

Influence of Skipped Spawning and Misspecified Reproductive Schedules on Biological Reference Points in Sustainable Fisheries

DAVID H. SECOR*

Chesapeake Biological Laboratory, Center for Environmental Science, University of Maryland,
1 Williams Street, Post Office Box 38, Solomons, Maryland 20688, USA

Abstract.—During the spawning season, adult striped bass *Morone saxatilis* can occur outside known spawning tributaries. This phenomenon has been observed in other fishes, suggesting that investigators have misspecified reproductive schedules by assuming annual spawning. Across a range of species, skipped (i.e., nonannual) spawning is positively correlated with longevity. Therefore, reproductive schedules that are misspecified due to skipped spawning or poorly known age at maturation are likely for many moderately to extremely long-lived species. To explore the relevance of misspecified reproductive schedules on sustainable fisheries, a range of types of skipped spawning was modeled for the Chesapeake Bay striped bass population to test for effects on the biological reference point of egg production per recruit. The influence of misspecified reproductive rates was minor, particularly in relation to the effects of the two alternative size limits (46 and 71 cm) that are most commonly used in fisheries management. Among misspecification scenarios, reduced frequency of spawning later in life had the largest effect on reproductive rate. As fisheries management increasingly focuses on thresholds that promote resiliency, increased recognition of variation in reproductive schedules will probably place greater emphasis on conservation of age structure.

During their spawning season (April–June), anadromous striped bass *Morone saxatilis* in the mid-Atlantic region sometimes occur outside of their spawning tributaries. Evidence from electronic tagging, hydroacoustics, and otolith microchemistry have placed adult fish outside of spawning tributaries in North Carolina, Virginia, and Maryland during seasons of reproduction. In the Roanoke River, spring hydroacoustic surveys detected less than half the number of adults predicted for the 2001 run by Virtual Population Assessment (Hewitt 2003). In that same system, approximately 50% of the 19 females captured and released with biotelemetry tags into western Albemarle Sound during winter entered the adjacent Roanoke River during the next spring (Carmichael 1995; Carmichael al. 1998). For adults sampled from several Chesapeake Bay spawning tributaries, analysis of life history profiles

based on otolith Sr:Ca ratios indicated nonannual spawning in a minority of females (Secor and Piccoli 2007).

Increasingly state-of-the-art approaches, such as electronic tagging, bioacoustics, and otolith chemistry, are providing evidence that striped bass and other fishes sometimes occur outside their spawning areas during spawning seasons. The purpose of this paper is to provide a prospectus on the role of reproductive schedule misspecification in sustainable fisheries management by using Chesapeake Bay striped bass as a model.

Evidence supports the generality of skipped spawning (SS), particularly for long-lived migratory fishes with large energetic demands for reproduction (Rideout et al. 2005; Jørgensen et al. 2006). While the term SS is somewhat teleological, there is now precedence for its usage. Skipped spawning need not reference some deviation from an iteroparous fish's imperative to spawn every year, but SS ostensibly represents the investigator's misspecification of reproductive rates. Increasingly, SS has been observed in cases where a spawning migration is coupled with reproduction. More broadly, SS includes nonannual oogenesis, which can occur in both sedentary and migratory fishes (Rideout et al. 2005). Equipped with information from new discoveries on the spatial behaviors of individuals (Block et al. 2005; Able and Grothues 2007; Secor 2007), the focus of this paper is on striped bass and other species that as adults (or at assumed sizes at maturity) sometime occur in nonreproductive habitats during their expected spawning periods. Thus, delayed maturation is also included as a category of misspecified reproductive rates. Delayed maturation is a teleological term (again conforming to precedence) and represents the investigator's misspecification of maturation, which is probably variable and incompletely known.

Skipped spawning implies an iteroparous life history, which is common among migratory fishes. Iteroparity is favored when larval and juvenile mortality is high and unpredictable (Charnov and Schaffer 1973; Schaffer and Elson 1975; Secor 2007). Skipped spawning is modeled as the result of a trade-off between current and future reproduction (Bull and

* E-mail: secor@cbl.umces.edu

Shine 1979; Rideout et al. 2005). By foregoing spawning, an individual may incur survival and growth advantages in the current year to maximize its lifetime reproductive success. Therefore, SS is expected to be positively correlated with reproductive life span (Rideout et al. 2005).

