Marine Resources Monitoring, Assessment and Prediction Program: Report on the Status of the Life History of Snowy Grouper, *Hyporthodus niveatus*, for the SEDAR36 Standard Stock Assessment

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SEDAR36-WP-08

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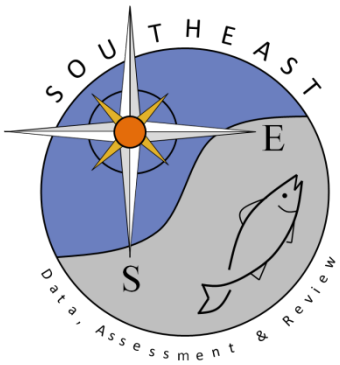
***Addendum added to reflect changes made during the assessment process. Final data are found in the addendum.**



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Introduction

The snowy grouper, *Epinephelus niveatus*, is a commercially important deepwater species that occurs in the western Atlantic from Massachusetts to Brazil, including Bermuda, Cuba, the Bahamas, and the Gulf of Mexico (Carpenter, 2002). Stray specimens have been collected in the Canadian Atlantic (Scott and Scott, 1988). Along the coast of the southeast United States, adult snowy grouper are predominantly found on the upper continental slope (> 75 m; Lee et al., 1985) at depths of 116-259 m (Low and Ulrich, 1983; Moore and Labisky, 1984; Parker and Ross, 1986), whereas juveniles are more common at shallower depths (Moore and Labisky, 1984). Low and Ulrich (1983) and Wyanski et al. (2000) noted a positive correlation between total length (TL) and water depth off South Carolina. Most fishing for this species occurs in habitats characterized by rocky ledges, cliffs, and swift currents (Matheson and Huntsman, 1984).

The two earliest studies of snowy grouper life history used sectioned sagittal otoliths to determine that the species can live 15-17 yr (Matheson and Huntsman, 1984; Moore and Labisky, 1984), with potential to live at least 25 yr (Matheson and Huntsman, 1984). A more recent study by Wyanski et al. (2000) estimated the age of 2,263 snowy grouper by examining sectioned otoliths from specimens collected on research and commercial vessels operating off North Carolina and South Carolina during 1979-1985 and 1993-1995. The maximum age reported from each gear type and time period ranged from 21 – 29 yr. That the maximum age is in the upper 20s was validated in an unpublished study designed to measure Radiocarbon (^{14}C), released via atmospheric testing of nuclear weapons from approximately 1950 through 1970, in otolith cores of four deepwater species, including snowy grouper (n=21), in the snapper/grouper complex of the South Atlantic Bight (Cape Hatteras to southern tip of Florida). The amount of ^{14}C was compared to ^{14}C decay in a known standard and then the year of hatching for that fish as calculated from the otolith derived age (Unpublished final report; SEDAR36-WP09). The oldest fish among the 21 specimens was 27 yr old. Snowy grouper are slow growing, as the estimates of *k* in the von Bertalanffy growth model have ranged from 0.07 to 0.12 in the life history studies to date (Matheson and Huntsman, 1984; Moore and Labisky, 1984; Wyanski et al., 2000).

The snowy grouper is a protogynous hermaphrodite that reaches sexual maturity between the ages of 3 and 8 yr (Wyanski et al., 2000), most by the age of 5 yr (Moore and Libisky, 1984) to 7 yr (Wyanski et al., 2000). There is evidence that the number of males in the population decreased between the 1970s and the 1990s (Wyanski et al., 2000).

Snowy grouper are captured primarily in commercial fisheries off the southeastern United States (Parker and Mays, 1998). Most are caught with snapper reels[1] (handlines) and bottom longlines. Starting in 1991, the longline fishery was restricted to waters deeper than 91 m by the South Atlantic Fishery Management Council (SAFMC, 1991). Fishing for snowy grouper has occurred off the Carolinas

[1] Snapper reels are commonly known as "bandits" or "one-armed bandits" by fishermen due to the remote similarity between early snapper reels and gambling slot machines, and because luck is involved in what is caught. The early mechanical reels have typically been replaced by 12 volt DC automobile starter motors or hydraulic systems.

since the mid-1950s (Huntsman, 1976), with annual landings along the Atlantic coast of the southeastern United States averaging 146.0 mt (321,800 lb) during 1981-2005 (Figure 1). Landings varied widely during 1981-1999, a period characterized as having minimal fisheries regulations and thereby giving commercial fishers the flexibility to shift between fisheries (i.e., from bottom longline to swordfish) to optimize their earnings. For example, the same 1983 peak occurred in South Carolina landings of snowy grouper and was attributed to an approximate doubling in the number of vessels as the bottom longline fishery developed (Low et al., 1987). By 1985, landings had returned to pre-expansion levels because the average production per trip was decreasing, which led many fishers to shift efforts to the pelagic longline fishery for swordfish when the fish returned to the fishing area.

Starting in 2006, the SAFMC phased in over a three year period an increasingly restrictive trip limit and annual quota (Amendment 13C; see http://www.safmc.net/Library/SnapperGrouper/tabid/415/Default.aspx). The annual quota has remained around 36 mt (80,000 lb) since 2008 and in 2009 the SAFMC allocated 95% of the quota to the commercial sector (See Amendment 15B; http://www.safmc.net/Library/SnapperGrouper/tabid/415/Default.aspx. To reduce the bycatch mortality of speckled hind and Warsaw grouper, two other deepwater reef species with overfished populations, there was a prohibition on harvest and retention of snowy grouper, blueline tilefish, yellowedge grouper, misty grouper, queen snapper, and silk snapper caught at depths beyond 240 feet (73 m) in federal waters in the South Atlantic effective January 31, 2011 (See Amendment 17B; http://www.safmc.net/LinkClick.aspx?fileticket=9BXhV2vGiyM%3d&tabid=415). Effective May 10, 2012, this prohibition has been eliminated.

Stock assessment history

The initial and only SEDAR stock assessment was a benchmark assessment that took place in 2004. The Assessment Workshop concluded that snowy grouper was overfished and overfishing was occurring as of 2002, the terminal year in the incorporated data. A standard assessment is scheduled for June 2013.

In the Review Consensus produced by the Review Workshop Panel, several criticisms/suggestions were presented that should be addressed if possible before the 2013 assessment, including the following (SEDAR 4 Stock Assessment Report 1, 2004):

- Aging differences between MARMAP and the NMFS Beaufort Lab indicate questions remain regarding age determination protocols, the validity of age-related data, and their use in age structured models. Ages from a preliminary bomb-radiocarbon validation study indicate that the MARMAP ages could be too low. The Assessment workshop concluded that NMFS' ages used in the assessments were preferable for determining von Bertalanffy growth curves. Regarding ageing methods, the Review Panel recommends that ageing validation should be accomplished prior to addressing concerns over differences in age determinations between the various labs.
- The Review Workshop recommended that stratification by length and development of appropriate age-length keys be considered as a possibly more effective and economical

approach to inferring age composition than attempting random age sampling. Regardless of the method ultimately chosen, it is most important to provide adequate age and length sampling through a rigorous and statistically valid sampling program.

- A clear unit stock definition was not provided in the data workshop. A single South Atlantic stock was apparently assumed. This assumption was considered reasonable, based on the likelihood of restricted movement of adults in or out of the region, as well as the likely broad dispersal of their planktonic larvae. Modeling of the dispersal of other snapper and grouper larvae has suggested both local and long-distance transport of larvae prior to settlement. Future assessments should consider whether to include the snowy grouper from the Gulf of Mexico or Mid-Atlantic because of possible larval diffusion.
- Age composition data were limited and possibly biased due to clumped sampling. The Stock Assessment Workshop did not include age composition data for years where there were fewer than 25 age samples. A question was raised as to whether 25 age samples were adequate, and whether such limited sampling enabled tracking of cohorts. The response was that age data actually served only to aid in determining selectivities. A suggestion was made to model selectivities based on size instead of age. The analysts said that they would move in that direction in future SEDAR assessments.
- The Panel recommended that better information should be collected related to sex ratios and maturity at age, and that the fisheries implications of protogynous hermaphroditism in snowy grouper be more fully evaluated in future assessments.

Purpose of present study

The purpose of the present study was to provide updated life history data (age composition, growth parameters, age at maturity and at sex transition, proportion of spawners at age) for the Standard Assessment in June 2013 and to compare new data with earlier data to determine what effects the management measures implemented since 2006 have had on the population of snowy grouper off the Atlantic coast of the southeastern United States.

