ICES Journal of Marine Science, 57: 808–815. 2000
doi:10.1006/jmsc.2000.0560, available online at http://www.idealibrary.com on IDEAL®

Longevity and resilience of Chesapeake Bay striped bass

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Secor, D. H. 2000. Longevity and resilience of Chesapeake Bay striped bass. – ICES Journal of Marine Science, 57: 808–815.

Since the early 1960s, the Chesapeake Bay striped bass population has undergone a large cycle of abundance, recovering to record levels during the 1990s. Changes in age structure over this period were examined to determine contributions of old females (>13 yr) to the recovery. In 1992, in a sample of large female striped bass, 10 yr of absent year classes (1972–1981) were observed corresponding to a period of recruitment overfishing. Fishery-independent stock assessments conducted 1985–1990 by Maryland Department of Natural Resources indicated that old females, while present in small numbers, made relatively small contributions to annual egg production during the period of recovery. Abundances, weighted for age-specific fecundity, indicated that older fish were probably the most important contributors to recruitment throughout the 1970s and early 1980s. Egg production after 1986 was principally contributed by young females, those produced after 1981. Demographic analysis also supports the view that a Maryland fishing moratorium designed to protect year classes after 1981 stimulated recovery. Longevities of >30 yr documented in this study suggest that striped bass populations can persist during long periods of poor recruitment due to a long reproductive lifespan. Longevity may have also conferred resiliency against an extended period of recruitment overfishing in the Chesapeake Bay.

Key words: age structure, Chesapeake Bay, longevity, moratorium, overfishing, recruitment, striped bass.

Received 9 November 1998; accepted 29 November 1999.

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Introduction

Due to a decline in recruitment of Chesapeake Bay striped bass, a moratorium on harvests was enforced in Maryland waters from 1985 to 1989. By the early 1980s, catch statistics, spawning stock assessments, and juvenile indices had all indicated that production of age 0+ striped bass had declined below a level necessary for replacement of the spawning population (Goodyear *et al.*, 1985). Maryland's striped bass moratorium ended in 1989 due to a high abundance of age 0+ striped bass in the Chesapeake Bay which exceeded the trigger level prescribed by the Atlantic States Marine Fisheries Commission (ASMFC, 1990). Large striped bass recruitments have subsequently been observed in 1989, 1993, and 1996 (MD DNR, 1996).

The effect of the moratorium in restoring striped bass stocks has been heralded as one of few recent success stories in fisheries science and management. However, despite the recovery of Chesapeake Bay striped bass, Jensen (1993) admonished that moratoria or partial moratoria have not been effective for other Chesapeake Bay species (most notably American shad and shortnose sturgeon). Thus, the causes of the striped bass decline and recovery may be due to unique life history traits or habitat requirements, which should be given due consideration in their management (Hutchings and Myers, 1993; Secor, 2000).

This study provides a demographic analysis of the recovery of female striped bass in three Chesapeake Bay tributaries. By utilizing a recent otolith-based demographic study (Secor *et al.*, 1995) and MD Department of Natural Resources (MD DNR, 1996) spawning stock assessments (1985–1995) I examine the hypothesis that recovery of striped bass was due to its unique life history attributes which include high fecundity (Mihursky *et al.*, 1987) and long reproductive lifespan (Merriman, 1941; Secor *et al.*, 1995).

Methods

Age structure was initially examined for sample of very large females (≥91 cm TL) taken during May 1992 from