Reproductive schedules and their misspecification have potential consequences for the effects of exploitation on population sustainability and recovery. Departures from assumed iteroparous reproductive schedules can range from a single missed spawning event early in life to extremely delayed maturity, emulating semelparity. Here, five classes of SS (Table 1) are introduced that have relevance to stock assessment and exploitation thresholds. These scenarios are applied to Chesapeake Bay striped bass to investigate how misspecified reproductive rates affect biological reference points and sustainable fishing rates.

Methods

To investigate SS patterns and their association with longevity, I examined species included in a review by Rideout et al. (2005) as well as additional species. Studies were selected based upon the lack of expected occurrence during a spawning migration or on a spawning ground. The focus was narrowed to the paired behaviors of spawning and migration, which have been highlighted in the recent literature, rather than on lack of spawning once the spawning ground had been reached. Approaches for identifying non-occurrence of spawning migrations include mark-recapture in sequential years (Schaffer and Elson 1975; Quinn and Ross 1985), comparison of adult abundances in foraging and spawning habitats (Bell et al. 1992; Livingston et al. 1997), electronic tagging (Carmichael et al. 1998), and microstructural or microchemical analysis of hard parts (Roussow 1957; Engelhard and Heino 2005; Secor and Piccoli 2007). Gross histological approaches were also included if they were applied to support nonannual spawning migrations (Kennedy 1953, 1954; Schwalme and Chouinard 1999). On a population basis, whether the same individuals consistently forgo spawning year after year or whether the pool of individuals that exhibit SS changes over time, the net effect on a population level is that spawning interval is the inverse of the SS fraction (e.g., if SS = 50%, then the population's spawning interval is 2 years). The proportion of SS was fit to the \log_{10} (maximum age) for each species, as obtained from FishBase (www.fishbase.org) and Carey and Judge (2002).

To evaluate the effects of misspecified reproductive rates on a fishery's sustainability, scenarios of

fecundity schedule, exploitation schedule, and SS were compared using the biological reference point of egg production per recruit (EPR). This rather elemental life table approach evaluates the sensitivity of reproductive rates to changes in demographic schedules and is a favored approach for many diadromous species (Dorazio 1995; Boreman 1997; Boreman and Friedland 2003; ICES 2006). This threshold is typically included in the suite of biological reference points against which stock assessments are compared and is particularly useful in establishing thresholds protective of recruitment overfishing (Goodyear 1989; Murawski et al. 2001; Fogarty and Gendron 2004). An important caveat in applying this reference point alone is the lack of inclusion of density-dependent changes in vital rates and recruitment (i.e., stock–recruitment relationships; Rochet 2000). To compute EPR, the value (E) of lifetime egg production under conditions of no exploitation is estimated as:

$$E = \sum_{t=1}^a N_t \times L_t \times S_t,$$

where N is cohort abundance, L is fecundity, S is the proportion of fish that are spawning, t designates age-class, and a is maximum age. In this instance, initial cohort size ($t = 1$) was arbitrarily set to 1 so that N_t is interpreted as survival probability to age t . Lifetime egg production under varying exploitation rates and reproductive schedules are then compared with E as a fraction, termed percent of maximum eggs per recruit or %EPR (Boreman 1997). Parameters and scenarios for the EPR analysis (Table 2) were simplified for the Chesapeake Bay striped bass population (i.e., assumptions were a constant rate of instantaneous annual natural mortality M , complete and instantaneous [knife-edge] maturity, and recruitment to the fishery at specified ages) to sharpen contrasts. Percent EPR was examined across a range of fishing mortality rates (instantaneous annual fishing mortality rate $F = 0.1$ – 0.4 ; annual fishing mortality rate = 10–33%).

