# Spawning in the nick of time? Effect of adult demographics on spawning behaviour and recruitment in Chesapeake Bay striped bass

## David H. Secor

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Striped bass (*Morone saxatilis*) is an iteroparous anadromous species that spawns dispersive offspring into freshwater habitats and exhibits a high fecundity and high embryo and larval mortality rates. Field studies indicate that temperature differentially affects spawning behaviour and larval survival, and periods of high egg production are often mis-timed for optimal larval survival. I hypothesize that age structure of females may be an important determinant in reducing variability in recruitment through its influence on spawning behaviour. Age diversity of Chesapeake Bay female striped bass is indexed according to expectations of age-specific reproductive values in an unexploited population. The age diversity index was positively correlated to spawning dispersion (egg presence ratio) and 0+ juvenile abundance during the recent period of population recovery (1985–1995). Diversity in age structure and spawning behaviour may contribute to a storage effect, because in most years minority behaviours would result in sustained recruitment. A diverse age structure may thus contribute to an accumulation of spawning stock biomass and increase the future likelihood of dominant year classes.

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Key words: age composition, age truncation, Chesapeake Bay, egg production per recruit, longevity, spawning behaviour, stock-recruitment, storage effect, striped bass, year-class strength.

*D. H. Secor, University of Maryland Center for Environmental Science, Chesapeake Biological Laboratory, PO Box 38, Solomons, MD 20688, USA. Tel: +1 410 326 7229; fax: +1 410 326 7318; e-mail: secor@cbl.umces.edu*

## Introduction

Striped bass is a long-lived anadromous species that supports important estuarine and coastal fisheries along the east coast of North America. Tagging and genetic studies show that Chesapeake Bay is the major source of recruits for coastal fisheries (Boreman and Lewis, 1987; Fabrizio, 1987; Wirgin *et al.*, 1993). During the 1970s in Chesapeake Bay, extremely high rates of exploitation on premigratory juvenile striped bass (F>2.0; Gibson, 1993) and degraded nursery habitats (Hall *et al.*, 1993) were believed to have led to recruitment failure. By the early 1980s, catch statistics, spawning stock assessments, and juvenile indices had all indicated that production of juveniles had declined below a level necessary for replacement of the spawning stock (Goodyear *et al.*, 1985). The State of Maryland instituted a moratorium on striped bass harvests in their portion of Chesapeake Bay from 1985 to 1989. Stock rebuilding was observed

by the early 1990s and exceptionally high year-class strengths occurred in the mid-1990s (MD DNR, 1996). Simultaneous improvement in spawning stock biomass and recruitment is consistent with the expectation of increased likelihood of good year classes under conditions of high spawning stock biomass (Fogarty, 1993).

Year-class strength in striped bass is believed to be controlled by density independent forces related to variability in the spawning environment; these cause differential survival of offspring (Ulanowicz and Polgar, 1980; Goodyear and Christiansen, 1984; Rutherford and Houde, 1995; Secor and Houde, 1995). Striped bass are event spawners, spawning dispersive offspring into freshwater habitats. They exhibit high individual fecundities and high embryo and larval mortality rates (>15% d$^{-1}$; Houde, 1996). Early survival of eggs and larvae has been related principally to spring-time temperature conditions (Secor and Houde, 1995), but may also be influenced by
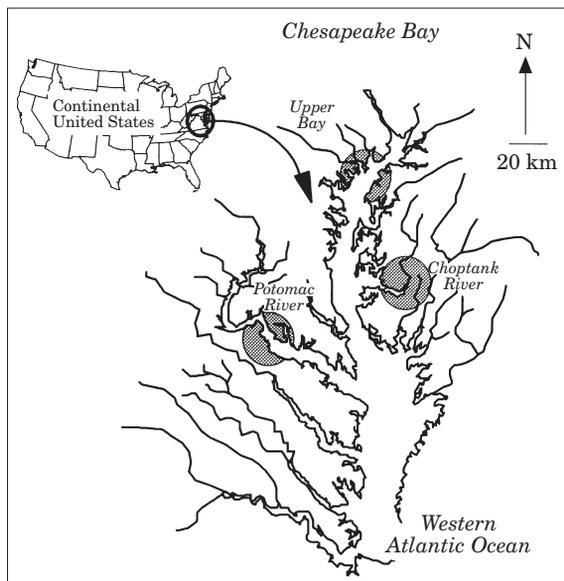
Figure 1. Chesapeake Bay, USA. Locations of spawning and nursery tributaries sampled for female age structure, spawning dispersion, and of juvenile abundance of striped bass are indicated. Spawning grounds are shaded.