Methods

Specimen collection

During 1979-2012, Snowy Grouper were obtained from commercial boats, research vessels, and headboats, primarily off North Carolina and South Carolina. All specimens (n = 5,314) were collected between 29.66 and 34.73°N at depths of 18‑302 m, but only seven specimens were collected south of 31°N. Fishery-independent samples were collected during cruises of the MARMAP (Marine Resources Monitoring Assessment and Prediction) and South East Fishery Independent Survey (SEFIS) Programs with bottom longlines (see Harris et al., 2004), Kali poles (an off-bottom longline), snapper reels, rods and reels, and chevron traps (Collins, 1990). The SEFIS Program began sampling in 2010 and uses chevron traps and rods and reels for sampling gears. Specimens (n = 1854) from all fishery-independent sampling efforts were collected between 29.66 and 34.61°N at depths of 35-226 m.

Samples have been collected annually through fishery-independent sampling by the MARMAP and SEFIS; since the terminal year (2002) of the previous assessment, 710 specimens have been collected for life history analysis (Table 1). In addition, MARMAP staff obtained funding in 2008 through the Cooperative Research Program (NOAA/NMFS) to contract with a commercial bottom longliner from South Carolina to collect 3000 specimens total of three deepwater reef fish species, one of which was snowy grouper; this effort resulted in the capture of nearly 1,100 snowy grouper in 2008-2009.

After collection, whole Snowy Grouper were weighed to the nearest gram (g) and total length (TL) and standard length were measured to the nearest mm. Note that a mid-line length, equivalent to fork length, was measured for some specimens. The left sagittal otolith, and the right sagitta when time permitted, were removed and stored dry prior to processing. Samples of gonad tissues were removed and stored in 11% seawater formalin for later histological processing.

Age and growth

Each otolith was embedded in paraffin (1979–85) or an epoxy resin (1990s and later) and sectioned (0.5 mm thickness) along a dorsoventral plane through the focus with a single high-concentration diamond wheel on a Buehler Isomet low-speed saw. Otolith sections were mounted on glass slides with Crystalbond thermoplastic or a liquid mounting medium (Accu-mount 60 or Cytoseal) and examined under a dissecting microscope (7.5 to 63X) with reflected and transmitted light. Before 1996, the sections were covered with cedar wood oil prior to examination

Otolith sections were examined independently by two readers and re-examined jointly when differences in age estimation occurred. Aging was done without knowledge of specimen length or date of capture. If disagreement persisted, the specimen was eliminated from age analyses. In addition, we made assessments of section quality and edge type (Table 2) for specimens collected from 2003-2012; these variables have not been assessed in our samples collected prior to 2003. The edge type data will not be used in the SEDAR36 assessment, as was the case for the case for the benchmark assessment (SEDAR4, 2004); age analyses will be based on counts of growth increments (annuli).

Workshops were held in Charleston SC (March 2009) and NOAA SEFSC-Beaufort Laboratory (October 2012) in preparation for SEDAR 36. The goal of the workshop was to (1) compare sample preparation

and method of interpreting growth increments in the sagittal otoliths from Snowy Grouper, with an emphasis on addressing difficulties and issues previously encountered by staff at labs in the southeast region, including the Gulf of Mexico (see SEDAR36-DW09 for results). In addition, an age validation study has been completed since SEDAR4 (see SEDAR36-RD07 for results).

Reproduction

Following capture and dissection, the posterior portion of the gonads were fixed for 7–14 d in 11% seawater–formalin solution buffered with marble chips and transferred to 50% isopropanol for an additional 7–14 d. Reproductive tissue was processed in automated tissue processors and blocked in paraffin. Three transverse sections (6–8 um thick) were cut from each sample with a rotary microtome, mounted on glass slides, stained with double-strength Gill hematoxylin, and counterstained with eosin-y. Sections were viewed under a compound microscope at 20-400X magnification, and sex and reproductive class were determined without knowledge of capture date, specimen length, or specimen age. Two readers independently determined sex and reproductive state using histological criteria (see Wyanski 2000). When assignments differed, the readers re-examined the section simultaneously to determine reproductive state.

Females were considered to be in spawning condition if they possessed oocytes undergoing maturation (i.e., fusing of yolk globules, germinal vesicle migration and breakdown), hydrated oocytes, or postovulatory follicles). Specimens with developing, ripe, spent, or resting gonads were considered sexually mature. For females, this definition of sexual maturity included specimens with oocyte development at or beyond the cortical granule stage and specimens with beta, gamma, or delta stages of atresia. To ensure that females were correctly assigned to either the immature or resting categories, the length-frequency histogram of females with evidence of certain maturity (e.g., those that were developing, ripe, or spent) was compared with the histograms for immature and resting females. Females of uncertain maturity were excluded from maturity analyses. Specimens undergoing sex transition (female to male) were considered males, as these specimens would likely have spawned as males in the next spawning season.

Analyses

All analyses were done using, EXCEL, SAS or “R” software. Results were considered significant at P-values less than 0.05. To estimate age at 50% maturity and age at 50% male (A_{50}), the PROBIT procedure (SAS Institute, Inc., 1990) was used to fit gompit, logit, or probit models to age data in 1-yr (maturity) or 3-yr bins (proportion male). The LOGISTIC procedure was used to determine which model to use in the PROBIT procedure.

Results

Weight conversion

An equation to convert gutted fish weight (g) to whole fish weight (g) was not available at the time of SEDAR4. Based on mostly fishery-dependent samples collected by the MARMAP program, the following equation was generated:

Whole wt = gutted wt*1.082 (adj r^2 = 1.00; n = 502)

Age and growth

Parameters of the von Bertalanffy growth model were estimated for all MARMAP/SEFIS samples collected during 1979-2012, as well as a subset of only the fishery-independent samples collected by the programs (Table 3 and Figure 2). The results for the two datasets revealed very similar estimates of K and t_0, with the estimate of L_∞ based on all samples being slightly higher (1007 vs. 962 mm TL) and closer to the maximum observed size (1137 mm) in the samples.

Reproduction

There was a high degree of overlap in the left tail of the length histograms of definitely mature and regenerating Snowy Grouper and modest overlap in the lengths of immature and all mature individuals, indicating that individuals were correctly assigned to the immature and regenerating classes (Figure 3).

In the overall dataset (1979-2012), the youngest mature female was Age 3, and the oldest immature female was Age 13 (Table 4); age at 50% maturity was 5.6 yr (Logistic model: 95% CI = 5.3-5.9 yr). Further probit analysis showed that individuals matured at older ages in 2008-2012 compared to 1979-1994 (Logistic model: period effect, $p < 0.0001$), as A_{50} increased from 5.0 to 5.8 yr (Table 4).

In the overall dataset (1979-2012), the youngest male was Age 5, and the oldest male was Age 32 (Table 5); age at 50% male was 18.2 yr (Normal model: 95% CI = 15.3-24.6 yr). Further probit analysis showed that individuals transitioned to male younger ages in 2008-2012 compared to 1979-1994 (Normal model: period effect, $p < 0.0016$), as A_{50} decreased from 18.9 to 16.0 yr (Table 5). Note that the asymptote of the proportion males curve approached 0.75, indicating that some of the oldest specimens do not transition to male. The oldest specimen in the overall dataset was an Age 35 female.

Samples collected during 2008-2012 revealed a similar spawning season (April through September) to that reported by Wyanski et al. (2000); however, five specimens with histological evidence of spawning (oocyte maturation or postovulatory follicles) were collected in January, March, and October.

To determine if age has an effect on spawning proportion, the data were also examined by 5-yr age groups within month. The results showed that the overall proportion of spawners in the age groups between Age 2 and Age 20 during the spawning season (April-September) was fairly consistent among age groups, ranging from 0.26 to 0.34 (Table 6). The proportion of spawners may increase at older ages, but sample sizes were very small ($n < 5$).

No estimates of the annual fecundity of Snowy Grouper are available, so three proxies for fecundity were generated (Gonad weight versus TL, whole fish weight, and age). The equation relating gonad weight to whole fish weight after natural log transformation had the highest r^2 value (0.50).

