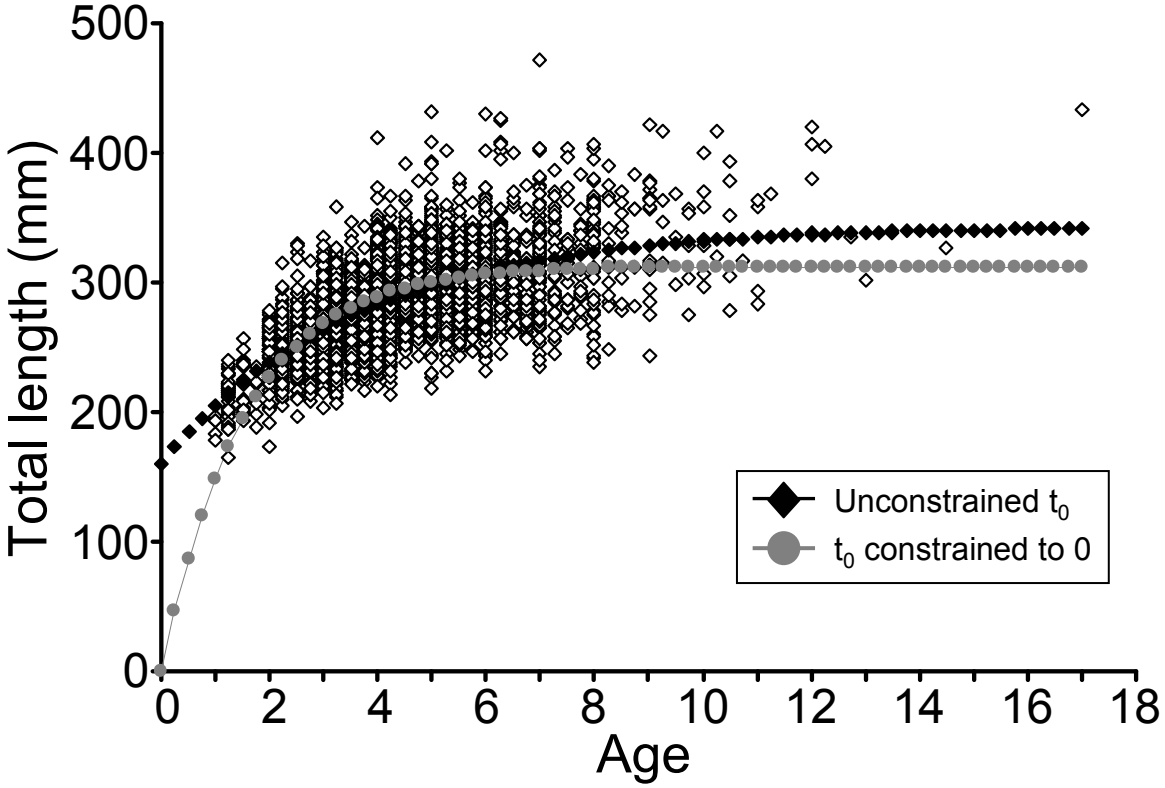

Figure A.14. Von Bertalanffy growth curves for all hook and line-caught red porgy from the northeastern Gulf of Mexico and raw age length data.

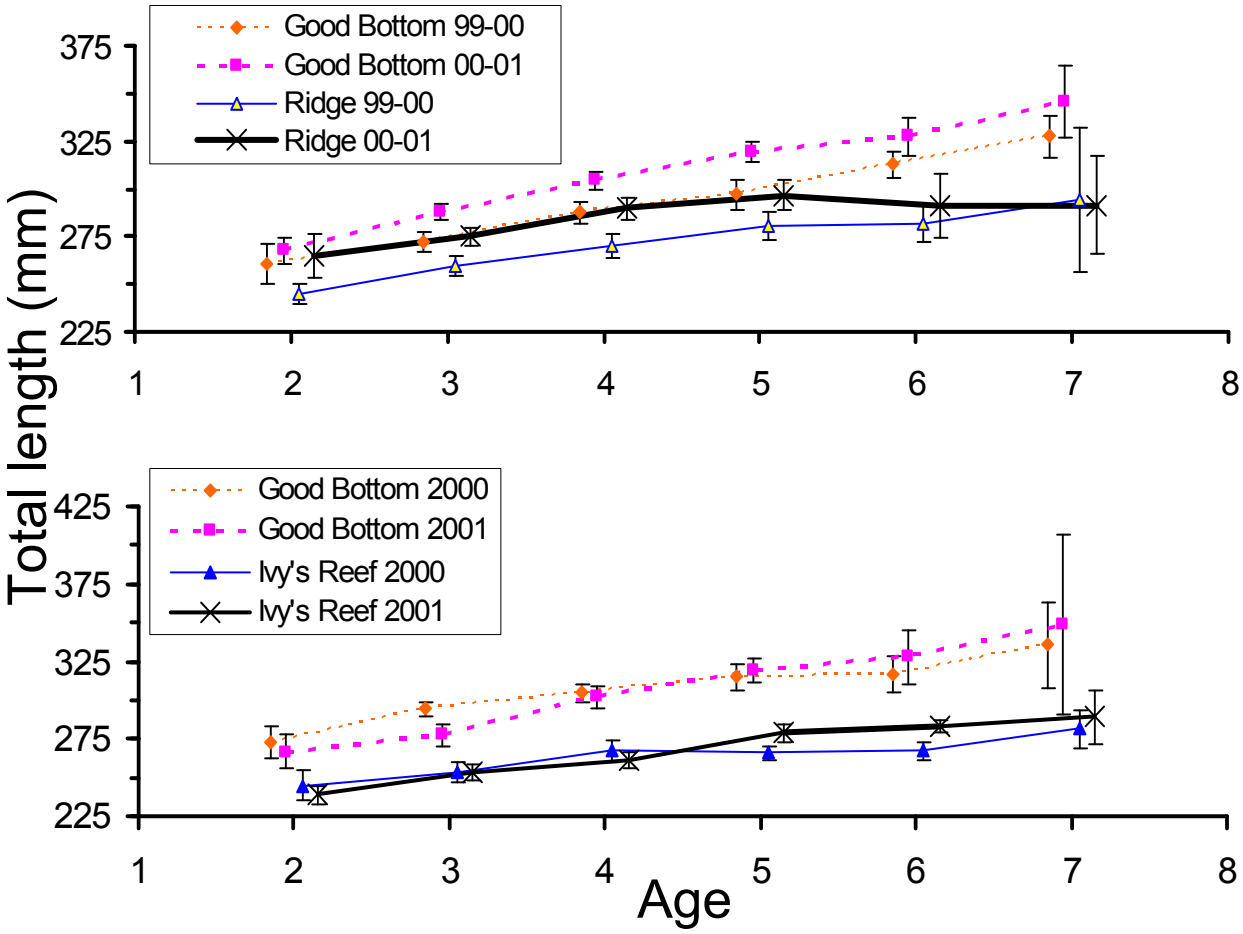

Figure A.15. Annual mean sizes at age and 95% C.L.'s of red porgy ages 2-7 for Good Bottom (GB) and Ridge during Jul 99 – Jun 00 and Jul 00 – Jul 01, and for GB and Ivy's Reef during Jun-Dec 2000 and Jan-Aug 2001.