Overfishing thresholds for %EPR are not stipulated across species, but precedence exists for a convention of 50% EPR for fishes with low lifetime reproductive rates (e.g., sturgeons, Acipenseridae), whereas 20% may be a protective threshold for a moderately long-lived, fecund marine species (e.g., Atlantic cod or striped bass; Mace 1994; Boreman 1997). The most recent fecundity schedule for Chesapeake Bay striped bass is based on data from 102 Choptank River females (75–119 cm total length) collected in 2001 (Richards et al. 2003). That study included a larger sample size and more representative length distribution than were used in previous fecundity schedule estimates (Mihursky et

TABLE 1.—Types of skipped spawning (SS; nonannual spawning and delayed maturation) in which absence of a fish's spawning migration has been observed. Hypothesized causes of SS types and consequences for population sustainability are speculated upon based on cited literature. Here, SS is used more narrowly than in previous reviews that also defined a lack of oogenesis on the spawning grounds as SS (Rideout et al. 2005; Jørgensen et al. 2006).

Type	Examples	Possible cause and consequences
Constant skipping	Modeling study on Arctic Atlantic cod <i>Gadus morhua</i> (Jørgensen et al. 2006); lake sturgeon <i>Acipenser fulvescens</i> (Roussow 1957)	Cause: An energetic threshold remains approximately constant with size and environmental variations, but is not met by annual energetic supply. Consequence: Constant spawning intervals have been applied to life table model approaches to estimate effects of exploitation on lifetime reproductive success (Beamesderfer et al. 1995; Gross et al. 2002) by decrementing annual fecundity by some fixed fraction ($100 - \%SS$). These models are insensitive to SS because the unexploited population and exploited population are affected by SS in the same way. If constant SS is occurring but not recognized, higher-than-expected recruitment at a given stock size will result.
Younger skipping	Modeling study on Arctic Atlantic cod (Jørgensen et al. 2006), for which the pattern of younger skipping overlays periodic pattern of skipping throughout life span; Chesapeake Bay striped bass (Secor and Piccoli 2007)	Cause: Initial spawning migration and reproduction require a disproportionate amount of stored energy in smaller, first-time spawners than in older adults. Maturation can also engender large physiological and behavioral transitions that cause first-time spawners to incur disproportionately greater costs. Consequence: Because reproductive rates are proportionately higher at young ages, younger skipping will shift the distribution of egg production to older ages.
Older skipping	Yellow perch <i>Perca flavescens</i> (Holmgren 2003); white sucker <i>Catostomus commersonii</i> (Trippel and Harvey 1988); Atlantic sturgeon <i>Acipenser oxyrinchus</i> and white sturgeon <i>Acipenser transmontanus</i> , for which carcasses of large females have been observed during the spawning season with no apparent agent of mortality (Blankenship 1997; Veinott et al. 1999)	Cause: Spawning and accessory costs scale positively to fish size. Such an effect could occur as large and old individuals approach asymptotic size and can no longer generate sufficient surplus production due to increased basal metabolic demands (Pauly 1981). The inability to recoup anaerobic debt incurred by spawning-related metabolism increases could be sublethal. For instance, increases in a 250 cm (total length) white sturgeon, full recovery of muscle glycogen stores is predicted to require over 5 d (Goolish 1991). Increased mortality risk with size could result in conservative energetic thresholds for spawning at older ages. Consequence: If egg production geometrically increases with fish size, SS in older fish could diminish the effective spawning stock biomass below expected levels (resulting in a higher realized recruitment level per spawner). Older skipping will shift reproductive rates to younger ages, leading to decreased generation times.
Event skipping	For white suckers (Trippel and Harvey 1988), environmental hypoxia precluded spawning in certain years	Cause: An episodic environmental event causes an entire population to undergo SS for a single calendar year. Consequence: The influence of event skipping on lifetime reproductive success will depend upon life span and is probably minimal in moderately long-lived species if such events are rare.
Delayed maturation	(Trippel and Harvey 1988) observed an extremely old white sucker (21 years) that had not yet spawned; Eastern Atlantic bluefin tuna <i>Thunnus thynnus</i> typically mature by age 3 (Corriero et al. 2005) but recent analysis by Block et al. (2005) indicated that some fish delay initial spawning until they reach ages >8.	Cause: Age and size at maturity show high phenotypic plasticity and are responsive to density and changing environments (Rijnsdorp 1989; Roff 1991). The same trade-offs between current and future reproduction that are acting on other SS types are probably also related to maturation delays. Alternatively, delayed maturation may indicate that a particular cohort or individual has never attained sufficient surplus production to enable spawning migration and reproduction. Consequence: Lifetime reproductive success is extremely sensitive to age at maturation (Roff 1992). In some species, delaying maturation even by 1–2 years can substantially depress lifetime reproductive rate.