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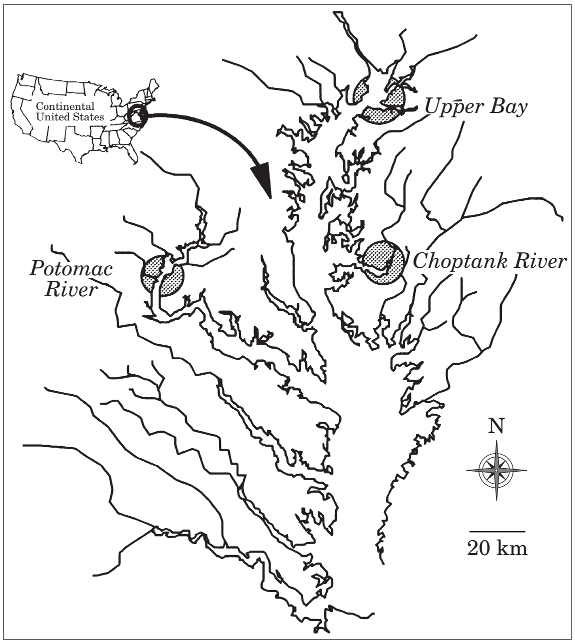

Figure 1. Chesapeake Bay, US. Locations of spawning and nursery tributaries sampled for female abundance and age structure, and 0+ juvenile abundance are indicated.

the MD Trophy Striped Bass Fishery. This recreational fishery was limited to Chesapeake mainstem waters and mostly comprised post-ovulatory females. Recreational catches were sampled for gonadal condition, scales and otoliths (sagittae) in Solomons, MD, at the mouth of the Patuxent River. Approximately 50% of landed fish were sampled in 1992. Efforts were made to ensure that all size classes were sampled in an unbiased manner. Because large fish were targeted in the fishery, the sample was likely skewed towards older individuals in the population. Among the 44 fish sampled, all were female and only two contained hydrated eggs; all others showed atretic ovaries. Females were probably emigrating from the Upper Bay region because peak spawning in the Upper Bay typically occurs in late April/early May (Rutherford and Houde, 1995) and thus would immediately precede the fishery. More southern tributaries (e.g. Patuxent and Potomac Rivers) have earlier spawning seasons (Rutherford and Houde, 1995; Secor and Houde, 1995) and emigrating females would be less vulnerable to the May fishery.

To evaluate annual changes in age structure during the period of recovery, data were obtained from Maryland state records of 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). Ripe females were sampled in drift gillnets of 7.6–25.4-cm stretched mesh. Sampling began during the first week of April and was terminated when striped bass were no longer caught in the nets (typically late May). Sampling locations were randomly chosen within each spawning reach and nets were fished five to seven times per week. Catch per unit effort (c.p.u.e.) for each age class was corrected for gillnet selectivity (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 from either direct interpretation of the scales annuli or from acetate impressions of the scales (MD DNR, 1996). Secor *et al.* (1995) validated otolith age estimates based upon tagged and recaptured striped bass and showed that scale annuli were reliable until age 8, whereafter the number of annuli in scales (t_{sc}) continued to increase with increasing annuli in otoliths (t_{ot}) by the regression:

$$t_{ot}=1.84t_{sc}-6.13 \quad r^2=0.85 \qquad (1)$$

This regression was used to correct scale ages. Based upon these ages, striped bass were assigned to three decadal generations: those produced prior to 1972, 1972–1981, and after 1981. Despite imprecision in regression (1), it was sufficiently robust to assign fish to these decadal groupings. Because the regression predicts that a scale annulus forms once every ca. 2 years, corrected age distributions contained gaps. Use of variance from regression (1) could fill in these intervals, but would also likely inflate representation of year classes. Therefore, the pattern of age classes was conserved in original scale data, under the assumption of constant ageing bias with increasing age.

MD DNR c.p.u.e. data were adjusted to weight for age-specific rates of fecundity (c.p.u.e.$_F$). Age-specific fecundity was modeled by the following two equations from Mihursky *et al.* (1987):

$$W_t=1747.26t_{sc}-5348.23 \quad r^2=0.94 \qquad (2)$$

$$F=206.82W-13\,097.60 \quad r^2=0.95, \qquad (3)$$

where W_t is weight in grams at age t_{sc} and F is the number of eggs. Estimated fecundities ranged 0.69×10^6 to 5.75×10^6. These fecundities were similar to those observed by Mihursky *et al.* (1987) which ranged between 0.17×10^6 and 6.05×10^6 for fish with scale-based age estimates of 3 and 16, respectively. The proportional contribution of each year class to annual egg production was estimated as:

$$\text{c.p.u.e.}_F=\text{c.p.u.e.}\times F\times10^{-6} \qquad (4)$$

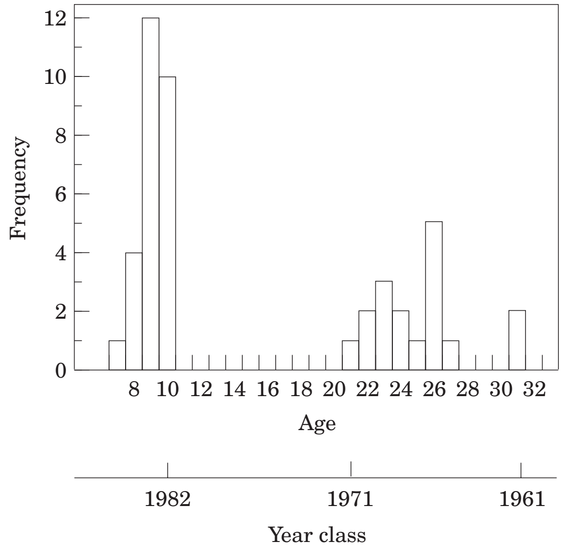

Figure 2. Age structure of Maryland trophy striped bass collected during May 1992. Ages estimated from annuli in sagittal otoliths.

Results

Age estimates of females collected during the MD Trophy Fishery (n=44; 91–130 cm TL) ranged 7–31 yr (Fig. 2). The distributions of ages and lengths of 1992 trophy striped bass were bimodal. Striped bass between 91–102 cm TL were 7–10 yr old; those between 109 and 130 cm TL were 21–31 years old. Thus, a 7-cm gap in length corresponded to a 10-year gap in age. Year classes 1972 to 1981 correspond to this gap. For convenience, I have termed this 10-year gap a "missing generation". Striped bass produced in earlier (prior to 1972) and later (after 1981) year classes are termed "old generation" and "new generation", respectively.

Analaysis of c.p.u.e.$_F$ indicated that the missing generation were minor contributors to spawning stock during 1985–1995 (Figs 3–5). In the Upper Bay, highest amplitude c.p.u.e.$_F$ values were mostly associated with old and new generations. Only in 1992, 1993, and 1995 were high contributions to reproductive potential associated with missing generation year classes and in these instances, 1980 or 1981 year classes contributed highest

