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Age Validation and Reproductive Biology of Bluefish, *Pomatomus saltatrix,* Along the East Coast of United States

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AGE VALIDATION AND REPRODUCTIVE BIOLOGY OF BLUEFISH, *POMATOMUS SALTATRIX*, ALONG THE EAST COAST OF UNITED STATES

by

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ABSTRACT

AGE VALIDATION AND REPRODUCTIVE BIOLOGY OF BLUEFISH, *POMATOMUS SALTATRIX*, ALONG THE EAST COAST OF UNITED STATES

Eric Robillard
Old Dominion University, 2006
Director: Dr. Cynthia M. Jones

I describe a new preparation technique that increases readability of otoliths, along with criteria for the interpretation of otolith microstructure of bluefish, *Pomatomus saltatrix*, collected from Florida to New York during 2001-2003 (n=2652). I validated annulus formation in otoliths for ages 1 to 8 using marginal increment analysis and thus extended validation by four years to include the preponderance of age classes in the catch. Although otoliths are typically superior for ageing, bluefish are routinely aged with scales; thus a side-by-side comparison of otoliths versus scales is necessary before otoliths can supplant scales. When compared, precision was highest with sectioned otoliths, exceeding 87% across all years, and exceeding 99% within 1 year up to ages 13. In contrast, scales tended to over age age-1 through age-5, and under aged age-7 and older in comparison with sectioned otoliths. Having demonstrated the value of otoliths, I used ages estimated from them to evaluate age distribution of various gears used in the fishery and calculated growth parameters and batch fecundity. When I evaluated my coastwide collections, I noted that gears caught different age ranges yet there were no significant differences in the von Bertalanffy growth parameters compared by sex, year, and between the South Atlantic and Middle Atlantic Bights using likelihood-ratio tests. The estimated Atlantic von Bertalanffy model growth parameters were L_{inf}= 815.3mm ±15.3, k = 0.311 ± 0.03, t_0 = -.301 ± 0.18. Histology, trends in gonadosomatic index, and oocyte diameter frequencies were used to determine bluefish spawning locations and patterns. Bluefish are multiple spawners with indeterminate fecundity. The presence of all stages of development in fully mature ovaries indicates that bluefish have asynchronous oocyte development. Mean age at first maturity for bluefish provided evidence for larger sizes than previously estimated with females maturing at 1.90 years and 480 mm. Histological samples showed imminent spawning in Florida and North

Carolina during March to April, and from April to August in Virginia to New York, supporting the hypothesis of continuous spawning from South Atlantic Bight to Middle Atlantic Bight. My estimates of fecundity at size are lower than previously published results.

This thesis is dedicated to my wife, Holly A. Robillard, who through her love and understanding gave me the strength to achieve, what I consider, the hardest challenge I have had to face to date: graduate school.

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CHAPTER I

GENERAL INTRODUCTION

1.1. Bluefish life history

Bluefish (*Pomatomus saltatrix*) can be found globally in temperate and warm temperate zones (Briggs, 1960; Champagnat, 1983). They are generally recognized as a single species. It is the only member of its family, the Pomatomidae, which is closely related to the family Carangidae (jacks, pompano, etc.) In North America they live along the Atlantic seaboard from Nova Scotia south, around the tip of Florida, and along the Gulf Coast to northern Mexico (Pottern et al., 1989). Their world wide range also includes the Caribbean, the Azores, the Mediterranean Sea, the Black Sea, northwest and southern Africa, and the entire coast of Australia (Wilk, 1977).

Bluefish is considered an apex piscivorous predator, relying primarily on vision to detect prey (Wilk, 1977). The food habits of offshore, newly hatched larvae, are composed of mainly zooplankton, including larvae of other pelagic-spawning fishes (Norcross et al., 1974; Kendall and Walford, 1979; Kendall and Naplin, 1981). Young of the year arriving in coastal nursery areas feed mostly on piscine prey like anchovies (*Anchoa mitchilli)*, striped killifish (*Fundulus majalis)*, and silversides (*Menidia menidia)* (Olla et al., 1985; Friedland et al., 1988; Pottern et al., 1989). Adult bluefish typically consume schooling species such as alewives (*Alosa pseudoharengus)*, menhaden (*Brevoortia tyrannus)*, spot (*Leiostomus xanthurus)*, smaller bluefish and many other species (Richards, 1976; Buckel et al., 1999).

The model for this thesis is Fishery Bulletin.

Bluefish along the East Coast of United States are migratory, spending their summers from New England to Cape Hatteras, North Carolina, and their winters around Florida and the Gulf Stream (Pottern et al., 1989). Smaller bluefish travel close to shore during both the spring and fall migration. Larger fish travel near shore in their northern range, but are hypothesized to move offshore during the southern migration in dispersed groups close to the coast (Lund and Maltezos, 1970; Wilk, 1977). There also appears to be a non-migratory population in southern Florida and the Gulf of Mexico regions (Barger et al., 1978; Kendall and Walford, 1979; Pottern et al., 1989). Genetic studies have failed to find, however, any temporally stable differences in population structure, thus supporting the hypothesis of a single unit stock with differing migratory and spawning patterns (Graves et al., 1992).

1.2. Previous hypotheses

Bluefish support one of the most important recreational fisheries in the U.S., and accounts for approximately 30% of the total weight of all species captured by anglers along the East Coast (Pottern et al., 1989; MAFMC, 1998). Total landings of bluefish in the Mid-Atlantic, however, have declined by 80% over the last 15 years (Gibson and Lazar, 1998; NMFS, 2005[1]). This decline has alarmed anglers and fisheries managers alike and scientists have attributed the decline to several factors. Among the more popular hypotheses are: 1) increased competition for food by striped bass (*Morone saxatilis*) during the juvenile (young-of-the-year; YOY) stage; 2) decreased survival or supply of larvae of the spring-spawned cohort; 3) changes in oceanographic conditions or in essential fish habitat are also popular hypotheses (De Luca, 2000). Changes in the

[1] Pers. Comm. National Marine Fisheries Service, Fisheries Statistics Division, Silver Spring, MD.

reproductive fitness (fecundity) of bluefish have also been implicated as a potential cause for the decline of this population (DeLuca, 2000), but only one paper (Lassitter, 1962) has been published on the direct measurement of bluefish fecundity.

The potential effect on competition between young of the year striped bass and bluefish was studied by Buckel and McKown (2002). They compared habitat and diet between the two species. They showed these two species are seldom found together and there seems to be very low overlap in the diets. They concluded there was no evidence for competitive interactions between juvenile striped bass and bluefish. This study did not support the theory of increased competition for food by striped bass during the juvenile stages.

The yearly recruitment pattern of bluefish in the Middle Atlantic Bight is complex and bimodal. Recruits first occur in bays and estuaries in late May and early June (Nyman and Conover, 1988). These are hypothesized to be progeny of the spring-spawning group, as evidenced by distributions of larvae and back-calculated hatch dates obtained from YOY fish collected in estuaries and bays along the South Atlantic Bight (SAB) and mid-Atlantic coast (McBride et al., 1993). The second pulse of recruits results from local spawning within the Middle Atlantic Bight (MAB), in mid-shelf waters (Chiarella and Conover, 1990; McBride and Conover, 1991). Evidence for this local, summer-spawning is derived from three pieces of information. The first is the presence of high concentrations of small larvae on the continental shelf during mid-summer (Cowen et al., 1993). The second is the presence of ripe fish in near coastal waters, and consistently high gonadosomatic index from July to September (Chiarella and Conover,

1990). Finally is the occurrence of YOY bluefish in bays and estuaries with back-calculated hatch dates of mid summer (July).

There are two competing hypotheses concerning the formation of this bimodal recruitment. The first proposes that there are two distinct spawning episodes, the first occurring in the SAB in the spring, and the second in the summer in the MAB. This hypothesis was first proposed by Kendal and Walford (1979), who, looked at the distribution of larvae collected from ichtyoplankton surveys, found two distinct groupings of larvae, and concluded they were formed by two main spawning events. Further evidence for the two-spawning event was provided by Chiarella and Conover (1990), who found that fish collected in New York had low gonadosomatic indices in June. These low indices were followed by an increase that peaked in mid-July, coinciding with the presence of larvae in the Middle Atlantic Bight (MAB). They concluded that the low indices were due to a cessation of spawning from the South Atlantic Bight (SAB) to the MAB and that fish spawning off of New York in late June, July and August were part of the second spawning event.

The second hypothesis to explain the bimodality of recruitment to estuaries was proposed by Hare and Cowen (1993). They used gonadosomatic indices, larval abundance, and distribution for both SAB and MAB to develop a transport model. The model described a complicated interplay between large and mesoscale physical oceanographic processes and features, including the Gulf Stream, Warm Core Rings, and hydrographic fronts (Hare and Cowen, 1996). The model predicts that as the fish spawn in the SAB on the continental shelf, the larvae are subsequently transported by the Gulf Stream carrying them north-northeast along the edge of the continental shelf south of

Cape Hatteras at ca. 100 to 200 cm/s (Pierce and Joyce, 1988; Joyce et al., 1990; Hare and Cowen, 1996). For the larvae to reach the estuaries in the MAB, they need to cross the Gulf Stream or else they would be advected into the Slope Sea. Hare and Cowen (1996), proposed that larvae are advected from the Gulf Stream to the MAB through the formation of Warm Core Ring streamers. These are ribbons of Gulf Stream water which are carried around the western side of the warm-core rings and which deposit Gulf Stream water at the MAB shelf break. The model demonstrated that with continuous spawning, a bimodality in recruitment was formed as a result of physical oceanographic processes.

There is considerable interest in the determination of the relative contribution of each spawning period to year class strength (Conover et al., 2000), as there is some suggestion that the contribution of recruitment from the spring and summer-spawning components has changed. It appears that these spring-spawned recruits have been lost (Conover et al., 2000) and it is hypothesized the loss could result from decreased survival or supply of larvae from changes in oceanographic conditions.

If the relative contribution of spring- and summer-spawned components has changed, knowledge of the age-specific fecundity is critical to establishing where in the life cycle this change is manifested. Estimates of fecundity for bluefish are almost entirely lacking, however, and the only published estimates are based on the work of Lassiter (1962), who made direct observations on gonads. He found that fecundity of 3 to 4 year old bluefish from the coast of North Carolina ranged between 0.6 and 1.4 million eggs, but did not indicate whether bluefish were batch or total spawners. Clearly, such estimates are inadequate for addressing population level questions that need total annual

fecundity, maturity schedules, and age-specific fecundity estimates to form the basis of Spawning Potential Ration (SPR) models. Fortunately, techniques for the estimation of fecundity are well developed (Luna, 1968; Hunter et al., 1985; Hunter and Macewicz, 1985; Hunter et al., 1992; West, 1990; Wells, 1994) and coupled with appropriate age information, allow examination of potential effects on recruitment of over fishing, and formulation of likely management actions that could increase reproductive success (Sissenwine and Shepherd, 1987; Mace and Sissenwine, 1993; Lowerre-Barbieri, 1996; Barbieri et al., 1997).

The resiliency and persistence of exploited fish populations depend on age-specific survival and fecundity i.e. fitness. Changes in population structure, abundance, and longevity can dramatically alter the prospects that a population will rebound from exploitation (Rugolo et al., 1994). In theory, with heavier exploitation survivors should grow faster and become more fecund at a given age. As the mean age of the population declines (juvenescence) as the result of harvest, the lifetime reproductive potential of the population may be diminished. Thus the estimate of fitness provides a first and critical step in interpreting any of the other hypotheses. Once age-specific survival and fecundity are known, then the causes for population decline can be modeled and specific hypotheses tested.

1.3. Objectives

In this project, I focused on a general research question concerning growth and fecundity of bluefish as a vehicle for addressing the basic building blocks of a rationally managed fishery. To properly assess the role of reproduction in the apparent population

decline, or to properly determine which other life stages are important for study, I assessed three components of life-time reproductive fitness. First, I determined the reproductive spawning mode. Are bluefish batch or total spawners? Moreover, if bluefish are batch spawners, are they synchronous or asynchronous spawners? Without this knowledge total fecundity may be underestimated. Second, I validated age structure to age the population. Without a validated age structure, age-specific population parameters (natural mortality, maximum age, size-at-age) of the underlying population dynamics may be under- or over-estimated. The third component necessary to determine lifetime reproductive fitness and to assess changes in fitness over time is the age-specific fecundity and age at first maturity. Finally, I summarize these results and discuss implications.

CHAPTER II

AGE-VALIDATION AND GROWTH OF BLUEFISH (*POMATOMUS SALTATRIX*) ALONG THE EAST COAST OF THE UNITED STATES

2.1. Introduction

Bluefish are a migratory pelagic species (Briggs, 1960; Champagnat, 1983; Pottern et al., 1989; Juanes et al., 1996), whose broad distribution along the U.S. East Coast is accomplished through temporal coastwide migrations in loosely aggregated groups of like-sized fish (Wilk, 1977), while maintaining its integrity as a unit stock (Graves et al., 1992). This population has shown substantial recent declines. The fishery, which is one of the most important recreational fisheries in the United States, accounts for approximately 30% of the total weight of all species captured by anglers along the East Coast (Pottern et al., 1989; MAFMC, 1998). However, recreational landings have declined from 95.2 million pounds in 1981 to a low of 11.7 million pounds in 2002. Although commercial landings are a minor component of the fishery, they have followed a similar trend, declining from a high of 16.5 million pounds in 1981 to a low of 6.8 million pounds in 2002. This represents an overall reduction of over 80% of total bluefish landings in the Mid-Atlantic over the last 20 years (Gibson and Lazar, 1998).

Fittingly for such an important recreational species, a great deal of research has been directed to recruitment studies in bluefish by tracking juveniles in the Middle Atlantic Bight (Norcross et al., 1974; Nyman and Conover, 1988; McBride and Conover, 1991; Creaser and Perkins, 1994; McBride et al., 1995; Munch and Conover, 2000; Epifanio and Garvine, 2001; Able et al., 2003; Conover et al., 2003). Surprisingly, much

less research has been directed to the study of adult bluefish related to age and growth on the East Coast of United States (Richards, 1976; Barger, 1990; Terceiro and Ross, 1993; Salerno et al., 2001), perhaps because of the difficulty in sampling such a wide-ranging species.

Because bluefish are managed with age-based stock assessments, it is crucial that age estimates are accurate and precise over the fully exploited age classes (Beamish and McFarlane, 1983; Campana, 2001). Scientists have pointed out the apparent lack of intermediate-age bluefish along the U.S. East Coast suggests potential problems with age assignments (Wilson and Degnbol, 2002). Currently, bluefish ages are assigned based on scales (Barger, 1990; Lucena and O'Brien, 2001; Salerno et al., 2001; Sipe and Chittenden, 2002). Although the accuracy of scale-based ageing was validated by lab-rearing and mark and recapture studies (Wilk, 1977), conditions in the laboratory may not reflect those in nature for a fish as migratory as bluefish and, further, age classes for the mark-recapture study were not described. Precision also has been low when ageing bluefish with scales, especially for older fish (Sipe and Chittenden, 2002; Wilson and Degnbol, 2002). Further, no studies have examined the possibility of scale ages being biased toward under-ageing bluefish, especially at older ages. As a result, there is a concern that ageing with scales could lead to inaccuracies of as much as three years in age assignments, affecting estimates of the biological characteristics of this species such as growth (Wilson, 2000). To address this concern, Sipe and Chittenden (2002) compared scale ages with those of otoliths, opercula, and vertebrae and concluded that sectioned otoliths were the best structure because otoliths had the clearest marks and gave the highest precision. They identified two problems, however, in using otoliths: 1)

validation studies had not been conducted; and 2) fish older than age-four showed low precision (Barger, 1990; Sipe and Chittenden, 2002). Furthermore, their study did not determine if age assignment bias occurred between the various ageing structures.

In this study, I used a new processing technique for otoliths to increase readability of older bluefish, and include criteria for the interpretation of otolith microstructure. For accuracy, I validated otolith annuli formation through age 8 using marginal increment analysis. I conducted age determination with scales using Barger's (1990) interpretation methodology and compared between and within readers' precision as well as determined bias between both hard parts. Using the validated otolith ageing technique, I evaluated gear characteristics by evaluating size and age distributions of the catch and estimated growth parameters for bluefish and compared the size-at-age of the population along the Atlantic coast.

2.2. Methods

2.2.1. Field Collections

A total of 2652 bluefish were collected for analysis between April 2001 and August 2003 (Figure 2.1; Table 2.1). All fish were measured for total length (TL, mm), fork length (FL, mm), standard length (SL, mm), and total weight (TW, g). Sagittal otoliths and scales were removed and stored dry for age determination. In the first year pilot project, I identified major recreational and commercial gears that harvest adult bluefish. I found fish size varied spatially and between recreational and commercial fisheries; therefore, it was necessary to obtain bluefish from both fishing sectors to cover the full size range of adults. In Florida, specimens were mostly available from

recreational fisheries. Bluefish in North Carolina are mainly caught with gillnets, so I collected almost exclusively from commercial gillnet fishers there. In Virginia, fish were collected offshore from recreational charter boats and inshore from gill nets, pound nets, and haul seine landings. All fish from New Jersey and New York were collected from recreational charter boats. To represent the entire age range, I emphasized sampling larger specimens.

2.2.2. Development of otolith ageing technique

I randomly selected either the right or left otolith for analysis. Each otolith was mounted onto a standard microscope slide with Crystalbond™ adhesive with its distal surface upwards. The slide was secured to a Buehler Isomet saw equipped with two Norton diamond wafering blades separated with a 0.4 mm stainless steel spacer positioned to straddle the focus of the otolith.

I used a "bake and thin-section" technique that was developed at the Center for Quantitative fisheries Ecology (CQFE) by Stephen Wischnowski. The otolith section was placed into a ceramic "Coors" spot plate well and baked in a Thermolyne 1400 furnace at 400°C. Baking time was dependent on otolith size and gauged to achieve a light caramel color. The baked thin-sectioned otolith was placed on a labeled glass slide and covered with a thin layer of Flo-texx® mounting medium. This medium provided enhanced contrast and greater readability by increasing light transmission through the sections.

Otoliths were examined using a Leica MZ-12 dissecting microscope with transmitted light and dark-field polarization at between 8 and 20 times magnification. All samples ($n = 2648$) were aged in chronological order by collection date, without

Table 2.1

Sample size, fork length range, and age range for bluefish collected by year and by state. Periods of no sampling effort are categorize as N/S. Periods with sampling effort with no samples collected are left as blanks.