al. 1987; Olsen and Rulifson 1992). The Chesapeake Bay ("southern group") maturity schedule constructed by Berlinsky et al. (1995) was used here because the study was recent and relied on an appropriately mixed

sample of both mature and immature individuals from Rhode Island coastal waters. The selected maturity schedule was modified according to the five differing reproductive schedules (Table 2).

TABLE 2.—Spawning fractions used for comparisons of egg production per recruit in Chesapeake Bay striped bass based on various scenarios of skipped spawning (SS). Fecundity schedule from Richards et al. (2003). Longevity and maturity schedules are from Secor et al. (1995) and Berlinsky et al. (1995).

SS scenario ^a	Age							
	3	4	5	6	7	8	9	
Baseline (B) ^b	0	0.12	0.34	0.77	1.0	1.0	1.0	
Skip 50% early (E)	0	0.06	0.17	0.39	0.50	1.0	1.0	
Skip 50% late (L)			50% annual spawning after age 20					
Skip after first spawn (V)	0	0.12	0.22	0.55	0.57	0.77	1.0	
Delay by 1 year (D)	0	0	0.12	0.34	0.77	1.0	1.0	
Accelerate by 1 year (A)	0.12	0.34	0.77	1.0	1.0	1.0	1.0	

^a Two minimum size limits for harvest by the fishery were modeled: 46 cm total length (knife-edge recruitment at age 4) and 71 cm total length (knife-edge recruitment at age 8).

^b Baseline longevity was 35 years; natural mortality for ages 1–35 was assumed constant at 0.09 (instantaneous annual rate); baseline spawning frequency was annual.

Results and Discussion

Longevity and Skipped Spawning

Twenty-one marine and freshwater species were identified as exhibiting SS, and the annual SS rate (percent of sample) ranged from 9% to 86% (Figure 1). The 21 species represent a diverse set of fishes, most of which are important to commercial and recreational

fisheries or are threatened or endangered. A linear regression was fitted to the data:

$$\%SS = -33.76 + [50.85 \times \log_{10}(\text{maximum age})]$$

($r^2 = 0.47$, $n = 21$, $P = 0.001$). Freshwater and marine taxa did not deviate in the association between %SS and longevity, but sturgeons represented extreme