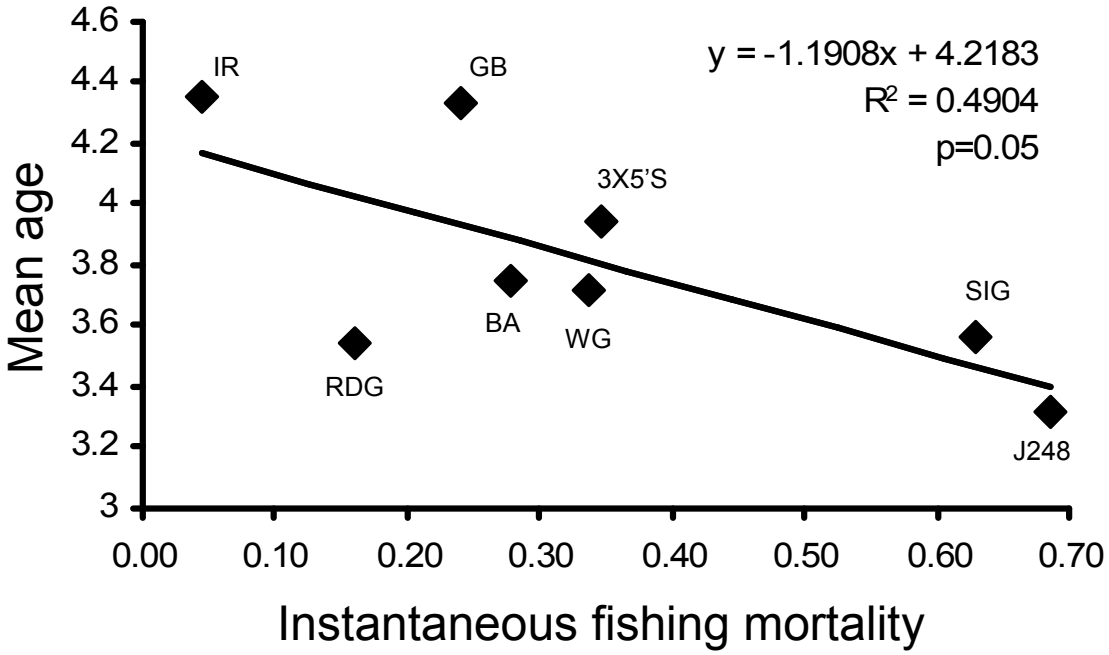

Figure A.16. Regression of mean age on instantaneous fishing mortality rate calculated using site-specific M's and Robson-Chapman Z's.

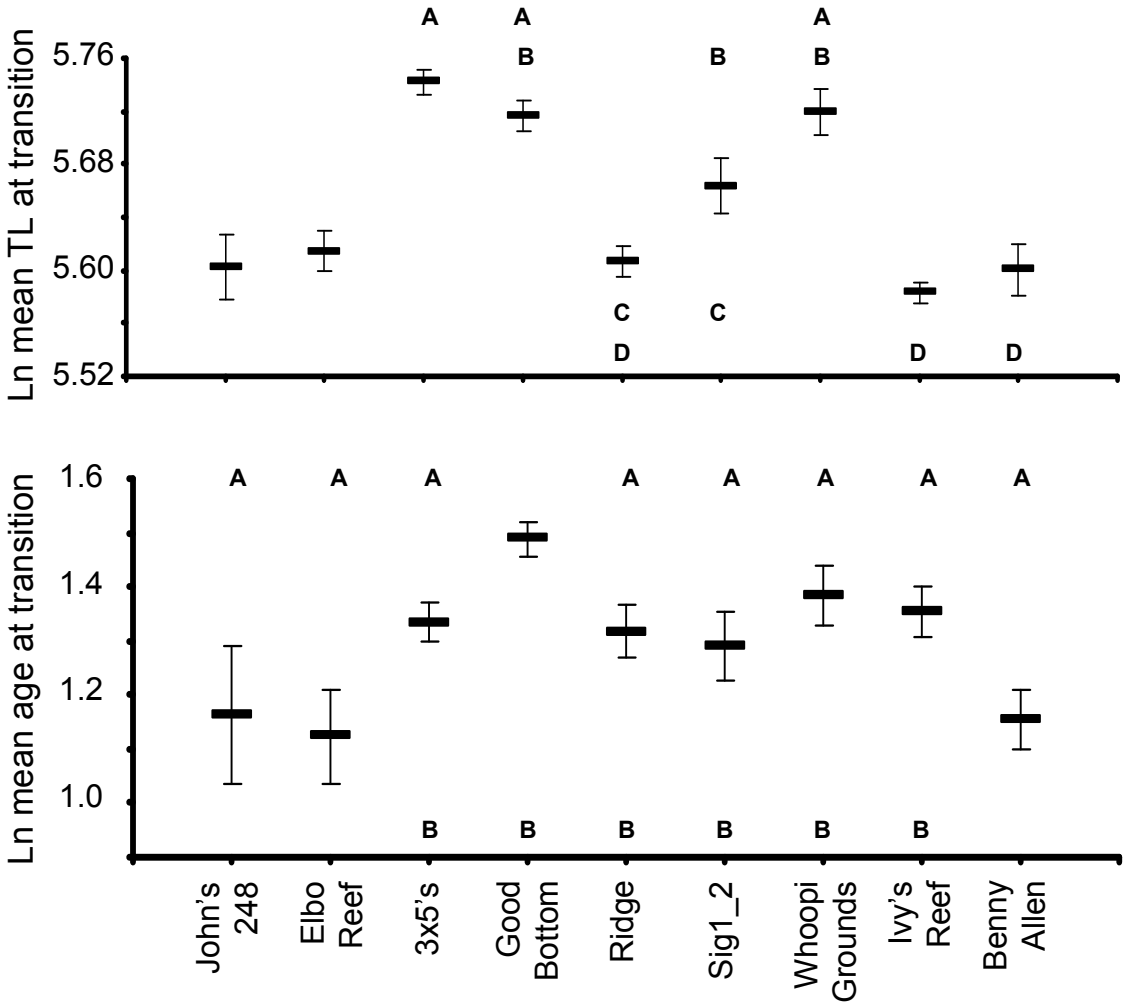

Figure A.17. Ln mean ± SE size (mm TL) at transition (upper panel) and age at transition (lower panel) of red porgy by site. Letters identify groups of sites which Tukey's HSD test indicated were not significantly different at α=0.05. John's 248 and Elbo Reef were excluded from the size at transition analyses because of their small sample sizes.

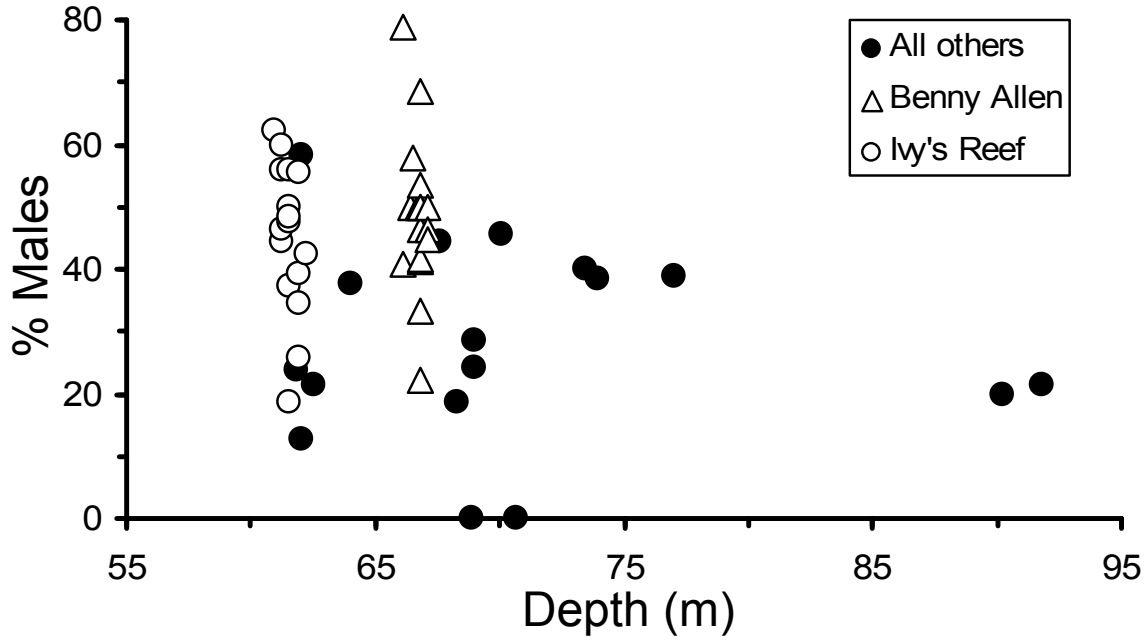

Figure A.18. Percent males by depth for Benny Allen, Ivy's Reef, and all other collections, including non-standard sites. Only collections with >4 fish were included in analysis.

