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Multiple spawning and the dynamics of fish populations: inferences from an individual-based simulation model

Susan K. Lowerre-Barbieri, James M. Lowerre, and Luiz R. Barbieri

Abstract: We used an individual-based Monte Carlo simulation model to assess how aspects associated with multiple spawning (within a spawning season) affected survivorship, lifetime fecundity, cohort egg production, and yield-per-recruit of a highly exploited species. To make our model more realistic, we included and tested the effects of individual variability in growth and a seasonal growth pattern. Birth months influenced when fish first matured and became vulnerable to the fishery. There was a sixfold increase in mature fish at the beginning of their first spawning season associated with having been born early versus late the previous season. Early born fish had a lower average life-span than later born fish. Although early born fish had lower survivorship they produced the most eggs because of an early size at first maturity, low fishing mortality in the first year, and their larger size at age. These results suggest multiple spawning can have important implications for recruitment and adult population dynamics.

Résumé : Nous avons utilisé un modèle de simulation Monte Carlo fondé sur l'individu pour évaluer comment les aspects connexes au frai multiple (au sein d'une saison de frai) influent sur la survie, la fécondité pendant la durée de vie, la production d'oeufs de la cohorte et le rendement par recrue d'une espèce fortement exploitée. Afin de rendre le modèle plus réaliste, nous avons inclus et testé les effets de la variabilité individuelle de la croissance et d'un régime de croissance saisonnier. Le mois de la naissance influe sur le moment où le poisson devient mature et vulnérable à la pêche. Il y avait une augmentation par un facteur de six des poissons matures au début de leur première saison de frai qui découlait du fait qu'ils étaient nés tôt, comparativement à tard au cours de la saison antérieure. Les poissons nés plus tôt présentaient une durée de vie moyenne inférieure. Bien que les poissons nés plus tôt avaient un taux de survie inférieur, ils produisaient le plus d'oeufs à cause d'une taille à maturité atteinte plus tôt, d'une faible mortalité par pêche au cours de la première année et d'une taille à l'âge plus importante. Ces résultats portent à croire que le frai multiple peut avoir des incidences importantes pour le recrutement et la dynamique de la population adulte.

[Traduit par la Rédaction]

Introduction

Although it has become increasingly recognized that managers need information on how fishing affects reproductive output (Prager et al. 1987; Murphy et al. 1994; Schirripa and Goodyear 1994), traditional models rarely incorporate the dynamic patterns of multiple spawners. This is due in part to the fact that scientists have only recently realized many fish have indeterminate fecundity (Hunter et al. 1985). Prior to this, it was assumed that most fish had determinate fecundity, i.e., annual fecundity can be estimated from the standing stock of advanced oocytes within the ovary before spawning has been initiated (Hunter et al. 1985). In addition, it was assumed that egg production was proportional to spawning biomass. However, more recent work has indi-

cated that numerous species are multiple spawners with indeterminate fecundity (e.g., northern anchovy, *Engraulis mordax* (Hunter and Macewicz 1985); bay anchovy, *Anchoa mitchilli* (Luo and Musick 1991); Atlantic croaker, *Micropogonias undulatus* (Barbieri et al. 1994)), which continuously mature new spawning batches throughout a typically protracted spawning season. For these species, spawning biomass cannot be assumed to be a good indicator of annual reproductive potential (Parrish et al. 1986).

The multiple spawning pattern of these fishes affects their life history in a number of important ways. For example, the extended spawning period of most multiple spawners (regardless of whether they have determinate or indeterminate fecundity), in conjunction with the plasticity of fish growth, insures a large size-at-age range. This large range of sizes at age will affect when fish mature, with individual fish often maturing at different months within a spawning season or even different years (Luo and Musick 1991). It will similarly affect when fish first become vulnerable to capture in a managed fishery with minimum size limits, which may cause differential adult survivorship associated with birth date (i.e., early or late in the spawning season) and hence affect the size and age composition of the breeding population and potentially drive the evolution of the stocks (Law and Grey 1989; Murphy et al. 1994).

Because fecundity of a multiple spawner is determined by

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S.K. Lowerre-Barbieri¹ and L.R. Barbieri.¹ University of Georgia Marine Institute, Sapelo Island, GA 31327, U.S.A.
J.M. Lowerre. 5607 Ravenel Lane, Springfield, VA 22151, U.S.A.

¹Present address: Tequesta Field Laboratory, Florida Marine Research Institute, Florida Department of Environmental Protection, 19100 SE Federal Highway, Tequesta, FL 33469-1712, U.S.A.

size at first maturity, batch fecundity, spawning frequency, and seasonal spawning duration, there is potential for a much higher level of variability than with determinate fecundity. Batch fecundity and first maturity are both closely related to size and will vary because of multiple spawners' wide size-at-age range. Batch fecundity-at-size has also been shown to vary individually and for some species to vary between seasons (Hunter et al. 1985; Kjesbu et al. 1996). In addition, spawning frequency and duration have been found to vary within season and between seasons (Kjesbu et al. 1996; Lowerre-Barbieri et al. 1996b), as well as by age (Parrish et al. 1986) and individually (Kjesbu et al. 1996).