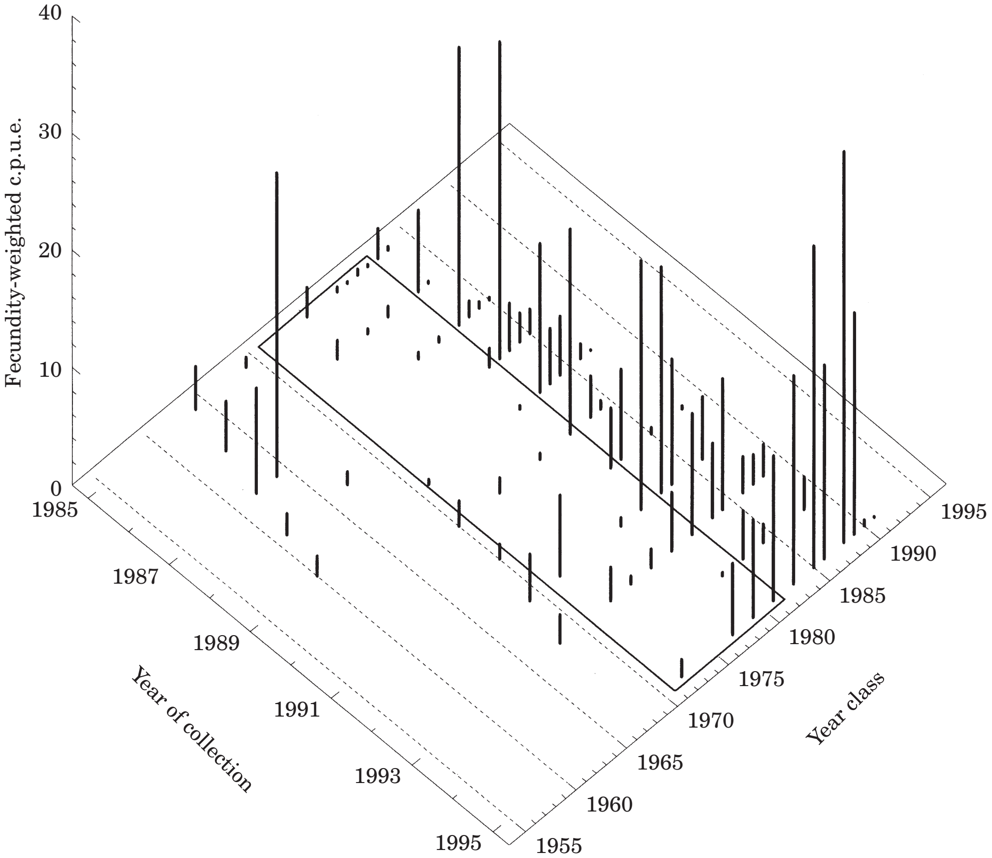

Figure 3. Temporal pattern of year-class contributions to potential egg productions (c.p.u.e.$_F$) in the Upper Bay, Maryland. Year class is predicted based upon corrected scale ages (t_{ot}). White rectangular area on graph indicates nominal missing generation.