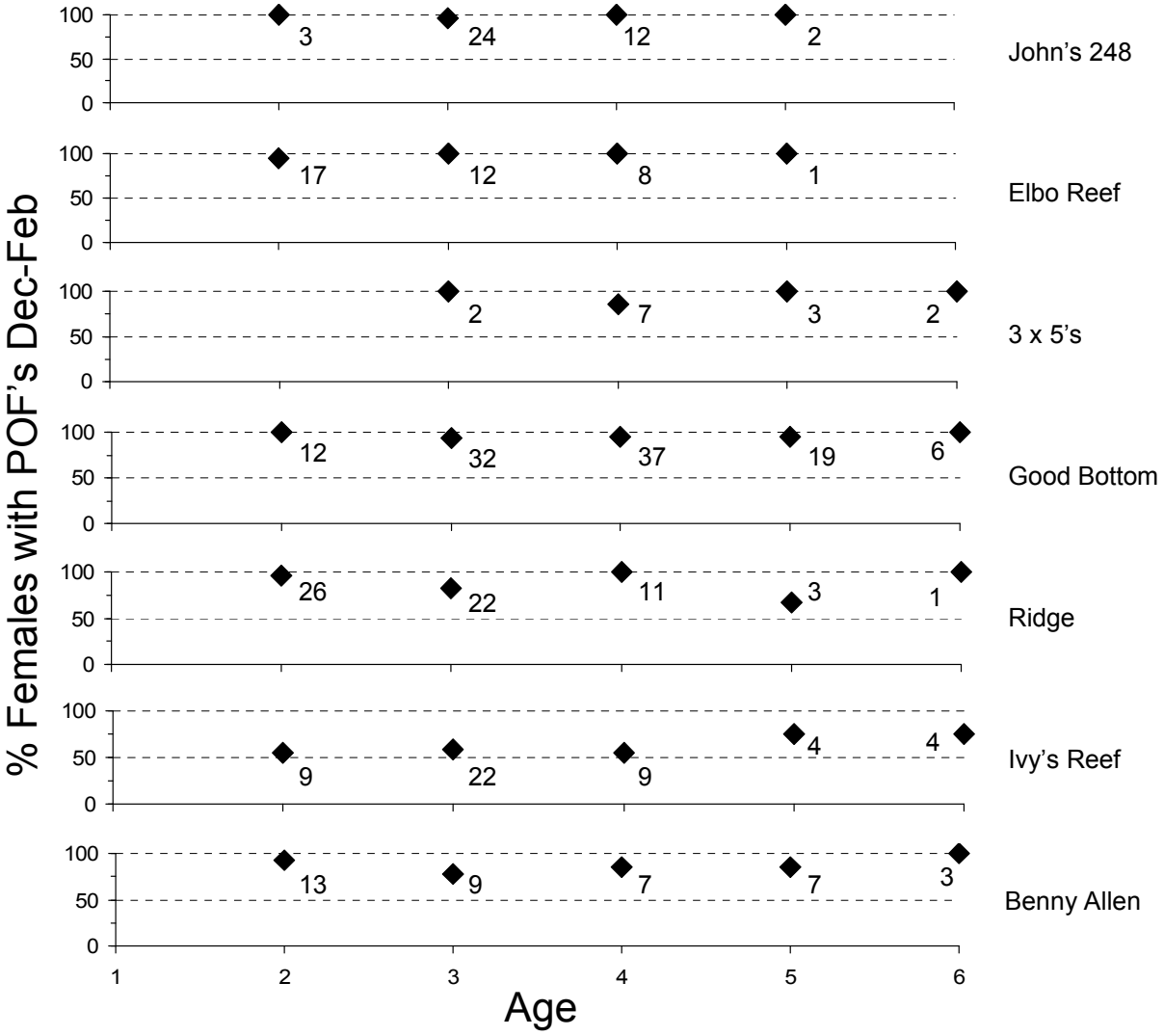

Figure A.19. Percentages of mature female red porgy (as indicated by the presence of POF's) by age during Dec-Feb for seven of the standard sites. Numbers adjacent to data points are total number of mature + immature females at each site.

APPENDIX B

SUPPLEMENTARY TABLES

Table B.1. Median and mean total lengths, standard errors, and size ranges for the nine standard sites by sex and overall. M = males, F = females, T = transitionals.

			Total Length (mm)			
Site	Sex	N	Range	Median	Mean	Std. Error
John's 248	M	42	253-326	287	289.3	2.6
Elbo Reef	M	36	222-335	280.5	281.9	3.4
3X5'S	M	38	268-382	332	331.0	3.6
Good Bottom	M	148	275-394	326	325.9	1.8
Ridge	M	86	246-340	284.5	288.0	1.9
Sig1_2	M	44	250-336	288	292.4	2.9
Whoopi Grounds	M	41	280-376	312	318.0	4.1
Ivy's Reef	M	187	227-364	275	275.9	1.2
Benny Allen	M	203	227-406	280	284.7	1.7
John's 248	F	99	213-304	255	255.4	1.8
Elbo Reef	F	82	213-292	247.5	250.1	2.2
3X5'S	F	138	221-400	300.5	301.3	2.1
Good Bottom	F	370	215-403	286	285.2	1.5
Ridge	F	188	188-341	258	259.9	1.9
Sig1_2	F	105	203-343	260	262.8	2.8
Whoopi Grounds	F	84	173-347	283	281.4	3.3
Ivy's Reef	F	173	187-331	244	245.9	1.6
Benny Allen	F	157	175-395	253	257.0	3.1
John's 248	T	6	253-292	269	271.3	6.6
Elbo Reef	T	7	264-297	270	274.6	4.1
3X5'S	T	58	263-355	312.5	312.6	3.0
Good Bottom	T	76	238-375	301.5	305.4	3.4
Ridge	T	39	229-310	273	272.9	3.0
Sig1_2	T	28	222-417	290.5	290.0	6.5
Whoopi Grounds	T	27	245-365	311	306.0	5.3
Ivy's Reef	T	56	237-330	266.5	266.4	2.3
Benny Allen	T	37	210-386	265	272.4	5.5
John's 248	All	147	213-326	264	265.7	1.9
Elbo Reef	All	125	213-335	263	260.6	2.2
3X5'S	All	234	221-400	310	308.9	1.7
Good Bottom	All	594	215-403	296	297.9	1.3
Ridge	All	313	188-341	270	269.2	1.5
Sig1_2	All	177	203-417	277	274.5	2.3
Whoopi Grounds	All	152	173-376	295	295.6	2.7
Ivy's Reef	All	416	187-364	262	262.1	1.1
Benny Allen	All	397	175-406	273	272.6	1.7

Table B.2 Site specific von Bertalanffy growth parameters and associated statistics.

Site	n	Size Range	Ages	t_0 unconstrained					
				t_0	95% C.I.	k	95% C.I.	L_4	95% C.I.
John's 248	146	213-326	1-7	-4.17	-6.99 to -1.34	0.2	0.04-0.36	338.8	282.2-395.3
Elbo Reef	124	213-335	1-12	-6.14	-10.34 to -1.93	0.12	0.01-0.23	386.9	278.3-495.5
3x5's	232	221-400	1-7	-2.07	-4.44 to 0.31	0.34	0.11-0.57	354.8	324.3-385.3
Good Bot.	568	215-403	1-11	-3.00	-4.36 to -1.64	0.22	0.14-0.30	369.8	346.1-393.4
Ridge	312	188-341	1-9	-1.48	-2.44 to -0.53	0.44	0.30-0.59	301.4	290.6-312.2
Sig 1_2	178	203-417	1-9	-4.95	-10.24 to 0.35	0.14	-0.04-0.32	388.4	249.3-527.5
Whoopi Gr.	150	173-376	1-13	-0.97	-2.35 to 0.42	0.44	0.21-0.68	336	314.5-357.5
Ivy's Reef	384	187-364	1-12	-3.22	-5.25 to -1.19	0.29	0.16-0.43	295.8	281.0-310.7
Benny Allen	396	179-406	1-14	-2.18	-3.50 to -0.86	0.27	0.16-0.38	337.5	312.5-362.6
				t_0 constrained to 0					
John's 248	146	213-326	1-7	0		1.12	1.00-1.24	277.7	273.5-281.9
Elbo Reef	124	213-335	1-12	0		0.88	0.78-0.99	281.4	274.4-288.5
3x5's	232	221-400	1-7	0		0.69	0.62-0.76	332.4	325.5-339.3
Good Bot.	568	215-403	1-11	0		0.59	0.55-0.62	328.4	324.1-332.7
Ridge	312	188-341	1-9	0		0.84	0.77-0.90	287.5	283.6-291.5
Sig 1_2	178	203-417	1-9	0		0.7	0.60-0.79	301.4	292.3-310.5
Whoopi Gr.	150	173-376	1-13	0		0.68	0.60-0.77	323.2	314.4-332.0
Ivy's Reef	384	187-364	1-12	0		0.81	0.75-0.87	275.7	272.7-278.8
Benny Allen	396	179-406	1-14	0		0.63	0.58-0.67	304.2	298.5-309.9

Table B.3. Results of Tukey's HSD test of mean size at age among the standard sites for ages 2-7. Lower case letters in bold indicate sites which were not significantly different at α=0.05. BA = Benny Allen, ER = Elbo Reef, GB = Good Bottom, IR = Ivy's Reef, J248 = John's 248, RDG = Ridge, S1_2 = Sig1_2, WG = Whoopi Grounds.