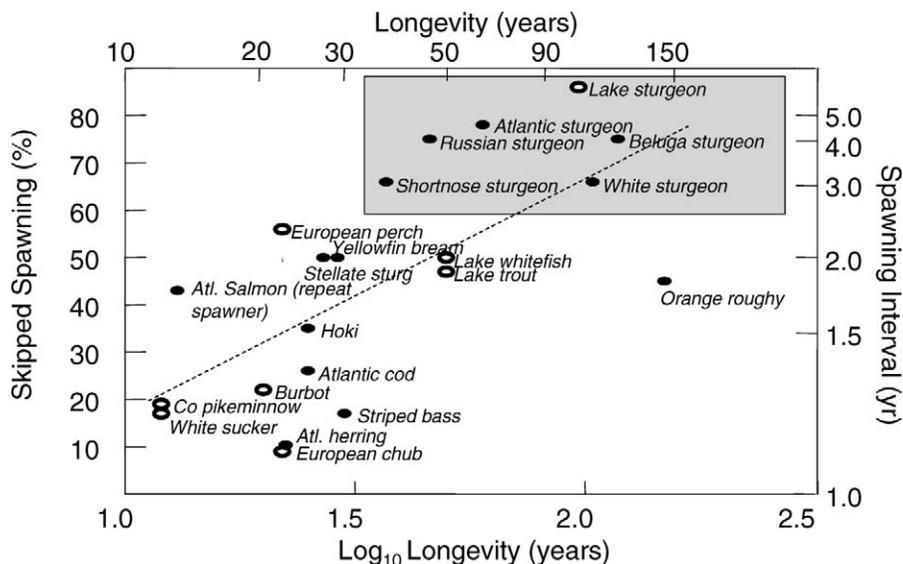


FIGURE 1.—Relation between skipped spawning (SS; expressed as percent of sample) or related spawning interval (years; $100/[\%SS]$) and longevity (years) in marine (shaded symbols) and freshwater (open symbols) fish species (dotted line = linear regression slope). The gray box delineates sturgeon data. Species include European chub *Leuciscus cephalus* (Fredrich et al. 2003); striped bass (Carmichael 1995; Hewitt 2003); white sucker (Trippel and Harvey 1989); Colorado pikeminnow *Ptychocheilus lucius* (Tyus 1990); burbot *Lota lota* (Pulliainen and Korhonen 1990); Atlantic cod (Schwalme and Chouinard 1999); hoki *Macruronus novaezelandiae* (Livingston et al. 1997); Atlantic salmon *Salmo salar* (Schaffer and Elson 1975); orange roughy *Hoplostethus atlanticus* (Bell et al. 1992); lake trout *Salvelinus namaycush* and lake whitefish *Coregonus clupeaformis* (Kennedy 1953, 1954); Atlantic herring *Clupea harengus* (Engelhard and Heino 2005); stellate sturgeon *Acipenser stellatus*, Russian sturgeon *Acipenser gueldenstaedtii*, and beluga sturgeon *Huso huso* (Secor et al. 2000); yellowfin bream *Acanthopagrus australis* (Pollock 1984); European perch *Perca fluviatilis* (Holmgren 2003); shortnose sturgeon *Acipenser brevirostrum*, white sturgeon, and Atlantic sturgeon (Gross et al. 2002); and lake sturgeon (Roussow 1957).

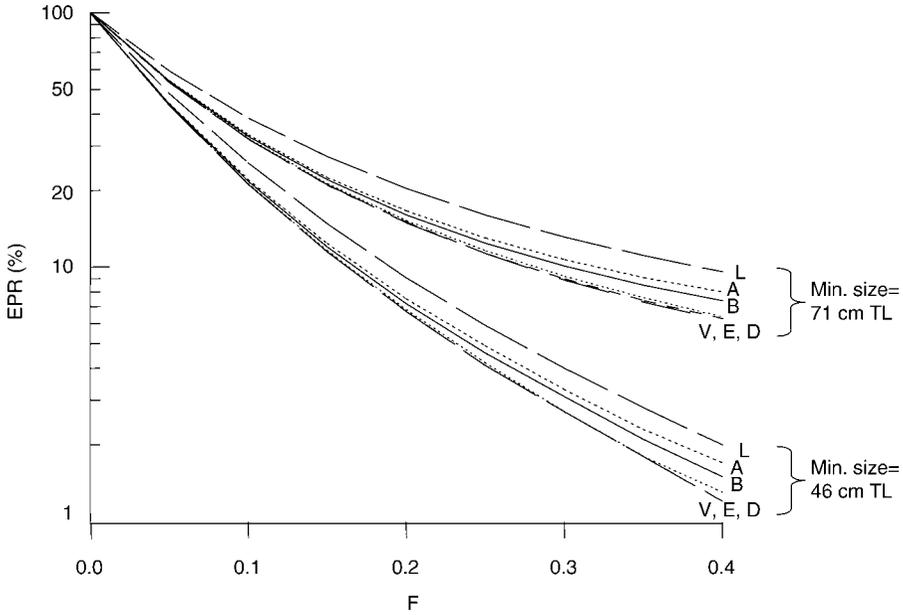


FIGURE 2.—Egg production per recruit (EPR) in a simulated population of Chesapeake Bay striped bass across a range of fishing mortality rates (F) for scenarios of skipped spawning, maximum fecundity, and two minimum harvestable size limits (46 and 71 cm total length [TL]). See Table 2 for code definitions and scenario descriptions.

values for both longevity and %SS (analysis of covariance [ANCOVA]: $P > 0.10$). Indeed, removal of sturgeon species resulted in a nonsignificant correlation ($P = 0.14$). In aquaculture, sturgeons also do not reproduce annually, indicating that oogenesis may require several years in this group (Doroshov et al. 1997; Williot et al. 2005). Still, the absence of annual reproduction is associated with a lack of annual spawning migrations in sturgeons (Chapman et al. 1996; Erickson and Webb 2007). For actinopterygian fishes other than sturgeons, SS was less than or equal to 50%, indicating that most fishes probably spawn at intervals once every 2 years or less.