Location	Period	2001			2002			2003		
		Sample size	Fork length range (mm)	Age range	Sample size	Fork length range (mm)	Age range	Sample size	Fork length range (mm)	Age range
New York	Jan-April	N/S	N/S	N/S						
	May-August	74	395-829	2-10	180	381-805	2-11	298	275-840	1-11
	Sept-Dec				38	474-813	2-11			
Virginia	Jan-April	63	365-762	2-7	95	254-731	1-9	12	402-597	2-4
	May-August	249	230-780	1-8	391	153-776	1-9	393	160-770	1-10
	Sept-Dec	123	286-844	1-12	230	280-789	1-7	42	420-769	1-9
North Carolina	Jan-April	N/S	N/S	N/S	181	189-860	1-12	240	463-860	3-13
	May-August	N/S	N/S	N/S	7	669-725	5-8			
	Sept-Dec	N/S	N/S	N/S						
Florida	Jan-April	N/S	N/S	N/S	N/S	N/S	N/S	36	676-870	5-12
	May-August	N/S	N/S	N/S	N/S	N/S	N/S			
	Sept-Dec	N/S	N/S	N/S	N/S	N/S	N/S			
Total Specimens		509			1122			1021		2652

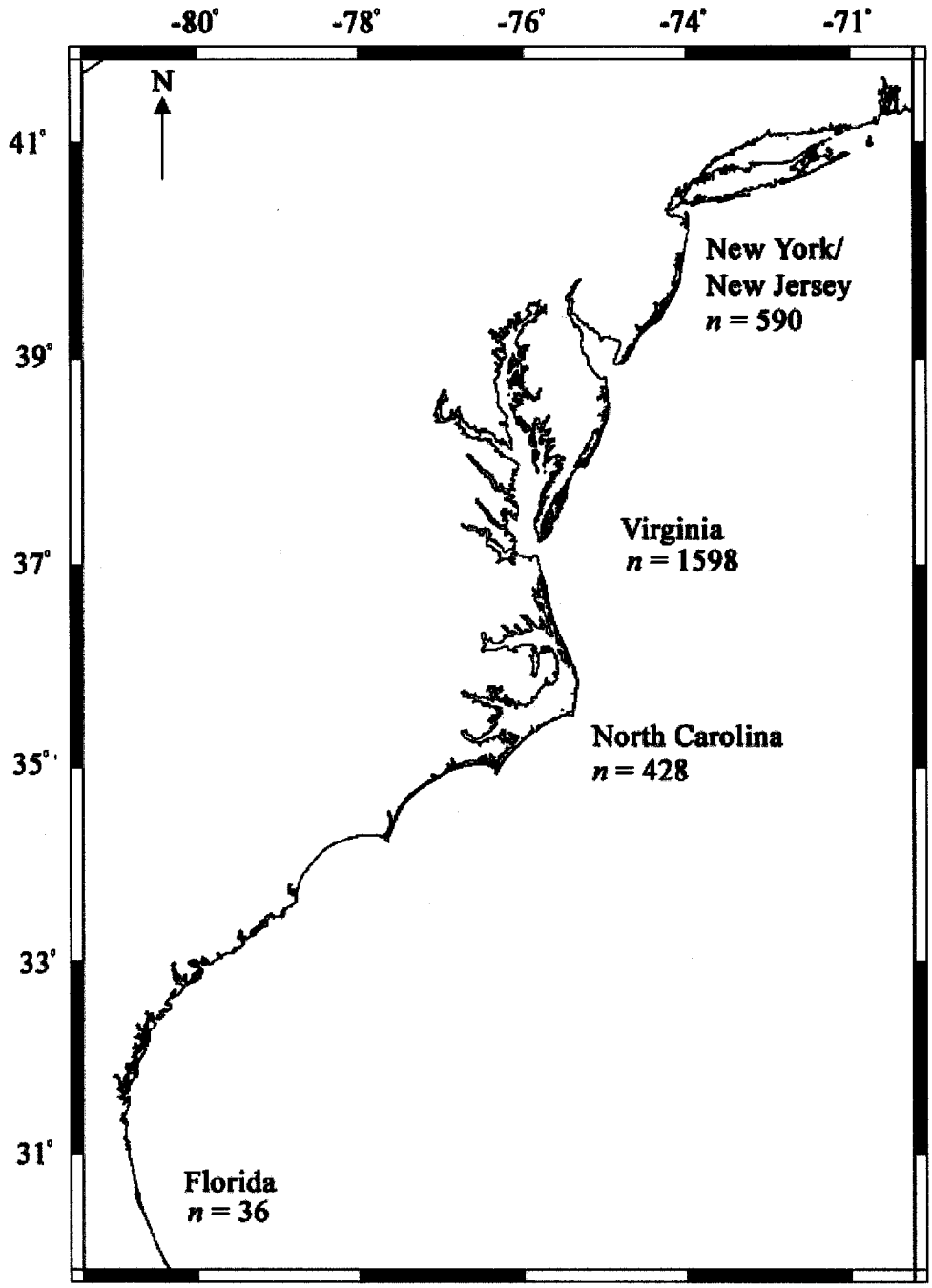

Figure 2.1
Map of the locations and numbers of bluefish collected from 2001 to 2003.

knowledge of previously estimated ages or the specimen lengths. Two readers independently read the sectioned otoliths.

2.2.3. Scale ageing technique

Scales were pressed onto acetate sheets (0.02 gauge) with a Carver Laboratory heated press using 12,000 psi at 130°C for 5 to 10 minutes. The impressions were viewed with a Bell and Howell microfiche reader for age determination. Annuli were defined as "a band of widely spaced circuli, usually with broken circuli in the anterior field and/or anastomosis in the lateral field, followed by a series of closely spaced circuli" (Barger, 1990). Two readers independently read the scale impressions.

2.2.4. Validation of annuli formation

I determined the periodicity of annulus formation on sectioned otoliths by marginal increment analysis. Otolith measurements were made with a digital image processing system using Image Pro 5 (MediaCybernetics, Inc.) attached to a Hitachi KP-D50 color digital camera on Leica MZ12 microscope. As stated by Campana (2001), this method may be difficult to carry out due to difficulties associated with viewing a partial increment affected by light refraction through an edge. However, this approach is valid if done with a rigorous protocol (Campana, 2001): 1) all samples were randomized before examination to prevent bias in measurements; 2) two consecutive years were examined; and 3) the validation was undertaken by year class to age 8. The translucent margin beyond the last opaque annulus was measured along the ventral side of the sulcal groove.

2.2.5. Measures of precision

A test for symmetry was used to detect systematic difference between the two readers (Hoenig et al., 1995). To measure reader otolith self-precision and age

reproducibility, each reader re-aged all fish collected in 2001 and a randomly selected subset of 50 fish from 2002 and 2003 (n = 596). To measure reader self-precision and age reproducibility from scale impressions, a random subset of 115 fish was selected. Between and within reader precision was measured using Chang's (1982) average coefficient of variation (CV) with the formula presented in Campana and Jones (1992).

2.1) $$100\% * \sqrt{\frac{\sum_{l=1}^{R} \frac{(X_{lk} - \overline{X}_k)^2}{R-1}}{\overline{X}_k}}$$

Where X_{lk} is the lth age determination of the kth fish, X_k is the mean age of the kth fish, and R is the number of times each fish is aged. A sub-sample of 10 specimens per age class was randomly selected (n = 110) to discern bias between otolith and scale ages using (1) a linear regression to test for the null hypothesis that the slope (β) of the linear regression of the counts for the scales and sectioned otoliths equaled 1; (2) a test of symmetry to detect systematic difference between the two ageing structures (Hoenig et al., 1995).

2.2.6. Growth

To evaluate variability in growth, observed length-at-age data based on otoliths were fitted with a von Bertalanffy Growth function (Ricker, 1975), by non-linear least squares regression S-PLUS® (version 6.1) as follows:

2.2) $$L_t = L_{\inf}(1 - e^{-k(t-t_0)})$$

where L_t is observed length at any given age; L_{inf}= asymptotic mean length (mm); t_o is the theoretical age at 0 length; k = the instantaneous growth rate (Brody coefficient) and t is the age defined as the estimated age plus the fractional age ((month of capture-6)/12)

using June 1 as the birth date, as it is hypothesized that bluefish spawn between March and August.

Likelihood ratio tests (Kimura, 1980) were used to determine if differences existed between von Bertalanffy parameter estimates between years, locations (SAB and MAB), and sexes for mean fork length-at-age data. Models were developed to assess the following hypotheses 1) different growth curves between years, locations, and sexes (H_Ω); 2) different growth curves with one growth parameter (L_{inf}, t_0, or K) equal ($H_{w1\text{-}3}$); and 3) the alternative hypotheses of no differences in growth curve parameters (H_{w4}).

2.3) $$H_\Omega : l_{ij} = l_{\infty i}\left(1 - e^{-k_i\left(t_{ij} - t_{01}\right)}\right)$$

2.4) $$H_{w1} : l_{ij} = l_{\infty}\left(1 - e^{-k_i\left(t_{ij} - t_{01}\right)}\right)$$

2.5) $$H_{w2} : l_{ij} = l_{\infty i}\left(1 - e^{-k\left(t_{ij} - t_{01}\right)}\right)$$

2.6) $$H_{w3} : l_{ij} = l_{\infty i}\left(1 - e^{-k_i\left(t_{ij} - t_{0}\right)}\right)$$

2.7) $$H_{w4} : l_{ij} = l_{\infty}\left(1 - e^{-k\left(t_{ij} - t_{0}\right)}\right)$$

When comparing two or more curves using likelihood ratios, a unconstrained null model that has common parameters is used to compare with more specific models. The statistics are developed by comparing the ratio of the two likelihoods (Kimura, 1980)

2.8) $$\Lambda = \frac{\left(2\pi\hat{\sigma}_w^2\right)^{-\frac{N}{2}} e^{\left(\frac{-N}{2}\right)}}{\left(2\pi\hat{\sigma}_\Omega^2\right)^{-\frac{N}{2}} e^{\left(\frac{-N}{2}\right)}} = \left(\frac{\hat{\sigma}_\Omega^2}{\hat{\sigma}_w^2}\right)^{\frac{N}{2}}$$

with the test statistic:

2.9) $$-2Ln(\Lambda) = -NLn\left(\frac{\hat{\sigma}_\Omega^2}{\hat{\sigma}_w^2}\right)$$

that takes a chi-squared distribution and is used to test the significance of differences between the unconstrained and specifically-constrained models (Kimura, 1980).

2.3. Results

2.3.1. Otolith ageing technique

Baking enhanced the microstructure of bluefish otolith thin sections and made age determination much easier, especially for animals with narrow annuli, or when otoliths had false annuli (Figure 2.2). The sectioning process also enhanced overall readability. When properly sectioned, the sulcal groove came to a sharp point within the middle of the focus; there was little "broadening" and distortion of the opaque growth zones, and a defined and delineated annulus was evident.

Typically the first opaque zone was found by locating the focus of the otolith, which was characterized as a visually distinct dark oblong region found in the center of the otolith (Figure 2.3). The first opaque zone was most visible proximal to the focus along the edge of the sulcal groove. Once located, the first opaque zone was followed outward from the sulcal groove towards the dorsal perimeter of the otolith. Often, but not always, the first opaque zone was associated with a very distinct crenellation on the dorsal surface and a prominent protrusion on the ventral surface (Figure 2.3). Unfortunately, both these landmarks had a tendency to become less prominent in older fish. Apparent rapid growth during the first year of life prevented the formation of a sharp delineation between opaque and translucent zones. When the exact location of the

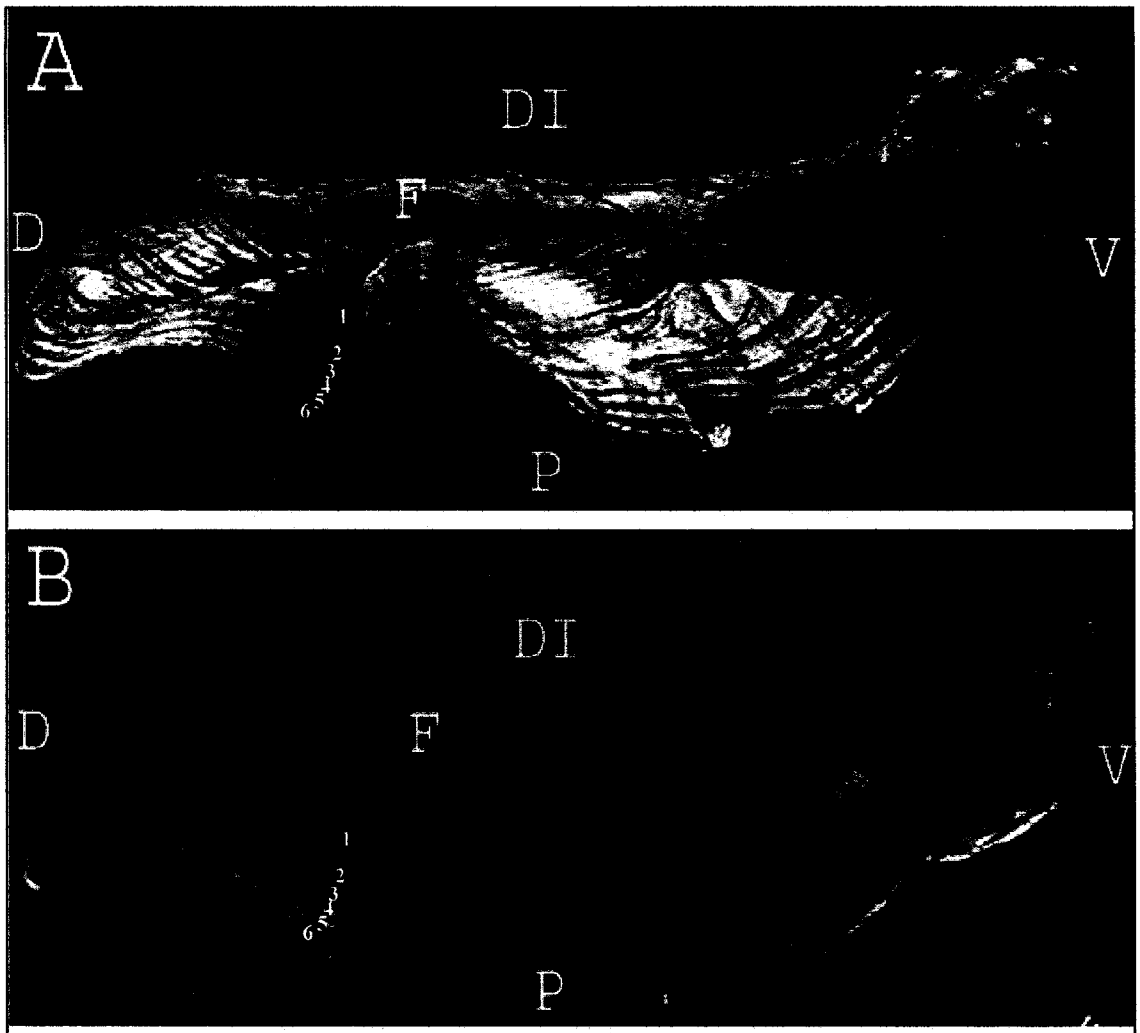

Figure 2.2
Transverse sectional view of an age 6+ bluefish collected from Virginia in June 2001. (A) Unbaked otolith; (B) Otolith baked at 400°C for 5 minutes. F = focus; SG = sulcal groove; DI= distal surface; D = dorsal end; P = proximal surface; V = ventral end.

first opaque zone was not clearly evident, and the otolith had been sectioned accurately, a combination of surface landscape (1st year crenellation) and the position of the second opaque zone were used to help determine the position of the first mark.

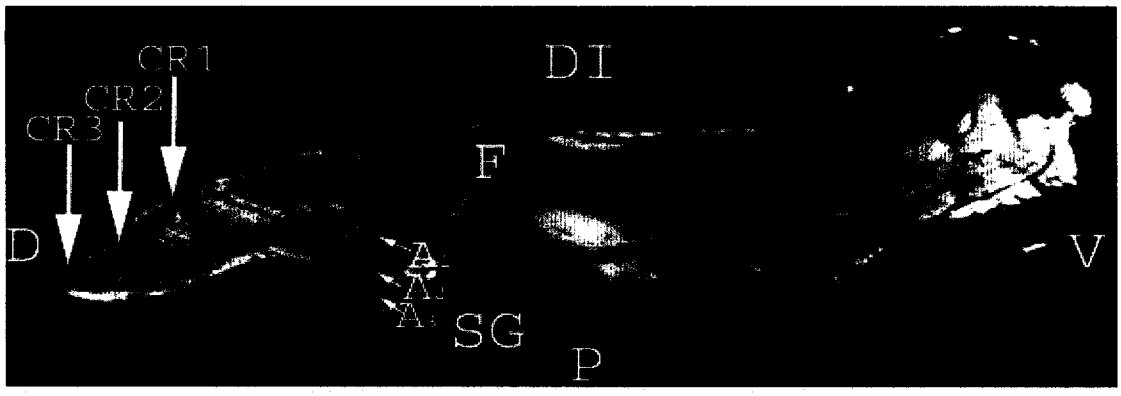

Figure 2.3
Transverse sectional view of an age 3 bluefish collected from Virginia in May 2003. A = annulus; CR = crenellation associated with annulus; F = focus; SG = sulcal groove; DI= distal surface; D = dorsal end; P = proximal surface; V = ventral end.

What appeared to be "double annuli" were occasionally observed in bluefish four years of age and older (Figure 2.4). This structure typically occurred within years 4 to 7, and was characterized by distinct and separate opaque zones in extremely close proximity to each other. Although it is not known if these structures represented one or two annuli, they generally occurred during times of reduced growth after maturation. "Double annuli" were considered to be one annulus when both opaque zones joined to form a central origin, with the origins being the sulcal groove and at the outer peripheral edge of the otolith. If these opaque zones did not meet to form a central origin they were counted as two annuli.

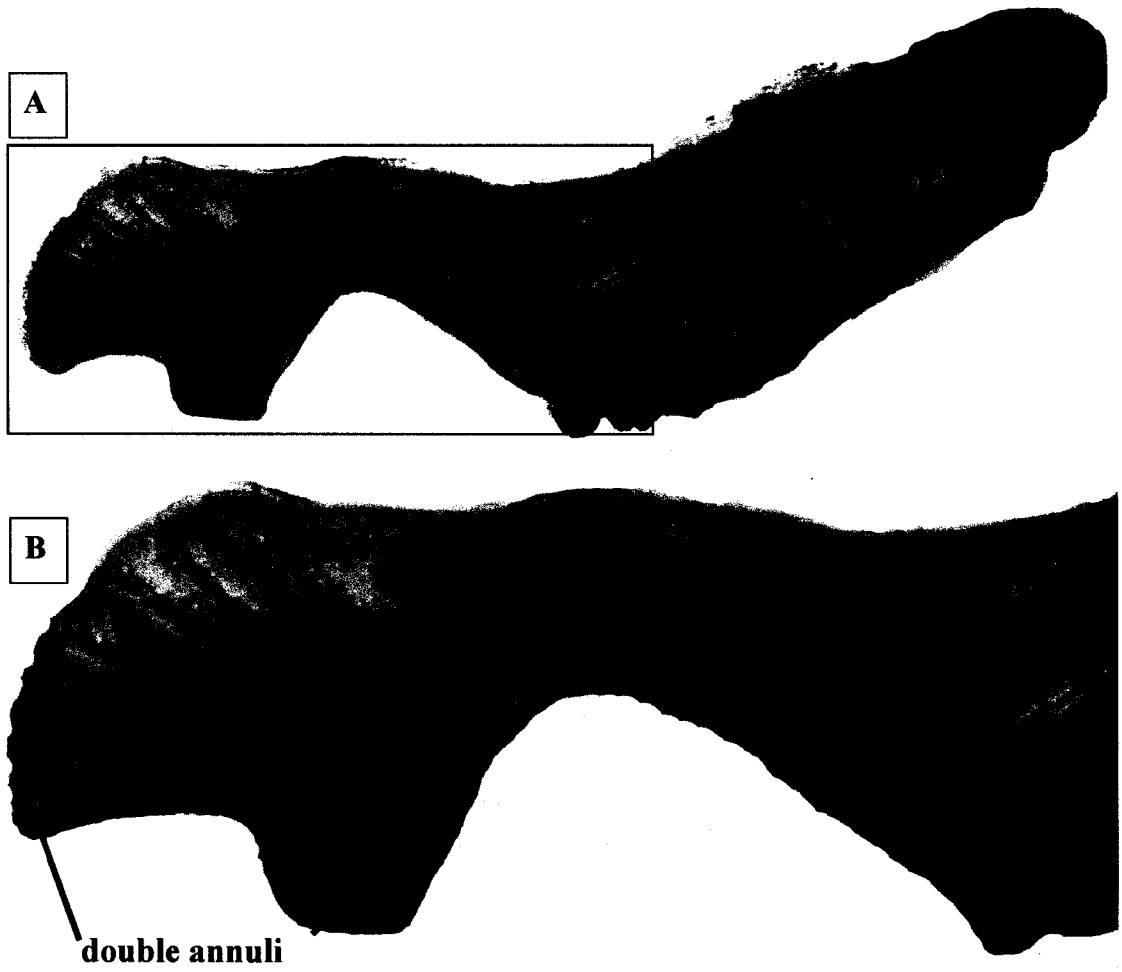

Figure 2.4
Transverse section of the sagittae of a 9-year-old male bluefish with an 812 mm fork length. (A) Sectioned magnified X1.2. (B) Sectioned magnified X 2 showing the presence of double annuli.