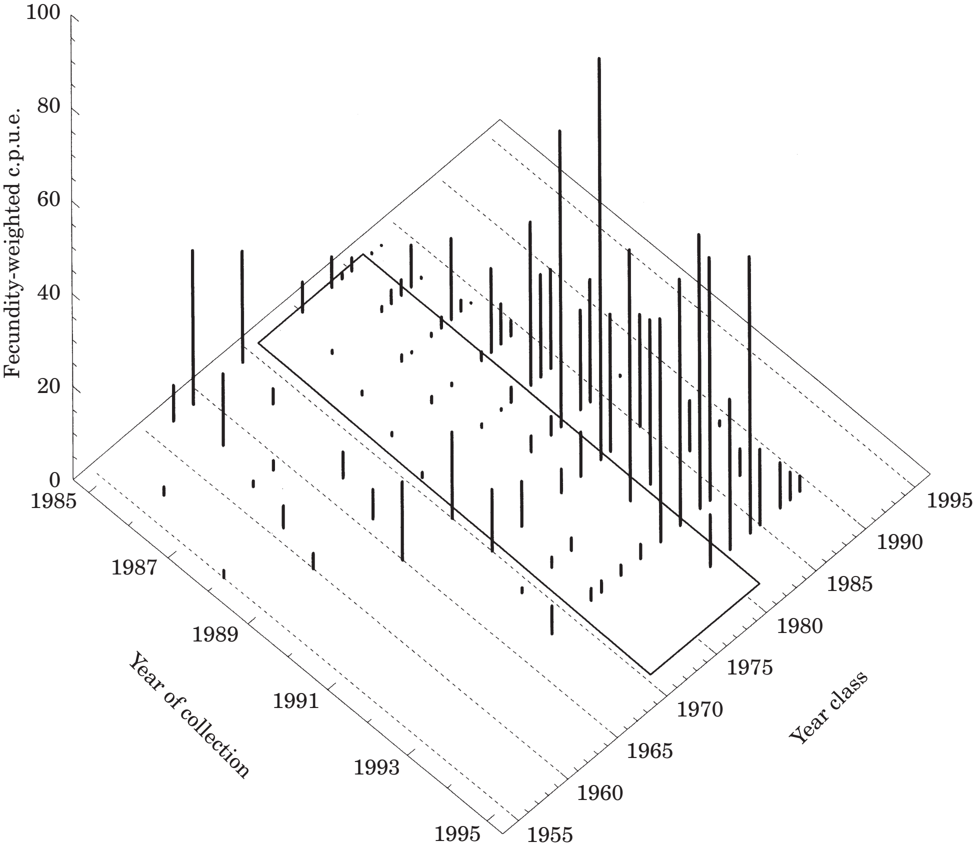

Figure 4. Temporal pattern of year-class contributions to potential egg productions (c.p.u.e.$_F$) in the Choptank River, Maryland. Year class is predicted based upon corrected scale ages (t_{ot}). White rectangular area on graph indicates nominal missing generation.

levels. A similar pattern was observed in the Choptank and Potomac Rivers, where missing generation contributions were absent or low except for 1979–1981 year class contributions during 1990–1995. Proportionately high c.p.u.e.$_F$ values (>30% of the year's potential egg production) were attributable to old generation females during the period 1985–1987 in all systems (Fig. 6). Relatively high contributions by missing generation year classes occurred for 1985, a year of very low potential egg production, in the Choptank and Potomac Rivers. New generation females contributed most to potential egg production during the period 1987–1995. As indicated above, missing generation year classes (principally 1979–1981) had proportionately high c.p.u.e.$_F$ values for 1990–1995.

Discussion

Missing generation

The absence of year classes 1972–1981, observed in the age-structure of "Trophy" striped bass, was a dramatic indication of past recruitment failure. While this sample of fish is biased towards older individuals, this should not alter the inference of a large gap in age structure. Given that females produced after 1981 were dominant in the distribution of ages, it seems unlikely that increased representation of smaller females would fill in the 1972–1981 year-class gap.

In contrast to the 1992 sample, MD DNR spawning stock assessments showed that some contribution to egg production by the "missing generation" did occur for 1985–1995 recruitments. However, this generation's abundances and potential contributions to annual egg production were relatively minor compared to old (1958–1971) and new (1982–1988) generations. Missing generation contributions mostly occurred from year classes 1979–1981. These year classes may have been misdesignated due to imprecision in adjusting scale-based ages.

The otolith–age vs. scale–age regression caused artificial gaps in age structure. Inclusion of slope variance could have been used to predict all age classes, but this would have artificially increased the number of age classes. The adjustment procedure probably resulted in reasonable estimates of generational year class