Age	Mean TL	n	Site	Age	Mean TL	n	Site	Age	Mean TL	n	Site
2	**a** 278.9	11	3X5s	4	**a** 313.9	71	3X5s	6	**a** 333.0	14	3X5s
2	**b a** 264.3	27	WG	4	**b a** 304.5	44	WG	6	**b a** 317.9	60	GB
2	**b** 255.8	51	GB	4	**c b** 297.1	142	GB	6	**b** 314.5	27	BA
2	**b c** 255.4	18	J248	4	**c d** 287.3	42	S1_2	6	**c** 289.8	18	RDG
2	**c** 246.9	72	RDG	4	**e d** 282.1	65	RDG	6	**c** 276.5	54	IR
2	**c** 245.1	27	S1_2	4	**e d** 279.5	97	BA				
2	**c** 243.3	42	ER	4	**e d** 275.7	42	J248	7	**a** 332.4	28	GB
2	**c** 242.2	78	BA	4	**f e** 270.9	35	ER	7	**a** 313.1	14	BA
2	**c** 239.9	38	IR	4	**f e** 262.5	81	IR	7	**b** 280.3	25	IR
3	**a** 296.3	83	3X5s	5	**a** 320.4	45	3X5s				
3	**b a** 290.7	43	WG	5	**b a** 314.7	21	WG				
3	**b** 280.4	144	GB	5	**b a** 310.3	111	GB				
3	**c** 267.3	73	S1_2	5	**c b** 298.0	20	S1_2				
3	**c** 267.1	95	RDG	5	**c** 290.7	13	J248				
3	**c** 266.2	107	BA	5	**c** 289.6	62	BA				
3	**d c** 260.6	52	J248	5	**c d** 287.9	39	RDG				
3	**d c** 258.4	33	ER	5	**d** 271.1	70	IR				
3	**d** 252.4	98	IR								

Table B.4. Mean age (yr) and standard error for each site by sex. Ages are ordered from oldest to youngest for each sex. BA = Benny Allen, ER = Elbo Reef, GB = Good Bottom, IR = Ivy's Reef, J248 = John's 248, RDG = Ridge, SIG = Sig1_2, WG = Whoopi Grounds.

Females				Transitionals				Males			
Site	n	Mean Age	Std. Error	Site	n	Mean Age	Std. Error	Site	n	Mean Age	Std. Error
3x5's	137	3.72	0.09	**GB**	75	4.61	0.16	**GB**	141	5.87	0.13
GB	351	3.66	0.07	**WG**	27	4.15	0.23	**IR**	172	5.30	0.12
IR	157	3.39	0.10	**IR**	55	4.11	0.19	**RDG**	85	4.82	0.17
WG	83	3.22	0.13	**3x5s**	57	3.93	0.14	**3x5s**	38	4.74	0.17
BA	157	3.11	0.11	**RDG**	39	3.90	0.18	**WG**	40	4.48	0.31
SIG	105	3.11	0.10	**SIG**	28	3.86	0.28	**J248**	42	4.45	0.16
RDG	187	2.88	0.08	**BA**	37	3.35	0.19	**SIG**	44	4.43	0.23
J248	99	2.83	0.11	**J248**	6	3.33	0.42	**ER**	36	4.36	0.29
ER	81	2.74	0.09	**ER**	7	3.14	0.26	**BA**	203	4.31	0.11

REFERENCES

Adams, S., B.D. Mapstone, G.R. Russ, and C.R. Davies. 2000. Geographic variation in the sex ratio, sex specific size, and age structure of *Plectropomus leopardus* (Serranidae) between reefs open and closed to fishing on the Great Barrier Reef. Can. J. Fish. Aquat. Sci. 57:1448-1458.

Aldenhoven, J.M. 1986. Local variation in mortality rates and life-expectancy estimates of the coral-reef fish *Centropyge bicolor* (Pisces: Pomacanthidae). Mar. Biol. 92:237-244.

Alekseev, F.E. 1982. Hermaphroditism in sparid fishes (Perciformes, Sparidae) I. Protogyny in porgies, *Pagrus pagrus, P. orphus, P. ehrenbergi* and *P. auriga*, from West Africa. J. Ichthyol., Eng. Transl., 22:85-94.

Alekseev, F.E. 1983. Hermaphroditism in porgies (Perciformes, Sparidae) I. Sexual structure of the populations, mechanism of its formation and evolution in scups, *Pagrus pagrus, P. orphus, P. ehrenbergi* and *P. auriga*. J. Ichthyol., Eng. Transl., 23:61-73.

Alonzo, S.H., and M. Mangel. 2004. The effects of size-selective fisheries on the stock dynamics of and sperm limitation in sex-changing fish. Fish. Bull. 102:1-13.

Armsworth, P.R. 2001. Effects of fishing on a protogynous hermaphrodite. Can. J. Fish. Aquat. Sci. 58:568-578.

Bagenal, T.B., and E. Braum. 1971. Eggs and early life history. *In* Methods for assessment of fish production in fresh waters. *Edited by* W.E. Ricker. Blackwell Sci. Publ., Oxford. pp. 166-198.

Bailey, K.M. 1997. Structural dynamics and ecology of flatfish populations. Neth. J. Sea Res. 37:269-280.

Ball, A.O., G.R. Sedberry, J.H. Wessel III, and R.W. Chapman. 2003. Large-scale genetic differentiation of *Pagrus pagrus* in the Atlantic. J. Fish Biol. 62:1232-1237.

Bannerot, S.W., W. Fox, Jr., and J.E. Powers. 1987. Reproductive strategies and the management of snappers and groupers in the Gulf of Mexico and Caribbean. *In* Tropical snappers and groupers: biology and fisheries management. *Edited by* J.J. Polovina and S. Ralston. Westview Press, Boulder, Colorado. pp. 561-603.

Bauchot, M.L., and J.C. Hureau. 1990. Sparidae. *In* Check-list of the fishes of the eastern tropical Atlantic (CLOFETA), Vol. 2. *Edited by* J.C.Quero, J.C. Hureau, C. Karrer, and A.Post. UNESCO, Paris and Lisbon.

Beaumariage, D.S. 1969. Returns from the 1965 Schlitz tagging program. Florida Bd. Cons. Mar. Res. Lab. Tech. Ser. No. 59.

Begg, G.A., J.A. Hare, and D.D. Sheehan. 1999. The role of life history parameters as indicators of stock structure. Fish. Res. 43:141-163.

Berg, E., and T. Pedersen. 2001. Variability in recruitment, growth and sexual maturity of coastal cod (*Gadus morhua* L.) in a fjord system in northern Norway. Fish. Res. 52:179-189.

Brown-Peterson, N., R. Thomas, and C.R. Arnold. 1988. Reproductive biology of the spotted seatrout, *Cynoscion nebulosus*, in south Texas. Fish. Bull. 86(2):373-388.

Buxton, C.D. 1990. The reproductive biology of *Chrysoblephus laticeps* and *C. cristiceps* (Teleostei: Sparidae). J. Zool., Lond. 220:497-511.

Buxton, C.D. 1992. The application of yield-per-recruit models to two South African sparid reef species, with special consideration to sex change. Fish. Res. 15:1-16.

Buxton, C.D. 1993. Life-history changes in exploited reef fishes on the east coast of South Africa. Env. Biol. Fishes 36:47-63.

Buxton, C.D., and J.C. Allen. 1989. Mark and recapture studies of two reef sparids in the Tsitsikamma Coastal National Park. Koedoe 32:39-45.