river flow, precipitation, pH, conductivity, and trace metals (Uphoff, 1989; Rutherford and Houde, 1995).

Similar to Atlantic herring (Lambert, 1987) and cod (Hutchings and Myers, 1993), large, old striped bass may spawn earlier than small and young individuals (Cowan *et al.*, 1993). Increased age diversity in the spawning stock may increase the temporal and spatial frequency of spawning (spawning dispersion) and thereby increase the probability that some offspring will encounter favourable conditions (Lambert, 1990). I construct indices of spawning dispersion (egg presence ratio) and age diversity (Shannon-Weiner index of age-specific reproductive values) for Chesapeake Bay female striped bass in three important tributaries during the period 1985–1995 (Fig. 1). Correlations among these indices were used to address the following hypotheses:

- Diversity in female age structure is positively related to spawning dispersion.
- Production of juveniles is positively associated with diversity in female age structure.

## Methods

Female age composition and abundance data were obtained from Maryland state records of spawning stock assessments conducted in the spawning reaches of the Upper Bay region and Choptank and Potomac rivers from 1985 to 1995 (Fig. 1; MD DNR, 1996). Deployed gear was drift gillnets of 7.6 to 25.4 cm stretched mesh. Sampling began during the first week of April and was

terminated when striped bass were no longer caught (typically late May). Sampling locations were randomly chosen within each spawning reach and nets were fished five to seven times per week. Age-specific catch per unit effort ($CPUE_t$) estimates were corrected for selectivity differences due to size, sex, and sampling site (MD DNR, 1996). The $CPUE_t$ was adjusted to reflect age-dependent patterns in fecundity as:

$$CPUE_{fec,t} = CPUE_t * m_t \qquad (1)$$

where $m_t$=age-specific fecundity. To support comparisons across systems, $CPUE_{fec,t}$ for each system was indexed to the maximum annual value and the ratio was $log_e$ transformed to meet assumptions of normality. My assumption that, for all systems, maximal values occurred during 1985–1996 is supported by historical records (MD DNR, 1996).

All striped bass were measured for total length and sexed by expression of gonadal products. Scales (n=4–10) were removed from the left side above the lateral line and below the first dorsal fin. Age was estimated by interpretation of annuli (rings) either directly from scales or from acetate impressions of the scales (MD DNR, 1996). Secor *et al.* (1995b), using validated otolith age estimates based on tagged and recaptured fish, showed that the number of annuli in scales was only reliable until age 8 years, when after the number of annuli in scales ($t_{sc}$) continued to increase with increasing annuli in otoliths ($t_{ot}$) by the regression:

$$t_{(9...35)} = 1.84\, t_{sc} - 6.13\ (r^2 = 0.71) \qquad (2)$$

This regression was used to correct scale-derived ages. Because the regression predicts that a scale annulus forms once every ca. 2 years, the corrected age distributions contained gaps. Use of variance estimates could fill in these intervals, but would also inflate estimates of age diversity. I therefore chose to conserve the pattern of diversity in original scale data under the assumption of constant ageing bias after age 8 years.