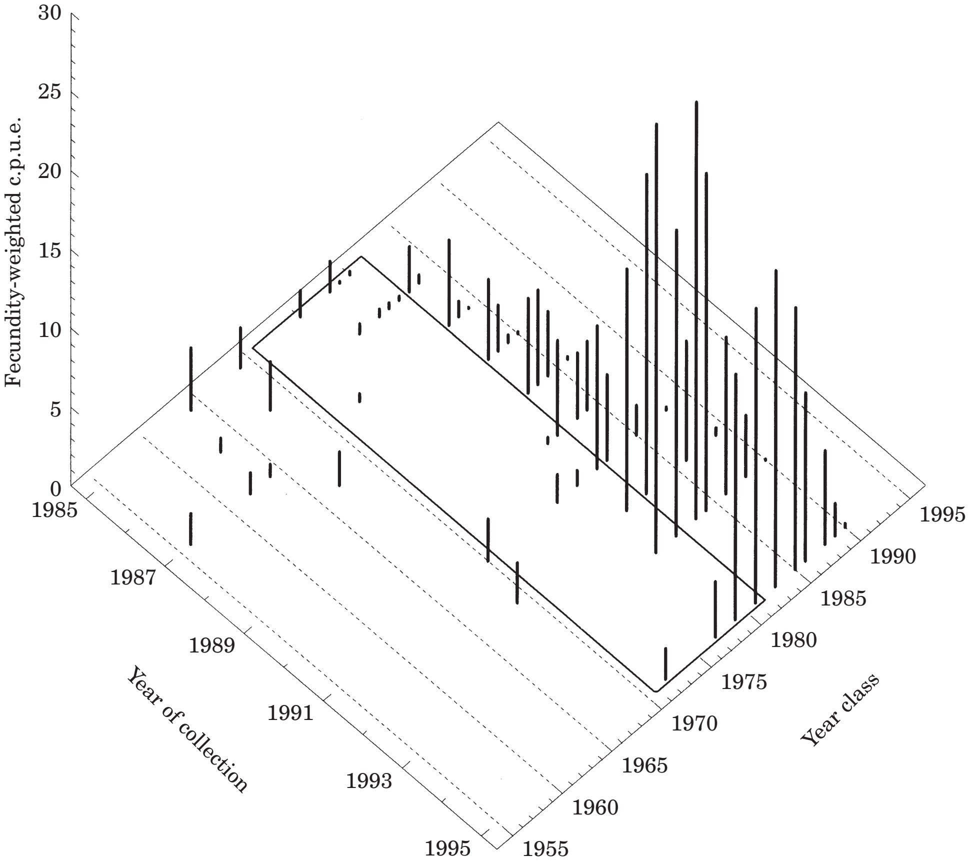

Figure 5. Temporal pattern of year-class contributions to potential egg productions (c.p.u.e.$_F$) in the Potomac River. Year class is predicted based upon corrected scale ages (t_{ot}). White rectangular area on graph indicates nominal missing generation.

designations of c.p.u.e. Still, on an annual level, year-class assignment was imprecise, particularly for those near generational boundaries (e.g. 1971–1972 and 1981–1982). Year-class 1979–1981 females could have been new generation striped bass which were erroneously placed into the missing generation category. Absence of missing generation females for sample years prior to 1990 supports this view.

Low abundances of missing generation females is consistent with the apparent lack of strong year classes during the 1972–1981 period (Fig. 7). Although the mean juvenile index for the missing generation was not significantly different than that of old or new generation striped bass (analysis of variance on geometric means; $p>0.05$), year-class abundances were typically low during this period. Early controversy on the cause of striped bass recruitment decline in the Chesapeake Bay contrasted effects due to overfishing and environmental degradation of nurseries (Goodyear, 1985a). The view that higher year-class strengths are due to improved habitats is inconsistent with exceptionally high year classes in 1989, 1993, and 1996. These strong year classes occurred without a demonstrable improvement of nursery habitats over the past 10 yr (Chesapeake Bay Program, 1995).

Striped Bass Moratorium

The primary goal of the MD Striped Bass Moratorium was to permit the 1982 year class, a moderately strong year class, to recruit fully into the spawning population. Strong contributions of the 1982 year class to potential egg productions were observed as early as 1987 (maturation of females ranges 4–8 years). The 1982 year class contributed >90% of egg production during 1989, when a high juvenile index was recorded. Declining contributions from old generation females and absence of significant contributions from missing generation females during the early 1980s indicated that the population was on the verge of collapse (ASMFC, 1990). Without protection of immature striped bass in the Chesapeake Bay, the reservoir of old generation striped bass could no longer be expected to support reproduction into the late 1980s.