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Table 1: Number by year of snowy grouper collected since the benchmark assessment (SEDAR4, 2004) during fishery-independent (FI) sampling by the MARMAP (Year=2003 to present) and SEFIS Programs (Year=2010-2012) and during fishery-dependent (FD) sampling by the MARMAP program through a study funded by the Cooperative Research Program. Transverse sections of a sagittal otolith and histological sections of gonadal tissue were examined by two readers independently to assess age, sex, and reproductive state.

Year	# of FI specimens	# of FD specimens	# of oto. exam.	# of histo. exam.
2003	71		71	
2004	32		32	
2005	40		40	
2006	43		43	
2007	26	1	26	
2008	63	949	1012	1012
2009	30	140	170	170
2010	128	3	128	128
2011	157		157	157
2012	120		120	120
Total	710	1093	1799	1587

Table 2. Classification of otolith edge type and quality.

EDGE TYPE - Code description
1 Opaque zone on the edge.

2 Narrow translucent zone on edge Width less than about 30% of previous increment

3 Medium translucent zone on edge Width about 30-60% of previous increment

4 Wide translucent zone on edge Width more than about 60% of previous increment

READABILITY - Code description and analysis consequence
A Unreadable Omit otolith from analysis

B Very difficult to read Age estimate between readers are expected to be >2 year for young, and > 4 yrs for old fish (>10 yrs) Agreement on age may be difficult to reach, in which case otoliths should be classified as A and omitted from the analysis.

C Fair readability Age estimates between readers should be within 2 year in young, and within 4 years in old fish (>10 yrs). Agreement after second reading is expected after some discussion.

D Good readability Age estimates between readers should be within 1 year for young, to 2 years in old fish (> 10 years). Agreement after second reading is expected without much discussion.

E Excellent readability Age estimates between readers should be the same.

Table 3. von Bertalanffy growth model parameters for Snowy Grouper based on data collected by the MARMAP and SEFIS Programs during 1979-2012.

Model	L inf	SE	K	SE	t_0	SE
All MARMAP/SEFIS data	1007	14.69	0.12	0.005	-1.42	0.11
MARMAP/SEFIS, fish. Independ. data	961.5	18.17	0.13	0.008	-1.40	0.18

Table 4. Proportion of mature female Snowy Grouper by age class (# of increments) during two periods.

Age		1979-1994		2008-2012		1979-2012
	n=	Prop.mat.	n=	Prop.mat.	n=	Prop.mat.
1	7	0.00	2	0.00	9	0.00
2	31	0.00	24	0.00	55	0.00
3	31	0.06	70	0.03	101	0.04
4	50	0.22	107	0.22	157	0.22
5	47	0.49	154	0.43	201	0.44
6	47	0.87	310	0.57	357	0.61
7	53	0.94	209	0.70	262	0.75
8	39	0.92	165	0.81	204	0.83
9	19	1.00	71	0.85	90	0.88
10	27	1.00	64	0.92	91	0.95
11	16	1.00	19	0.89	35	0.94
12	10	1.00	12	0.83	22	0.91
13	6	1.00	1	0.00	7	0.86
14	3	1.00	3	1.00	6	1.00
15	7	1.00	1	1.00	8	1.00
16	8	1.00			8	1.00
17	6	1.00			6	1.00
18	8	1.00			8	1.00
19	4	1.00			4	1.00
20+	6	1.00	2	1.00	8	1.00
Total	425		1214		1639	

		LR X^2						
Data	Model	p	Intercept	SE	Increment	SE	A50 (yr)	95% CI
1979-1994	Logistic	0.99	-6.574	0.728	1.324	0.140	5.0	4.7-5.2
2008-2012	Logistic	0.0014	-3.661	0.808	0.633	0.128	5.8	5.0-6.4
1979-2012	Logistic	0.0107	-4.025	0.424	0.717	0.069	5.6	5.3-5.9

Table 5. Proportion of male Snowy Grouper by age class (# of increments) during two periods.

Age	Age midpoint	n=	1979-1994 Prop. male	n =	2008-2012 Prop. male	n =	1979-2012 Prop. male
2-4	3	13	0.00	25	0.00	38	0.00
5-7	6	114	0.00	401	0.03	515	0.03
8-10	9	84	0.02	287	0.12	371	0.10
11-13	12	38	0.16	43	0.37	81	0.27
14-16	15	34	0.47	6	0.33	40	0.45
17-19	18	29	0.38	2	1.00	31	0.42
20-22	21	12	0.67	2	0.50	14	0.64
23-35	29	7	0.71	2	0.50	9	0.67
Total		331		768		1099	

		LR X^2						
Data	Model	p	Intercept	SE	Increment	SE	A50 (yr)	95% CI
1979-1994	Normal	0.0077	-3.197	0.579	0.169	0.039	18.9	15.8-26.7
2008-2012	Normal	0.0266	-2.758	0.607	0.173	0.068	16.0	11.8-186.0
1979-2012	Normal	0.0073	-2.636	0.276	0.145	0.025	18.2	15.3-24.6

Table 6. Proportion of spawning female Snowy Grouper among all adult females (active+inactive) by 5-yr age groups within month. Spawners had at least one indicator of imminent or recent spawning (i.e., migratory nucleus oocytes, hydrated oocytes, and postovulatory follicles).

	# of increments											
Month	2-5	n=	6-10	n=	11-15	n=	16-20	n=	21-25	n=	26-35	n=	Total
Jan	0.00	5	0.07	30									35
Feb													
Mar	0.00	17	0.02	42	0.00	3	0.00	1					63
Apr	0.00	9	0.10	72	0.13	8	0.00	3					92
May	0.35	20	0.40	146	0.67	12	0.83	6	1.00	1			185
Jun	0.40	10	0.22	76	0.43	7							93
Jul	0.38	21	0.46	108	0.00	2	1.00	1			1.00	1	133
Aug	0.21	24	0.47	117	0.29	24	0.17	12	0.50	2			179
Sep	0.00	7	0.13	62	0.20	10	0.17	6	0.00	1			86
Oct	0.00	9	0.02	56	0.25	4							69
Nov	0.00	3	0.00	15									18
Dec													
Total (Apr-Sep)		91		581		63		28		4		1	768
Total (all)		125		724		70		29		4		1	953
Avg. monthy prop. spawners, Apr-Sep	**0.22**		**0.30**		**0.29**		**0.43**		**0.50**		**1.00**		
Prop. spawners, Apr-Sep	**0.26**		**0.34**		**0.33**		**0.32**		**0.50**		**1.00**		

Table 7. Potential proxies for an estimate of individual fecundity in Snowy Grouper. Fish wt = whole fish weight.

Proxy	Units	Equation	a	SE	b	SE	Adj. r^2	n	Range of x
Gonad wt vs TL	g, mm	y = a + bx	-541.8	75.9	0.972	0.105	0.37	144	530-1006
Gonad wt vs TL	g, mm	y=exp(a*x)	0.0066	6.50E-05			0.35	144	530-1006
Gonad wt vs Fish wt	g, g	y = a + bx	-57.4	25.3	0.038	0.004	0.42	122	1500-20430
Gonad wt vs Fish wt	g, g	ln y = a + b (ln x)	-7.39	1.09	1.414	0.128	0.50	122	1500-20430
Gonad wt vs age	g, yr	y = a + bx	16.8	37.6	14.376	3.821	0.11	108	5-21

Figure 1. Commercial landings of snowy grouper along the Atlantic coast of the southeastern United States for all gear types, primarily snapper reels and bottom longlines (Pers. comm., National Marine Fisheries Service, Fisheries Statistics Division, February 22, 2012). Reference line in 2006 indicates beginning of management measures to reduce fishing mortality by implementation of annual quotas and trip limits.