Buxton, C.D., and P.A. Garratt. 1990. Alternative reproductive styles in seabreams (Pisces:Sparidae). Environ. Biol. Fishes 28:113-124.

Camus, P.A., and M. Lima. 2002. Populations, metapopulations, and the open-closed dilemma: the conflict between operational and natural population concepts. Oikos 97(3):433-438.

Cárdenas, S., and Á. Calvo. 2003. Reproducción en el mar y en cautividad del Pargo Común o Bocinegro, *Pagrus pagrus* (Pisces: Sparidae). [Natural and captive reproduction of common seabream or red porgy, *Pagrus pagrus* (Pisces: Sparidae)]. CIVA 2003: 468-480. url: http://www.civa2003.org.

Chapman, D.G., and D.S. Robson. 1960. The analysis of a catch curve. Biometrics 16:354-368.

Charnov, E.L. 1982. The theory of sex allocation. Princeton University Press, Princeton, NJ.

Choat, J.H. 1998. The question of spatial scale in reef fish studies. *In* ReeFish ’95: recruitment and population dynamics of coral reef fishes. *Edited by* G.P. Jones, P.J. Doherty, B.M. Mapstone, and L. Howlett. CRC Reef Research Centre, Townsville, Aus. pp. 83-86.

Christensen, J.M. 1964. Burning of otoliths, a technique for age determination of soles and other fish. J. Du Conseil 29(1):73-81.

Ciechomski, J.D., and G. Weiss. 1973. Desove y disarrollo embrionario y larval del besugo,

Pagrus pagrus (Linne) en el Mar de Argentina (Pisces, Sparidae). Physis Rev. Assoc. Argent. Cienc. Nat., Secc. A., 32(85):481-487.

Ciechomski, J.D., and M.C. Cassia. 1974. Reproduccion y fecundidad del besugo, *Pagrus pagrus* (Linne) en el Mar de Argentina (Pisces, Sparidae). Physis Rev. Assoc. Argent. Cienc. Nat., Sec. A., 33(87):443-452.

Clavijo, I. 1982. Aspects of the reproductive biology of the redband parrotfish *Sparisoma aurofrenatum.* Ph.D. Dissertation. Univ. Puerto Rico, Mayaguez, Puerto Rico.

Clifton, K.E. 1995. Asynchronous food availability on neighbouring Caribbean coral reefs determines seasonal patterns of growth and reproduction for the herbivorous parrotfish *Scarus iserti*. Mar. Ecol. Prog. Ser. 116:39-46.

Coleman, F.C., C.C. Koenig, and L.A. Collins. 1996. Reproductive styles of shallow-water groupers (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. Environ. Biol. Fish. 47:129-141.

Coleman, F.C., C.C. Koenig, A. Eklund, and C.B. Grimes. 1999. Management and conservation of temperate reef fishes in the snapper-grouper complex of the southeastern United States. American Fisheries Society Symposium 23:233-242.

Collins, M.R. 1990. A comparison of three fish trap designs. Fish. Res. 9:325-332.

Collins, M.R., and G.R. Sedberry. 1991. Status of vermilion snapper and red porgy stocks off South Carolina. Trans. Am. Fish. Soc. 120:116-120.

Collins, M.R., S.B. Van Sant, and G.R. Sedberry. 1996. Age validation, movements, and growth rates of tagged gag (*Mycteroperca microlepis*), black sea bass (*Centropristis striata*), and red porgy (*Pagrus pagrus*). *In* Biology, fisheries and culture of tropical groupers and snappers. *Edited by* F. Arraguin-Sanchez, J.L. Munro, M.C. Balgos, and D. Pauley. ICLARM Conf. Proc. 48. pp. 158-162.

Costa, P.A.S., E.B. Fagundes-Netto, L.R. Gaelzer, P.S. Lacerda, and W.M. Monteiro-Ribas. 1997. Crescimento e ciclo reprodutivo do pargo-rosa (*Pagrus pagrus* Linnaeus, 1758) na região do Cabo Frio, Rio de Janeiro. Nerítica, Curitiba 11:139-154.

Cotrina, C.P. 1986. Estudios biológicos sobre peces costeros con datos de dos campañas de investigación realizadas en 1981. V. El besugo (*Sparus pagrus*). Publ. Com. Tec. Mix. Fr. Mar. 1 (1):53-59.

Cotrina, C.P., and H.E. Christiansen. 1994. El comportamiento reproductivo del besugo (*Pagrus pagrus*) en el ecosistema Costero Bonaerense. Rev. Invest. Des. Pesq. 9:25-58.

Cotrina, C.P., and M.C. Raimondo. 1997. Estudio de edad y crecimiento del besugo (*Pagrus pagrus*) del sector Costero Bonaerense. Rev. Invest. Des. Pesq. 11:95-118.

Cowen, R.K. 1990. Sex change and life history patterns of the labrid *Semicossyphus pulcher*, across an environmental gradient. Copeia 1990(3):787-795.

Crowder, L.B., S.J. Lyman, W.F. Figueira, and J. Priddy. 2000. Source-sink population dynamics and the problem of siting marine reserves. Bull. Mar. Sci. 66(3):799-820.

Davies, C.R. 1995. Patterns of movement of three species of coral reef fish on the Great Barrier Reef. Ph.D. thesis, James Cook University, North Queensland, Australia.

Domeier, M.L., and P.L. Collin. 1997. Tropical reef fish spawning aggregations: defined and reviewed. Bull. Mar. Sci. 60(3):698-726.

Dudgeon, C.L., N. Gust, and D. Blair. 2000. No apparent genetic basis to demographic differences in scarid fishes across continental shelf of the Great Barrier Reef. Mar. Biol. 137:1059-1066.

Ferreira, B.P., and G.R. Russ. 1995. Population structure of the leopard coralgrouper, *Plectropomus leopardus*, on fished and unfished reefs off Townsville, Central Great Barrier Reef, Australia. Fish. Bull. 93(4):629-642.

Fischer, E.A., and C.W. Petersen. 1987. The evolution of sexual patterns in the seabasses. BioScience 37:482-489.

Garratt, P.A. 1993. Spawning of riverbream, *Acanthopagrus berda*, in Kosi estuary. S. Afr. J. Zool. 28(1):26-31.

Ghiselin, M.T. 1969. The evolution of hermaphroditism among animals. Quart. Rev. Biol. 44:189-208.

Gilmore, R.G., and R.S. Jones. 1992. Color variation and associated behavior in the epinepheline groupers, *Mycterperca microlepis* (Goode and Bean) and *M. phenax* Jordan and Swain. Bull. Mar. Sci. 51(1):83-103.

Griffiths, M.H., and C.G. Wilke. 2002. Long-term movement patterns of five temperate reef fishes (Pisces:Sparidae): implications for marine reserves. Mar. Freshwater Res. 53:233-244.

Grimes, C.B., C.S. Manooch, and G.R. Huntsman. 1982. Reef and rock outcropping fishes of the outer continental shelf of North Carolina and South Carolina, and ecological notes on the red porgy and vermilion snapper. Bull. Mar. Sci. 32(1):277-289.

Grimm, V., K. Reise, and M. Strasser. 2003. Marine metapopulations: a useful concept? Helgol Mar. Res. 56:222-228.

Gust, N. 2004. Variation in the population biology of protogynous coral reef fishes over tens of kilometers. Can. J. Fish. Aquat. Sci. 61:205-218.

Gust, N., J.H. Choat, and M.I. McCormick. 2001. Spatial variability in reef fish distribution, abundance, size and biomass: a multi-scale analysis. Mar. Ecol. Prog. Ser. 214:237-251.

Gust, N., J.H. Choat, and J.L. Ackerman. 2002. Demographic plasticity in tropical reef fishes. Mar. Biol. 140:1039-1051.

Gunderson, D.R. 1972. Evidence that Pacific ocean perch (*Sebastes alutus*) in Queen Charlotte Sound form aggregations that have different biological characteristics. J. Fish. Res. Board Can. 29(7):1061-1070.

Hanski, I. and OE Gaggiotti (Eds.). 2004. Ecology, genetics, and evolution of metapopulations **:** **s**tandard methods for inventory and monitoring. Academic Press, San Diego, USA.