Traditional yield- and eggs-per-recruit models, although useful, greatly oversimplify how fishing affects multiple spawners. These models combine many individuals into one group (i.e., all fish of a particular age or size), assuming these fish will mature, spawn, grow, and die at the same rates over their life-spans. Although this level of aggregation may produce worthwhile results depending on the questions being asked, ecologists have become aware that individual variability can have a decisive influence on population dynamics and that populations exhibiting substantial individual variation in characteristics important to survival might better be analyzed at a lower level of aggregation (Crowder et al. 1992; Rice et al. 1993).

Based on these considerations, we developed an individual-based Monte Carlo simulation model (IBM) to assess how various aspects associated with multiple spawning affect survivorship, lifetime fecundity, cohort egg production, and yield-per-recruit (YPR). Input data came from a 4-year field study of weakfish, *Cynoscion regalis*, conducted in Chesapeake Bay (Lowerre-Barbieri 1994). Our reasons for choosing an IBM were twofold: (i) we were specifically interested in incorporating the individual variability observed in both growth and reproductive parameters of multiple spawners; and (ii) the flexibility of this modeling approach made it relatively easy to incorporate a large degree of biological detail in the current model, as well as to augment it in the future. Our overall objective was to build as realistic a model as possible, given the available data. Using a set of baseline parameters, we looked at how fishing and reproduction interacted both at the cohort and individual level (i.e., when fish matured and became vulnerable to the fishery and how birth date affected survivorship and fecundity). We then tested how different aspects of this model affected estimates of yield and egg production. Specifically, we addressed (i) the effect of a large range of size at age on vulnerability to the fishery and time of maturity; (ii) the effect of individual variability in growth on yield and egg production; (iii) the interaction between seasonal growth and an extended spawning season; (iv) the effect of differential reproductive output within the spawning season (e.g., more eggs produced at the beginning or end of the season); and (v) differential survivorship.

We chose to model weakfish because it is a multiple spawner with indeterminate fecundity and an extended spawning season and because detailed reproductive data were available (Lowerre-Barbieri et al. 1996a, 1996b). Weakfish are most abundant and heavily exploited in waters of the Atlantic from North Carolina to New York. Although weakfish are considered a unit stock, they are highly migra-

tory, overwintering off of North Carolina and in the spring moving northward and inshore to estuarine feeding and spawning grounds. Because of this pattern, they may experience differing fishing pressure depending on season and location, similar to a number of other commercially and recreationally important species along the east coast of the United States.

Methods

Model description

Using a Monte Carlo simulation, individual adult growth, mortality, and egg production of a weakfish year-class were followed on a monthly basis. To keep computing time and the amount of output data reasonable, simulations were based on 4000 fish. Simulations started on January 1 of the first year of life and ran for 25 years (maximum reported age under high exploitation is 17 years; Lowerre-Barbieri et al. 1995). We assumed age-1 fish were made up of four subcohorts, corresponding to birth months, as weakfish spawn from May to August (Lowerre-Barbieri et al. 1996a). To focus on the effect of birth date without the potentially confounding effect of differential growth, we assumed all subcohorts exhibited the same growth rate from birth to January 1.

Each subcohort had a different mean size at age 1 (L_1), with earlier born subcohorts being larger than late-born ones. We assumed that the predicted von Bertalanffy TL at age 1 (178 mm based on fish collected in April and May; Lowerre-Barbieri et al. 1995) was a good estimate of mean L_1 on May 1. Because it is difficult to daily age Chesapeake Bay weakfish (Szedlmayer et al. 1991), it was not possible to assign birth dates to these fish. Therefore, we assumed that mean L_1 corresponded to an average birth date, which was assumed to be in the middle of the spawning season (30 June) making them 304 days old. Based on this estimate, we calculated an average daily growth rate of 0.59 mm per day (i.e., 178 mm TL/304 days) and applied it to subcohort-specific ages using a midmonth birth date, resulting in the following L_1 s: (i) 207 mm TL for May; (ii) 188 mm TL for June; (iii) 171 mm TL for July; and (iv) 152 mm TL for August. Individual L_1 s for each subcohort were then simulated based on a random sample from a bivariate normal population with the given means and a coefficient of variation (CV) of 10%. This CV was chosen because it generated what we considered a conservative range of L_1 s (100–260 mm TL), based on our field observations (140–255 mm TL; Lowerre-Barbieri et al. 1995) and those reported by Chao and Musick (1977) for April and May (65–330 mm TL; 1977).

Growth was simulated using a seasonally modified von Bertalanffy growth model and compared with that based on the regular von Bertalanffy growth curve. We chose to incorporate this because most temperate water fish demonstrate seasonal growth (Moreau 1987). However, the weakfish migrational pattern makes it difficult to obtain data on seasonal growth (Lowerre-Barbieri et al. 1995). Based on weakfish life history and Chesapeake Bay water temperatures, we modeled growth to be zero in December and maximum in June. Seasonal growth curves were estimated using the following equation:

$$l_t = L_\infty(1 - e^{-K(t-t_0) + \frac{6K}{\pi} \left[\sin\left(\frac{\pi}{6}(t-12)\right) - \sin\left(\frac{\pi}{6}(t_0-12)\right) \right]})$$

where l_t is the length at time t , L_∞ is the asymptotic length, K is the Brody growth coefficient, t_0 is the hypothetical time at which length equals zero, t is the time in months.