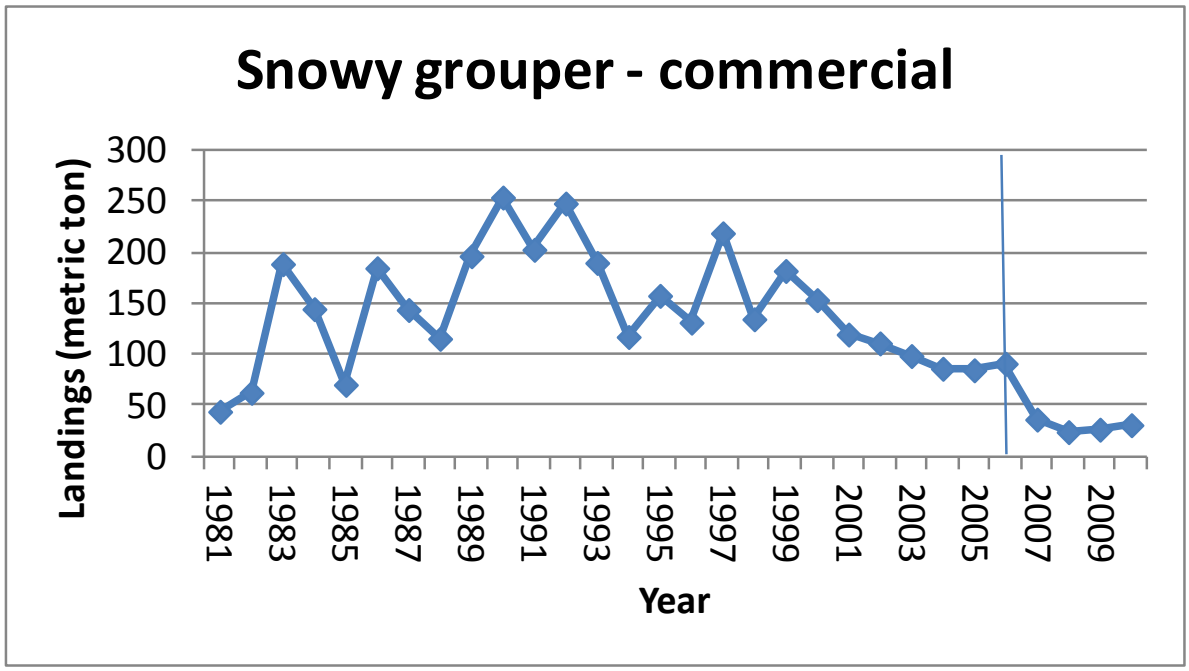
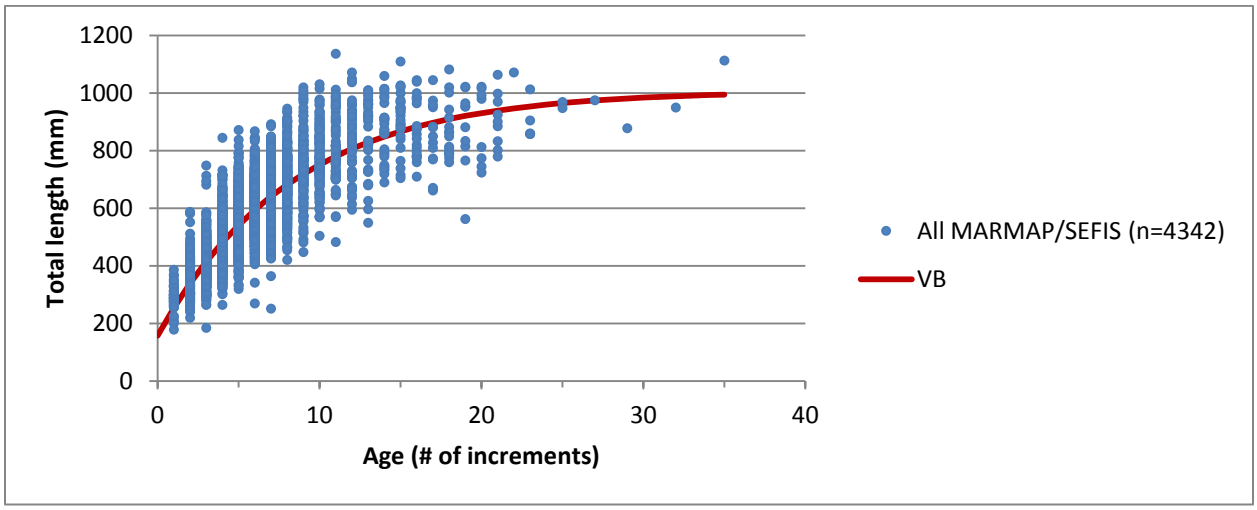


Figure 2. Observed and predicted sizes at age of Snowy Grouper captured by the MARMAP and SEFIS Programs, 1979-2012. **A)** All fishery-independent and fishery-dependent samples, **B)** All fishery-independent samples. VB = von Bertalanffy growth model (no constraints).

A)



B)

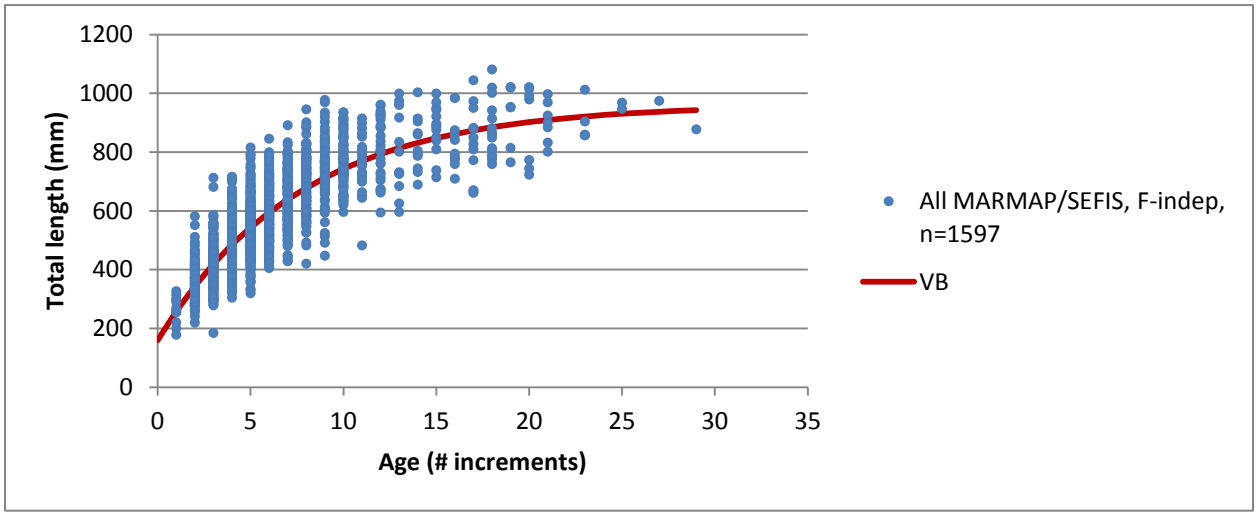
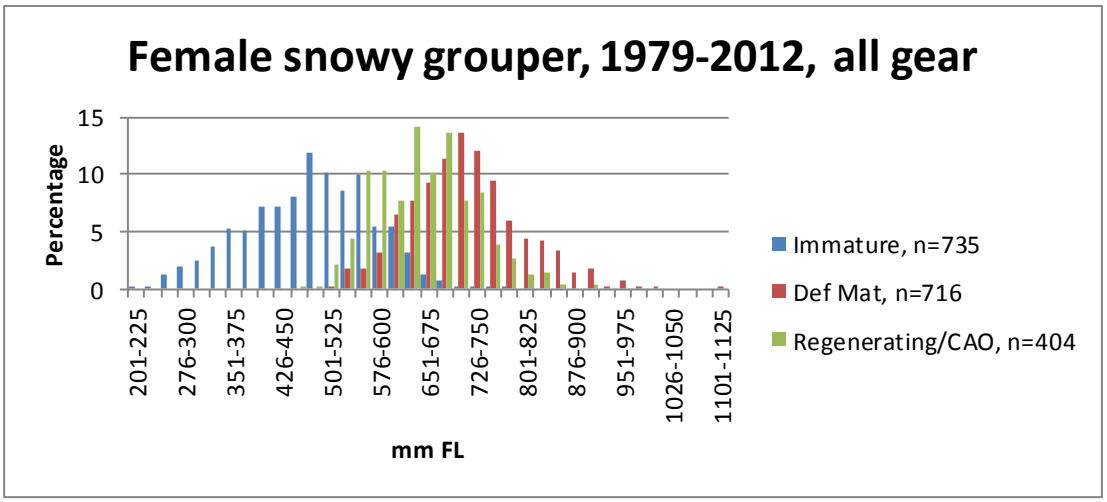


Figure 3. A comparison of length-frequency histograms for Snowy Grouper specimens collected during 1979-2012 that were categorized as immature, definitely mature, or resting. Definitely mature specimens were developing, ripe, or spent.