Hanski, I., and D. Simberloff. 1997. The metapopulation approach, its history, conceptual domain, and application to conservation. *In* Metapopulation biology: ecology, genetics, and evolution. *Edited by* I. Hanski and M.E. Gilpin. Academic Press, San Diego, CA. pp. 5-26.

Harris, P.J., and J.C. McGovern. 1997. Changes in the life history of red porgy, *Pagrus pagrus*, from the southeastern United States, 1972-1994. Fish. Bull. 95:732-747.

Hart, A.M., and G.R. Russ. 1996. Response of herbivorous fishes to crown-of-thorns starfish *Acanthaster planci* outbreaks. III. Age, growth, mortality and maturity indices of *Acanthurus nigrofuscus*. Mar. Ecol. Prog. Ser. 136:25-35.

Hastings, A., and S. Harrison. 1994. Metapopulation dynamics and genetics. Annual Reviews in Ecology and Systematics 25:167-188.

Hoenig, J.M. 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. 82:898-903.

Hood, P.B., and A.K. Johnson. 2000. Age, growth, mortality, and reproduction of red porgy, *Pagrus pagrus* from the eastern Gulf of Mexico. Fish. Bull. 98:723-735.

Hussain, N., S. Akatsu, and C. El-Zahr. 1981. Spawning, egg and larval development, and growth of *Acanthopagrus cuvieri* (Sparidae). Aquaculture 22:125-136.

Huntsman, G.R., and W.E. Schaaf. 1994. Simulation of the impact of fishing on reproduction of a protogynous grouper, the graysby. N. Amer. J. Fish. Man. 14:41-52.

Ingram, G.W., Jr. 2001. Stock structure of gray triggerfish, *Balistes capriscus*, on multiple spatial scales in the Gulf of Mexico. Ph.D. thesis, Univ. South Alabama, Mobile, AL.

Jones, G.P. 1980. Growth and reproduction in the protogynous hermaphrodite *Pseudolabrus celidotus* (Pisces:Labridae) in New Zealand. Copeia 1980(4):660-675.

Jones, G.P. 1987. Competitive interactions among adults and juveniles in a coral reef fish. Ecology 68(5):1534-1547.

Jones, G.P. 1991. Postrecruitment processes in the ecology of coral reef fish populations: a multifactorial perspective. *In* The ecology of fishes on coral reefs. *Edited by* P.F. Sale. Academic Press, Orlando, FL. pp. 294-328.

Kingsford, M.J., and J.M. Hughes. 2005. Patterns of growth, mortality, and size of the tropical damselfish *Acanthochromis polyacanthus* across the continental shelf of the Great Barrier Reef. Fish. Bull. 103:561-573.

Kodric-Brown, A. 1998. Sexual dichromatism and temporary color changes in the reproduction of fishes. Amer. Zool. 38:70-81.

Koenig, C.C., F.C. Coleman, L.A. Collins, Y. Sadovy, and P.L. Collins. 1996. Reproduction in gag (*Mycteroperca microlepis*) (Pisces: Serranidae) in the eastern Gulf of Mexico and the consequences of fishing spawning aggregations. *In* Biology, fisheries and culture of tropical groupers and snappers. *Edited by* F. Arreguin-Sanchez, J.L. Munro, M.C. Balgos, and D. Pauly. ICLARM Conf. Proc. 48. pp. 307-323.

Koenig, C.C., F.C. Coleman, C.B. Grimes, G.R. Fitzhugh, K.M. Scanlon, C.T. Gledhill, and M. Grace. 2000. Protection of fish spawning habitat for the conservation of warm-temperate reef-fish fisheries of the shelf-edge reefs of Florida. Bull. Mar. Sci. 66(3):593-616.

Kokokiris, L., S. Bruslé, M. Kentouri, and A. Fostier. 1999. Sexual maturity and hermaphroditism of the red porgy *Pagrus pagrus* (Teleostei: Sparidae). Mar. Biol. 134:621-629.

Kokokiris, F. Le Menn, M. Kentouri, M. Kagara, and A. Fostier. 2001. Seasonal cycle of gonadal development and serum levels of vitellogenin of the red porgy *Pagrus pagrus* (Teleostei: Sparidae). Mar. Biol. 139:549-559.

Kolios, P., S. Kiritsis, and N. Katribusas. 1997. Larval-rearing and growout of the red porgy (*Pagrus pagrus*) in the Riopesca hatchery (Greece). Hydrobiologia 358:321-325.

Kritzer, J.P. 2002. Variation in the population biology of stripey bass *Lutjanus carponotatus* within and between two island groups on the Great Barrier Reef. Mar. Ecol. Prog. Ser. 243:191-207.

Kritzer, J.P., and P.F. Sale. 2004. Metapopulation ecology in the sea: from Levins♠ model to marine ecology and fisheries science. Fish and Fisheries 5:131-140.

Kritzer, J.P., C.R. Davies, and B.D. Mapstone. 2001. Characterizing fish populations: effects of sample size and population structure on the precision of demographic parameter estimates. Can. J. Fish. Aquat. Sci. 58(8):1557-1568.

Kuehl, R.O. 1994. Statistical principles of research design and analysis. Duxbury Press, Belmont, CA.

Labropoulou, M., A. Machias, and N. Tsimenides. 1999. Habitat selection and diet of juvenile red porgy, *Pagrus pagrus* (Linnaeus, 1758). Fish. Bull. 97:495-507.

Law, R. 2000. Fishing, selection, and phenotypic evolution. ICES J. Mar. Sci. 57:659-668.

Leu, M.-Y. 1994. Natural spawning and larval rearing of silver bream, *Rhabdosargus sarba* (Forsskål), in captivity. Aquaculture 120:115-122.

Levin, P.S. 1993. Habitat structure, conspecific presence and spatial variation in the recruitment of a temperate reef fish. Oecologia 94:176-185.

Levin, S.A. 1992. The problem of pattern and scale in ecology. Ecology 73(6):1943-1967.

Levins, R. 1970. Extinction. *In*: Some mathematical problems in biology. *Edited by* M. Desternhaber. American Mathematical Society, Providence, RI. pp. 77-107.

Lutnesky, M.M.F. 1988. Sexual dimorphism, dichromatism, and protogynous hermaphroditism in the pomacanthid angelfish, *Centropyge potteri*. Pacific Science 42(1-2):126.

Lutnesky, M.M.F. 1994. Density-dependent protogynous sex change in territorial-haremic fishes: models and evidence. Behav. Ecol. 5:375-383.

Man, A., R. Law, and N.V.C. Polunin. 1995. Role of marine reserves in recruitment to reef fisheries: a metapopulation model. Biological Conservation 71:197-204.

Manooch, C.S. 1975. A study of the taxonomy, exploitation, life history, ecology and tagging of the red porgy, *Pagrus pagrus* Linnaeus, of the Carolinas. Ph.D. thesis, North Carolina State Univ., Raleigh, NC.

Manooch, C.S. 1976. Reproductive cycle, fecundity, and sex ratios of the red porgy, *Pagrus pagrus* (Pisces: Sparidae) in North Carolina. Fish. Bull., U.S. 74:775-781.

Manooch, C.S. 1977. Foods of the red porgy, *Pagrus pagrus* Linnaeus (Pisces: Sparidae) from North Carolina and South Carolina. Bull. Mar. Sci. 27(4):776-787.

Manooch, C.S., and W.W. Hassler. 1978. Synopsis of biological data on the red porgy, *Pagrus pagrus* (Linnaeus). NOAA Tech. Rep. NMFS Circ. 412.

Manooch, C.S., and G.R. Huntsman. 1977. Age, growth, and mortality of the red porgy, *Pagrus*

pagrus. Trans. Am. Fish. Soc. 106:26-33.

Marconato, A., V. Tessari, and G. Marin. 1995. The mating system of *Xyrichthys novacula*: Sperm economy and fertilization success. J. Fish Biol. 47:292-301.

McGovern, J.C., D.M. Wyanski, O. Pashuk, C.S. Manooch II, and G.R. Sedberry. 1998. Changes in the sex ratio and size at maturity of gag, *Mycteroperca microlepis*, from the Atlantic coast of the southeastern United States during 1976-1995. Fish. Bull. 96:797-807.

McPherson, E., A. García, and A. Gordoa. 2000. Direct estimation of natural mortality rates for littoral marine fishes using populational data from a marine reserve. Mar. Biol. 137:1067-1076.