Three TLs per month were calculated for each fish: at the beginning of the month, the end of the month, and the mean for the month (the average of these two). An estimated annual t_0 of -0.13 and a mean L_∞ of 919 mm TL (Lowerre-Barbieri et al. 1995) were

used for all fish because there is no data on subcohort-specific growth. The annual t_0 was converted to a monthly t_0 to conform to the model's time frame. Individual L_∞ s were simulated with the given mean, a CV of 10%, and a 0.95 correlation between individual L_1 s and L_∞ s. This generated a reasonable range of L_∞ s (550–1250 mm TL; maximum reported TL when highly exploited is 960 mm TL (Villoso 1989) and weakfish have a large size-at-age range). Individual Brody growth coefficients (K) were then generated based on the given t_0 , L_1 , and L_∞ for each fish.

Whether a fish died in any given month was dependent on its size and the monthly natural mortality (M) and fishing mortality (F) rates. If a fish's TL was $< TL$ at first capture (l_c), then the probability it died was calculated as $1 - e^{-M}$. If its TL was $> l_c$, then the probability it died was calculated as $1 - e^{-(M+F)}$. For a fish that died, the probability it was caught was calculated as $F/F + M$. Because of a lack of data, M was assumed to be evenly distributed over the year and throughout a cohort's life-span. A monthly M of 0.0167 was used, which corresponds to an annual rate of approximately 0.20 (Lowerre-Barbieri 1994). There are no published estimates of total mortality (Z) or F for weakfish in Chesapeake Bay. The most recently reported is a mean Z of 1.08 for the years 1956–1958 (Vaughan et al. 1991). We chose to use this, although outdated, as it was similar to the recent coastwide annual Z of 1.2, and weakfish are considered a unit stock (Vaughan et al. 1991). Because there are fewer fisheries targeting weakfish during November–March (the months when weakfish are migrating or overwintering off North Carolina), we assumed a lower F . Thus, an annual F of 1.08 was broken down to a monthly F of 0.114 for April–October (the months most weakfish occur in Chesapeake Bay) with a 50% decrease in F (0.057) in November–March.

Size at first capture also differed temporally (i.e., whether it was a month in which weakfish occurred in Chesapeake Bay or not). For April through October, l_c was set at 305 mm TL (12 in.) based on the 1993 minimum size regulations in the Chesapeake Bay region of 305 mm TL in Maryland and 305 mm for recreational and gill nets in Virginia. Based on the landings reported from the North Carolina winter trawl fishery (Ross 1991), we chose a conservative l_c of 200 mm TL for November through March. Recruitment to the fishing gear was assumed to be knife-edged.

Spawning was initiated if a fish was alive during a month within the spawning season (May–August) and the fish was mature. The size-at-first-maturity range was based on field studies in which females < 170 mm TL were immature and > 210 mm were mature (Lowerre-Barbieri et al. 1996a). Thus, within the spawning season the probability a fish was mature was assigned as (i) 0% if TL < 170 mm; (ii) 50%, if $170 \text{ mm} < \text{TL} < 210 \text{ mm}$; and (iii) 100% if TL > 210 mm. Once a fish initiated spawning it continued to spawn. All fish were assumed to be female.

Batch fecundity (BF) was based on an individual fish's mean monthly TL and a field-generated BF to TL relationship (Lowerre-Barbieri et al. 1996b). The relationship used was

$$\text{BF} = -349\,558 + 1544 \text{ TL} \quad R^2 = 0.53, n = 62$$

Although this function was linear for the size range sampled (296–429 mm TL), BF to TL is most likely nonlinear at smaller sizes (e.g., this relationship predicts negative BF for fish < 226 mm TL). Thus, a correction factor was used for mature females between 170 mm and 226 mm TL. Batch fecundities for these smaller fish were estimated by multiplying the predicted BF of that fish in the same month at age 3 (age when all fish are big enough to produce a positive BF) by the following ratio:

$$\frac{\text{TL}_{\text{current}} - 170}{\text{TL}_{\text{age3}} - 170}$$

where 170 mm TL is the size at which a fish can first become mature.

Monthly egg production of mature fish was calculated as BF times spawning frequency. Individual monthly spawning frequencies were simulated based on a random sample from a bivariate normal population with a season-long mean spawning frequency of one spawn every 3 days or 10 times per month (Lowerre-Barbieri et al. 1996b) and a CV of 10%. Individual annual egg production was calculated as the summation of monthly egg production over the spawning season (May–August).

Model output

The model, based on the above calculations, was adapted to generate two different types of output: (i) summary statistics, both annual and for the cohort as a whole, and (ii) output for individual fish. For simplicity, we will refer to these as the production version (summary statistics) and the individual version. To make statistical comparisons, the production model was programmed to execute 30 runs using the same input data (i.e., growth parameters, etc.), changing only the initial random number seed. This run size was chosen a priori because a sample size of 30 approximates the normal distribution (Lindgren 1976). Output was saved separately for each run and consisted of egg production, spawning biomass, number of fish that died naturally, number caught, number still alive, and yield for each year the program ran. Yield was calculated as the summation of individual total gutted weights of caught fish. Total gutted weight (TGW) refers to total weight minus the stomach, as weakfish can eat fish up to a third of their own weight (Lowerre-Barbieri et al. 1995). Total length (mm) was converted to TGW (g) using the equation from Lowerre-Barbieri et al. (1995):

$$\text{TGW} = 4.7 \times 10^{-6} \text{ TL}^{3.13} \quad R^2 = 0.99, n = 950$$

Yield per recruit (in grams) was calculated as total yield divided by the number of fish that did not die from natural mortality before reaching a catchable size (200 mm TL).