ADDENDUM

Marine Resources Monitoring, Assessment and Prediction Program: Report on the Status of the Life History of Snowy Grouper, *Hyporthodus niveatus*, for the SEDAR36 Standard Stock Assessment

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SEDAR36-WP08 (**2nd Revision**)
Revised after requests by assessment team for additional analyses

MARMAP Technical Report # 2013-007

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Introduction

The snowy grouper, *Epinephelus niveatus*, is a commercially important deepwater species that occurs in the western Atlantic from Massachusetts to Brazil, including Bermuda, Cuba, the Bahamas, and the Gulf of Mexico (Carpenter, 2002). Stray specimens have been collected in the Canadian Atlantic (Scott and Scott, 1988). Along the coast of the southeast United States, adult snowy grouper are predominantly found on the upper continental slope (> 75 m; Lee et al., 1985) at depths of 116-259 m (Low and Ulrich, 1983; Moore and Labisky, 1984; Parker and Ross, 1986), whereas juveniles are more common at shallower depths (Moore and Labisky, 1984). Low and Ulrich (1983) and Wyanski et al. (2000) noted a positive correlation between total length (TL) and water depth off South Carolina. Most fishing for this species occurs in habitats characterized by rocky ledges, cliffs, and swift currents (Matheson and Huntsman, 1984).

The two earliest studies of snowy grouper life history used sectioned sagittal otoliths to determine that the species can live 15-17 yr (Matheson and Huntsman, 1984; Moore and Labisky, 1984), with potential to live at least 25 yr (Matheson and Huntsman, 1984). A more recent study by Wyanski et al. (2000) estimated the age of 2,263 snowy grouper by examining sectioned otoliths from specimens collected on research and commercial vessels operating off North Carolina and South Carolina during 1979-1985 and 1993-1995. The maximum age reported from each gear type and time period ranged from 21 – 29 yr. That the maximum age is in the upper 20s was validated in an unpublished study designed to measure Radiocarbon (^{14}C), released via atmospheric testing of nuclear weapons from approximately 1950 through 1970, in otolith cores of four deepwater species, including snowy grouper (n=21), in the snapper/grouper complex of the South Atlantic Bight (Cape Hatteras to southern tip of Florida). The amount of ^{14}C was compared to ^{14}C decay in a known standard and then the year of hatching for that fish as calculated from the otolith derived age (Harris, 2005). The oldest fish among the 21 specimens was 27 yr old. Snowy grouper are slow growing, as the estimates of *k* in the von Bertalanffy growth model have ranged from 0.07 to 0.12 in the life history studies to date (Matheson and Huntsman, 1984; Moore and Labisky, 1984; Wyanski et al., 2000).

The snowy grouper is a protogynous hermaphrodite that reaches sexual maturity between the ages of 3 and 8 yr (Wyanski et al., 2000), most by the age of 5 yr (Moore and Libisky, 1984) to 7 yr (Wyanski et al., 2000). There is evidence that the number of males in the population decreased between the 1970s and the 1990s (Wyanski et al., 2000).

Snowy grouper are captured primarily in commercial fisheries off the southeastern United States (Parker and Mays, 1998). Most are caught with snapper reels[1] (handlines) and bottom longlines. Starting in 1991, the longline fishery was restricted to waters deeper than 91 m by the South Atlantic Fishery Management Council (SAFMC, 1991). Fishing for snowy grouper has occurred off the Carolinas

[1] Snapper reels are commonly known as "bandits" or "one-armed bandits" by fishermen due to the remote similarity between early snapper reels and gambling slot machines, and because luck is involved in what is caught. The early mechanical reels have typically been replaced by 12 volt DC automobile starter motors or hydraulic systems.

since the mid-1950s (Huntsman, 1976), with annual landings along the Atlantic coast of the southeastern United States averaging 146.0 mt (321,800 lb) during 1981-2005 (Figure 1). Landings varied widely during 1981-1999, a period characterized as having minimal fisheries regulations and thereby giving commercial fishers the flexibility to shift between fisheries (i.e., from bottom longline to swordfish) to optimize their earnings. For example, the same 1983 peak occurred in South Carolina landings of snowy grouper and was attributed to an approximate doubling in the number of vessels as the bottom longline fishery developed (Low et al., 1987). By 1985, landings had returned to pre-expansion levels because the average production per trip was decreasing, which led many fishers to shift efforts to the pelagic longline fishery for swordfish when the fish returned to the fishing area.

Starting in 2006, the SAFMC phased in over a three year period an increasingly restrictive trip limit and annual quota (Amendment 13C; see http://www.safmc.net/Library/SnapperGrouper/tabid/415/Default.aspx). The annual quota has remained around 36 mt (80,000 lb) since 2008 and in 2009 the SAFMC allocated 95% of the quota to the commercial sector (See Amendment 15B; http://www.safmc.net/Library/SnapperGrouper/tabid/415/Default.aspx. To reduce the bycatch mortality of speckled hind and Warsaw grouper, two other deepwater reef species with overfished populations, there was a prohibition on harvest and retention of snowy grouper, blueline tilefish, yellowedge grouper, misty grouper, queen snapper, and silk snapper caught at depths beyond 240 feet (73 m) in federal waters in the South Atlantic effective January 31, 2011 (See Amendment 17B; http://www.safmc.net/LinkClick.aspx?fileticket=9BXhV2vGiyM%3d&tabid=415). Effective May 10, 2012, this prohibition has been eliminated.

Stock assessment history

The initial and only SEDAR stock assessment was a benchmark assessment that took place in 2004. The Assessment Workshop concluded that snowy grouper was overfished and overfishing was occurring as of 2002, the terminal year in the incorporated data. A standard assessment is scheduled for June 2013.

In the Review Consensus produced by the Review Workshop Panel, several criticisms/suggestions were presented that should be addressed if possible before the 2013 assessment, including the following (SEDAR 4 Stock Assessment Report 1, 2004):

- Aging differences between MARMAP and the NMFS Beaufort Lab indicate questions remain regarding age determination protocols, the validity of age-related data, and their use in age structured models. Ages from a preliminary bomb-radiocarbon validation study indicate that the MARMAP ages could be too low. The Assessment workshop concluded that NMFS' ages used in the assessments were preferable for determining von Bertalanffy growth curves. Regarding ageing methods, the Review Panel recommends that ageing validation should be accomplished prior to addressing concerns over differences in age determinations between the various labs.
- The Review Workshop recommended that stratification by length and development of appropriate age-length keys be considered as a possibly more effective and economical

approach to inferring age composition than attempting random age sampling. Regardless of the method ultimately chosen, it is most important to provide adequate age and length sampling through a rigorous and statistically valid sampling program.

- A clear unit stock definition was not provided in the data workshop. A single South Atlantic stock was apparently assumed. This assumption was considered reasonable, based on the likelihood of restricted movement of adults in or out of the region, as well as the likely broad dispersal of their planktonic larvae. Modeling of the dispersal of other snapper and grouper larvae has suggested both local and long-distance transport of larvae prior to settlement. Future assessments should consider whether to include the snowy grouper from the Gulf of Mexico or Mid-Atlantic because of possible larval diffusion.
- Age composition data were limited and possibly biased due to clumped sampling. The Stock Assessment Workshop did not include age composition data for years where there were fewer than 25 age samples. A question was raised as to whether 25 age samples were adequate, and whether such limited sampling enabled tracking of cohorts. The response was that age data actually served only to aid in determining selectivities. A suggestion was made to model selectivities based on size instead of age. The analysts said that they would move in that direction in future SEDAR assessments.
- The Panel recommended that better information should be collected related to sex ratios and maturity at age, and that the fisheries implications of protogynous hermaphroditism in snowy grouper be more fully evaluated in future assessments.

Purpose of present study

The purpose of the present study was to provide updated life history data (age composition, growth parameters, age at maturity and at sex transition, proportion of spawners at age) for the Standard Assessment in June 2013 and to compare new data with earlier data to determine what effects the management measures implemented since 2006 have had on the population of snowy grouper off the Atlantic coast of the southeastern United States.

Methods

Specimen collection

During 1979-2012, Snowy Grouper were obtained from commercial boats, research vessels, and headboats, primarily off North Carolina and South Carolina. All specimens (n = 5,314) were collected between 29.66 and 34.73°N at depths of 18–302 m, but only seven specimens were collected south of 31°N. Fishery-independent samples were collected during cruises of the MARMAP (Marine Resources Monitoring Assessment and Prediction) and South East Fishery Independent Survey (SEFIS) Programs with bottom longlines (see Harris et al., 2004), Kali poles (an off-bottom longline), snapper reels, rods and reels, and chevron traps (Collins, 1990). The SEFIS Program began sampling in 2010 and uses chevron traps and rods and reels for sampling gears. Specimens (n = 1854) from all fishery-independent sampling efforts were collected between 29.66 and 34.61°N at depths of 35-226 m.