2.3.2. Sectioned otolith validation

Marginal increment analysis revealed one trough per year (Figure 2.5). The trough was visible between April and May, and was broad, lasting until September before the marginal width increased to a maximum between December and January. Fish 3, 4 and 5 years old showed a temporal shift in formation of this trough. For those ages, the rough began later, during June and July, again lasting until September. Overall, the mean

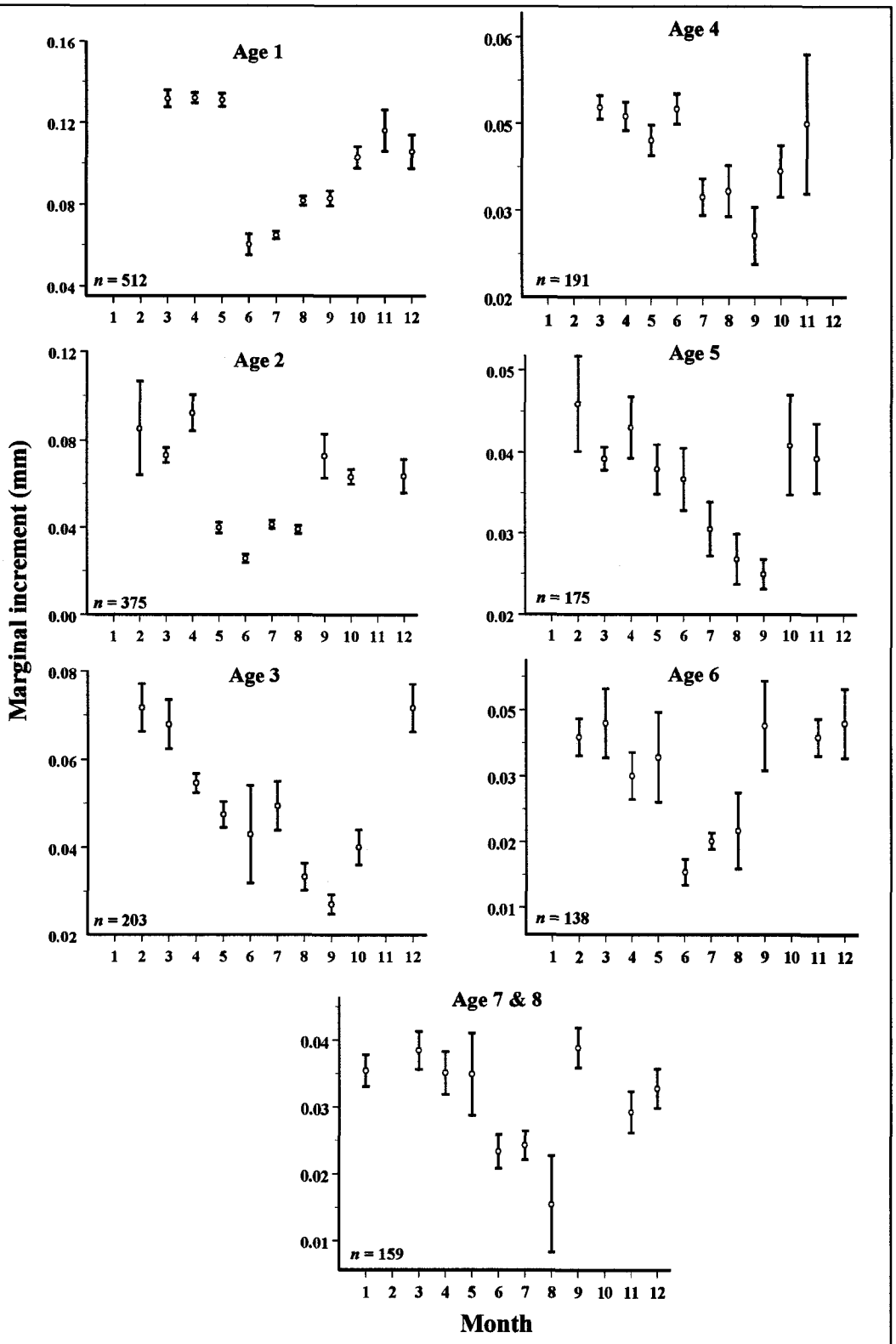

Figure 2.5
Mean monthly otolith marginal increments for bluefish ages 1 to 8 collected along the Atlantic coast 2001-2003. Vertical bars are +/– 1 Standard Error.

monthly marginal increment showed only one trough during the year, therefore, I concluded only one annulus was formed per year on bluefish for ages one through eight.

2.3.3. Between and within reader precision

Using sectioned otoliths, ages were assigned to 2591 of the 2652 (97.6%) bluefish collected. Within-reader agreements for sectioned otolith age readings were (reader 1 = 96.1% and reader 2 = 90.9%) and 99.3% accounted for disagreements of +/- 1 year (Figure 2.6). The measurement of reader self-precision was also high for both readers (reader 1's CV = 1.1% and reader 2's CV = 3.0%). Between-reader agreements for sectioned otolith age readings were 87.1% overall and for disagreements that were within a year, 99.5% (Figure 2.6). The average between-reader coefficient of variation was 2.7%. There was no evidence of systematic disagreement between reader 1 and reader 2 at the $\alpha = 0.05$ level (test of symmetry, $\chi^2 = 27.3$, df = 18, P = 0.09).

Ageing precision with sectioned otoliths was similar between older fish ($\geq$ age 5, $n = 829$) and younger fish. Within-reader agreements for sectioned otolith age readings were (reader 1 = 91.2% and reader 2 = 78.0%) and 97.8% accounted for disagreements of +/- 1 year. The measurement of reader self-precision was also high for both readers (reader 1's CV = 1.0% and reader 2's CV = 2.9%). Between reader agreement was slightly lower (75%) overall but 98.6% of this disagreement was within one year. The average between-reader coefficient of variation was 3.0% and there was no evidence of systematic disagreement between reader 1 and reader 2 (test of symmetry, $\chi^2 = 21.4$, df = 15, P = 0.12).

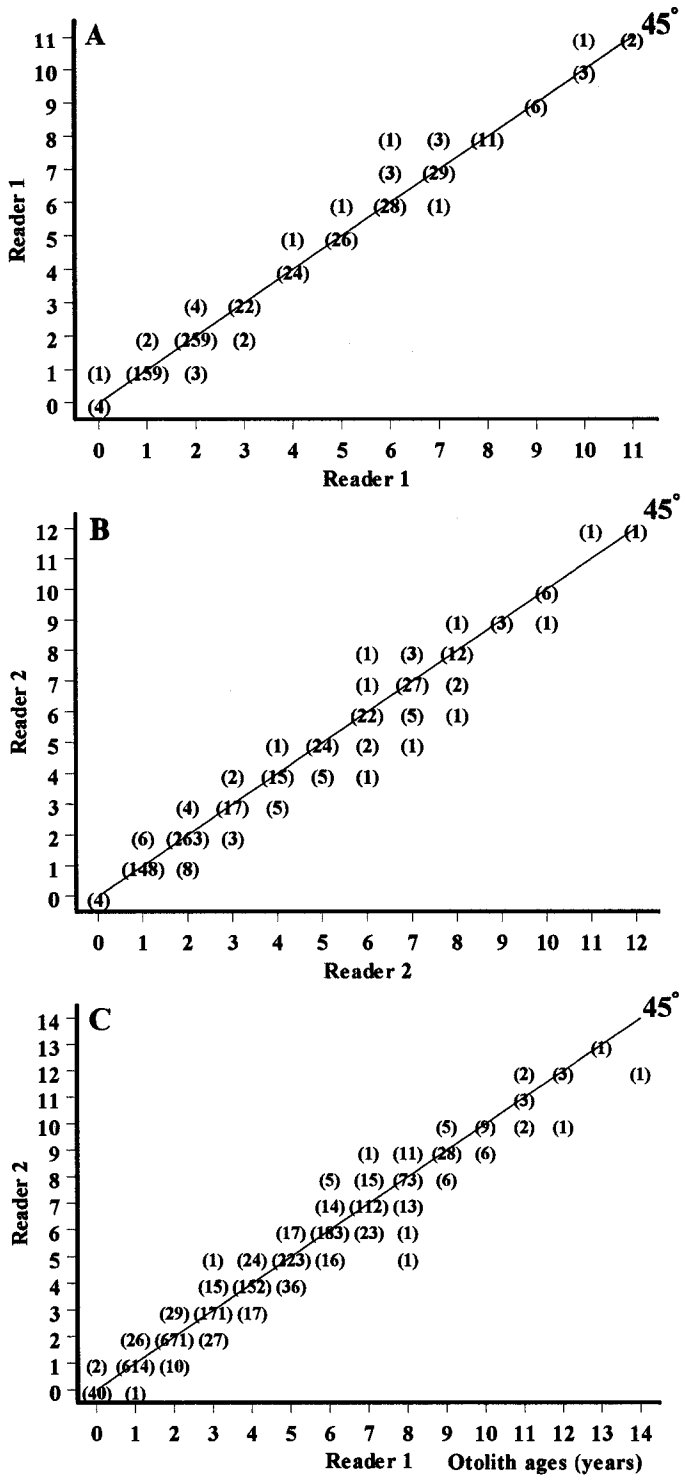

Figure 2.6

Agreement plots for pair wise comparisons between replicate annulus counts for sectioned otoliths of bluefish along the East Coast. (A) within reader 1, (B) within reader 2, (C) between reader 1 and reader 2. The 45^0 line represents 100% agreement. Numbers of observations are indicated in each parenthesis.

Within-reader agreements for scale age readings (n = 115) were lower than those for sectioned otoliths with reader 1 = 80.8% and reader 2 = 60.8% and 95.6% accounting for disagreements of +/- 1 year (Figure 2.7). The measurement of reader self-precision was higher for reader 1 (reader 1's CV = 3.92%) than for reader 2 (reader 2's CV = 12.78%). Between-reader agreements for scale age readings were 64% overall and 92% for disagreements that were within a year (Figure 2.7). The average between-reader coefficient of variation was 10.8%. There was no evidence of systematic disagreement between reader 1 and reader 2 at the $\alpha = 0.05$ level (test of symmetry, $\chi^2 = 24.9$, df = 17, P = 0.09).

2.3.4. Bias between scale and otolith ages

Counts based on aging by scales did not agree well with sectioned otolith counts. Scales ages (n = 110) showed 34% overall agreement with sectioned otoliths and 66% of the disagreements were within 1 year (Figure 2.8). Overall the C.V. between scale and otolith ages was 18.1%. The linear regression t-test rejected the null hypothesis that $\beta = 1$ ($P < 0.05$), thus implying significant differences in presumed age count between scales and sectioned otoliths. Scales generally over aged age-1 through age-5, and under aged age-7 plus when compared to sectioned otoliths (Figure 2.8). The test of symmetry ($\chi^2 = 34.08$, df = 33, P = 0.41), however, failed to reject the null hypothesis that there is no systematic difference in counts between structures.

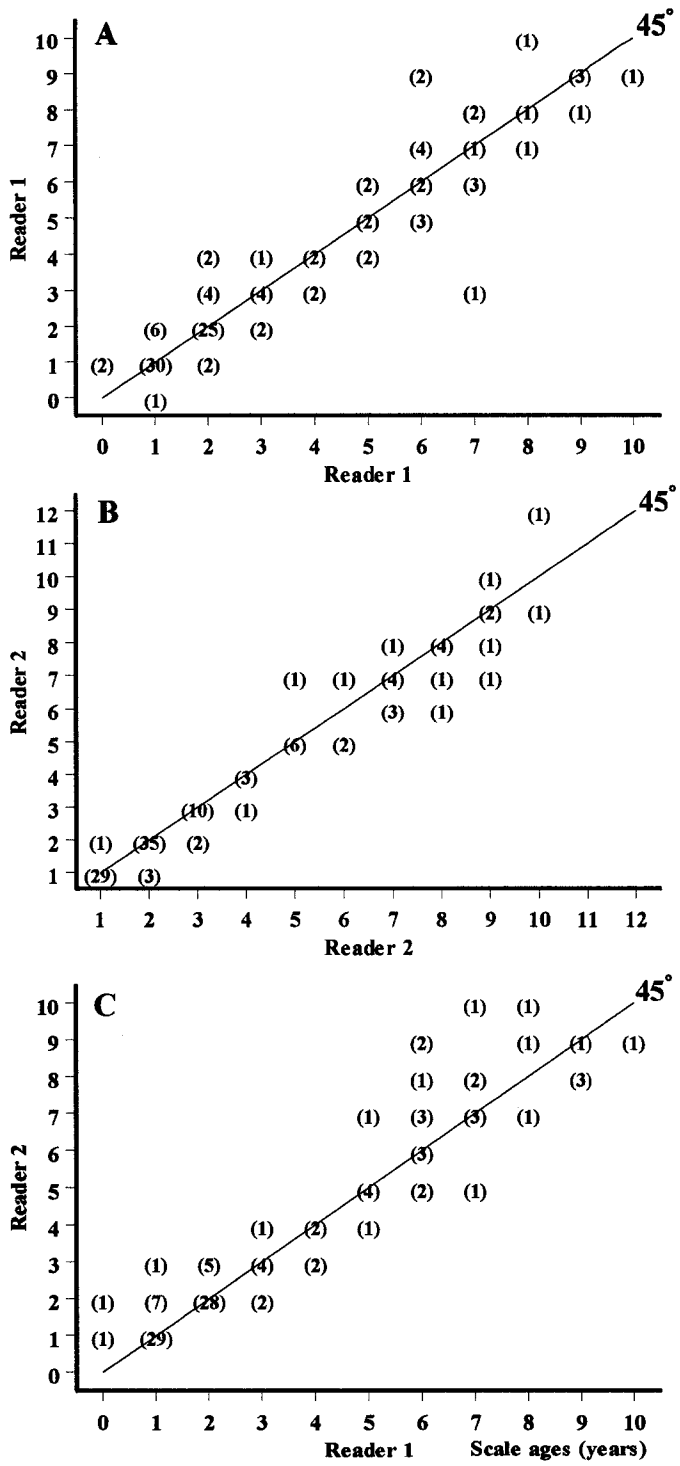

Figure 2.7

Agreement plots for pair wise comparisons between replicate annulus counts for scale impressions of bluefish along the East Coast. (A) within reader 1, (B) within reader 2, (C) between reader 1 and reader 2. The 45^0 line represents 100% agreement. Numbers of observations are indicated in each parenthesis.

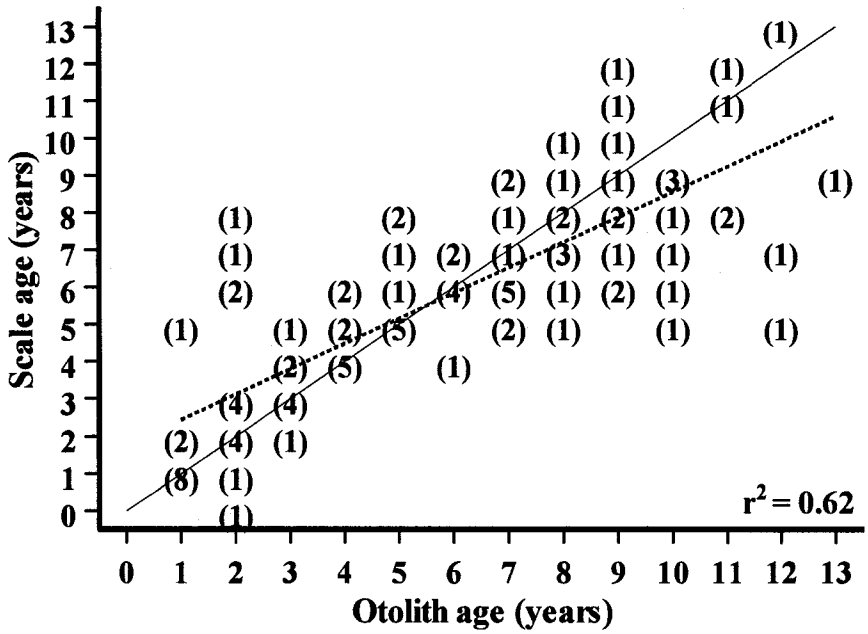

Figure 2.8
Plot of scale impressions estimated age versus sectioned otolith estimated age. The dashed line represents the best fit (OLS) between the two methods. The solid line reflects the 1:1 slope and perfect agreement. Numbers of observations are indicated in each parenthesis.

2.3.5. Age, Catch, and Gear Interactions

As expected, I found significant differences in the length frequency distributions between gears, fishing sectors, and across areas during this study (Figure 2.9). Much of this variability can be attributed to the types of gear interacting with the spatial distribution of fish rather than an absence of fish of a particular size class. For example, in almost all months, the size frequency of bluefish collected in Virginia commercial gears was heavily skewed to smaller (mean = 401.01 FL, SD = 135.42, n = 1314) and younger fish (mean age = 2, SD = 1.66, n = 1314). In contrast, bluefish collected using charter boats immediately offshore of the Chesapeake Bay, were larger (mean = 660.31 FL, SD = 109.64, n = 194) and older fish (mean age = 5.47, SD = 2.15, n

= 194) and note that they were simply not available to the commercial fishery. In contrast, the commercial fishery off North Carolina, which is dominated by ocean gill netting, collected substantially larger (mean = 595.6 FL, SD = 142.1, n = 515) and older fish (mean age = 4.63, SD = 2.15, n = 515) than the commercial fishery in Virginia (Figure 2.9, Figure 2.10). As a result, the distribution of sizes among my sample was bimodal, suggesting it is an artifact of sampling (Figure 2.11). Even so, as bluefish is a unit stock and because it is highly migratory in like-sized groups, samples from one region or fishing sector are not expected to represent the entire size or age range of this species. Nonetheless, as growth analysis does not rely on sampling the population proportionally, it was appropriate to pool fish for growth analysis given the extensive temporal and spatial collections.