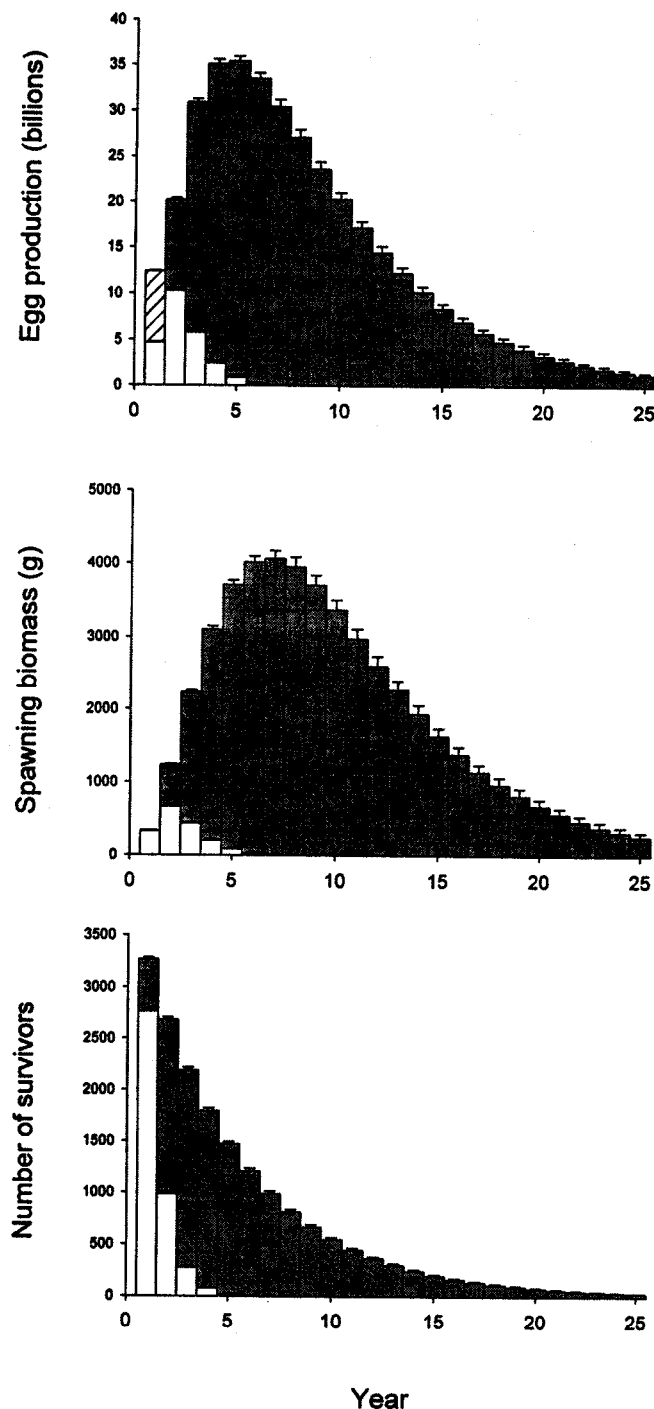
The individual version was run 10 times for each set of parameters being assessed. This number of runs was chosen to minimize the effects due to random variability, yet keep the amount of output data manageable. The individual version provided output for each fish consisting of: subcohort, status (alive, died naturally, caught), TL, TW, age in months, cumulative egg production, L_1 , and L_∞ .

Simulations

For baseline data, the models were run with F as outlined above, seasonal growth, equal subcohort sizes, individually variable growth, and fecundity calculated as the product of batch fecundity and spawning frequency (later sections will refer to the use of these parameters as the "baseline model"). These results were compared with those of a virgin stock. To explore the effect of this fishing regime on individuals, size at capture and month of capture were analyzed for each year fish survived. To evaluate the effect of individuals maturing at different times, egg production from the baseline model was compared with that if the model was run with all fish maturing before their first spawning season.

To evaluate the effect of individual variability in growth, the production model was run with subcohort-constant L_1 s and L_∞ s. This output was compared with that from the baseline parameters. The effect of individual variability in growth on when fish matured and became vulnerable to fishing was also examined by running the individual baseline model with no mortality. To assess when fish matured, the individual model was run for 5 months (beginning of the spawning season) and 8 months (end of the spawning season). To determine when fish became vulnerable to the Chesapeake Bay fishery, the model was run for 10 months (end of the first fishing season), 16 months (beginning of the second season), and 22 months (end of the second season). These results were then compared with those from the individual model when there was no variability in growth.

Fig. 1. Annual mean ($n = 30$ runs) egg production and spawning biomass ($\pm 1SD$) for a virgin (shaded bar) and fished (open bar) stock. Hatched bar indicates mean egg production in year 1 of a fished stock if all fish matured by the beginning of their first spawning season.