Diversity in age composition for adult females (t>4) was indexed according to expectations of age-specific reproductive values in an unexploited population. Reproductive values ($R_t$) were modelled as:

$$R_t = l_t\, m_t \qquad (3)$$

where $l_t$ is survival to time t and m=fecundity. Instantaneous natural mortality rate starting at age 1 year was estimated to be 0.12 year$^{-1}$ based on a longevity of 35 years (Vetter, 1988). This longevity record is supported by the literature, which reports ages up to 31 years (Merriman, 1941; Secor *et al.*, 1995b). Olsen and Rulifson (1992) observed that the variables age and
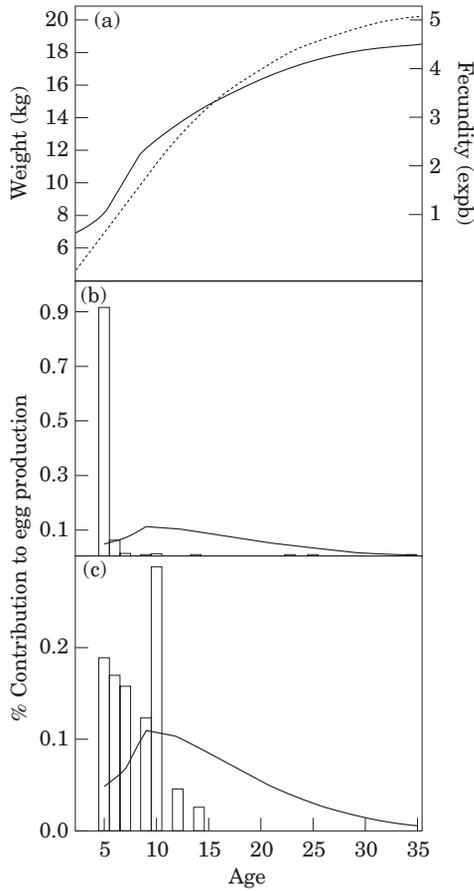
Figure 2. Age-specific models for Chesapeake Bay striped bass. (a) Growth (dashed line) and fecundity (solid line). (b) and (c) Expected percentage contribution to egg production under unexploited conditions (solid line) compared to the observed contributions (open bars) in the Choptank River in 1987 (b; $\%H_{max}=0.14$) and 1994 (c; $\%H_{max}=0.64$).

weight yielded best estimates of fecundity for ages 5–10, and >10 years, respectively. Therefore, age-specific fecundity was modelled based on two equations (Fig. 2a; Olsen and Rulifson, 1992):

$$m_{(5-10)} = -311\ 247 + 168\ 945\ t \qquad (r^2=0.71) \qquad (4)$$

$$m_{(11-35)} = -94\ 322 + 225\ 921\ w_t \qquad (r^2=0.83) \qquad (5)$$

where,

$$w_t = 21.21\ (1 - \exp^{(-0.106\ (t+3.5))})^3 \qquad (r^2=0.90) \qquad (6)$$

Weight at age ($w_t$) was modelled based on otolith-derived ages for females between 5 and 31 years of age (Fig. 2a; Secor et al., 1995b). Maximum or "ideal" diversity in the unexploited population was estimated using the Shannon-Weiner Diversity Index ($H_{max}$) based

on the fraction of egg production attributable to each age class ($p_t$) in an unexploited population:

$$p_t = R_t \left( \sum_{t=5}^{N} R_t \right)^{-1}$$

where N is the oldest age and t is the age predicted by Equation (2).

Observed age diversity ($H_t$) was estimated from the spawning stock monitoring programme based on:

$$q_t = CPUE_{fec,t} \left( \sum_{t=5}^{N} CPUE_{fec,t} \right)^{-1} \qquad (7)$$

where $q_t$ is the fraction of egg production attributable to an age class ($CPUE_{fec,t}$). Finally, the fraction of maximum (ideal) age diversity realized is estimated as:

$$H_t\ (H_{max})^{-1} \qquad (8)$$

As a second index of age diversity, the absolute number of age classes present in the spawning stock, $N_a$, was also used. Lambert (1987) termed this index "age span".