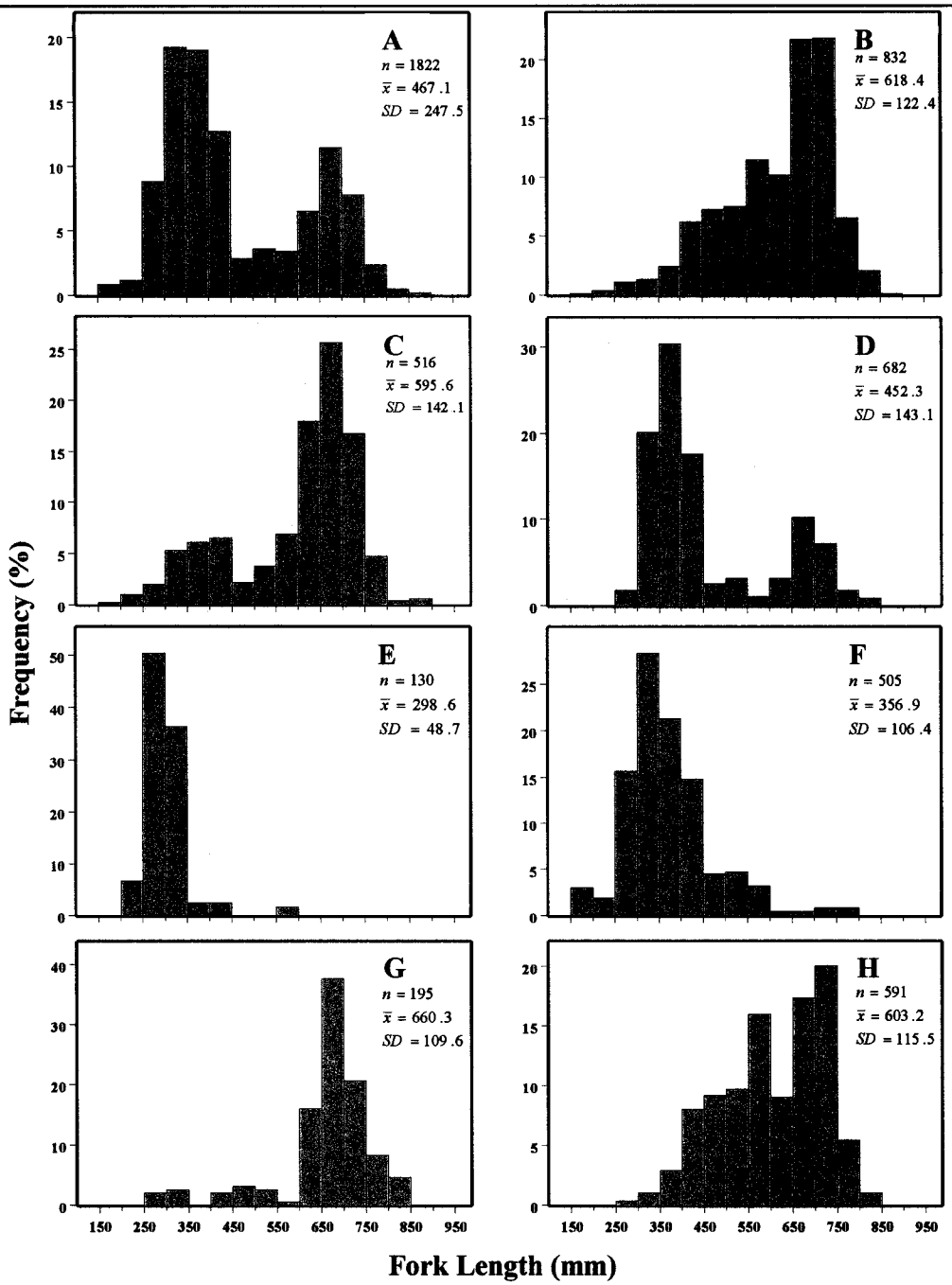

Figure 2.9

Fork-length frequency distribution of bluefish collected between 2001 and 2003. (A) Commercial gear (pound net, gill net, haul seine) from Virginia and North Carolina; (B) from recreational sector (New York: party boats, New Jersey/Virginia: charter boats); (C) gill nets in North Carolina; (D) gill nets in Virginia; (E) haul seine in Virginia; (F) pound net in Virginia; (G) charter boats in Virginia; (H) party boats in New York/New Jersey. Note different scales on the Y axis.

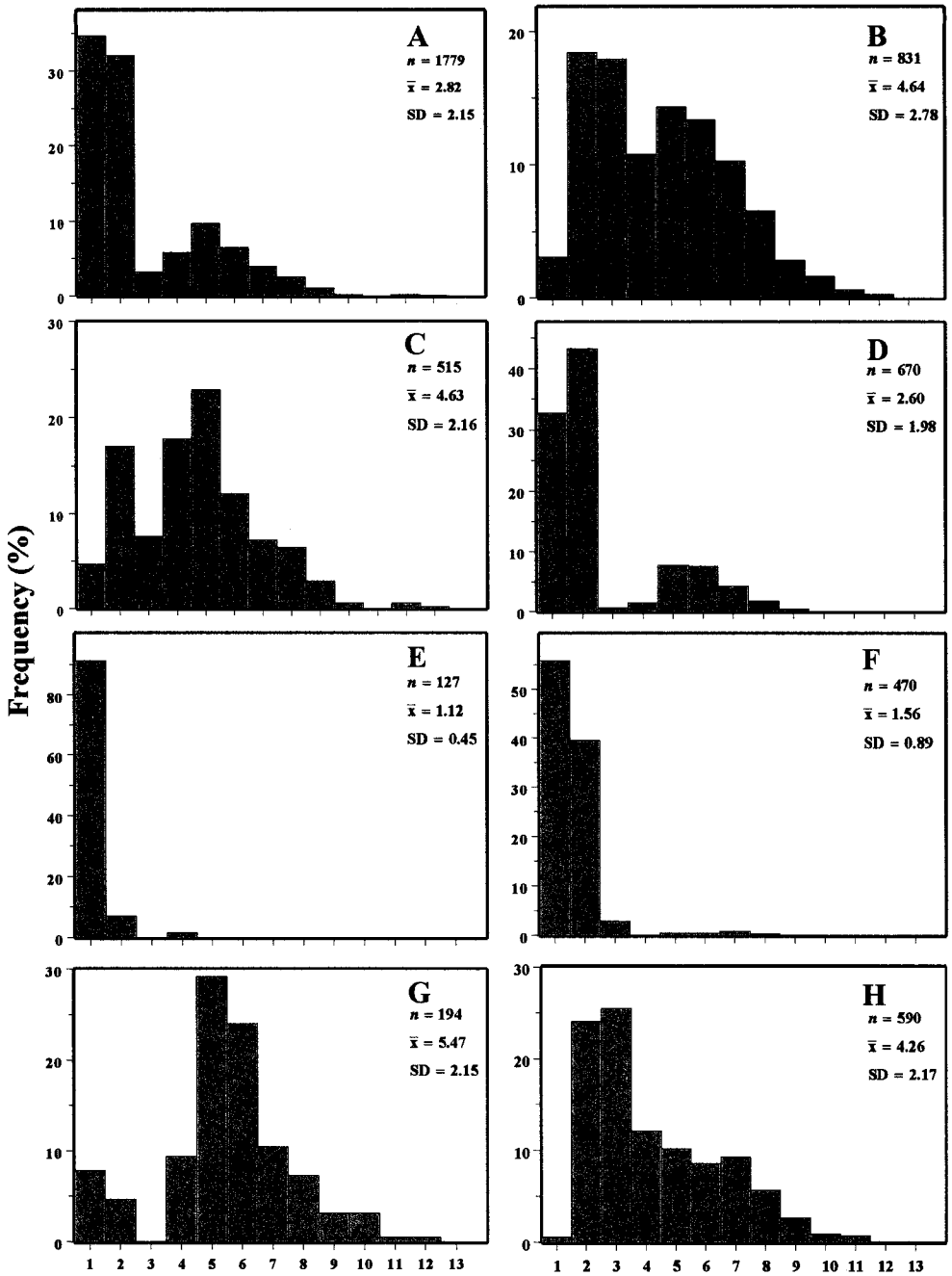

Figure 2.10

Age-frequency distribution of bluefish collected between 2001 and 2003. (A) Commercial gear (pound net, gill net, haul seine) from Virginia and North Carolina; (B) from the recreational sector (New York: party boats, New Jersey/Virginia: charter boats); (C) gill nets in North Carolina; (D) gill nets in Virginia; (E) haul seine in Virginia; (F) pound net in Virginia; (G) charter boats in Virginia; (H) party boats in New York/New Jersey. Note different scales on the Y axis.

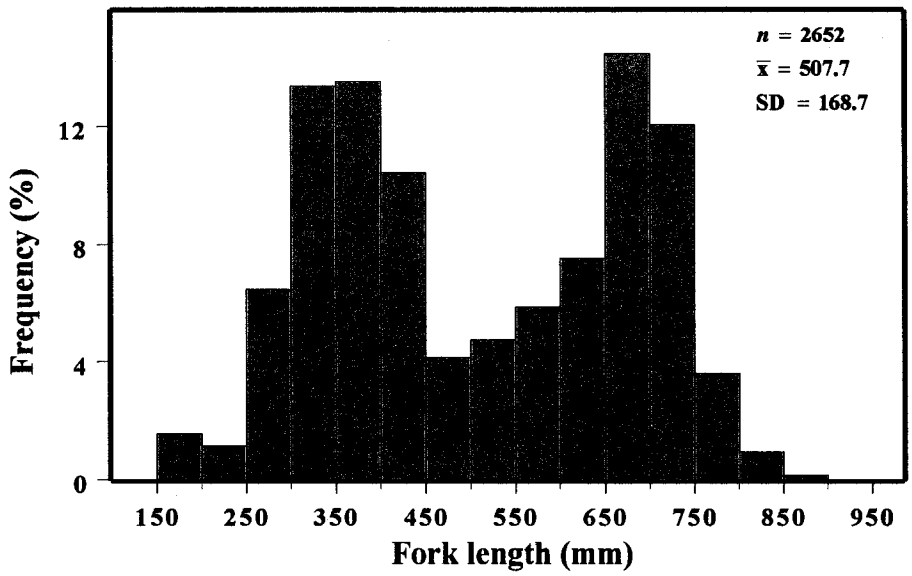

Figure 2.11
Length-frequency histogram (n = 2652) of bluefish from the East Coast of United States. Specimens were collected from recreational and commercial fisheries from 2001 to 2003.

2.3.6. Growth Parameters:

Bluefish grew rapidly until the age of 5-7 years after which the growth slowed considerably (Figure 2.12). Comparisons between the von Bertalanffy curves demonstrated that the null model, which assumed common growth coefficients for females and males, was not significantly different (χ^2 = 1.55, df = 3, P>0.6) than models with separate parameters by sex. Therefore, both males and females were pooled and their growth coefficients compared by year and location using the likelihood-ratio tests (Table 2.2 and Table 2.3). The growth curves of pooled sexes were not significantly different by year and by location (Table 2.2 and Table 2.3), and were combined. The estimated growth parameters were L_{inf}= 815.3mm ±15.30, k = 0.31 ± 0.03, t_0 = -0.30 ± 0.18 (r^2 = 0.927) (Figure 2.12).

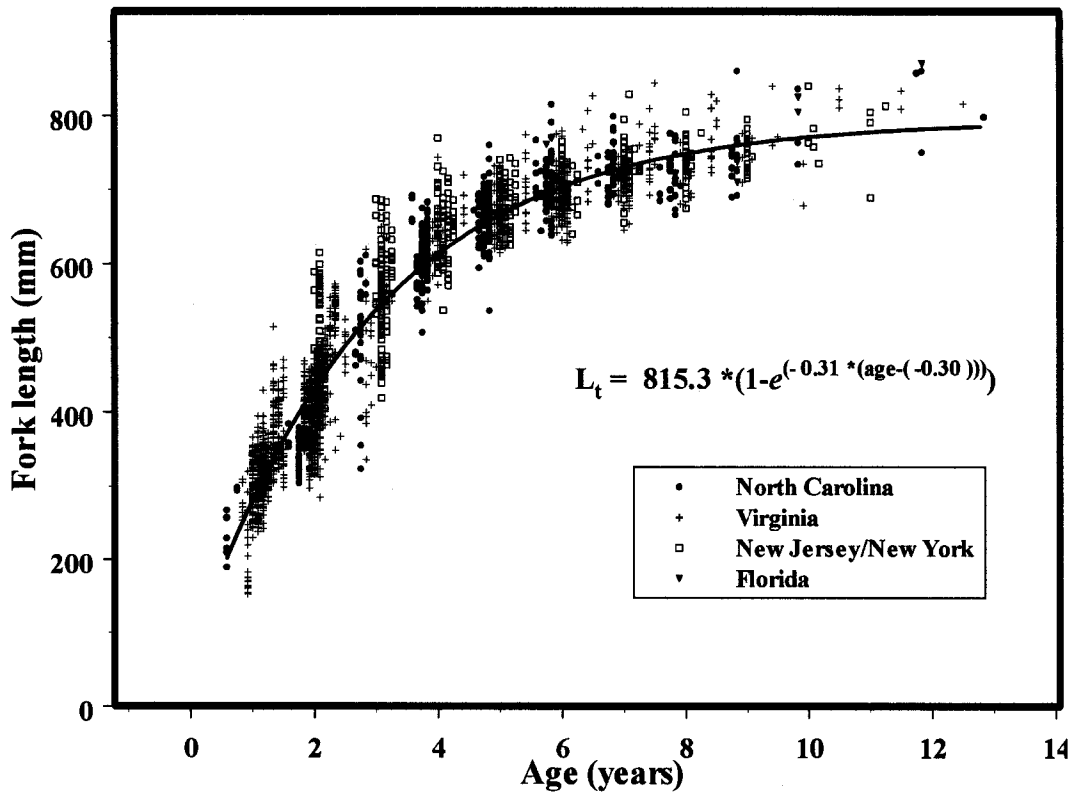

Figure 2.12
Observed fork length at age and fitted von Bertalanffy model for bluefish collected along the East Coast of the United States from 2001 to 2003. Sexes are combined.

2.4. Discussion

This study demonstrates that sectioned otoliths can be used to estimate bluefish ages accurately and precisely over 99% of the exploited age classes. With the marginal increment analysis on sectioned otoliths, bluefish age 1 to 8 were validated for accuracy. Furthermore, with the thin-section and bake method I reached high reproducibility of otolith age estimates.

I was able to validate bluefish age estimates through marginal increment analysis through age eight. My results concur with previous studies that show annulus formation

to occur between April and mid June (Barger, 1990; Terceiro and Ross, 1993). Fish 3 through 5 years old, however, showed a temporal shift in annulus formation. For those ages, annulus formation began during June and July and lasted until September. I cannot explain this shift in annulus formation, except that it could not be attributed to any artifact in sampling, because these ages were taken in a variety of gears throughout the sampling season. Despite the temporal shift, there was only one trough per year validating the annual periodicity of annulus formation.

Bluefish otoliths are more difficult to use than otoliths of many other species because their otoliths are thin and fragile and the annuli become less defined with increasing age. Nevertheless, with the thin-section and bake technique, there was good within-reader agreement with both readers capable of exactly reproducing their age estimates in over 90% of the samples. Between-reader overall agreement of age estimates using sectioned otoliths clearly demonstrated that with the thin section and bake method and proper training, sectioned otoliths are readily interpreted. Furthermore, the between-reader agreement showed no evidence of systematic disagreement and the average coefficient of variation was low. Not only are these results an improvement over the previous study that validated annuli only to age 4 (Sipe and Chittenden, 2002) in that otoliths were validated to age eight, but more importantly, precision for older fish was also improved.

Table 2.2
The estimated growth curves using mean fork length of bluefish along the East Coast of the United States with standard error in parentheses.

Comparison	n	L_{inf}	K	T_o
Sex				
Male	1073	823.4 (16.7)	0.270 (0.02)	-0.830 (0.23)
Female	1421	818.7 (14.1)	0.297 (0.02)	-0.644 (0.22)
Both sexes combined	2494	820.8 (10.3)	0.283 (0.01)	-0.735 (0.15)
Year				
2001	488	823.3 (17.0)	0.338 (0.04)	-0.367 (0.22)
2002	1086	808.8 (27.7)	0.291 (0.05)	-0.680 (0.39)
2003	975	815.9 (12.7)	0.291 (0.02)	-0.735 (0.20)
All years combined	2549	814.6 (11.2)	0.309 (0.02)	-0.572 (0.16)
Location				
SAB	464	821.1 (20.0)	0.308 (0.03)	-0.062 (0.20)
MAB	2090	808.6 (14.4)	0.316 (0.03)	-0.548 (0.20)
Locations combined	2554	815.3 (15.3)	0.311 (0.03)	-0.301 (0.18)

In contrast to otoliths, scale marks were often difficult to interpret due to false marks, crowding on the edge and frequent regenerated scales. The same difficulties were found using scales to age bluefish in previous studies (Lassiter, 1962; Richards, 1976; Sipe and Chittenden, 2002). As a result, both within and between reader agreements were lower when compared to sectioned otoliths. Within-reader agreement using scales averaged 70%, which is very similar to the 67% reported by Sipe and Chittenden (2002).

Table 2.3
Summary of maximum likelihood tests of differences between sexes, location, and years for mean fork length-at-age data fitted to the von Bertalanffy growth model for bluefish collected between 2001 and 2003.

Comparison	Sample Sizes	$\chi 2$	df	*P*
Sex				
Male vs. Female	1073 and 1421	1.55	3	0.67
Location				
SAB vs MAB	444 and 2090	14.68	3	0.06
Year				
2001 vs 2002	490 and 1088	6.78	3	0.07
2001 vs 2003	490 and 976	7.13	3	0.067
2002 vs 2003	1088 and 976	0.92	3	0.81

My between-reader agreement of 64% is very similar to the 67 % and 62% reported by Barger (1990) and Sipe and Chittenden (2002), respectively. My results are lower than the 97% agreement using scales reported by Salerno et al. (2001). Their data set, however, was limited to younger fish with very few fish over 30 inches. My between-reader agreement did increase to 80% with fish < 5 years old. These results demonstrate that although reasonable precision can be achieved using scales from younger bluefish, precision of age estimates decreases considerably for older bluefish.

Because bluefish travel in large, loosely aggregated groups of like-sized fish, I found that gear interactions in different areas have an effect on the overall size and age distribution of my samples. Bluefish are easier to sample using the commercial fishery, but its gears do not capture the complete size and age range in any location. Recreational gears target older and larger fish but are also not representative of the bluefish population. This gear interaction resulted in bimodality in size and age frequencies of my samples. This bimodality in age frequencies has been reported in previous studies and has

been a concern in bluefish stock assessment, especially when using integrated catch-at-age analysis (Wilson and Degnbol, 2002). Therefore a variety of gears and locations along the East Coast should be sampled to adequately represent the size composition of the bluefish population. This does not hinder analysis of catch-at-age statistics, but it adds complexity to population studies.

Growth rates between sexes agree with previous studies (Lassiter, 1962; Richards, 1976; Barger, 1990; Salerno et al., 2001), and there were no statistical differences between years and areas. Statistical results show equal growth parameters between the South Atlantic and Middle Atlantic Bights, thus providing little evidence for strong environmental signals to confound growth in animals that may remain resident in the South Atlantic Bight, or those which migrate north during summer. While this study was the first to represent bluefish size composition and otolith-based age along the U.S. East Coast, proportion at age of the population needs to be ascertained using fisheries independent sampling.

Finally, this study clearly shows I have surmounted the bluefish age determination problems. Using bluefish sectioned otoliths will produce accurate and precise age estimates needed in modeling population age structure and estimating rates of population growth, but have also shown the complexity of sampling bluefish along the East Coast of the U.S. I was able to collect age and growth data that is not spatially restricted with all bluefish size and age range represented which was not previously available.