Similarly, to evaluate other effects, specific parameters were changed (as outlined below), while the remainder of the parameters were kept at their baseline values. Seasonal growth was evaluated by running the production model with the regular von Bertalanffy curve. To evaluate the effect of subcohorts corresponding to the extended spawning season of a multiple spawner, the production model was run with all subcohorts having the same mean L_1 of 178 mm, and the output was compared with that of the baseline

model. Because spawning activity within the spawning season can vary, with peak egg production sometimes occurring early and in other years late in the season (Lowerre-Barbieri et al. 1996a), we assessed three theoretical subcohort regimes: (i) equal subcohort sizes ($n = 4000$); (ii) decreasing subcohort sizes with later birth months ($n = 3995$); and (iii) increasing subcohort sizes with later birth months ($n = 3995$). Decreasing subcohort runs had 50% fewer fish per subcohort for each consecutive birth month (i.e., May, 2130; June, 1065; July, 533; August, 267). Increasing subcohort runs had the opposite. The production model was run for each of these subcohort regimes for both a fished and virgin stock. To look at differential survivorship, the individual model was run for each subcohort regime for a fished stock.

Results

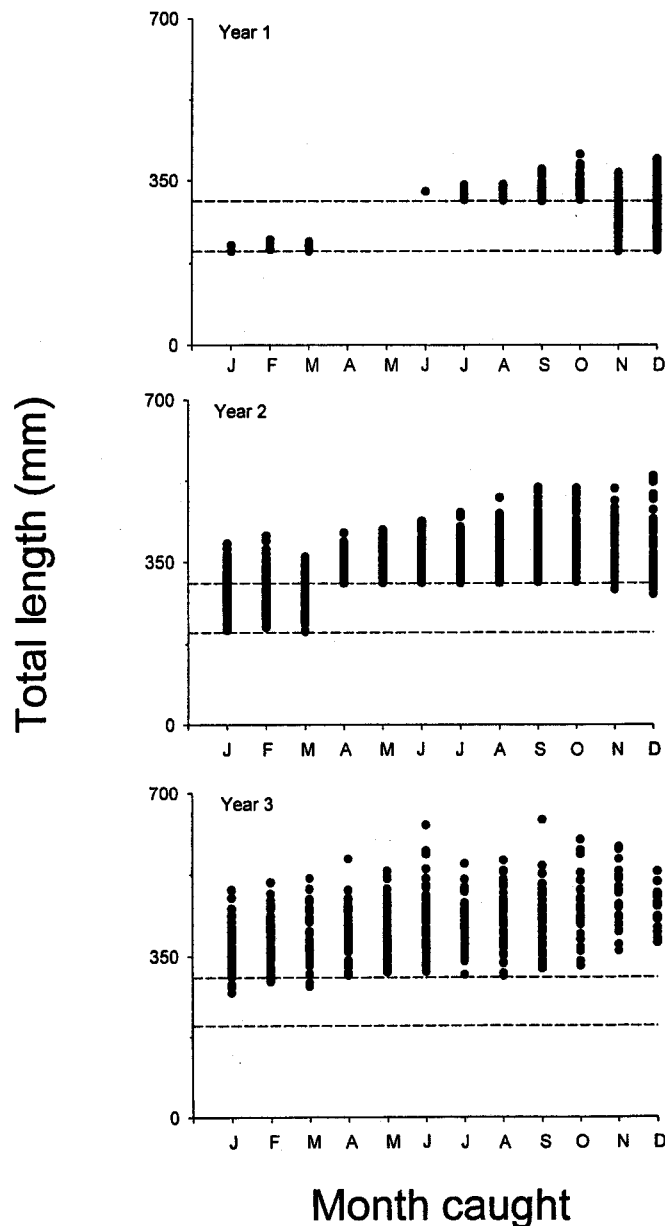
The baseline model

The baseline fishing regime greatly reduced egg production and the ages contributing to the spawning biomass (Fig. 1). Mean cohort egg production for a virgin stock was 358.3×10^9 eggs but varied by as much as 8.9% between runs. Fishing reduced egg production by 93%. In year 1, egg production by a fished stock was similar to that of a virgin stock, although the fished stock had an average of 16% fewer survivors (Fig. 1). The relative contribution this year-class made to cohort egg production, however, was 19 times greater for the fished stock than the virgin. In year 2 the fished stock's egg production peaked (10.3×10^9 eggs, 42% of cohort egg production), whereas virgin egg production was 20.2×10^9 eggs but only 6% of cohort egg production. Virgin egg production did not peak until year 5, while egg production by the fished stock was negligible by year 6 (<1%).

Although most fish were caught in their first 3 years of life, their vulnerability to fishing differed within each of these years ($F = 0.057$, $l_c = 200$ mm TL for November–March; $F = 0.114$, $l_c = 305$ for April–October) affecting egg production. Few fish were large enough to be caught during their first spawning season (Figs. 2 and 3). Although F decreased in November and December, most fish caught in year 1 (63%) were captured during these months because of the concurrent decrease in l_c (to 200 mm TL). In year 2, many fish were vulnerable in January–March (Fig. 2), effectively decreasing the number of 2-year-old spawners. By November most 2-year-olds were larger than the Chesapeake Bay l_c of 305 mm TL, so when F decreased, so did the number of fish caught (Fig. 3). By year 3, the smaller l_c in North Carolina had little effect, as most fish had grown past 305 mm TL (Fig. 2).

Birth date (subcohort) affected when fish became vulnerable to fishing (Fig. 4) and consequently their average life-span. Only age 1 fish born in May were large enough to be captured by the trawl fishery in North Carolina in January–March ($l_c = 200$ mm TL). No age 1 fish were large enough to be captured in April and May in Chesapeake Bay ($l_c = 305$ mm TL). However, May-born fish became vulnerable in June. In contrast, August-born fish were not caught until November and December when l_c again dropped to 200 mm TL. Consequently, the May subcohort had the lowest average life-span of 16.9 months and the August subcohort the longest average life-span of 20.8 months.