Using historical ichthyoplankton surveys, Uphoff (1993, 1997) computed an "egg presence ratio" ($E_p$), which is the fraction of plankton tows containing >0 eggs, and used this as a surrogate for egg production to make predictions on stock-recruitment relations. He demonstrated positive correlations between $E_p$ and recruitment for several Chesapeake Bay spawning tributaries. I used these estimates as an index of spawning dispersion. The domain of $E_p$ represents the number of cells in a matrix of rows (dates) and columns (sampling stations). The greater the number of cells occupied by positive tows, the greater the spatial and temporal frequency of spawning for a given year. Unfortunately, systems were not sampled in all years. The Upper Bay was monitored in 1985, 1988, and 1989; the Choptank River was monitored in 1985–1991 and 1994; and the Potomac River in 1987–1989.

Juvenile abundance in the Chesapeake Bay has been monitored since 1956. The 0+ index is estimated from replicate hauls of a $30.5 \times 1.24$ m bagless beach seine (mesh=6.4 mm) at fixed stations in the Upper Bay (7 stations), Choptank River (4 stations), and Potomac River (7 stations). Stations are sampled three times per year in July, August, and September. The year-class strength ($YOY_t$) is calculated as the geometric mean of samples for each nursery tributary (MD DNR, 1996). To support comparisons across systems, $YOY_t$ for each system was indexed to the maximum annual value and the ratio was $\log_e$ transformed to meet assumptions of normality. As with $CPUE_{fec,t}$ values, I assumed that maximal values occurred for all systems during the 1985–1995 period.
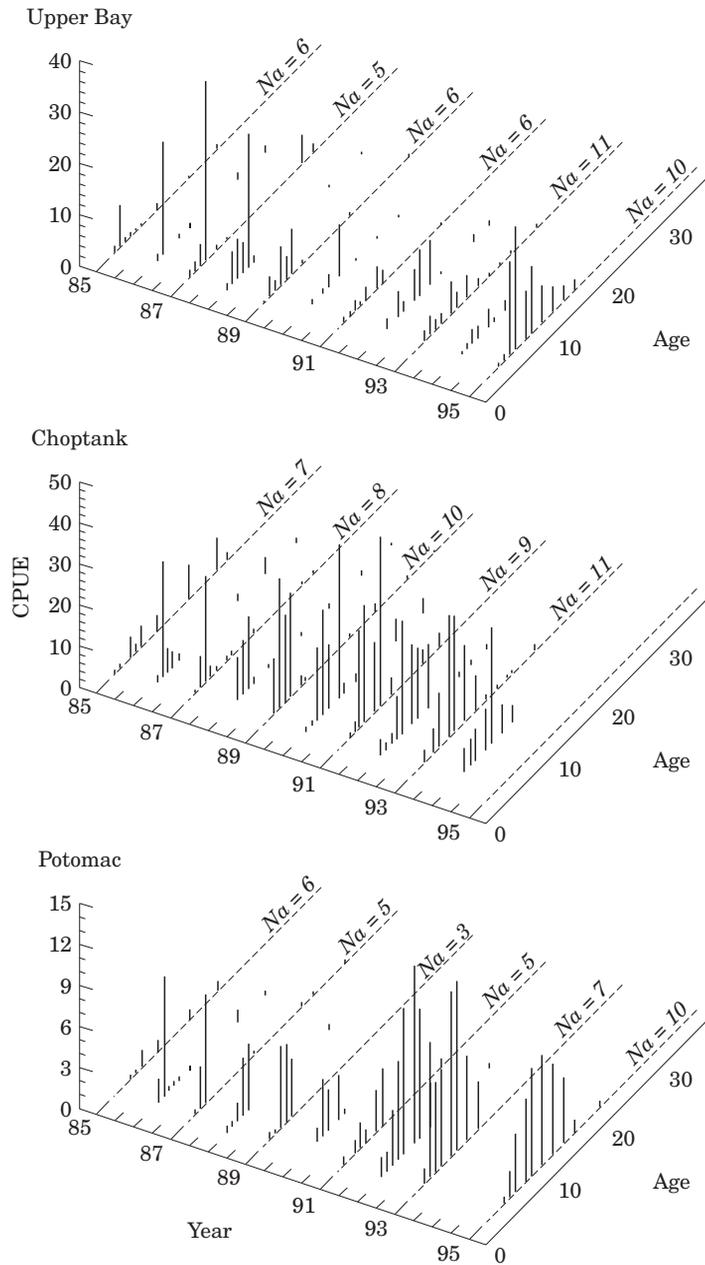
Figure 3. Female abundance of striped bass by age group (CPUE$_t$) for the Upper Bay and Choptank and Potomac rivers, Chesapeake Bay, 1985–1995. Estimated age-span (Na) in each year and system are also indicated. Abundances of immature females (t<5) are also shown.