Samples have been collected annually through fishery-independent sampling by the MARMAP and SEFIS; since the terminal year (2002) of the previous assessment, 710 specimens have been collected for life history analysis (Table 1). In addition, MARMAP staff obtained funding in 2008 through the Cooperative Research Program (NOAA/NMFS) to contract with a commercial bottom longliner from South Carolina to collect 3000 specimens total of three deepwater reef fish species, one of which was snowy grouper; this effort resulted in the capture of nearly 1,100 snowy grouper in 2008-2009.

After collection, whole Snowy Grouper were weighed to the nearest gram (g) and total length (TL) and standard length were measured to the nearest mm. Note that a mid-line length, equivalent to fork length, was measured for some specimens. The left sagittal otolith, and the right sagitta when time permitted, were removed and stored dry prior to processing. Samples of gonad tissues were removed and stored in 11% seawater formalin for later histological processing.

Age and growth

Each otolith was embedded in paraffin (1979–85) or an epoxy resin (1990s and later) and sectioned (0.5 mm thickness) along a dorsoventral plane through the focus with a single high-concentration diamond wheel on a Buehler Isomet low-speed saw. Otolith sections were mounted on glass slides with Crystalbond thermoplastic or a liquid mounting medium (Accu-mount 60 or Cytoseal) and examined under a dissecting microscope (7.5 to 63X) with reflected and transmitted light. Before 1996, the sections were covered with cedar wood oil prior to examination

Otolith sections were examined independently by two readers and re-examined jointly when differences in age estimation occurred. Aging was done without knowledge of specimen length or date of capture. If disagreement persisted, the specimen was eliminated from age analyses. In addition, we made assessments of section quality and edge type (Table 2) for specimens collected from 2003-2012; these variables have not been assessed in our samples collected prior to 2003. The edge type data will not be used in the SEDAR36 assessment, as was the case for the case for the benchmark assessment (SEDAR 4 Stock Assessment Report 1, 2004); age analyses will be based on counts of growth increments (annuli).

Workshops were held in Charleston SC (March 2009) and NOAA SEFSC-Beaufort Laboratory (October 2012) in preparation for SEDAR36. The goal of the workshop was to (1) compare sample preparation and

method of interpreting growth increments in the sagittal otoliths from Snowy Grouper, with an emphasis on addressing difficulties and issues previously encountered by staff at labs in the southeast region, including the Gulf of Mexico (see Wyanski et al., 2013). In addition, an age validation study has been completed since SEDAR04 (see Harris (2005)).

Reproduction

Following capture and dissection, the posterior portion of the gonads were fixed for 7–14 d in 11% seawater–formalin solution buffered with marble chips and transferred to 50% isopropanol for an additional 7–14 d. Reproductive tissue was processed in automated tissue processors and blocked in paraffin. Three transverse sections (6–8 um thick) were cut from each sample with a rotary microtome, mounted on glass slides, stained with double-strength Gill hematoxylin, and counterstained with eosin-y. Sections were viewed under a compound microscope at 20-400X magnification, and sex and reproductive class were determined without knowledge of capture date, specimen length, or specimen age. Two readers independently determined sex and reproductive state using histological criteria (see Wyanski 2000). When assignments differed, the readers re-examined the section simultaneously to determine reproductive state.

Females were considered to be in spawning condition if they possessed oocytes undergoing maturation (i.e., fusing of yolk globules, germinal vesicle migration and breakdown), hydrated oocytes, or postovulatory follicles). Specimens with developing, ripe, spent, or resting gonads were considered sexually mature. For females, this definition of sexual maturity included specimens with oocyte development at or beyond the cortical granule stage and specimens with beta, gamma, or delta stages of atresia. To ensure that females were correctly assigned to either the immature or resting categories, the length-frequency histogram of females with evidence of certain maturity (e.g., those that were developing, ripe, or spent) was compared with the histograms for immature and resting females. Females of uncertain maturity were excluded from maturity analyses. Specimens undergoing sex transition (female to male) were considered males, as these specimens would likely have spawned as males in the next spawning season.

Analyses

All analyses were done using, EXCEL, SAS or “R” software. Results were considered significant at P-values less than 0.05. To estimate age at 50% maturity and age at 50% male (A_{50}), the PROBIT procedure (SAS Institute, Inc., 1990) was used to fit gompit, logit, or probit models to age data in 1-yr (maturity) or 3-yr bins (proportion male). The LOGISTIC procedure was used to determine which model to use in the PROBIT procedure.

Results

Weight conversion

An equation to convert gutted fish weight (g) to whole fish weight (g) was not available at the time of SEDAR04. Based on mostly fishery-dependent samples collected by the MARMAP program, the following equation was generated:

Whole wt = gutted wt*1.082 (adj r^2 = 1.00; n = 502)

Age and growth

Parameters of the von Bertalanffy growth model were estimated for all MARMAP/SEFIS samples collected during 1979-2012, as well as a subset of only the fishery-independent samples collected by the programs (Table 3 and Figure 2). The results for the two datasets revealed very similar estimates of K and t_0, with the estimate of L_∞ based on all samples being slightly higher (1007 vs. 962 mm TL) and closer to the maximum observed size (1137 mm) in the samples.

Reproduction

There was a high degree of overlap in the left tail of the length histograms of definitely mature and regenerating Snowy Grouper and modest overlap in the lengths of immature and all mature individuals, indicating that individuals were correctly assigned to the immature and regenerating classes (Figure 3).

In the overall dataset (1979-2012), the youngest mature female was Age 3, and the oldest immature female was Age 13 (Table 4); age at 50% maturity was 5.6 yr (Logistic model: 95% CI = 5.3-5.9 yr). Further probit analysis showed that individuals matured at older ages in 2008-2012 compared to 1979-1994 (Logistic model: period effect, $p < 0.0001$), as A_{50} increased from 5.0 to 5.8 yr (Table 4).

In the overall dataset (1979-2012), the youngest male was Age 5, and the oldest male was Age 32 (Table 5); age at 50% male was 17.0 yr (Normal model: 95% CI = 15.8-18.5 yr). Omitting the Age 35 female produced this narrower 95% confidence interval. Further probit analysis showed that individuals transitioned to male at younger ages in 2008-2012 compared to 1979-1994 (Normal model: period effect, $p < 0.0001$), as A_{50} decreased from 18.1 to 13.7 yr (Table 5). Note that some of the oldest specimens do not transition to male, as the oldest specimen in the overall dataset was an Age 35 female.

Samples collected during 2008-2012 revealed a similar spawning season (April through September) to that reported by Wyanski et al. (2000); however, five specimens with histological evidence of spawning (oocyte maturation or postovulatory follicles) were collected in January, March, and October.

To determine if age has an effect on spawning proportion, the data were also examined by 1-yr age groups within month. The results showed that the overall proportion of spawners in the age groups between Age 5 and Age 35 during the spawning season (April-September) was fairly consistent among age groups, ranging from 0.26 to 0.36 (Table 6) for all ages except Age 10 (0.41). The proportion of spawners may increase at older ages (20-35 yr), but sample sizes were very small (total n = 7).

No estimates of the annual fecundity of Snowy Grouper are available, so three proxies for fecundity were generated (Gonad weight versus TL, whole fish weight, and age). The equation relating gonad weight to whole fish weight after natural log transformation had the highest r^2 value (0.50; Table 7).

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Table 1: Number by year of snowy grouper collected since the benchmark assessment (SEDAR 4 Stock Assessment Report 1. 2004) during fishery-independent (FI) sampling by the MARMAP (Year=2003 to present) and SEFIS Programs (Year=2010-2012) and during fishery-dependent (FD) sampling by the MARMAP program through a study funded by the Cooperative Research Program. Transverse sections of a sagittal otolith and histological sections of gonadal tissue were examined by two readers independently to assess age, sex, and reproductive state.

Year	# of FI specimens	# of FD specimens	# of oto. exam.	# of histo. exam.
2003	71		71	
2004	32		32	
2005	40		40	
2006	43		43	
2007	26	1	26	
2008	63	949	1012	1012
2009	30	140	170	170
2010	128	3	128	128
2011	157		157	157
2012	120		120	120
Total	710	1093	1799	1587

Table 2. Classification of otolith edge type and quality.