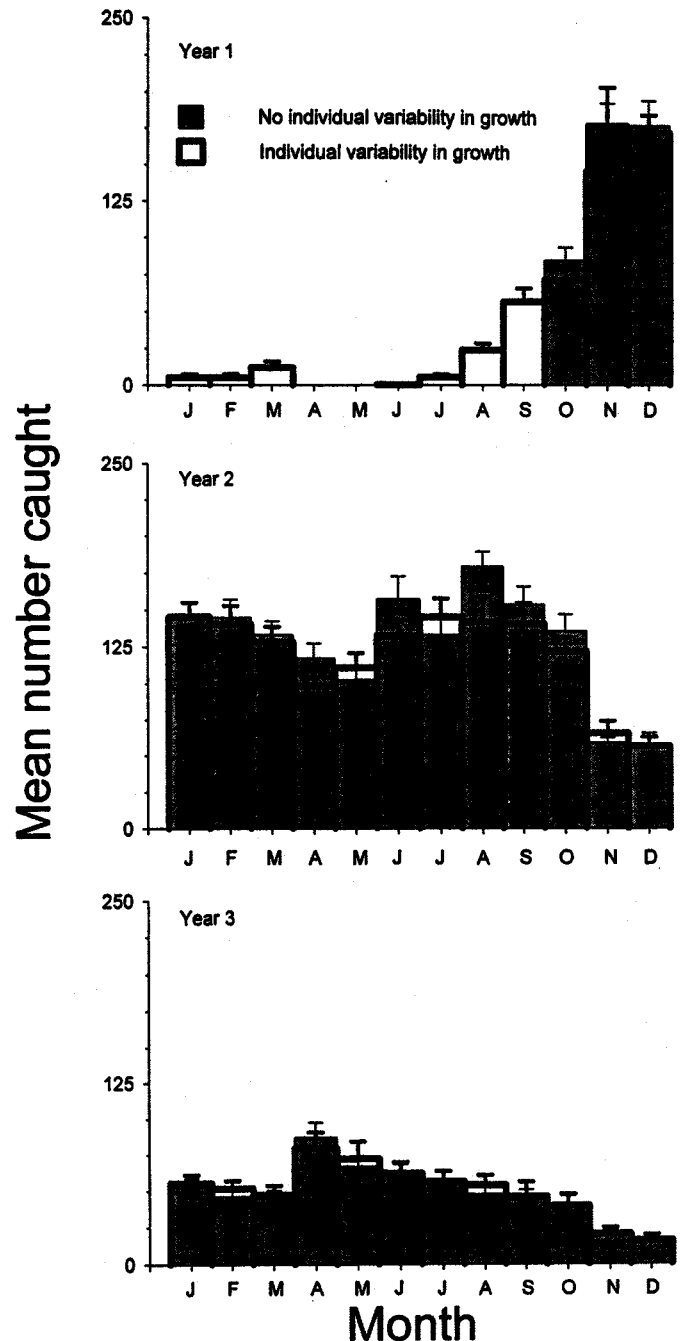
Fig. 2. Total length (TL) and month when individual fish (solid circles) were caught with baseline parameters for years 1–3. Broken lines are size (TL) at first capture of 200 mm during winter months and 305 mm in Chesapeake Bay.



Birth date also affected when fish matured, with August-born females maturing the slowest. Only 14% of August-born fish were mature by May of their first year compared with 80% of May-born fish. Similarly, all May-born fish matured by the end of the first spawning season but only 87% of August-born fish. Because of this and larger batch fecundities (due to larger body size), early born fish had greater average lifetime fecundities than later born (e.g., May born, 6.9×10^9 ; August born, 5.1×10^9).

This differential maturity affected which subcohort produced the most eggs and overall cohort egg production. Had all fish been mature by the beginning of their first spawning season, the June and July subcohorts would have had the greatest lifetime fecundities (June, 81.6×10^9 ; July, $83.2 \times$

Fig. 3. Mean number of fish caught ($n = 30$ runs) by month ($\pm 1SD$) in the first 3 years of life, with and without individual variability in growth.