## Results

Age diversity indices, $N_a$ and $\%H_{max}$, increased in all systems during the 1985–1995 period. $Na_t$ rose by 4–7 age classes (Fig. 3). For $\%H_{max}$, values in 1985 and 1986 were relatively high (Fig. 4) despite low numbers of mature age classes, the apparent result of equal disper-

sion among relatively few mature age classes. Diversity collapsed during 1987 among systems and rose steadily afterwards. A clear example of the large change in $\%H_{max}$ is shown for the Choptank River in 1987 and 1994 (Fig. 2b, c); 5-year-olds dominated in 1987 and $H_t$ was 14% of $H_{max}$. In 1994, increased number of age classes and their relative contributions to population
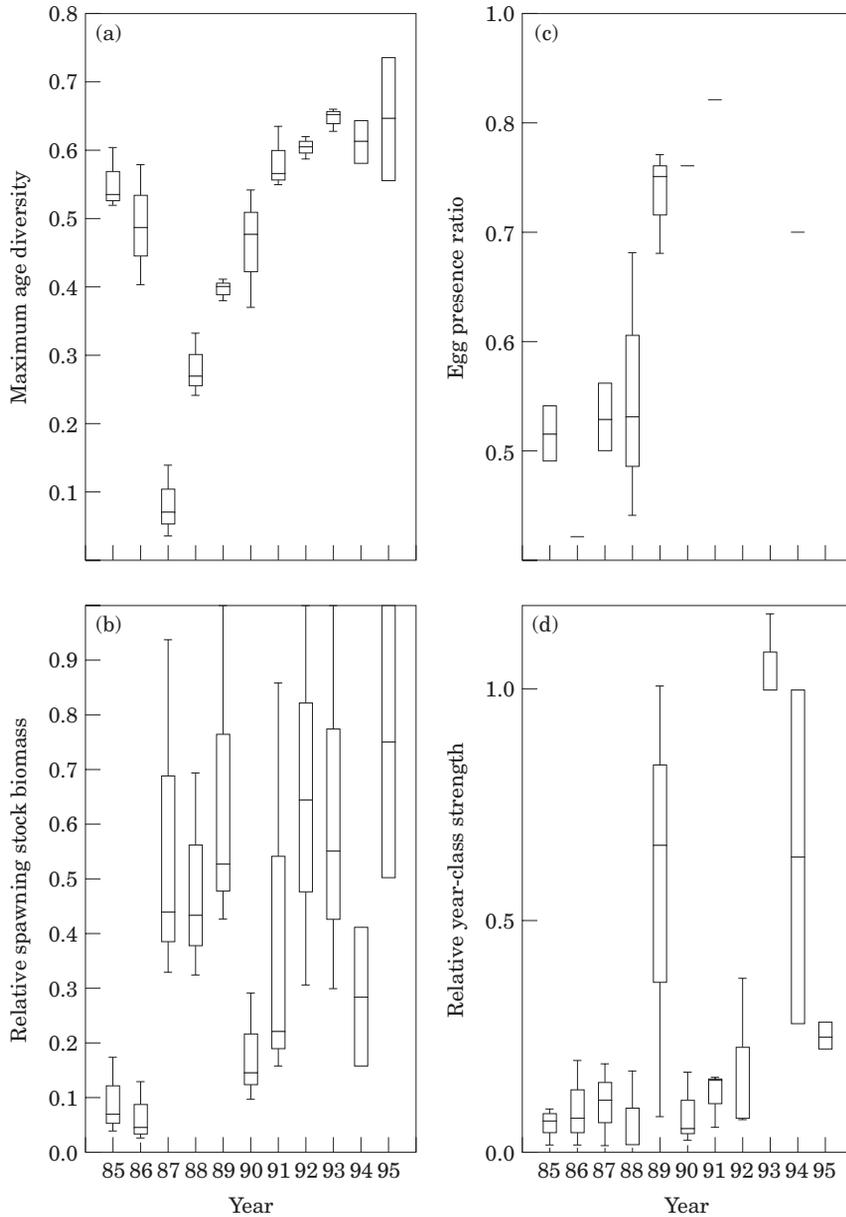
Figure 4. Box whisker plots of population parameters of striped bass for three Chesapeake Bay tributaries combined, 1985–1995: (a) proportion maximum age diversity ($H_{max}$); (b) relative spawning stock biomass; (c) egg presence ratio; (d) relative year-class strength.