McQuinn, I.H. 1997. Metapopulations and the Atlantic herring. Rev. Fish Biol. Fish. 7:297-329.

Meekan, M.G., J.L. Ackerman, and G.M. Wellington. 2001. Demography and age structures of coral reef damselfishes in the tropical eastern Pacific Ocean. Mar. Ecol. Prog. Ser. 12:223-232.

Mihelakakis, A., T. Yoshimatsu, and C. Tsolkas. 2001. Spawning in captivity and early life history of cultured red porgy, *Pagrus pagrus*. Aquaculture 199:333-352.

Moran, M., C. Burton, and N. Caputi. 1998. Sexual and local variation in head morphology of snapper, *Pagrus auratus*, Sparidae, in the Shark Bay region of western Australia. Mar. Freshwater Res. 50:27-34.

Moran, M., C. Burton, and J. Jenke. 2003. Long-term movement patterns of continental shelf and inner gulf snapper (*Pagrus auratus*, Sparidae) from tagging in the Shark Bay region of Western Australia. Mar. Freshwater Res. 54:913-922.

Murie, D.J., and D.C. Parkyn. 2005. Age and growth of white grunt (*Haemulon plumieri*): a comparison of two populations along the west coast of Florida. Bull. Mar. Sci. 76(1):73-93.

Murphy, M.D. 1997. Bias in Chapman-Robson and least-squares estimators of mortality rates for steady-state populations. Fish. Bull. 95(4):863-868.

Negpen, C.S. 1977. The biology of the hottentot *Pachymetopon blochii* (Val.) and the silverfish *Argyrozona argyrozona* (Val.) along the Cape south west coast. Sea Fish. Branch Inv. Rep. No. 105:1-35.

Nelson, R.S. 1988. A study of the life history, ecology, and population dynamics of four sympatric reef predators (*Rhomboplites aurorubens*, *Lutjanus campechanus*, Lutjanidae; *Haemulon melanurum*, Haemulidae; and *Pagrus pagrus*, Sparidae) on the East and West Flower Garden Banks, northwestern Gulf of Mexico. Ph.D. thesis, North Carolina State Univ., Raleigh, NC.

Newman, S.J., D.McB. Williams, and G.R. Russ. 1996. Variability in the population structure of *Lutjanus adetii* (Castelnau, 1873) and *L. quinquelineatus* (Bloch, 1790) among reefs in the central Great Barrier Reef, Australia. Fish. Bull. 94:313-329.

Olsen, E.M., H. Knutsen, J. Gjosater, P.E. Jorde, J.A. Knutsen, and N.C. Stenseth. 2004. Life-history variation among local populations of Atlantic cod from the Norwegian Skagerrak coast. J. Fish Biol. 64:1725-1730.

Pajuelo, J.G., and J.M. Lorenzo. 1996. Life history of the red porgy *Pagrus pagrus* (Teleostei:Sparidae) off the Canary Islands, central east Atlantic. Fish. Res. 28:163-177.

Pajuelo, J.G., and J.M. Lorenzo. 1999. Life history of black seabream, *Spondyliosoma cantharus*, off the Canary Islands, central-east Atlantic. Environ. Biol. Fishes 54:325-336.

Parker, R.O., Jr. 1990. Tagging studies and diver observations of fish populations on live-bottom reefs of the U.S. southeastern coast. Bull. Mar. Sci. 46(3):749-760.

Pauly, D. 1980. On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. J. Cons. Int. Explor. Mer. 39(2):175-192.

Petersen, C.W., and R.R. Warner. 2002. The ecological context of reproductive behavior. *In* Coral reef fishes: dynamics and diversity in a complex ecosystem. *Edited by* P.F. Sale. Academic Press, San Diego, CA. pp. 103-118.

Potts, G.W. 1984. Parental behavior in temperate marine teleosts with special reference to the development of nest structures. *In* Fish reproduction, strategies and tactics. *Edited by* G.W. Potts and R.J. Wootton. Academic Press, London. pp. 223-244.

Potts, J.C., and C.S. Manooch III. 2002. Estimated ages of red porgy (*Pagrus pagrus*) from fishery-dependent and fishery-independent data and a comparison of growth parameters. Fish. Bull. 100(1):81-89.

Pulliam, H.R. 1988. Sources, sinks, and population regulation. Am. Nat. 132(5):652-661.

Randall, J.E., and H.A. Randall. 1963. The spawning and early development of the Atlantic parrot fish, *Sparisoma rubripinne*, with notes on other scarid and labrid fishes. Zoologica N.Y. 48:49-60.

Ricker, W.E. 1975. Computation and interpretation of biological statistics of fish populations. Bull. Fish. Res. Board Can. 191:1-382.

Robertson, D.R. 1972. Social control of sex reversal in a coral reef fish. Science 177:1007-1009.

Robertson, D.R., J.H. Choat, J.M. Posada, J. Pitt, and J.L. Ackerman. 2005. Ocean surgeonfish *Acanthurus bahianus*. II. Fishing effects on longevity, size and abundance? Mar. Ecol. Prog. Ser. 295:245-256.

Robson, D.S., and D.G. Chapman. 1961. Catch curves and mortality rates. Trans. Am. Fish. Soc. 90:181-189.

Rodd, F.H., and D.N. Reznick. 1997. Variation in the demography of guppy populations: the importance of predation and life histories. Ecology 78(2):405-418.

Roede, M.J. 1972. Color as related to size, sex, and behavior in seven labrid fish species. *In* Studies on the fauna of Curacao and other Caribbean islands. Vol. XLII. *Edited by* P.W. Hummelinck and L.J. van der Steen. Martinus Nijhoff, The Hague, Netherlands.

Ross, R.M., G.M. Losey, and M. Diamond. 1983. Sex change in a coral-reef fish: dependence of stimulation and inhibition on relative size. Science 221:574-575.

Roumillat, W.A., and C.W. Waltz. 1993. Biology of the red porgy *Pagrus pagrus* from the southeastern United States. Data report 1993 MARMAP, South Carolina Wildlife and Marine Resources Department, Charleston, SC.

Sadovy, Y., and D.Y. Shapiro. 1987. Criteria for the diagnosis of hermaphroditism in fishes. Copeia 1987(1):136-156.

Sale, P. 1998. Appropriate spatial scales for studies of reef-fish ecology. Austral. J. Ecol. 23:202-208.

SAS Institute Inc. 1999. SAS/STAT user's guide, version 8. SAS Institute Inc., Cary, NC.

Schultz, E.T., and R.R. Warner. 1991. Phenotypic plasticity in life-history traits of female *Thalassoma bifasciatum* (Pisces: Labridae) 2. Correlation of fecundity and growth rate in comparative studies. Environ. Biol. Fishes 30:333-344.

Serafim, M.P.P., and H.M. Krug. 1995. Age and growth of the red porgy, *Pagrus pagrus* (Linnaeus, 1758) (Pisces: Sparidae), in Azorean waters. Arquipelago. Life and Marine Sciences 13A:11-20.

Shapiro, D.Y. 1980. Serial female sex changes after simultaneous removal of males from social groups of a coral reef fish. Science 209:1136-1137.

Shapiro, D.Y. 1981a. Size, maturation and the social control of sex reversal in the coral reef fish *Anthias squamipinnis* (Peters). J. Zool. (London) 193:105-128.

Shapiro, D.Y. 1981b. Sequence of coloration changes during sex reversal in the tropical marine fish *Anthias squamipinnis* (Peters). Bull. Mar. Sci. 31(2):383-398.

Shapiro, D.Y. 1984. Detrimental effects of intensive fishing over spawning aggregations of a commercially important grouper. Sea Grant Proj. R/LR-06-1 Annual Rep.

Shapiro, D.Y. 1987. Reproduction in groupers. *In* Tropical snappers and groupers: biology and fisheries management. *Edited by* J.J. Polovina and S. Ralston. Westview Press, Boulder, Colorado. pp. 295-327.

Shapiro, D.Y. 1991. Intraspecific variability in social systems of coral reef fishes. *In* The ecology of fishes on coral reefs. *Edited by* P.F. Sale. Academic Press, San Diego, CA, pp. 331-355.

Shapiro, D.Y., and R. Lubbock. 1980. Group sex ratio and sex reversal. J. Theor. Biol. 82:411-426.