CHAPTER III

REPRODUCTIVE BIOLOGY OF BLUEFISH (*POMATOMUS SALTATRIX*) ALONG THE EAST COAST OF THE UNITED STATES

3.1. Introduction

Estimates of the fecundity of bluefish (*Pomatomus saltatrix*) along the U.S. Atlantic coast are almost entirely lacking, and the only published estimates are based on the work of Lassiter (1962) who made direct observations on 10 female gonads. He found that fecundity of 2 to 3 year old bluefish sampled from the coast of North Carolina ranged between 0.6 and 1.4 million eggs, but did not indicate whether bluefish were batch or total spawners. This value has since been used to define reproductive capacity of bluefish (MAFMC, 1998). However, Hunter et al. (1985) demonstrated that most marine pelagic fish are batch spawners, and the low gonadosomatic index (GSI) described for bluefish (Chiarella and Conover, 1990) are typical of batch spawning. If so, then bluefish fecundity based on Lassiter's (1962) estimates may be underestimated, potentially underestimating bluefish productivity. Both, Conand (1975) and Haimovici and Krug (1996) showed that bluefish in Africa and Brazil were batch spawners, further suggesting that current views about East Coast bluefish reproduction need revision. Fortunately, techniques for the estimation of fecundity are well developed (Luna, 1968; Hunter et al., 1985; Hunter and Macewicz, 1985; Hunter et al., 1992; West, 1990; Wells, 1994) and, coupled with appropriate age information, provide the basis for the estimation of baseline information on the reproductive strategy of bluefish along the East Coast. Such information will be critical to assess the potential effects of over-fishing on recruitment,

and to formulate likely management actions that could increase reproductive success (Sissenwine and Shepherd, 1987; Mace and Sissenwine, 1993; Barbieri et al., 1994; Lowerre-Barbieri, 1996).

Because direct observations of bluefish gonads have been limited, scientists have looked at distribution of larvae to infer spawning locations and times. Using these studies as a proxy for bluefish spawning pattern, the annual recruitment pattern in the Middle Atlantic Bight (MAB) is bimodal based on a wave of juvenile recruits arriving in the spring followed by local production in the MAB producing the second wave during summer. There are two competing hypotheses that have attempted to explain this recruitment bimodality without directly observing the gonad development. Hare and Cowen (1993) hypothesized that the bimodality in recruitment in the MAB resulted from physical oceanographic processes interacting with continual spawning during the northward spawning migration. The model theorizes that, as fish spawn in the South Atlantic Bight (SAB) on the continental shelf during early spring, the larvae are transported north by the Gulf Stream and variability in its transport and cross shelf processes determine the recruitment of fish to the MAB. The model predicts that with continuous spawning, bimodality in recruitment can result from physical oceanographic processes, and local production (Hare and Cowen, 1996).

The second and more commonly accepted hypothesis suggests two distinct spawning episodes: the first occurring in the SAB in the spring and the second in the summer in the MAB with a hiatus in spawning during the migration north. Three pieces of information support this hypothesis: 1) egg and larval distributions along the East Coast (Kendall and Walford, 1979); 2) back-calculated hatch dates in MAB, off Long

Island (McBride and Conover, 1991); and 3) summer gonadosomatic index (GSI) from animals collected off Long Island only (Chiarella and Conover, 1990). Kendall and Walford (1979), found two distinct groupings of larvae, which they concluded were formed by two main spawning events. Chiarella and Conover (1990) provided further support for discrete spawning episodes as fish they collected in New York had low gonadosomatic indices in June. These low indices were followed by an increase that reached a peak in mid-July, and coincided with the presence of larvae in the MAB. Therefore, they concluded the low indices were due to a cessation of spawning from the SAB to the MAB and that fish spawning off New York in late June, July, and August were part of the second spawning event. To appropriately test which of these two hypotheses best reflects oocyte production, it would be necessary to directly sample gonads from the adult population over its entire range concurrently.

In this study, I describe the reproductive strategy of bluefish along the U.S. East Coast by directly sampling gonads using trends in gonadosomatic index (GSI), histology, and oocyte-diameter frequencies. Estimates of age-specific batch fecundity and sexual maturity are also calculated. Finally, I document changes in the reproductive state of female bluefish during migration and the spawning season and use these to evaluate the hypotheses of continuous spawning versus two discrete spawning episodes.

3.2. Methods

3.2.1 Field sampling

A total of 2652 bluefish were collected between April 2001 and August 2003 across states, and fishing (commercial, recreational) sectors, using various gears (Figure

3.1; Table 3.1). Broad sampling is necessary due to the migration of bluefish and because bluefish may spawn offshore from the mid-shelf to the continental slope of the Atlantic U.S. coast (Chiarella and Conover, 1990; Smith et al., 1994).

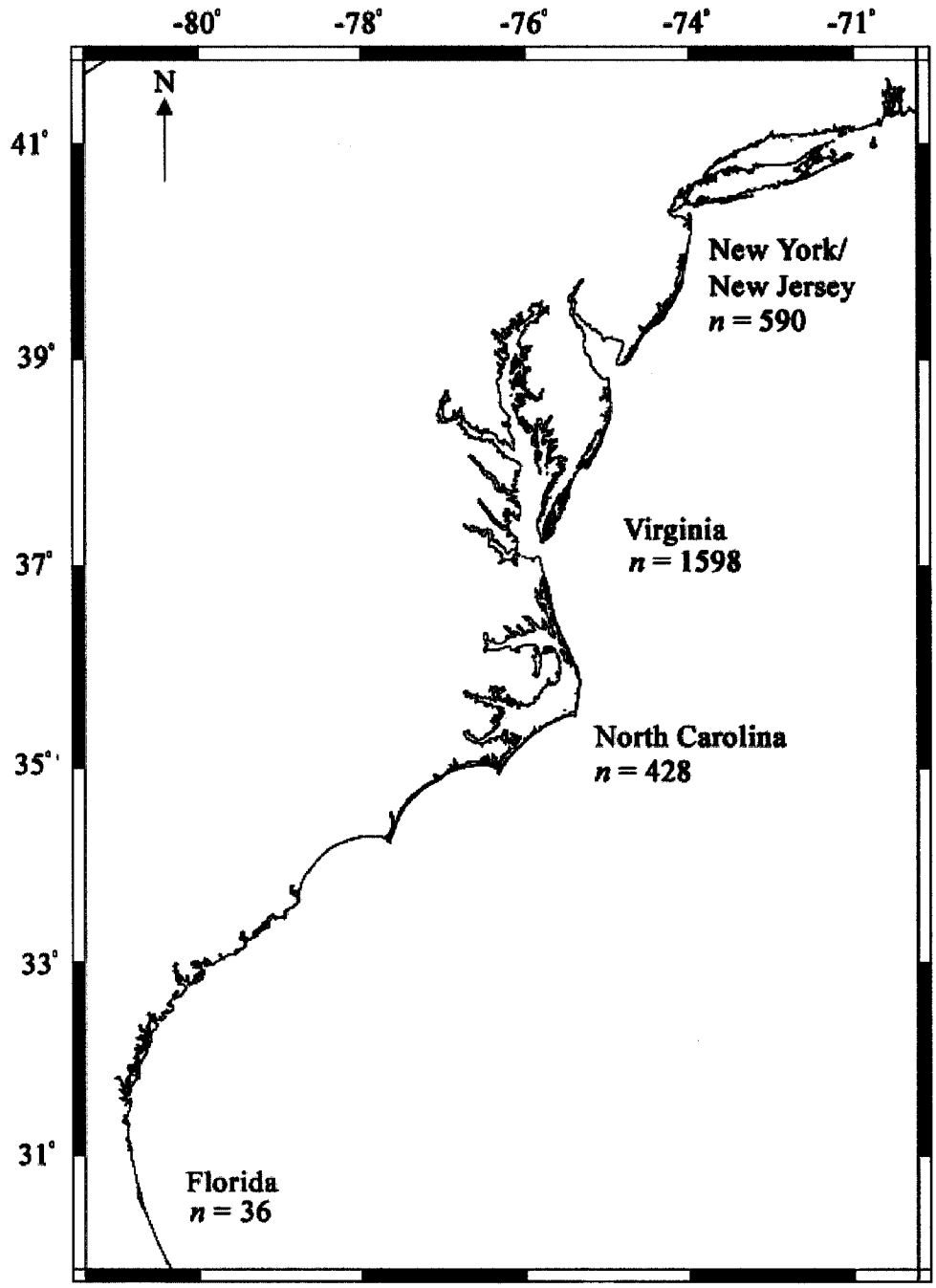

Figure 3.1
Map of the locations and numbers of bluefish collected from 2001 to 2003.

Because there are few directed fisheries, commercial or recreational, I used multiple sampling schemes to target bluefish over space and time. I sampled commercial fisheries in Florida, North Carolina and Virginia. However, only two locations of the directed bluefish fisheries, the commercial gill net fishery in North Carolina and the recreational head boat charter fishery in New York/New Jersey, occurred in known bluefish spawning habitat. Historical commercial landings data from North Carolina indicate that the commercial fishery operates from January through May (NMFS, 2005[2]). Therefore in North Carolina, I sampled the commercial fish catch bi-weekly from January until bluefish were no longer targeted and landed by the fishery (usually by April). In general, I purchased between 3 and 4 boxes of large bluefish (50 lbs. box^{-1}) bi-weekly. For the head boat fishery in New York, sampling commenced the first week of June and proceeded weekly to bi-weekly until the end of September when GSI values declined. I supplemented my sampling of specimens from New York and New Jersey collections by sampling fish from a variety of bluefish tournaments in June and July. In Virginia, bluefish were sampled year round as part of the ongoing Virginia Marine Resource Commission's (VMRC) Stock Assessment Program. The commercial samples, however, only represented smaller fish principally captured by fixed pound nets and gill nets located within the Chesapeake Bay. Consequently, since there was no directed fishery for offshore bluefish, I sampled bi-weekly using private charter boat trips from May until August. Colleagues at the Fish and Wildlife Research Institute conducted sampling of the commercial and recreational fishery along the east coast of Florida from January through August.

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[2] Pers. Comm. National Marine Fisheries Service, Fisheries Statistics Division, Silver Spring, MD.

Table 3.1

Sample size (*n*), fork length range, and sub-sample of bluefish females analyzed using histology collected by year and by state. Periods of no sampling effort are categorize as N/S. Periods with sampling effort with no samples collected are left as blanks.

Location	Period	2001			2002			2003		
		n ♀+♂	Fork length range (mm)	# of ♀ histology	*n* ♀+♂	Fork length range (mm)	# of ♀ histology	*n* ♀+♂	Fork length range (mm)	# of ♀ histology
New York	Jan-April	N/S	N/S	N/S						
	May-August	74	395-829	43	180	381-805	93	298	275-840	114
	Sept-Dec				38	474-813	8			
Virginia	Jan-April	63	365-762	0	95	254-731	1	12	402-597	0
	May-August	249	230-780	6	391	153-776	41	393	160-770	68
	Sept-Dec	123	286-844	0	230	280-789	0	42	420-769	0
North Carolina	Jan-April	N/S	N/S	N/S	181	189-860	36	240	463-860	80
	May-August	N/S	N/S	N/S	7	669-725	2			
	Sept-Dec	N/S	N/S	N/S						
Florida	Jan-April	N/S	N/S	N/S	N/S	N/S	N/S	36	676-870	23
	May-August	N/S	N/S	N/S	N/S	N/S	N/S			
	Sept-Dec	N/S	N/S	N/S	N/S	N/S	N/S			
Total Specimens		509			1122			1021		2652

3.2.2. General Biological data

All specimens were measured for total length (TL, mm), standard length (SL, mm), fork length (FL, mm), total weight (TW, g), gonad (ovary) weight (GW, nearest 1g) and somatic weight (TW-GW, g). Ovaries and testes were assigned a gross maturity stage based on macroscopic appearance (Table 3.2) and ovaries were preserved in 10% buffered formalin. Sagittal otoliths were removed and stored dry for age determination. All statistical analyses were performed using S-PLUS® (version 6.1).

3.2.3. Development of otolith ageing technique

Ageing methodology followed the "thin-section and bake" technique. Briefly, the otolith section was placed into a ceramic "Coors" spot plate well and baked in a Thermolyne 1400 furnace at 400°C. Baking time was dependent on otolith size and gauged by color, with a light caramel color desired. The baked thin-section was placed on a labeled glass slide and covered with a thin layer of Flo-texx® mounting medium. Otoliths were examined using a Leica MZ-12 dissecting microscope with transmitted light and dark-field polarization at between 8 and 20 times magnification. All samples were aged in chronological order by collection date, without knowledge of previously estimated ages or the specimen lengths. Two readers independently read the sectioned otoliths.

3.2.4. Gonadosomatic Index

I calculated the gonadosomatic index (GSI) for all mature females (stages 3-7) using the formula:

3.1) (GW/SW)*100

Where GW = gonad weight (g), and SW = somatic weight (g) and is expressed as a percentage of the total fish weight.

Table 3.2

Description of gonadal developmental stages for bluefish along the East Coast of U.S.

Stage	Macroscopic Description
1. Immature	Ovaries very small and translucent, look like ribbon
2. Developing	Ovaries ranging from small to medium, orange in color with no opaque oocytes present
3. Mature	Ovaries large, pale yellow in color, opaque oocytes can be detected, little ovarian vascularization with no signs of previous spawning
4. Gravid	Ovaries very large, clear hydrated oocytes visible among opaque oocytes, giving a speckled appearance
5. Spawning	Ovaries large, clear oocytes have been ovulated and are visible as a collective strip amongst yolked oocytes
6. Spent	Ovaries quite flacid and small, mustard to orange in color, may contain clear fluid
7. Recovering	Ovaries very small, dark orange to marron in color, no opaque oocytes present, membrane thicker than immature fish

Stage	Microscopic Description
1. Immature	Few oocytes with primary growth, oogonia predominate, no atresia present
2. Developing	Early vitellogenesis: oogonia, primary oocytes, cortical alveoli and a few partially yolked oocytes present
3. Mature	Late vitellogenesis: oogonia, primary oocytes to oocytes with yolk vesicle and yolk globules present
4. Gravid	Final oocyte maturation (FOM): primary oocytes to oocytes with yolk vesicle and yolk globules present with nucleus migration
5. Spawning	Hydrated: primary oocytes to oocytes with nucleus migration, hydrated oocytes present, postovulatory follicles (POF) may be present
6. Spent	Primary to cortical alveoli oocytes present, atretic partially and advanced yolked oocytes, degenerating POFs
7. Recovering	Similar to stage-1 with few oocytes with primary growth, oogonia predominate, but atresia present in this stage

3.2.5. Histological analysis of gonads

A sub-sample of 514 female ovaries was taken based on macroscopic examination (stage >2) for histological analysis from the central portion of one lobe of each gonad. Samples were embedded in paraffin, sectioned to 5-6 μm thickness and stained with Harris' hematoxylin and eosin Y. Seven stages of maturity (Table 3.2) and atresia stages were distinguished based on the histological criteria of Hunter and Macewicz (1985) and Lowerre-Barbieri et al. (1996). Presence of atresia was the key factor in determining if a fish had previously spawned and therefore classified as a recovering stage 7 instead of an immature stage 1.

To determine the most appropriate site in the ovary from which to take sub-samples to determine batch fecundity, the number of oocytes per gram was determined for 3 regions of ovaries of 30 fish. Samples of ovary were taken at anterior, middle and posterior parts of the ovary. There were no significant differences in number of advanced oocytes between each region (ANOVA, $F = 0.20$, df = 2, $p = 0.079$). Therefore, batch fecundity was estimated using the mean of three sub-samples taken from the anterior, middle and posterior of the ovary for 39 fish from New York and Virginia.

Two methods were used to calculate batch fecundity. For females with hydrated oocytes ($n = 4$), the hydrated oocyte method was used (Hunter et al., 1985). In this method, a sub-sample of the gonad was weighed to the nearest 0.1 mg and the number of hydrated oocytes was counted. An estimation of batch fecundity was calculated as the product of the hydrated oocyte density (hydrated count/subsample weight) times the weight of the gonads for both lobes. For females that were fully mature but not hydrated ($n = 35$), an oocyte size-frequency distribution method was used (Hunter et al., 1985;

MacGregor, 1957). With this method the most advance modal group of oocytes size classes is determined visually by constructing a size-frequency distribution of the oocytes from each fish. The total number of oocytes that constitute the most advanced mode was assumed to be the spawning batch. This method yields results similar to the hydrated method when highly advanced oocytes (> 0.45 mm) are used (Hunter and Goldberg, 1980; Laroche and Richardson, 1980). Exponential regression was used to determine the relationship between batch fecundity and total length and somatic weight.

3.2.6. Size and age at maturity

Size and age at maturity were estimated from 1040 females 170-975 mm TL and ages 0-12 years (including the 514 used for histological analysis). Females were considered mature if yolked oocytes were present, and gonads were visually in macroscopic stages 3 to 7 (Table 3.2). To prevent recovering fish from being classified as immature, only fish collected during the spawning period between March and August were used in the analysis. To predict the probability that a female bluefish was mature based on its TL and age, I estimated maturity-at-length and at-age using logistic regressions. Binary maturity observations (0 = immature, 1 = mature) and total length and age were fitted to logistic models using the function GLM, family = binomial in S-PLUS. The models used were

3.2) $$\pi(TL) = P(Y = 1 | TL) = \frac{e^{\beta 0 + \beta 1 * TL}}{1 + e^{\beta 0 + \beta 1 * TL}}$$

3.3) $$\pi(AGE) = P(Y = 1 | AGE) = \frac{e^{\beta 0 + \beta 1 * AGE}}{1 + e^{\beta 0 + \beta 1 * AGE}}$$

Where $P(Y = 1 | TL)$ = probability of female bluefish being mature at size TL;

$P(Y=1|AGE)$ = probability of female bluefish being mature at AGE; and β_0 and β_1 = regression coefficients for the intercept and length/age, respectively.

3.3. Results

3.3.1. General reproductive pattern

Oocyte development of bluefish collected along the East Coast was consistent with batch spawning. All stages of oocyte development were present in mature ovaries, indicating that bluefish have asynchronous oocyte development (Figure 3.2(A)). Examination of oocyte diameter distributions of whole oocyte samples revealed specific size ranges for each oocyte developmental stage. Primary growth oocytes were between 0.01 and 0.15 mm in diameter, while the cortical alveolar oil (lipid) globule stages ranged between >0.15-0.35 mm, and yolked oocytes ranged from 0.36 and 0.60 mm, while hydrated oocytes were greater than 0.7 mm in diameter. There was considerable overlap in oocyte diameter among stages, with no distinct modes except between yolked and hydrated oocytes, which were clearly separated (Figure 3.3), indicating that bluefish fecundity is indeterminate.