fecundity resulted in a relative $H_t$ of 64%. The large mode in abundance for the 1982 year class can be tracked during the late 1980s (Fig. 3). By 1990, other year classes protected by the moratorium were making large contributions and there was little remaining influence by the originally dominant year-class 1982 on age diversity.

Female abundance, as indexed by CPUE data, was variable among years and increased substantially in the Choptank during the late 1980s and in Potomac River during the early 1990s (Fig. 3). A general increase in fecundity-adjusted biomass was observed after 1986 (Fig. 4).

Egg presence ratio showed an abrupt shift to higher values after 1988 (Fig. 4) and was significantly and positively related to year-class strength (Fig. 5), as observed by Uphoff (1993). Age diversity and fecundity-adjusted abundance were positively but not significantly
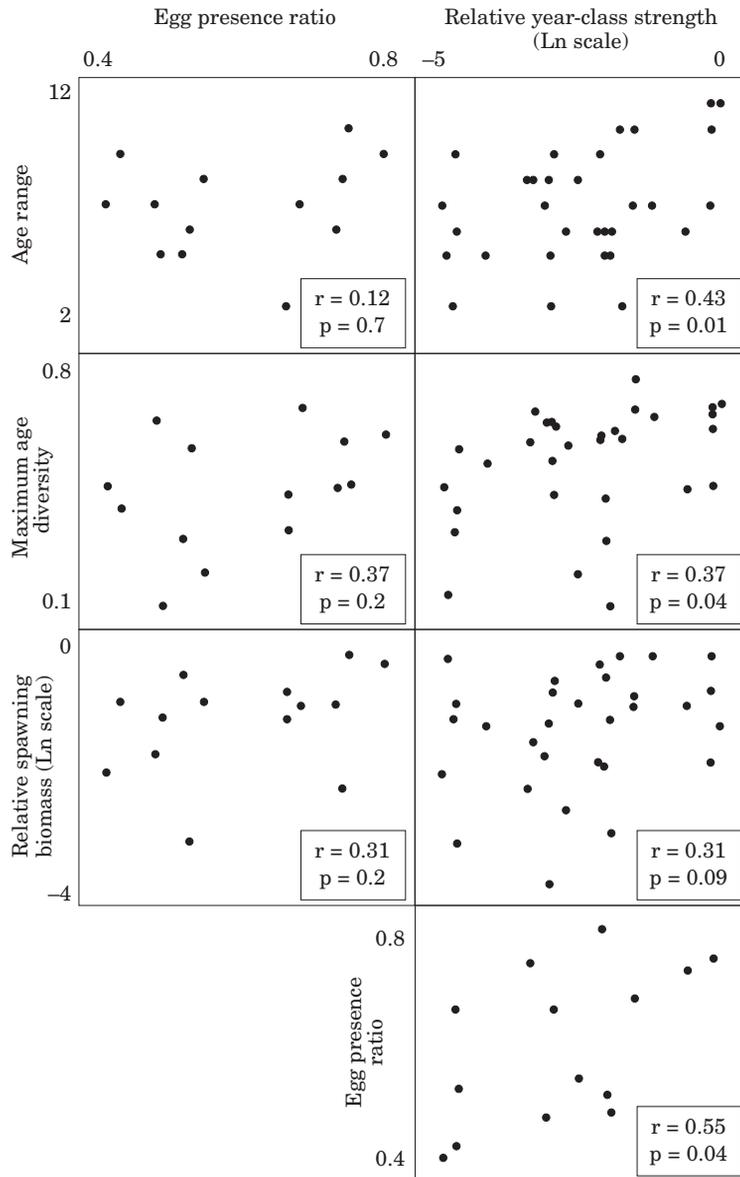
Figure 5. Correlations among egg presence ratio, relative year-class strength (ln scale), age range, maximum age diversity, and relative spawning biomass (ln scale) among years and Chesapeake Bay tributaries (Pearson correlation coefficients and p-values are indicated in each plot).