Sheaves, M.J., B.W. Molony, and A.J. Tobin. 1999. Spawning migrations and local movements of a tropical sparid fish. Mar. Biol. 133:123-128.

Shepard, G.R., and J.S. Idoine. 1993. Length-based analyses of yield and spawning biomass per recruit for black sea bass *Centropristis striata*, a protogynous hermaphrodite. Fish. Bull. 91:328-337.

Smale, M.J. 1988. Distribution and reproduction of the reef fish *Petrus rupestris* (Pisces: Sparidae) off the coast of South Africa. S. -Afr Tydskr. Dierk. 23(4):272-287.

Smedbol, R.K., and J.S. Wroblewski. 2002. Metapopulation theory and northern cod population structure: interdependency of subpopulations in recovery of a groundfish population. Fish. Res. 55:161-174.

Smedbol, R.K., A. McPherson, M.M. Hansen, and E. Kenchington. 2002. Myths and moderation in marine ♣metapopulations♣. Fish and Fisheries 3:20-35.

Smith, C.L. 1982. Patterns of reproduction in coral reef fishes. *In* The biological basis for reef fishery management. *Edited by* G.R. Huntsman, W.R. Nicholson and W.W. Fox, Jr. NOAA Tech. Memo. NMFS-SEFC-80, Beaufort Laboratory, Beaufort, NC. pp. 49-66.

Smith, G.B., H.M. Austin, S.A. Bortone, R.W. Hastings, and L.H. Ogren. 1975. Fishes of the Florida Middle Ground with comments on ecology and zoogeography. Fla. Mar. Res. Publ. 9.

Smith, P.J. 1986. Spawning behavior of snapper, *Chrysophrys auratus*, in captivity. N. Z. J. Mar. Freshw. Res. 20:513-515.

Sokal, R.R., and F.J. Rohlf. 1969. Biometry. W.H. Freeman and Company, San Francisco, CA.

Stearns, S.C. 1976. Life-history tactics: a review of the ideas. Quart. Rev. Biol. 51:3-47.

Stearns, S.C. 1977. The evolution of life history traits: a critique of the theory and a review of the data. Ann. Rev. Ecol. Syst. 8:145-171.

Stephanou, D., G. Georgiou, and E. Shoukri. 1995. Reproduction and larval rearing of the common sea bream (*Pagrus pagrus*), an experimental culture. *In* Marine aquaculture finfish species diversification. CIHEAM-IAMZ, Cahiers Options Méditerranéennes 16: 79-87.

Stephenson, R.L. 1999. Stock complexity in fisheries management: a perspective of emerging issues related to population sub-units. Fish. Res. 43:247-249.

Stepkina, M.V. 1973. Some biological characterisitics of *Pagrus ehrenbergii* Val. J. Ich. 13(5):641-649.

Thompson, M.J., W.W. Schroeder, and N.W. Phillips. 1999. Ecology of live bottom habitats of the northeastern Gulf of Mexico: a community profile. U.S. Dept. Interior, U.S. Geological Service, Biological Resources Division, USGS/BRD/CR—1999-0001.

Thresher, R.E. 1984. Reproduction in reef fishes. T.H.F. Publications, Neptune City, NJ.

Trexler, J.C., and J. Travis. 1993. Nontraditional regression analyses. Ecology 74:1629-1637.

Trippel, E.A., and H.H. Harvey. 1990. Ovarian atresia and sex ratio imbalance in white sucker, *Catostomus commersoni*. J. Fish Biol. 36:231-239.

Tuck, G.N., and H.P. Possingham. 2000. Marine protected areas for spatially structured exploited stocks. Mar. Ecol. Prog. Ser. 192:89-101.

van Bruggen, A.C. 1965. Records and observations in the Port Elizabeth Oceanarium in 1960. Der Zoologische Garten, Leipzig. 31:184-202.

van der Heiden, A.M., and S.M. Pérez. 1992. Secondary sexual dimorphism and dichromatism in Gulf of California flatfishes. Copeia 1992(4):1077-1080.

van Rooij, J.M., J.P. Kok, and J.J. Videler. 1996. Local variability in population structure and density of the protogynous reef herbivore *Sparisoma viride* . Environ. Biol. Fishes 47:65-80.

Vassilopoulou, V.,and C. Papaconstantinou. 1992. Age, growth and mortality of the red porgy *Pagrus pagrus*, in the eastern Mediterranean Sea (Dodecanese, Greec). Vie Milieu 42: 51-55.

Vaughan, D.S. 1999. Population characteristics of the red porgy *Pagrus pagrus* from the U.S. southern Atlantic coast. South Atlantic Fisheries Management Council, Charleston, SC.

Vaughan, D.S., and M.H. Prager. 2002. Severe decline in abundance of the red porgy (*Pagrus*

pagrus) population off the southeastern United States. Fish. Bull. 100:351-375.

Vaughan, D.S., G.R. Huntsman, C.S. Manooch III, F.C. Rhode, and G.F. Ulrich. 1992. Population characteristics of the red porgy, *Pagrus pagrus*, stock of the Carolinas. Bull. Mar. Sci. 50:1-20.

Wallace, R.A., and K. Selman. 1981. Cellular and dynamic aspects of oocyte growth in teleosts. Amer. Zool. 21:325-343.

Walters, C.J., and S.J.D. Martell. 2004. Fisheries ecology and management. Princeton University Press, Princeton, NJ.

Warner, R.R. 1975. The adaptive significance of sequential hermaphroditism in animals. Am. Nat. 109:61-82.

Warner, R.R. 1984. Mating behavior and hermaphroditism in coral reef fishes. Am. Sci. 72:128-136.

Warner, R.R., and S.G. Hoffman. 1980. Local population size as a determinant of mating system and sexual composition in two tropical marine fishes (*Thalassoma* spp.). Evolution 34:508-518.

Warner, R.R., and D.R. Robertson. 1978. Sexual patterns in the labroid fishes of the western Caribbean, I: The wrasses (Labridae). Smithsonian Contributions in Zoology 254:1-27.

Williams, A.J., C.R. Davies, B.D. Mapstone, and G.R. Russ. 2003. Scales of spatial variation in demography of a large coral-reef fish - an exception to the typical model? Fish. Bull. 101:673-683.

Willis, T.J., D.M. Parsons, and R.C. Babcock. 2001. Evidence of long-term site fidelity of snapper (*Pagrus auratus*) within a marine reserve. N. Z. J. Mar. Freshw. Res. 35:581-590.

Wilson, K., and I.C.W. Hardy. 2002. Statistical analysis of sex ratios: an introduction. *In*: Sex ratios, concepts and research methods. *Edited by* I.C. W. Hardy. Cambridge University Press, Cambridge, England. pp 48-92.

Zar, J.H. 1999. Biostatistical Analysis. Fourth Edition. Prentice Hall, Upper Saddle River, NJ.

BIOGRAPHICAL SKETCH

Douglas Alan DeVries was born July 3, 1951 in Holland, Michigan, the son of Peter A. and Arlene (Brower) DeVries. He graduated from Pensacola High School in 1969 and from Pensacola Jr. College in 1971. At PJC he was privileged to be mentored by Dr. Keitz Haburay, an enthusiastic biologist and teacher who passed on his love of marine biology and inspired him to pursue a career in fisheries science. In 1973 he received a B.S. degree with a major in marine science from the University of West Florida in Pensacola, Florida. In September of 1973 he was commissioned an Ensign in the U.S. Navy, spent a couple months at sonar school in Key West, and then the next 2 ½ years at a small base in Barbados. Diving on the reefs of Barbados for those 2 ½ years provided many opportunities to observe and learn about the ecology of coral reefs. In August 1976 he ended his career in the Navy and entered graduate school at Texas A&M University under Dr. Mark Chittenden. Doug received his M.S. degree in Wildlife and Fisheries Science in 1979, with a thesis entitled "Aspects of the life history of the silver seatrout, *Cynoscion nothus*, in the Gulf of Mexico". In December 1978 he began his career as a fishery biologist with the North Carolina Division of Marine Fisheries (DMF) in Morehead City, NC. In June 1987 he left DMF and began working for the National Marine Fisheries Service in Panama City, Florida. He has continued working at the NMFS lab in Panama City ever since then. In August 1995 he entered the Ph.D. program in the Department of Biological Science at Florida State University.