EDGE TYPE - Code description
1 Opaque zone on the edge.

2 Narrow translucent zone on edge Width less than about 30% of previous increment

3 Medium translucent zone on edge Width about 30-60% of previous increment

4 Wide translucent zone on edge Width more than about 60% of previous increment

READABILITY - Code description and analysis consequence
A Unreadable Omit otolith from analysis

B Very difficult to read Age estimate between readers are expected to be >2 year for young, and > 4 yrs for old fish (>10 yrs) Agreement on age may be difficult to reach, in which case otoliths should be classified as A and omitted from the analysis.

C Fair readability Age estimates between readers should be within 2 year in young, and within 4 years in old fish (>10 yrs). Agreement after second reading is expected after some discussion.

D Good readability Age estimates between readers should be within 1 year for young, to 2 years in old fish (> 10 years). Agreement after second reading is expected without much discussion.

E Excellent readability Age estimates between readers should be the same.

Table 3. von Bertalanffy growth model parameters for Snowy Grouper based on data collected by the MARMAP and SEFIS Programs during 1979-2012.

Model	L inf	SE	K	SE	t_0	SE
All MARMAP/SEFIS data	1007	14.69	0.12	0.005	-1.42	0.11
MARMAP/SEFIS, fish. Independ. data	961.5	18.17	0.13	0.008	-1.40	0.18

Table 4. Proportion of mature female Snowy Grouper by age class (# of increments) during two periods and for all years combined. Predicted values were calculated with a logistic equation [predicted = 1 - 1/(1 + exp(a+b*age))] for all years combined; a= -4.025, b = 0.717. LR = log-likelihood ratio.

Age		1979-1994		2008-2012			1979-2012
	n=	Prop.mat.	n=	Prop.mat.	n=	Pred. mat	Prop.mat.
0						0.018	
1	7	0.00	2	0.00	9	0.035	0.00
2	31	0.00	24	0.00	55	0.070	0.00
3	31	0.06	70	0.03	101	0.133	0.04
4	50	0.22	107	0.22	157	0.239	0.22
5	47	0.49	154	0.43	201	0.392	0.44
6	47	0.87	310	0.57	357	0.569	0.61
7	53	0.94	209	0.70	262	0.730	0.75
8	39	0.92	165	0.81	204	0.847	0.83
9	19	1.00	71	0.85	90	0.919	0.88
10	27	1.00	64	0.92	91	0.959	0.95
11	16	1.00	19	0.89	35	0.979	0.94
12	10	1.00	12	0.83	22	0.990	0.91
13	6	1.00	1	0.00	7	0.995	0.86
14	3	1.00	3	1.00	6	0.998	1.00
15	7	1.00	1	1.00	8	0.999	1.00
16	8	1.00			8	0.999	1.00
17	6	1.00			6	1.000	1.00
18	8	1.00			8	1.000	1.00
19	4	1.00			4	1.000	1.00
20+	6	1.00	2	1.00	8		1.00
Total	425		1214		1639		

		LR X^2						
Data	Model	p	Intercept	SE	Increment	SE	A50 (yr)	95% CI
1979-1994	Logistic	0.99	-6.574	0.728	1.324	0.140	5.0	4.7-5.2
2008-2012	Logistic	0.0014	-3.661	0.808	0.633	0.128	5.8	5.0-6.4
1979-2012	Logistic	0.0107	-4.025	0.424	0.717	0.069	5.6	5.3-5.9

Table 5. Proportion of male Snowy Grouper by age class (# of increments) during two periods and for all years combined. Predicted values were calculated with cumulative normal distribution function in EXCEL [Predicted = NORMSDIST(a+b*age)] for all years combined; a= -2.847, b = 0.168. LR = log-likelihood ratio.

Age		1979-1994		2008-2012	1979-2012			
	n =	Obs. Prop. Male	n =	Obs. Prop. Male	n =	Obs. Prop. Male	Pred. Prop. Male - no Age 35	Pred. Prop. Male
0							0.002	0.003
1							0.004	0.005
2						0.000	0.006	0.008
3	2	0.00	2	0.00	4	0.000	0.010	0.012
4	11	0.00	23	0.00	34	0.000	0.015	0.018
5	23	0.00	69	0.04	92	0.033	0.022	0.026
6	41	0.00	178	0.01	219	0.009	0.033	0.036
7	50	0.00	154	0.05	204	0.039	0.047	0.050
8	36	0.00	143	0.07	179	0.056	0.066	0.068
9	20	0.05	70	0.14	90	0.122	0.090	0.091
10	28	0.04	74	0.20	102	0.157	0.121	0.119
11	17	0.06	23	0.26	40	0.175	0.158	0.152
12	13	0.23	19	0.47	32	0.375	0.202	0.191
13	8	0.25	1	1.00	9	0.333	0.252	0.235
14	6	0.50	4	0.25	10	0.400	0.308	0.285
15	15	0.53	1	0.00	16	0.500	0.369	0.339
16	13	0.38	1	1.00	14	0.429	0.434	0.397
17	9	0.33	1	1.00	10	0.400	0.501	0.457
18	13	0.38			13	0.385	0.567	0.518
19	7	0.43	1	1.00	8	0.500	0.632	0.579
20	5	0.60	2	0.50	7	0.571	0.693	0.638
21	7	0.71			7	0.714	0.749	0.693
22							0.800	0.745
23	3	0.33			3	0.333	0.843	0.792
24							0.880	0.833
25	2	1.00			2	1.000	0.910	0.868
26							0.935	0.898
27	1	1.00			1	1.000	0.953	0.923
28							0.968	0.943
29	1	1.00			1	1.000	0.978	0.958
30							0.985	0.970
31							0.991	0.979
32			1	1.00	1	1.000	0.994	0.986
33							0.996	0.990
34							0.998	0.994
35			1	0.00	1	0.000	0.999	0.996
	331		768		1099			

Table 5. (continued).

Comment	Data	Model	p	Intercept	SE	Increment	SE	A50 (yr)	95% CI
	1979-1994	Normal	0.5687	-3.564	0.352	0.197	0.024	18.1	16.8-19.8
	2008-2012	Normal	0.0026	-2.708	1.697	0.189	0.189	16.2	n/a
Age 35 female omitted	2008-2012	Normal	0.4085	-3.368	0.274	0.247	0.031	13.7	12.5-15.4
	1979-2012	Normal	0.0370	-2.714	0.494	0.153	0.045	17.7	14.1-30.3
Age 35 female omitted	1979-2012	Normal	0.3303	-2.847	0.152	0.168	0.014	17.0	15.8-18.5

Table 6. Proportion of spawning female Snowy Grouper among all adult females (active+inactive) by 5-yr age groups during the spawning season (April through September). Spawners had at least one indicator of imminent or recent spawning (i.e., migratory nucleus oocytes, hydrated oocytes, and postovulatory follicles).

	# of increments and sample size (n)															
Month	3-4	n=	5	n=	6	n=	7	n=	8	n=	9	n=	10	n=	11-35	n=	Total
Apr	0.00	1	0.00	8	0.00	25	0.21	24	0.08	12	0.00	7	0.25	4	0.09	11	92
May	0.00	4	0.44	16	0.30	30	0.49	43	0.38	42	0.47	15	0.31	16	0.74	19	185
Jun	0.00	3	0.57	7	0.17	12	0.23	26	0.20	20	0.31	13	0.20	5	0.43	7	93
Jul	0.29	7	0.43	14	0.42	38	0.50	28	0.53	19	0.13	8	0.60	15	0.50	4	133
Aug	0.00	7	0.29	17	0.38	24	0.48	23	0.52	33	0.56	18	0.42	19	0.26	38	179
Sep	0.00	2	0.00	5	0.08	12	0.00	21	0.14	14	0.20	5	0.40	10	0.18	17	86
Total		24		67		141		165		140		66		69		96	768
Avg. monthy proportion spawners, Apr-Sep	**0.05**		**0.29**		**0.22**		**0.32**		**0.31**		**0.28**		**0.36**		**0.37**		
Prop. spawners, Apr-Sep	**0.08**		**0.33**		**0.26**		**0.35**		**0.36**		**0.35**		**0.41**		**0.34**		0.34

Table 7. Potential proxies for an estimate of individual fecundity in Snowy Grouper. Fish wt = whole fish weight.