The presence of hydrated oocytes along with advanced yolked oocytes in individual ovaries indicates fish that recently spawned and are capable of continued spawning (Figure 3.4(A)). Similarly, ovaries containing post-ovulatory follicles (POFs) also contained advanced yolked oocytes (Figure 3.4(B)) an indicator for multiple batch spawning. Different patterns of atresia were found in bluefish ovaries depending on when they were collected in the spawning season. Early in the season, ovaries showed some

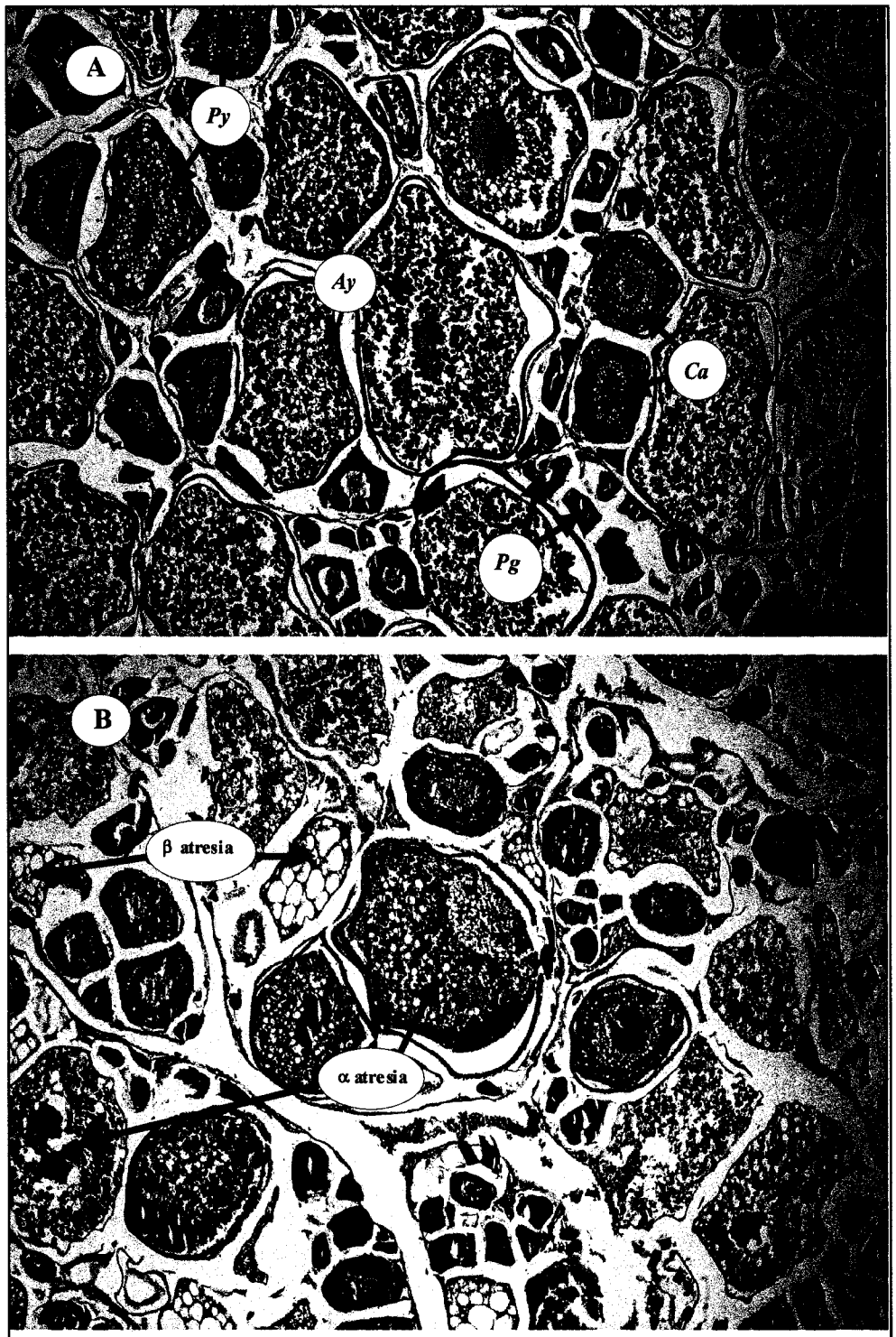

Figure 3.2
Histological sections of female bluefish gonads. (**A**) oocyte from a fully developed mature female with: primary growth (Pg), cortical alveoli (Ca), partially yolked (Py), and advanced yolked (Ay) oocytes. (**B**) oocytes from a fully spent ovary with α and β atresia.

early atresia (α-atresia) with surrounding healthy yolked oocytes. In this situation, the presence of many healthy oocytes along with the atretic oocytes did not signify complete resorption, as seen at the end of the spawning season. Later in the season, cessation of spawning was indicated by gonads containing healthy primary growth oocytes with all other oocytes being reabsorbed through the process of atresia (Figure 3.2 (B)), and was evidenced by α and β atresia (Hunter and Macewicz, 1985). In 2001 and 2002, α and β atresia occurred in late July, and were common by August, whereas in 2003, these types and amounts of atresia were mostly found at the end of August.

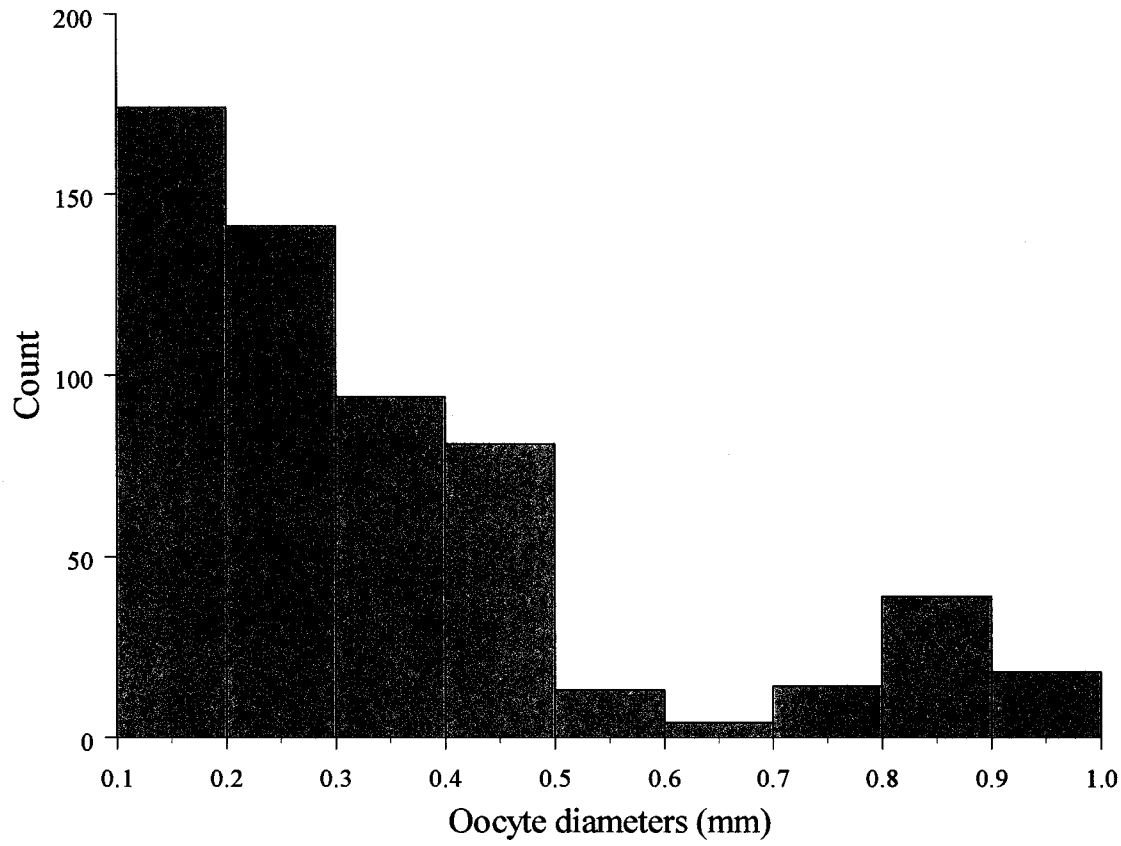

Figure 3.3
Frequency distribution of oocyte diameter measured from a 0.207 g sub-sample of the ovary of a hydrated female bluefish caught off New York coast at night.

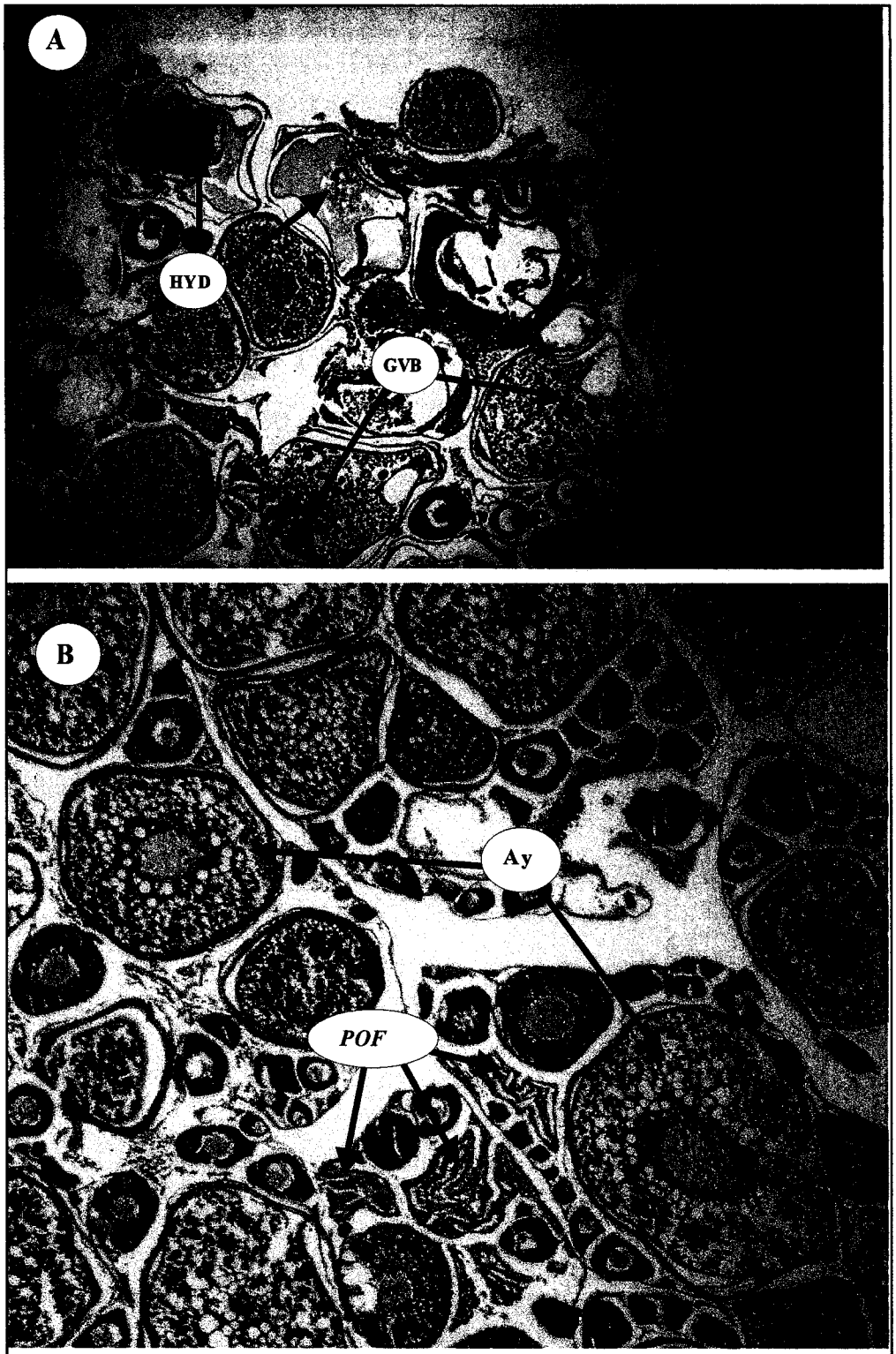

Figure 3.4
Histological sections of female bluefish. (**A**) oocytes from a hydrated female (HYD) with germinal vesicle breakdown (GVB). (**B**) fully mature female with advanced yolked (Ay) and postovulatory follicles (POF).

3.3.2. Spawning Pattern

3.3.2.1. By month:

Strong seasonal patterns in ovarian development were found that indicated spawning was continuous as bluefish migrated northward. Gonad development and commencement of spawning was asynchronous for bluefish, while cessation of spawning was synchronous. At the beginning of the season (January to March), some of the mature females that were analyzed histologically were still in recovery stages while others females were developing. Even in April to June, some females were in the recovering phases while others were spawning. At the end of the spawning season from late August to early September, all mature females collected were fully spent or recovering (Table 3.3).

Bluefish spawned from April through August over a broad region of the Atlantic coast, from North Carolina to New York. In all years, mean monthly GSI was low from January to March (GSI = 0.5 to 1), increased through April (GSI =1.5 to 2.2), and peaked between May and June (GSI = 1 to 4.5) before declining to pre-spawning levels by the end of August (Figure 3.5). Histological analysis of gonads supported this general conclusion based on the GSI. Although no ovaries in final maturation or hydration were found between January and March, most fish showed evidence of oocyte development, and as spring progressed all oocyte stages were found, including both recovering and spawning fish with POFs (Table 3.4). From May through August, most fish analyzed histologically were fully mature or spawning with oocytes in final maturation or hydrated. In 2002, however, histological evidence showed that by August, most fish were in spent stage with most remaining yolking oocytes atretic (Table 3.3).

Table 3.3

Percent maturity by state and by year of the number of mature females processed histologically (*n*). Reproductive phases consist of the following: Mature = vitellogenic oocytes, Spawning = final maturation and hydrated oocytes, Spent = primary to cortical alveoli with atretic yolked oocytes, Resting = primary oocytes with gamma or/and delta atretic oocytes.

Year		2001			2002							2003						
State	Stages	May	Jun	Jul	Mar	Apr	May	Jun	Jul	Aug	Sept	Feb	Mar	Apr	May	Jun	Jul	Aug
Florida	*n*												4	19				
	Mature												100%	63%				
	Spawning																	
	Spent													21%				
	Resting													16%				
North Carolina	*n*				13	23	2					7	33	40				
	Mature				46%	70%							36%	28%				
	Spawning													8%				
	Spent																	
	Resting				54%	30%	100%					100%	64%	64%				
Virginia	*n*	1	2	3		1	6	35							11	17	40	
	Mature	100%	50%			100%	33%	51%							36%	6%	30%	
	Spawning						50%	46%								88%	67%	
	Spent							3%										
	Resting		50%	100%			17%								64%	6%	3%	
NY/NJ	*n*		21	22				53	22	18	8					60	39	15
	Mature		10%	77%				64%	9%	6%						67%	41%	13%
	Spawning		90%	23%				21%								7%	59%	27%
	Spent							4%	77%	22%						7%		53%
	Resting							11%	14%	72%	100%					20%		7%
Total	*n*	1	23	25	13	24	8	88	22	18	8	7	37	59	11	77	79	15
	Mature	100%	13%	68%	46%	71%	25%	59%	9%	6%			43%	38%	36%	53%	35%	13%
	Spawning		83%	20%			38%	31%						6%		25%	64%	27%
	Spent							3%	77%	22%				7%		5%		53%
	Resting		4%	12%	54%	29%	37%	7%	14%	72%	100%	100%	57%	49%	64%	17%	1%	7%

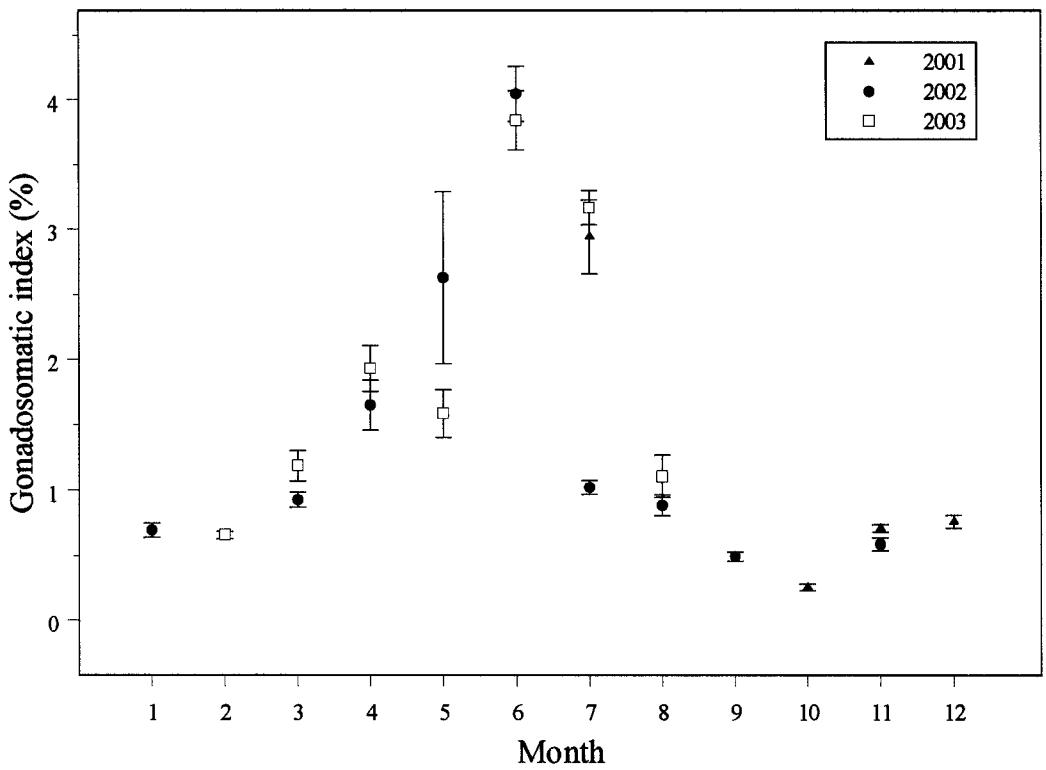

Figure 3.5
Mean monthly gonadosomatic index, +/- 1 Standard Error, and range of values for mature females bluefish collected along the East Coast of United States (*n* = 672).

3.3.2.2 By location:

Because of the migration of bluefish, the reproductive season was analyzed through space and time (Figure 3.6, Table 3.3). Fish collected in Florida between March and April of 2003 exhibited three distinct reproductive stages. Some of the fish were mature, with advanced vitellogenic oocytes while others were spent or recovering (GSI = 0.8 to 4.9). All fish showed evidence of atresia. During the same period of time, fish in North Carolina were in mature or recovering stages. In 2003, three female bluefish were found spawning in North Carolina in April as evidenced by the presence of POFs (Table

3.3). By May bluefish were captured in commercial fishing gear in Virginia and were reported at least as far north as New York (NMFS, 2003[3]). As bluefish migrated, their reproductive organs continued to develop with fewer fish being caught with gonads in recovering stages (Figure 3.7). In June, spawning occurred in Virginia and in New York with ovaries in final maturation and with presence of POFs. By July, spawning fish were common in New York and in Virginia. By August, spawning ceased (Table 3.3).

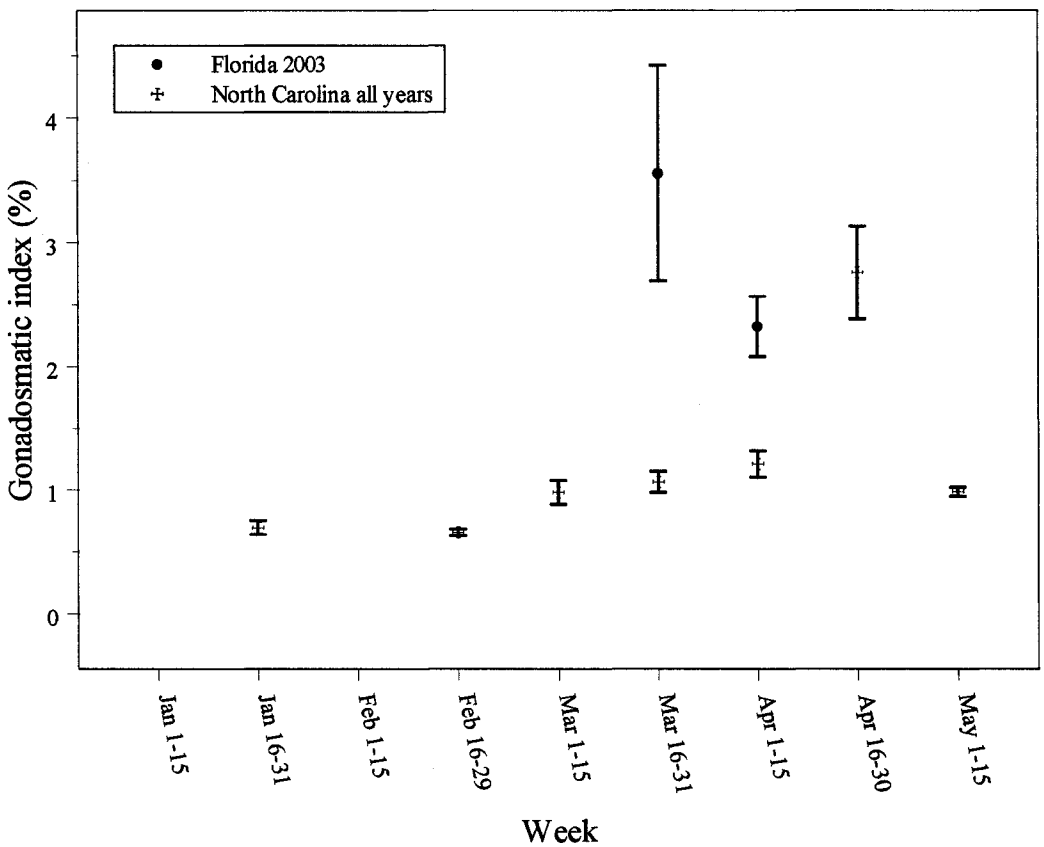

Figure 3.6
Mean bi-weekly gonadosomatic index, +/- 1 Standard Error, and range of values for mature females (n = 219) collected in Florida and North Carolina in 2002 and 2003.