related to $E_p$. $N_a$ showed no apparent relationship to $E_p$ (Fig. 5).

Relative year-class strength values were highest in 1989 and 1993–1994 (Fig. 4). The indices were highly dispersed in 1989 and 1994 due to high variance among systems. Both indices of age diversity, $H_{max}$ and $N_a$, were positively and significantly correlated with relative year-class strength (Fig. 5). Relative spawning biomass was less well correlated with year-class strength.

## Discussion

To establish a relationship between spawning stock age structure and recruitment, two associations are important: (1) time and place of spawning versus recruitment and (2) age structure versus time and place of spawning. While extensive research has addressed the effects of time and place of spawning on recruitment (Cushing, 1969; Lasker, 1975; Sinclair, 1988; Fortier and Gagne, 1990; Secor *et al.*, 1995a), very little research exists on

relating age composition to spawning behaviour (Lambert, 1987; Hutchings and Myers, 1993). Scalars of spawning dispersion remain under-developed. Lambert (1990) used the rate of decrease of ripe females during the spawning season. This index was inversely related to duration of spawning. By indirectly relating year-class span to duration of spawning season, Lambert inferred a positive correlation between the number of dominant year classes and recruitment. I used egg presence ratio as an index of spawning dispersion. While this ratio was not significantly related to measures of age diversity or spawning biomass, positive associations were observed, consistent with expectations.

Both temporal and spatial aspects of spawning behaviour are critical determinants in the production of striped bass 0+ juveniles. As observed initially by Uphoff (1993), $E_p$ was significantly and positively related to $YOY_t$. Increased spawning dispersion may compensate for variable temperature conditions on the spawning grounds, which often results in patterns of egg production that are mistimed for optimal larval survival (Rutherford and Houde, 1995; Secor and Houde, 1995). In general, periods of increasing temperature between 10 and 20°C cause spawning waves (Grant and Olney, 1991; Secor and Houde, 1995). Females not participating in spawning waves do not contribute much to annual egg production, but in some years survival of their offspring may serve to reduce annual variations in recruitment (Secor and Houde, 1995). Spatial placement of eggs in the nursery can also influence offspring survival. For instance, in the Choptank (Uphoff, 1989) and Nanticoke rivers (Houde and Secor, 1996), positive associations between water conductivity and larval survival were observed. Thus, spawning close to the salt-front may result in higher survival of offspring. However, high flows due to weather events could cause downriver advection of eggs and larvae near the salt-front, resulting in their complete mortality (Van den Avyle and Maynard, 1994; Secor et al., 1995a). Uncertainty in the fate of offspring spawned at different locations and times should promote dispersion in spawning effort by females. The observation that larger striped bass tend to spawn early in the season suggests that spawning behaviours that vary with size or age might be an effective means to hedge bets against environmental stochasticity.