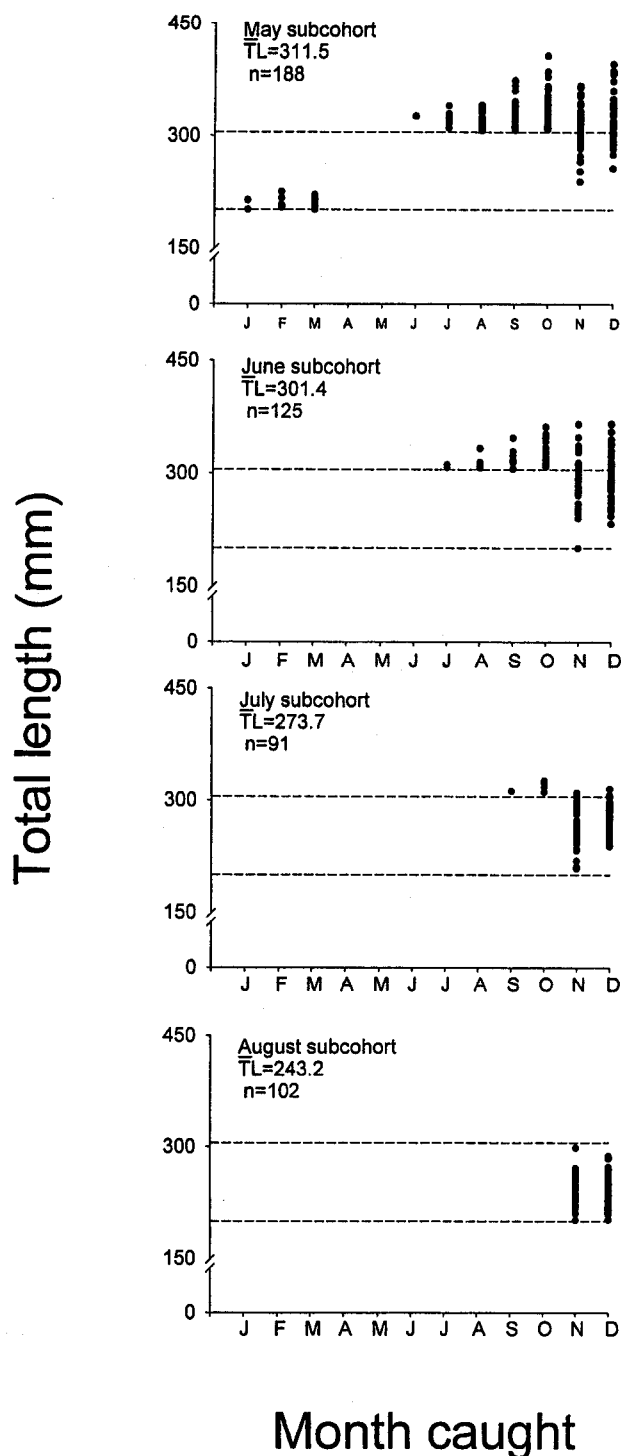


10^9) compared with early born (May, 80.1×10^9) and late born (August, 76.7×10^9). In addition, peak egg production would have been in year 1 and been more than double that with differential maturity (12.4×10^9 vs. 4.7×10^9 eggs), even though spawning biomass didn't peak until year 2 (Fig. 1).

Effect of individual variability in growth

Modeling all individuals in a subcohort with the same growth pattern resulted in higher egg production and YPR than when growth was modeled as individually variable

Fig. 4. Total length (TL) and month when individual age 1 fish (each dot) were caught by subcohort. The subcohort regime was equal sized. Broken lines are size (TL) at first capture of 200 mm during winter months and 305 mm in Chesapeake Bay. Number of fish caught and their mean TL are indicated for each subcohort.



(Fig. 5). Mean cohort egg production with subcohort-constant growth was 26.1×10^9 , significantly greater than 24.4×10^9 (t -test, $n = 60$, $P < 0.001$) with individually variable growth. Yield per recruit was also significantly greater

(t -test, $n = 60$, $P < 0.001$) with nonvariable growth (431.8 g) than when growth varied for individuals (422.3 g).

Although nonvariable growth still resulted in most fish being caught in the first 3 years of life and yield and egg production peaking in year 2, vulnerability to fishing differed somewhat. In year 1, nonvariable growth led to fewer fish being caught (Fig. 3) and a slightly higher egg production than with variable growth. This is primarily because with nonvariable growth fish did not become vulnerable to the fishery until October of their first year, while with variable growth some fish were vulnerable as early as January (Fig. 3). In addition, fish matured slightly faster with nonvariable growth, with 100% mature by the end of the first spawning season with nonvariable growth and 97% with variable growth. Catch rates continued to differ somewhat throughout year 2, with overall vulnerability being slightly greater with nonvariable growth, but by year 3, there was little difference (Fig. 3).

Seasonal growth model

When growth was modeled as seasonal, it resulted in higher egg production and YPR than nonseasonal growth. Mean egg production for a fished stock was significantly greater (t -test, $n = 60$, $P < 0.001$) when growth was modeled as seasonal (24.4×10^9) versus nonseasonal (23.5×10^9). Virtually all of the increased egg production occurred in year 1 because fish mature earlier with seasonal growth. By year 3, annual egg production became less for seasonal growth than nonseasonal growth. Similarly, YPR was significantly greater (t -test, $n = 60$, $P < 0.001$) when growth was modeled as seasonal (422.3) than nonseasonal (415.8) because of a larger mean size of fish caught in year 1 ($\bar{TL} = 288.4$ mm seasonal; 261.9 mm nonseasonal) and year 2 ($\bar{TL} = 388.4$ mm seasonal; 327.0 mm nonseasonal).

Effect of birth date on survivorship

Fish with smaller L_1 s showed greater survivorship. In 10 runs with equal-size subcohorts, the mean number of survivors \geq age 3 increased with later birth dates: 34.1, 43.2, 45.3, and 70.0 for the May, June, July, and August subcohorts, respectively. August subcohort survivorship was significantly greater than any other subcohort (ANOVA, $n = 40$, $P < 0.001$; Tukey's test, $P < 0.05$). This increased survivorship was due to the later birth date's smaller L_1 , with mean L_1 significantly smaller (ANOVA, $n = 20$, $P < 0.001$) for all fish surviving to ages ≥ 3 (169.0 mm) than those which died (179.1 mm). Mean number of survivors \geq age 3 was greater for the increasing subcohort regime (225), intermediate for the equal subcohort regime (193), and lowest for the decreasing regime (164). This was driven by the initial number of fish in the August subcohort (increasing subcohort regime, 2130; equal subcohort regime, 1000; decreasing subcohort regime, 267), which had a smaller mean L_1 .