[3] Pers. Comm. National Marine Fisheries Service, Fisheries Statistics Division, Silver Spring, MD.

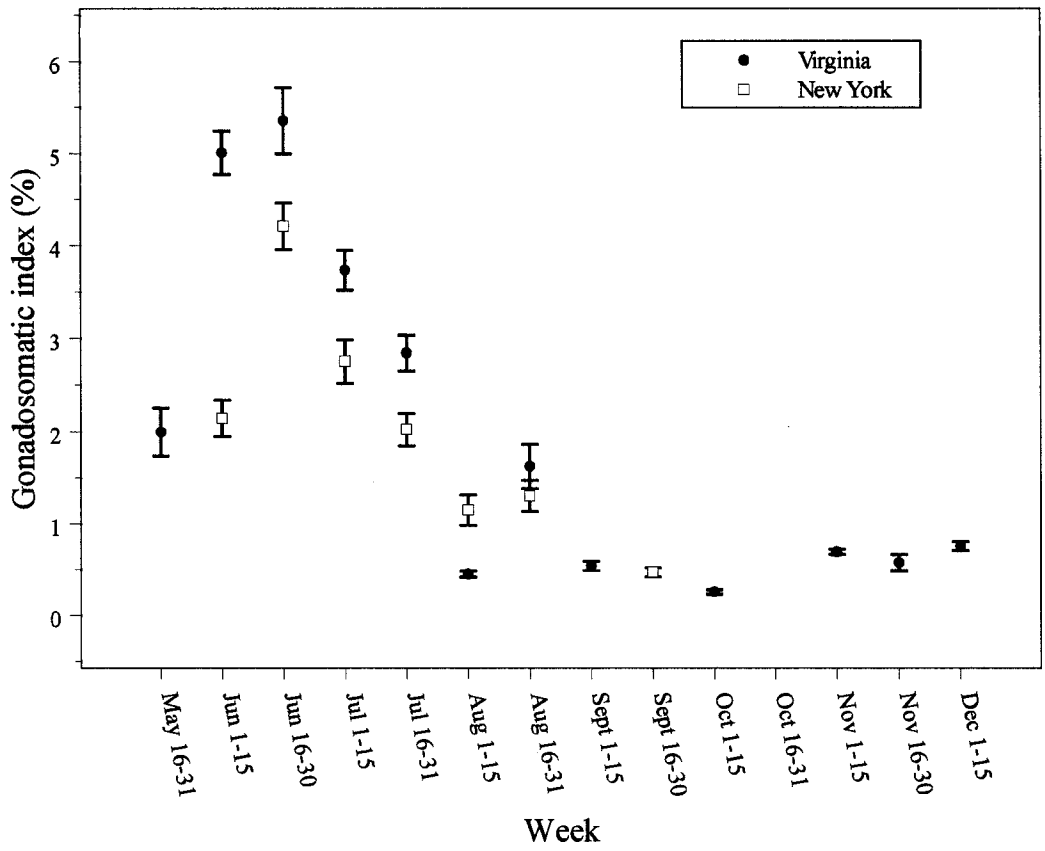

Figure 3.7
Mean bi-weekly gonadosomatic index, +/- 1 Standard Error, and range of values for mature female bluefish (n = 454) collected in Virginia and New York from 2001 to 2003.

3.3.3. Maturity

The mean age at 50% maturity estimated by logistic regression showed females matured at ~1.8 years (Figure 3.8), and that all fish were mature by age 5.

$$3.4) \qquad P(Y=1|AGE)=\frac{e^{-4.04+2.20*AGE}}{1+e^{-4.04+2.20*AGE}}$$

Histological examination confirmed that by age 2 bluefish were fully vitellogenic (stage 3) with advanced yolked oocytes suggesting they would spawn that year. No age 2

bluefish were collected however, in a gravid or spawning mode. The mean total length at 50% maturity (L_{50}) was 451 mm (Figure 3.9), and by 698 mm all fish were mature.

3.5) $$P(Y=1|TL)=\frac{e^{-7.44+0.016*TL}}{1+e^{-7.44+0.016*TL}}$$

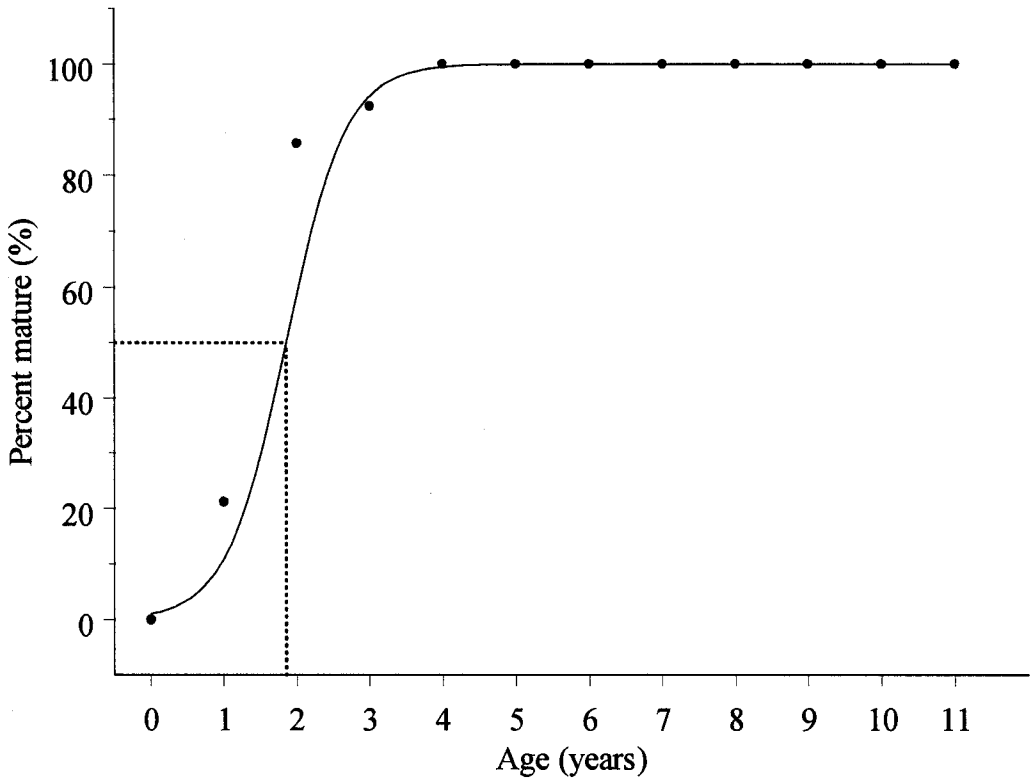

Figure 3.8

Logistic regression model for the estimated percent of sexually mature female bluefish as a function of age.

3.3.4. Fecundity

Batch fecundity of bluefish estimated using the hydrated oocyte method and the oocyte size-frequency gave similar results. Batch fecundity estimated using the hydrated oocyte method ranged from 232,279 oocytes for a 600 mm TL fish to 1,260,396 oocytes

for an 803 mm TL fish. The C.V. of batch fecundity using the hydrated oocyte method from three sub-samples of 4 specimens ranged from 1.2 to 9.04, with a mean of 4.4. Using the oocyte size-frequency method from three sub-samples of 26 specimens, batch fecundity ranged from 270,187 for a 725 mm TL female to 1,120,090 for a 745 mm TL fish. The CV's of estimates of batch fecundity using this method was 1 to 29, with a mean of 9.02.

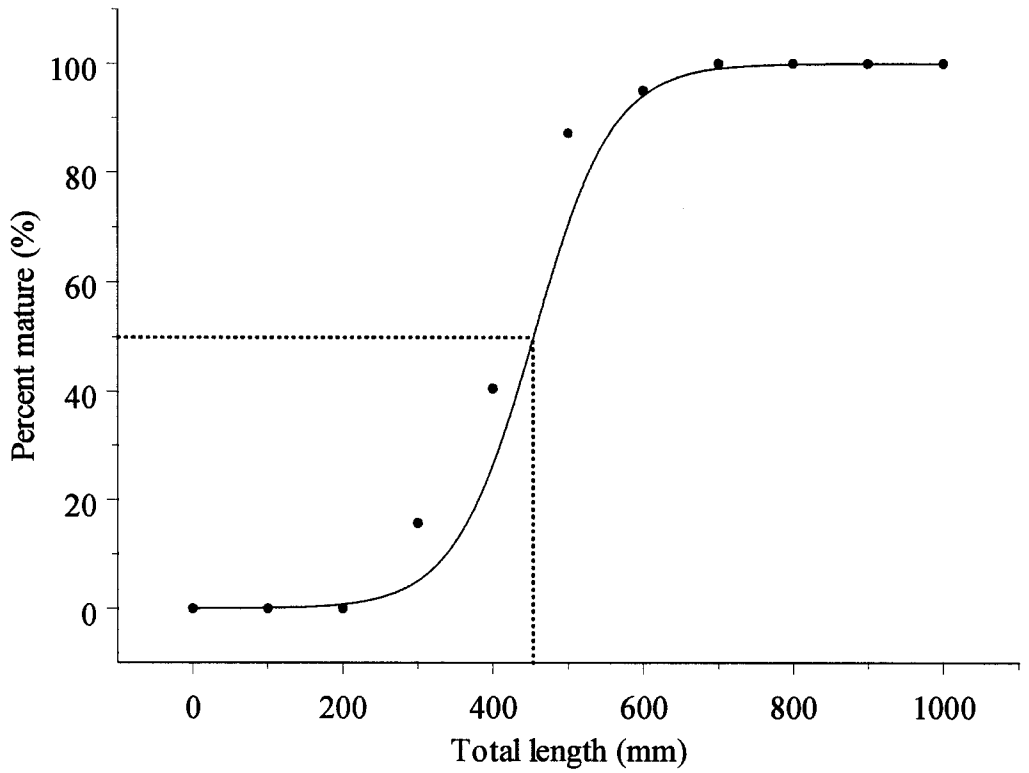

Figure 3.9
Logistic regression model for the estimated percent of sexually mature female bluefish as a function of total length.

There was no obvious relationship between batch fecundity (BF) and total length (TL), but for sake of comparison to previous estimates, I fitted the data with a simple exponential regression in the form:

3.6) $BF = 6{,}036.6e^{0.0053*TL}$ (Figure 3.10).

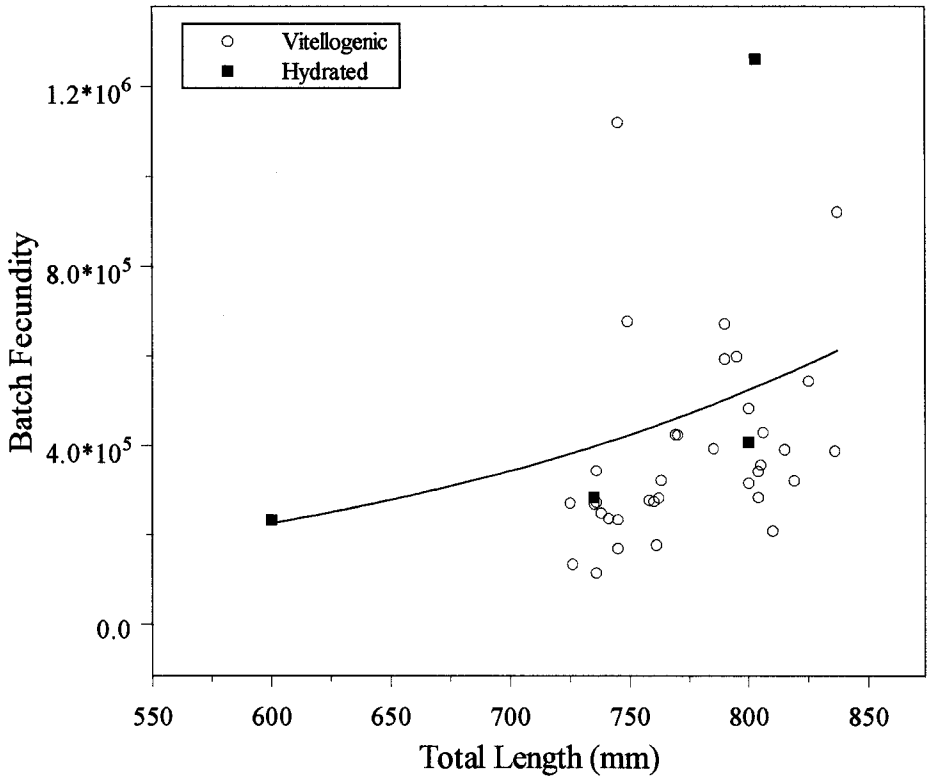

Figure 3.10
Relation between bluefish batch fecundity (number of hydrated ■ or late-stage ○ oocytes) and total length for two methods of estimating fecundity (hydrated, size-frequency distribution) in the Middle Atlantic Bight for 2002 and 2003.

There was also no obvious relationship between BF and somatic weight (SW), although I fitted the data with an exponential regression model in the form:

3.7) $BF = 62{,}991e^{0.0005*SW}$ (Figure 3.11).

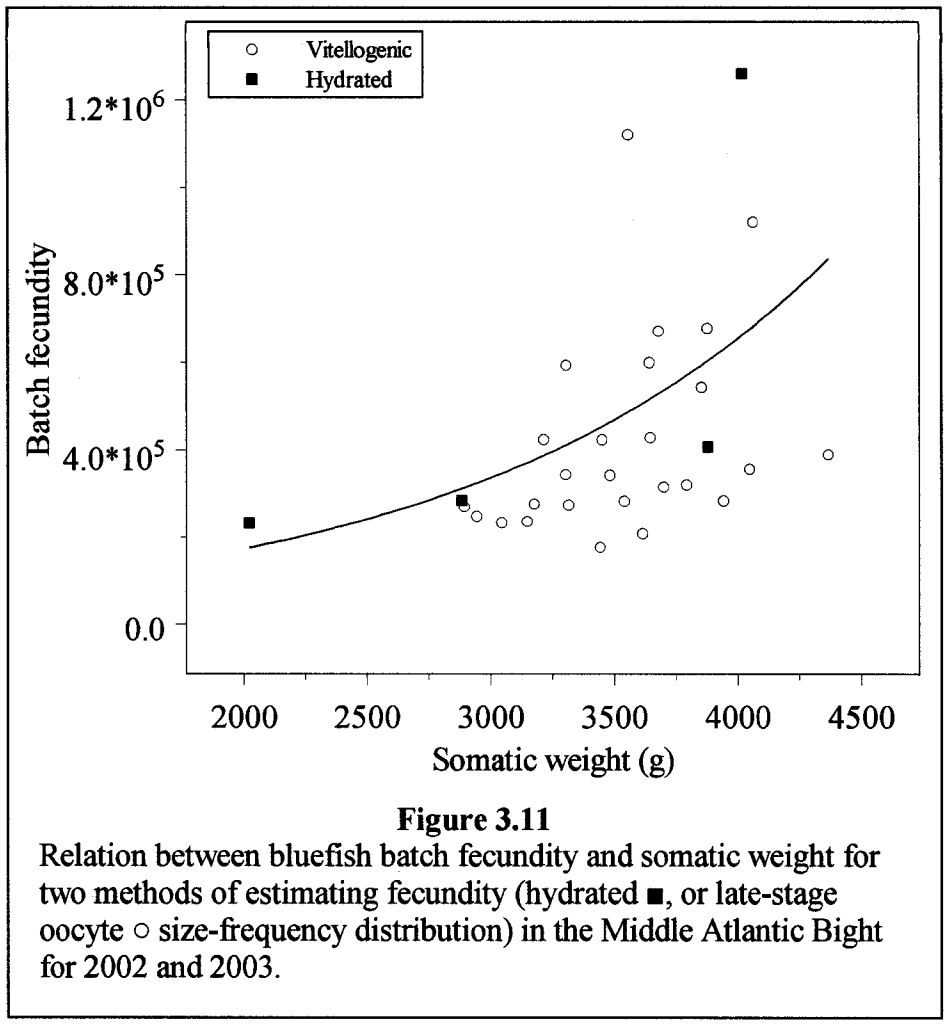

Figure 3.11
Relation between bluefish batch fecundity and somatic weight for two methods of estimating fecundity (hydrated ■, or late-stage oocyte ○ size-frequency distribution) in the Middle Atlantic Bight for 2002 and 2003.

3.4. Discussion

This study provides the first evidence that bluefish along the East Coast of United States are asynchronous, batch spawners, with a continual and protracted spawning pattern. This finding is supported by the seasonal oocyte development patterns that are characteristic of batch spawning. I found hydrated oocytes along with advanced yolked oocytes in the same fish, indicating that bluefish are capable of protracted spawning. Similarly, ovaries containing POFs also contained advanced yolked oocytes, providing further support that bluefish are multiple spawners. Moreover, the presence of all stages

of development in fully mature ovaries indicates that bluefish have asynchronous oocyte development. There is considerable overlap in oocyte diameter, however, with no distinct modes except between yolked and hydrated oocytes, which are clearly separated, indicating that bluefish fecundity is indeterminate.

Previous descriptions of the spawning season for bluefish are varied and are mostly based on recruitment and larval studies without direct observation of adult gonads, or on limited regional studies of reproductive status of adults (Kendall and Walford, 1979; Collins and Stender, 1987; Nyman and Conover, 1988; Chiarella and Conover, 1990; McBride and Conover, 1991; Hare and Cowen, 1993; McBride et al., 1993; Hare and Cowen, 1996; Munch and Conover, 2000). In contrast, I determined the direct correlation of spawning season for the SAB and MAB by analyzing mature females histologically over time and throughout a significant portion of their range. Although there was variability among years, in general the data, based on histological samples, show imminent spawning in Florida and North Carolina during March and April. This supports previous recruitment and larval studies that hypothesized spawning to occur in SAB during March and April (Kendall and Walford, 1979; Collins and Stender, 1987; Nyman and Conover, 1988; Hare and Cowen, 1993; McBride et al., 1993). These data also provide the first evidence to support the hypothesis of continuous spawning with no hiatus, but provide little information regarding the mechanisms for the bimodal recruitment patterns observed in the MAB. Bluefish collected from April to August showed imminent spawning with oocytes in final maturation or hydrated and POFs along the range from North Carolina to New York, indicating that bluefish spawn in the MAB from April to August. Bluefish caught in April in the SAB and MAB

demonstrate late vitellogenic oocytes and imminent spawning, supporting the hypothesis of continuous spawning (Hare and Cowen, 1993; Smith et al., 1994). Nevertheless, during the same time period, a larger percentage of fish were histologically classified as recovering, in collections from North Carolina than from Florida. Therefore, if spawning is continuous from SAB to MAB, it is only represented by a small contingent of migrating fish in North Carolina.