The dynamics of Chesapeake Bay striped bass are strongly determined by dominant year classes (Merriman, 1941). During the 1987–1989 period, one dominant year class (1982) occurred which depressed $H_t$. Contributions among age classes were similar after 1989 in all systems, which caused a rise in age diversity. In Icelandic cod, Marteinsdottir and Thorarinsson (1998) found that age diversity in a given year was positively correlated to the number of dominant year classes and abundance of older fish. Because striped bass have

longevity exceeding 30 years in age (Merriman, 1941; Secor et al., 1995b), several dominant year classes should simultaneously occur in an unfished population. Polymodal age distributions would result in increased spread of age distribution and presumably increased temporal and spatial variation in spawning (Lambert, 1990).

The index $\%H_{max}$ served as a useful scalar of age diversity and showed positive correlation to juvenile abundance. The index is complementary to the biological reference point, egg production per recruit (Mace, 1994; Boreman, 1997). In both instances, the relative contribution of each age class to egg production in an unexploited population is computed. The maximum diversity index is calculated based on the distribution of egg productions across ages. Observed diversity in reproductive values is contrasted with this ideal diversity. The Shannon-Weiner diversity index measures the evenness of contributions among ages, which seems reasonable given the large range of ages that can potentially contribute to egg production (Fig. 2). However, the well-known variability in year-class strength in striped bass will result in periodic depressions in $\%H_{max}$ which are not necessarily reflective of an "unhealthy" situation. This recommends the simultaneous use of measures such as Lambert's age-span.

Positive associations between egg presence ratio, age diversity, and year-class strength support the hypothesis that year-class strength is positively related to age structure of mature females due to its influence on spawning diversity. Still, these regressions cannot prove that spawning behaviour and female age are related. Indeed, effects of age diversity on $E_p$ were not statistically significant. Additional research on age structure of females as they arrive on the spawning ground (Lambert, 1987; Hutchings and Myers, 1993) is needed. Because striped bass egg size is positively related to female size (Zastrow et al., 1989), surveys of egg size could serve to demonstrate relationships between female age structure and spawning dispersion. The effect of larger egg size on larval viability in striped bass remains controversial, but differential survival of larvae due to maternal investment would be another means by which age structure could affect recruitment (Zastrow et al., 1989; Monteleone and Houde, 1992; Cowan et al., 1993).

Age structure and maternal influences on egg viability may serve as "storage mechanisms" (Chesson, 1984) that regulate abundance of iteroparous fishes by maintaining spawning biomass capable of producing dominant year classes. In periodic strategists like striped bass (Winemiller and Rose, 1992), moderately long reproductive lifespans and low adult mortality rates result in accumulation of spawning stock biomass. When environmental conditions favour recruitment, this large reproductive reservoir generates dominant year classes

which drive population growth. Diversity in age structure and spawning behaviour contribute to this storage effect. If minority spawning behaviours – for instance spawning during early or late parts of a season – in some years resulted in successful offspring, a diverse age composition should contribute to sustained annual recruitment and accumulation of spawning stock biomass.

Recovery of striped bass was due to its unique life history attributes, which include high fecundity and long reproductive lifespans. Lambert's prediction that reduction in year-class diversity renders a population more vulnerable to recruitment failures is consistent with the time series of year-class strengths observed for Chesapeake Bay striped bass. Lowest year-class strengths were observed during periods when age structure was severely truncated. Spawning stock biomass also was very low during the period of poor recruitment and it was not possible to statistically uncouple its effect from that of age structure. The two influences are probably inextricably linked in their contribution to population regulation. Sustained recruitment and accumulation of spawning stock biomass (storage mechanisms) may be accomplished by diversity of spawning behaviours and related diversity in age structure.

Through a moratorium on Maryland State harvests in the Chesapeake Bay, the 1982 year-class was effectively protected and became a dominant one. Ironically, most egg production in 1982 was attributable to striped bass >10 years in age (Secor, in press). Old remnant females produced during the 1960s were a hedge against a long period of recruitment overfishing which occurred during the 1970s. Striped bass epitomize periodic strategists, spreading risk of failed replacement through variability in spawning behaviour over many spawning seasons. This life history tactic indicates that a truncated age distribution would result in stock abundance being more closely linked to annual changes in year-class strength.

## Acknowledgements

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