Proxy	Units	Equation	a	SE	b	SE	Adj. r^2	n	Range of x
Gonad wt vs TL	g, mm	y = a + bx	-541.8	75.9	0.972	0.105	0.37	144	530-1006
Gonad wt vs TL	g, mm	y=exp(a*x)	0.0066	6.50E-05			0.35	144	530-1006
Gonad wt vs Fish wt	g, g	y = a + bx	-57.4	25.3	0.038	0.004	0.42	122	1500-20430
Gonad wt vs Fish wt	g, g	ln y = a + b (ln x)	-7.39	1.09	1.414	0.128	0.50	122	1500-20430
Gonad wt vs age	g, yr	y = a + bx	16.8	37.6	14.376	3.821	0.11	108	5-21

Figure 1. Commercial landings of snowy grouper along the Atlantic coast of the southeastern United States for all gear types, primarily snapper reels and bottom longlines (Pers. comm., National Marine Fisheries Service, Fisheries Statistics Division, February 22, 2012). Reference line in 2006 indicates beginning of management measures to reduce fishing mortality by implementation of annual quotas and trip limits.

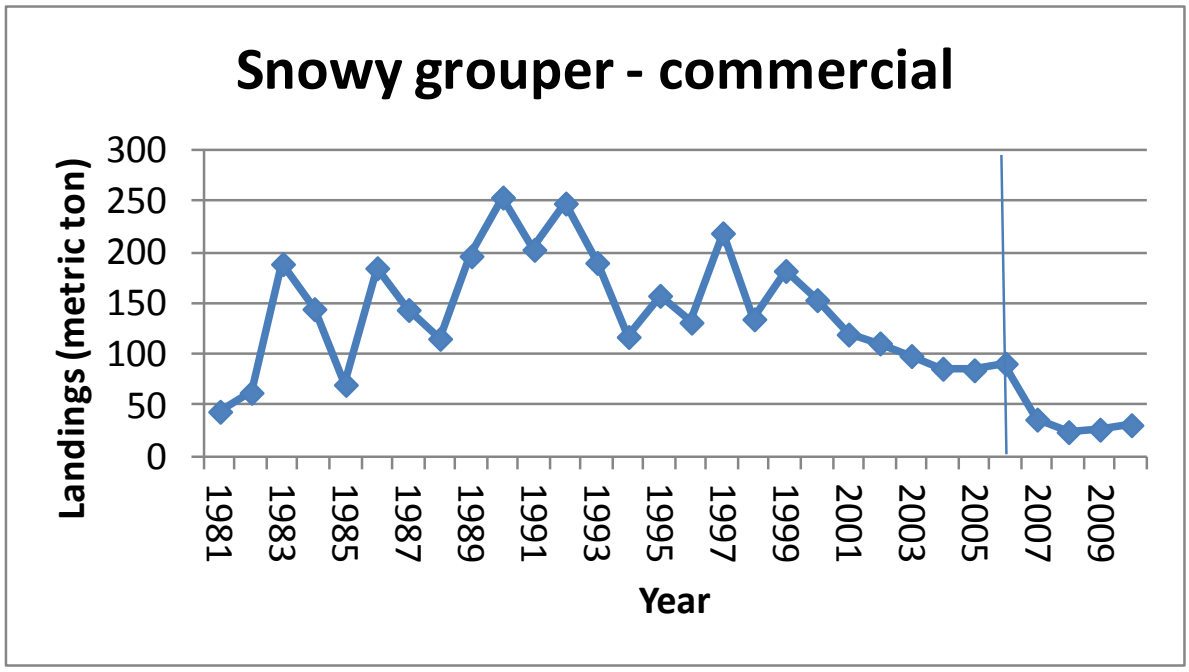
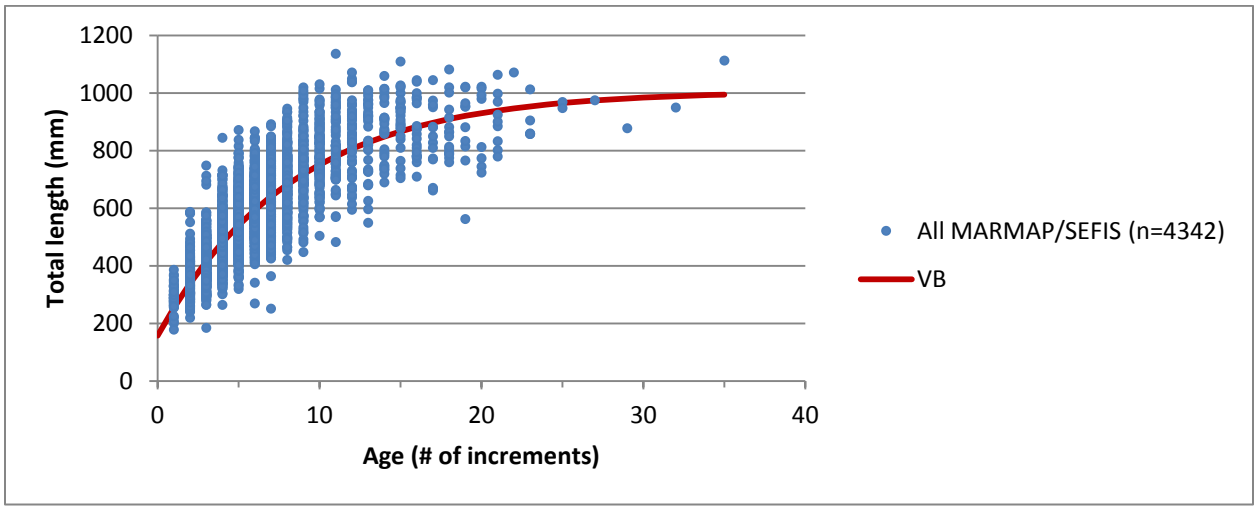


Figure 2. Observed and predicted sizes at age of Snowy Grouper captured by the MARMAP and SEFIS Programs, 1979-2012. **A)** All fishery-independent and fishery-dependent samples, **B)** All fishery-independent samples. VB = von Bertalanffy growth model (no constraints).

A)



B)

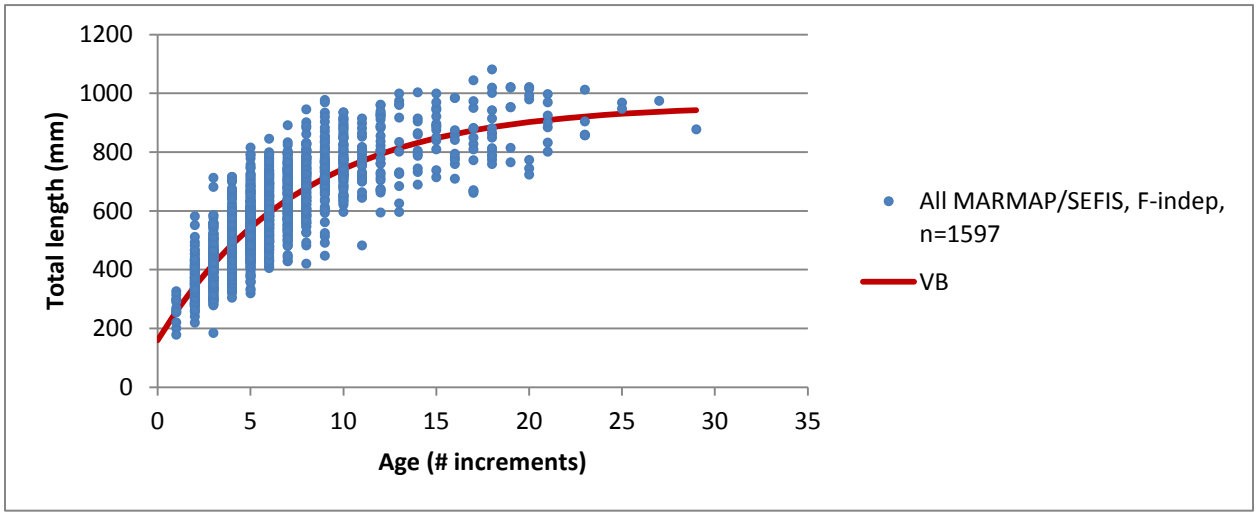


Figure 3. A comparison of length-frequency histograms for Snowy Grouper specimens collected during 1979-2012 that were categorized as immature, definitely mature, or resting. Definitely mature specimens were developing, ripe, or spent.