Various studies have used GSI values to describe reproductive seasonality in bluefish (Chiarella and Conover, 1990; Hare and Cowen, 1993), yet because of the multiple spawning patterns of bluefish, I found the highest GSI does not indicate peak spawning activity. For example, in 2003, the mean GSI peaked in June at 3.8 and declined to 3.2 in July. Yet, only 25% of the spawning females (gravid and spawning) were collected in June when GSI was at its highest as compared to 64% in July. Like Jons and Miranda (1997), I advise caution in using GSI levels for bluefish as indicators of spawning due, to their regional and temporal variations. Low GSI levels could represent recovering stages or the end of the spawning season, depending on the month analyzed. For example, bluefish collected in 2003 had GSI levels of 1 in August with 27% of the fish actively spawning, while in contrast, the same GSI level in March represented mostly fish in recovering stages.

My estimates of size and age at maturity of female bluefish were larger and older than current estimates for East Coast bluefish. Salerno et al. (2001) reported that the age at maturity for bluefish was 1.1 yrs and 334 mm based on scale ageing and macroscopic assessment of gonads, while I found that 50 % of the bluefish matured at 1.9 yrs and at a size of 480 mm. My results are more consistent with those of Conand (1975) who found

that size at maturity for West African bluefish was 430 mm using similar histological techniques. One reason for the discrepancy between my study and the current estimates produced by Salerno et al. (2001) may be explained by the fact that macroscopic examination of ovaries and GSI might include young, small fish that are unlikely to spawn that year. In my study, I assigned only fish that had begun yolking, and therefore were capable of spawning that season, as mature.

Previously, little fecundity information had been reported for bluefish. Lassiter (1962) made direct observations on gonads and found that fecundity of 2 to 3 year old bluefish (528 to 584 mm) examined from the coast of North Carolina ranged between 0.6 and 1.4 million eggs, but did not indicate whether bluefish were batch or total spawners. Conand (1975) calculated batch fecundity at 0.6 to 1.6 million eggs for fish ranging from 600 mm to 800 mm total length. My data revealed similar ranges in batch fecundity, from 0.2 to 1.4 million eggs for fish ranging from 600 to 840 mm TL, but my estimates of fecundity at size were lower than previously published results. I feel this is due to my strict criteria of only using females undergoing final maturation or fully hydrated females for fecundity estimation. The considerable overlap in oocyte diameter with no distinct modality complicates the use of the oocyte size-frequency distribution method (MacGregor 1957; Hunter et al. 1985) and will produce a broader range of coefficients of variation than the hydrated method. Nevertheless, there was no difference between fecundity estimates from the hydrated counts than from size-frequency counts. There was no relationship between batch fecundity and fish length and somatic weight over the size range of fish examined. However, given the exponential relationship, a few very large fish could have a significant impact on the overall fit of the curve. My estimates of

batch fecundity-at-size showed as much variability as observed by Conand (1975), for the size range of spawners I sampled. The lack of a strong relationship between fecundity and length or somatic weight is explained both by the paucity of large fish, but also by the nature of bluefish reproductive biology. At present there is no information on how or if batch size varies over the spawning season. If an individual's batch size changes over the spawning season or inter-annually, without knowledge of exactly what spawning event a female is undergoing, any relationship between fecundity and size based on the entire season will be highly variable.

My study shows bluefish are multiple spawners with indeterminate fecundity, indicating that the current available estimates of fecundity (Lassiter, 1962) based on determinate fecundity should be reconsidered before being used for management. For example, if each bluefish simply spawned twice each year, current estimates of fecundity would be doubled. Even though I was able to describe the spawning period and locations, I was unable to determine spawning frequency; therefore, future studies on the reproductive biology of bluefish should focus on sampling more frequently in the spawning locations and period to categorize the spawning frequency of bluefish, and temporal variability in batch fecundity.

CHAPTER IV

SUMMARY

The resiliency and persistence of exploited fish populations depend on age-specific survival and fecundity. Knowing the age of individual fish is necessary for longevity predictions, establishing growth rates, estimating age at maturity, and learning what periods of the life history of a fish population represent critical stages. Furthermore, to estimate reproductive capacity of the population, one must first estimate fecundity at age. I used a new technique to increase readability of otoliths along with criteria to interpret otolith microstructure and used ages estimated from them to evaluate age distribution in gears used in the fishery, size at age, and growth parameters from the catch. I also determined bluefish spawning location, spawning pattern and timing, and fecundity of bluefish along the U.S. East Coast. My study demonstrates that using bluefish sectioned otoliths will produce accurate and precise age estimates that are needed in modeling population age structure and for estimating rates of population growth. I am the first to describe that bluefish reproductive strategy is multiple spawning. As a result, the current available estimates of fecundity (Lassiter, 1962) based on determinate fecundity should be no longer considered for management.

This study finally puts to rest problems with age assignments that have caused trouble in the bluefish age-based stock assessment. I found that scales ages are biased with over-ageing younger fish, while under-ageing older fish. This bias could lead to inaccuracies that could affect the estimates of the biological characteristics of this species. In other fisheries, ageing error due to low accuracy has contributed to the serious

overexploitation of a population or species (Chilton and Beamish, 1982; Beamish and McFarlane, 1995). The problem is often one of age underestimation, which results in overly optimistic estimates of growth and mortality rate. With the new otolith processing technique used here, age estimates were precise and, coupled with the validation of the annulus formation, were also accurate. Therefore, future management of this species should be conducted with more accurate ages estimated from otoliths.

The results of this study provide the first evidence that bluefish along the East Coast of United States are asynchronous, batch spawners, with a continual and protracted spawning pattern. Lassiter (1962) published the only other study that made direct observations on gonads along the East Coast. His estimates of fecundity are higher than those I observed. This difference could be simply because his study was prior to the modern understanding that many marine pelagic fish are batch spawners. Management uses his fecundity results, however, to estimate numbers of young fish recruiting to the population, which could lead to over-optimistic estimates of recruitment.

I determined the direct correlation of spawning season for the SAB and MAB by analyzing mature females histologically. Although there was variability among years, in general, histological samples showed imminent spawning in Florida and North Carolina during March and April and North Carolina to New York from April to August. Given that bluefish caught in April in the SAB and MAB demonstrate late vitellogenic oocytes and imminent spawning, this study provides the first evidence to support the hypothesis of continuous spawning with no hiatus (Hare and Cowen 1993; Smith et al. 1994), resolving the two competing hypotheses that inferred spawning locations and times based on the abundance of juveniles.

In conclusion, my study clearly shows that I have surmounted the bluefish age determination problems. I demonstrated that using bluefish sectioned otoliths will produce accurate and precise age estimates needed in modeling population age structure and estimating rates of population growth. Furthermore, I estimated fecundity using the accepted proper techniques that, coupled with appropriate age information, provide the information critical to assess the potential effects of over-fishing on recruitment and to formulate likely management actions that could increase reproductive success.

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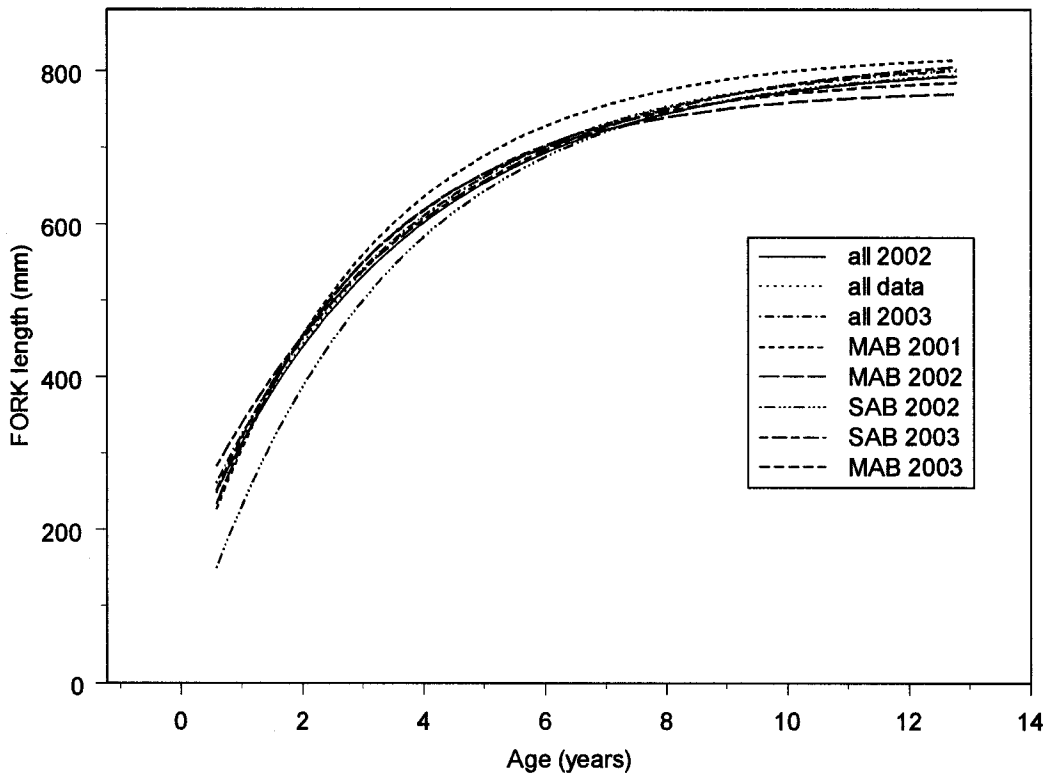
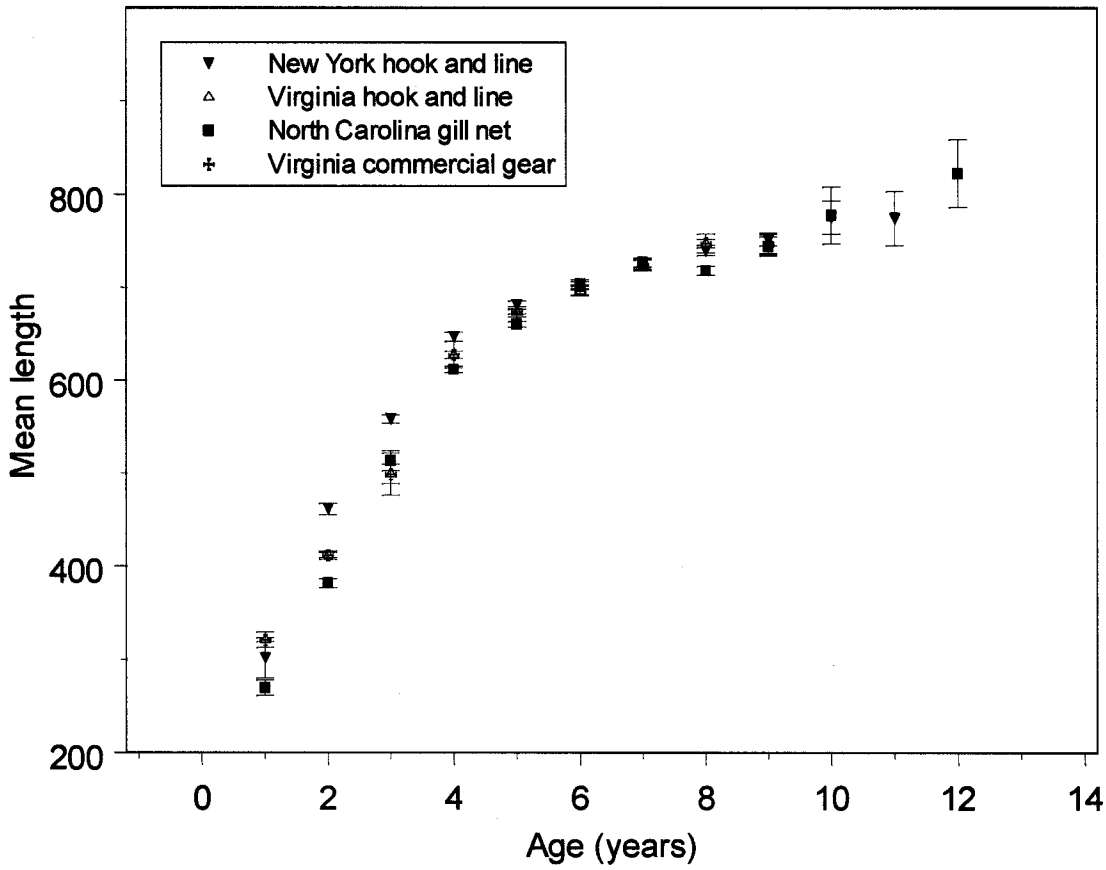
APPENDIX A

PLOT OF VON BERTALANFFY LENGTH-AT-AGE GROWTH CURVES FOR DIFFERENT YEARS AND AREAS



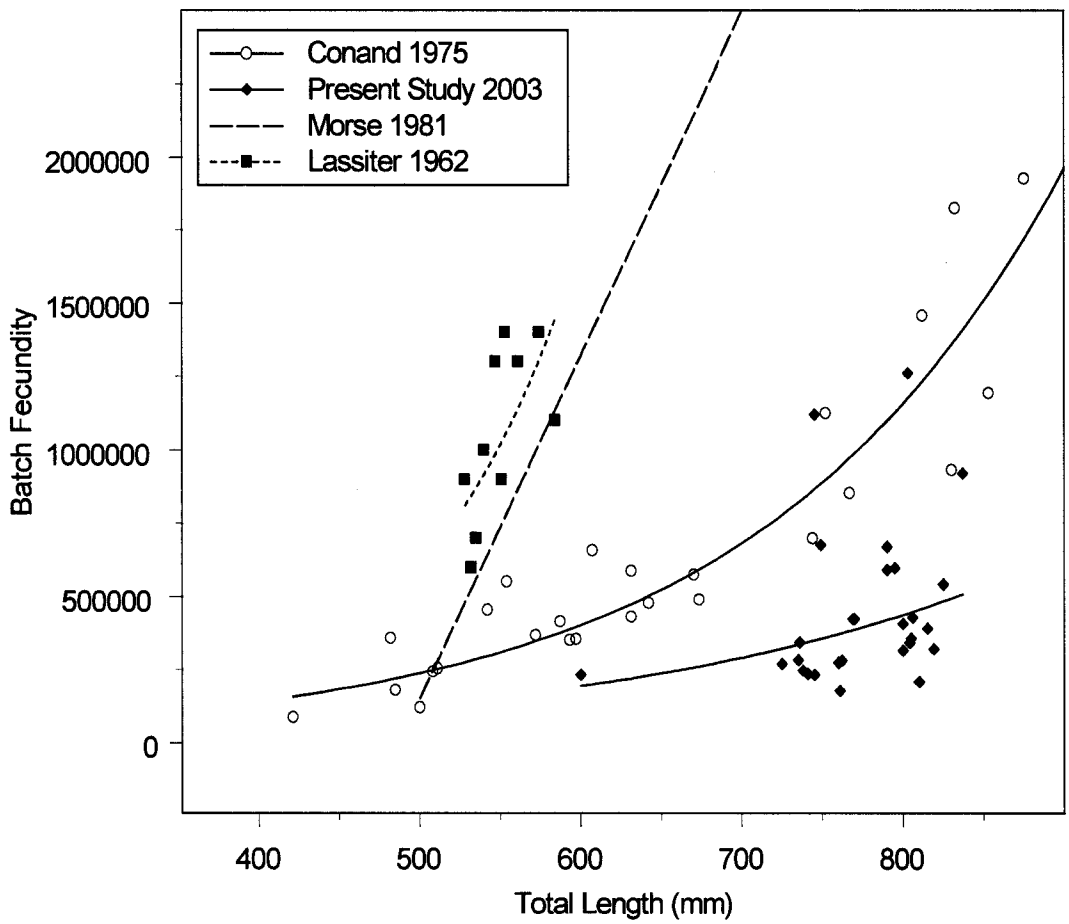
APPENDIX B

PLOT OF MEAN LENGTH-AT-AGE FOR DIFFERENT AREAS



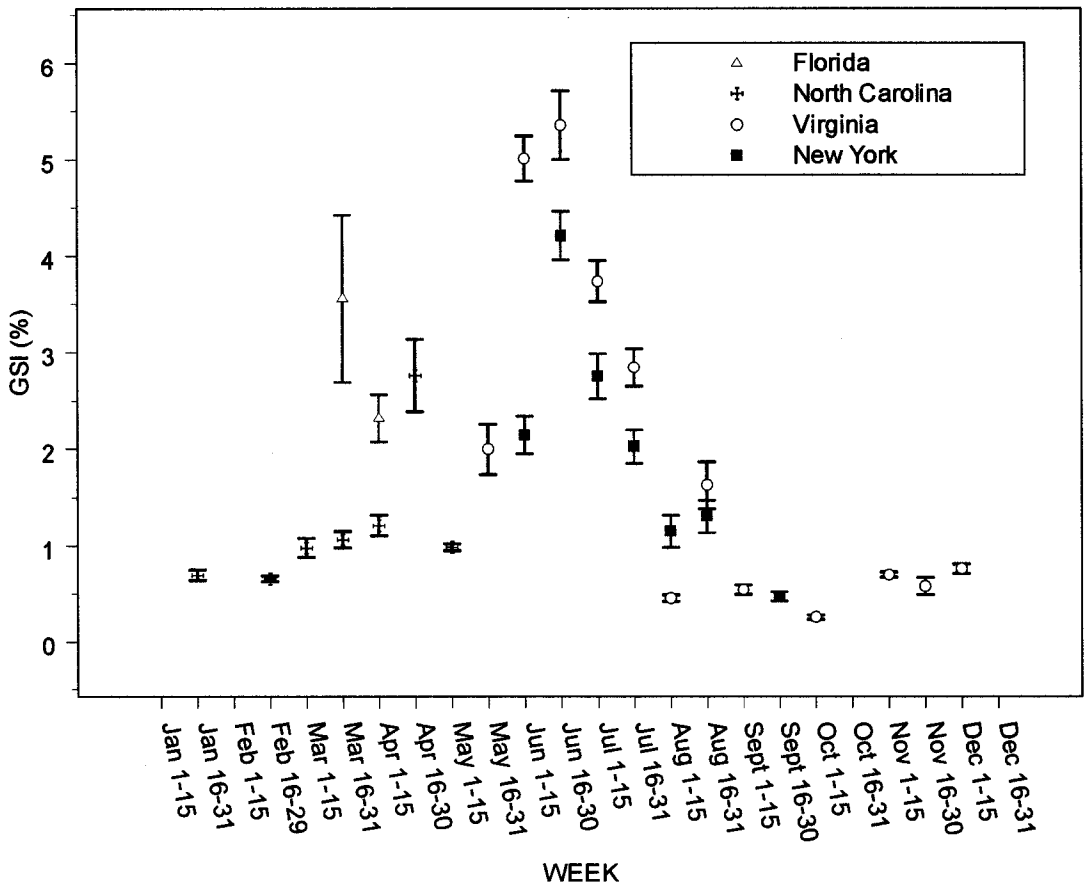
APPENDIX C

PLOT OF FECUNDITY BY LENGTH FROM DIFFERENT STUDIES



APPENDIX D

PLOT OF BI-WEEKLY GONADOSOMATIC INDEX FROM DIFFERENT AREAS



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