In an earlier literature review, Bull and Shine (1979) proposed that skipped reproduction in vertebrates results from migration and other “accessory” costs of reproduction (i.e., those associated with brood care and livebearing). Although parental care systems are frequent and diverse among fishes, migration is emphasized here because it is the principal accessory cost associated with reproduction by striped bass and other migratory marine fishes. The spawning migrations of anadromous species such as striped bass are well known to be seasonally directed behaviors (Carmichael et al. 1998; Secor and Piccoli 2007) that exceed hundreds of kilometers on an annual basis (e.g., Waldman et al. 1990). Migration is therefore expected to entail a significant accessory cost for striped bass,

which could lead to SS or other changes in their reproductive schedule.

Misspecified Reproductive Rates and Biological Reference Points

All scenarios of misspecified reproductive schedules had small to moderate effects on %EPR (Figure 2). Constant SS throughout life produced the same EPR curve as the baseline condition of no skipping (see Table 1) and is therefore not shown. Responses of EPR to fishing mortality were similar across all SS scenarios for each fishery type except for the scenario in which adults older than 20 years reproduced once every second year (termed “skip 50% late” in Table 2). In that case, a moderate shift toward a higher EPR was observed. The shift occurs due to the reduced role of older age-classes in lifetime reproductive rates. Thus, if older fish contribute less to egg production, an increased number of younger adults can be removed on a sustainable basis. This effect was moderate: a 9% increase in F under an EPR of 20% (F_{20}) at the smaller size limit (46 cm) and a 25% increase in F_{20} at the larger size limit (71 cm; Table 3). Contrasting the sustainable fishing rates between the two minimum size limits also highlights the influence of older striped bass on reproductive rates. At the larger, 71-cm size limit, reproductive rates were twofold higher at an F of 0.2 and threefold higher at an F of 0.3. The sensitivity of F_{20} to diminished values of older adults

TABLE 3.—Biological reference points for annual fishing mortality (F) at 20% egg production per recruit (F_{20}) under six scenarios of skipped spawning (SS; codes are defined in Table 2) and two minimum sizes (total length) for harvest by the fishery for Chesapeake Bay striped bass.

SS scenario	F_{20} at 46 cm	F_{20} at 71 cm
B	0.11	0.16
E	0.10	0.16
L	0.12	0.20
V	0.10	0.16
D	0.10	0.16
A	0.11	0.17

through removal of either eggs (older SS) or individuals (harvesting at a lower size limit) suggests that long life span coupled with annual spawning contributes a buffering effect against early changes to reproductive schedules. Other realistic scenarios of misspecified reproductive rates had differing effects; however, under the principal assumption of a relatively long life span (35 years), the effects on threshold F were proportionately minor.

In many species for which spawning is linked with migration behavior, state-of-the-art approaches for understanding migration (e.g., electronic tagging, hydroacoustics, and otolith microchemistry) will probably challenge current stock-level specifications of age at maturation, frequency of spawning, and reproductive life span that drive biological reference points (Marshall et al. 2003). For those species studied here, SS is associated with moderate to high longevity (>15 years) and is probably less than 50% per year for actinopterygians other than sturgeons. More important than misspecification of early reproductive schedules is the influence of older adults on lifetime reproductive rates; the age-mediated change in reproductive rates is known as the storage effect (Secor 2000, 2007; Frank and Brinkman 2001; Berkeley et al. 2004). As fisheries management increasingly focuses on thresholds that promote resiliency, increased recognition of variation in reproductive schedules will probably place greater emphasis on conservation of age structure.

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