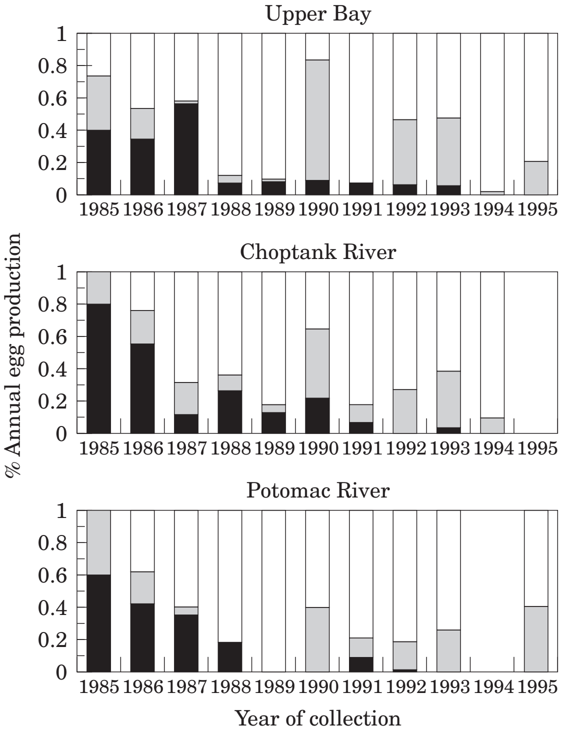

Figure 6. Relative contributions of generations of year classes to annual potential egg productions (1985–1995) for the Upper Bay, and Choptank and Potomac Rivers, Maryland. Black filled areas represent old generation (year classes 1955–1971), cross-hatched area represent missing generation (year classes 1972–1981), and open area represent new generation (year classes 1982–1993).

Historically (1924–1982), no creel limit occurred for Chesapeake Bay striped bass. Prior to 1990, the fishery was regulated chiefly through a slot limit and Maryland's fishery principally targeted striped bass less than 4 yr old. Minimum size limits were 25, 28, and 30 cm TL for the periods 1924–1953, 1954–1956, and 1957–1978, respectively. Female striped bass at these lengths are typically 2 yr old. A maximum weight limit of 6.8 kg (ca. 80–100 cm TL) began in 1941 and continued (the maximum size limit was changed to 81 cm TL in 1978) until 1990, when MD DNR began the spring "Trophy Season" (TL>91.4 cm). During the period 1962–1982, a limited commercial by-catch of fish over 6.8 kg was permitted. Demographic analyses showed that fish >5 yr in age were rarely caught and most harvested fish were 2 or 3 yr old (Merriman, 1941; Tiller, 1950; Vladykov and Wallace, 1952; Mansueti, 1961; Goodyear, 1985b).

Despite apparently high rates of exploitation of immature females, spawning stock biomass was still capable of producing good year classes throughout the 1960s (ASMFC, 1990). This was probably due to the maximum size limit. The immature females which survived 2–4 years of exploitation to become mature, and then reach sizes of ca. 6.8 kg were protected from exploitation. The maximum size limit served to protect old generation females from in-Bay exploitation throughout most of the 1970s and all of the 1980s.

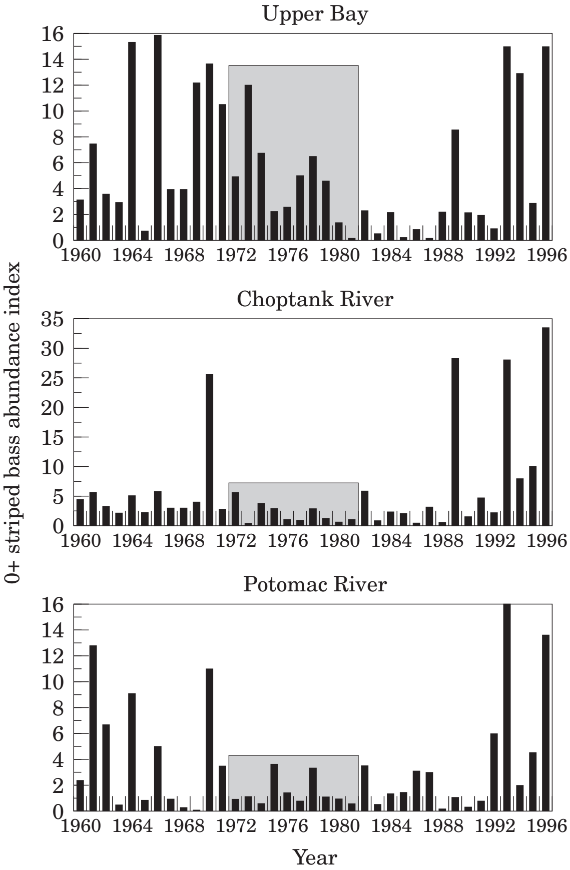

Figure 7. Indices of 0+ striped bass abundance for the Upper Bay, and Choptank and Potomac Rivers, Maryland. Missing generation year classes are designated by shaded boxes. Data from MD DNR (1996).

During the 1970s, improvement in fishing technology and a large increase in recreational anglers were viewed as possible causes of substantially increased rates of in-Bay exploitation (Florence, 1980; Goodyear, 1985a; ASMFC, 1990). Rates of fishing mortality were estimated to exceed 2.0 (ca. 90% yr^{-1}) during this period (Gibson, 1993). Thus under high rates of fishing from both commercial and recreational sectors, exploitation alone could have nearly extirpated entire year classes during 2–4 yr of in-Bay exploitation. High rates of fishing mortality on coastal stocks of immature and mature females (30 to 60% yr^{-1}; J. Boreman, National Marine Fisheries Service, Woods Hole, Massachusetts, pers. comm.) could also have contributed to the loss of 1972–1981 year classes. The Chesapeake Bay is the major contributor to coastal stocks (Merriman, 1941) and the coastal fishery historically had no size limits. Thus, females which survived to contribute to the coastal population (a proportion of the female population emigrates sometime after their third year of life (Dorazio *et al.*, 1994)) and subsequently recruited to the mature population would be fully exploited in coastal fisheries. Still, coastal exploitation rate during the 1970s was estimated to be substantially lower than in-Bay rates. For instance, 5 yr of in-Bay exploitation (F=2.0) would be expected to reduce a cohort by 22 000-fold. Whereas, 10 yr of coastal exploitation (F=0.35) would reduce a cohort by only 33-fold.

Old fish

The longevity of Chesapeake Bay striped bass found in our study surpassed that reported in the literature. Investigators have long suspected that large striped bass (e.g. >30 kg) were quite old but were not confident in using scale annuli for age determination. Merriman (1941) reported difficulty in assigning ages after 8 years using scales yet estimated that a 40-kg striped bass captured in Massachusetts coastal waters was 29–31 yr old. The two females I observed to be 31 yr old were 20–24 kg in weight. Because a systematic error occurred with scale ageing (Secor *et al.*, 1995), Merriman's fish could have been much older than he reported.

Longevity serves to increase the probability of individual replacement and population persistence. On an annual basis, it is clear that the probability of replacement for an individual female is quite low (Ulanowicz and Polgar, 1980; Secor and Houde, 1995; Secor, 2000). However, a population of 20- or 30-yr-old striped bass could replace itself by producing a good year class only once every 10–15 years. Apparently, for the Chesapeake Bay population, longevity as a life history tactic provided a degree of resiliency to long-term recruitment failure regardless of the cause of depressed or absent year classes. Current management practices in the US stipulate a 46-cm TL lower size limit, which provides an important measure of protection against recruitment overfishing.

For striped bass, longevity, high fecundities, and annual frequency of spawning (Secor and Piccoli, 1996) all serve to mitigate against the likelihood of annual failures in reproduction. Other anadromous species, for which moratoria or partial moratoria occur in the Chesapeake Bay (American shad, shortnose sturgeon and Atlantic sturgeon; Jensen, 1993) have much lower rates of lifetime reproduction (Carscadden and Leggett, 1975; Boreman, 1997) and are less resilient to series of poor annual recruitments.

Acknowledgements

J. Markham (MD DNR) assisted in the provision of data and reviewing this manuscript. Mark Trice assisted with striped bass collection and age determinations. Bunky's Charter Boat Service provided samples of trophy striped bass. This research was supported by the US Fish and Wildlife Service Emergency Striped Bass Study (F&W Contract 14-48-009-92-934 to Chesapeake Biological Laboratory). This is contribution no. 3275 of the University of Maryland Center for Environmental Science.

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