Effect of subcohorts

Modeling weakfish with four equal-sized subcohorts corresponding to birth months had a minimal effect on YPR and egg production. There was a wider L_1 distribution with subcohorts than without, which led to a slight but nonsignificant increase in egg production (24.4×10^9 vs. 24.6×10^9 eggs, t -test, $n = 60$, $P = 0.402$) and a slight but

significant decrease in YPR (422.3 vs. 417.0 g, t -test, $n = 60$, $P = 0.013$).

How fish were apportioned to the subcohorts, however, affected egg production and YPR. YPR differed significantly by subcohort regime (ANOVA, $n = 90$, $P = 0.0001$). It was largest (466.9 g) when subcohort size was decreasing (most fish in May subcohort), intermediate for equal subcohorts (422.3 g), and smallest (377.2 g) for increasing subcohort size (most fish in August subcohort). Counter-intuitively, given that weakfish growth becomes asymptotic at age 6, the greatest YPR did not occur with the subcohort regime producing the oldest survivors (increasing regime) because of its smaller number and size of fish caught in years 1 and 2 (Table 1).

Egg production also differed significantly by subcohort regime (ANOVA, $n = 90$, $P < 0.001$), with the decreasing subcohort regime producing the most eggs (Table 2). However, annual egg production was greater for the decreasing subcohort regime only in the first 2 years (Table 3). By year 3, egg production was similar for all three regimes, although somewhat larger for the increasing subcohort regime, which continued to be greater from this point on even though its spawning biomass did not become greater until year 6.

Discussion

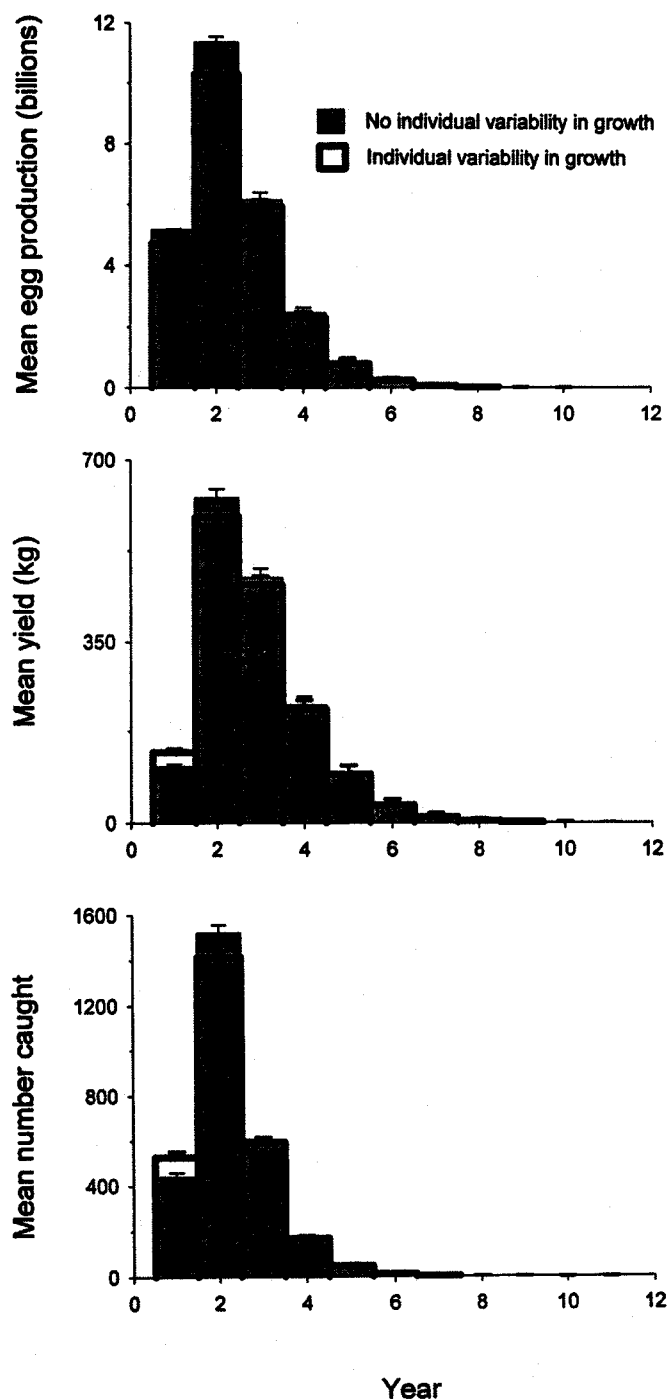
The baseline model

Our model incorporated aspects of multiple spawning and demonstrated how they can affect adult population dynamics. An obvious factor, which has been all but ignored, is the effect of a large range of birth dates from an extended spawning season (Cargnelli and Gross 1996). By simulating subcohorts corresponding to birth months with a 10% CV in individual growth we produced a realistic range of sizes at age 1. The differences in body size of subcohorts had far-reaching effects, including when fish matured and became vulnerable to the fishery, the size of cohort egg production and yield, and adult life-span.

There is concern that fisheries using a minimum size limit may act as a new selection pressure, causing earlier maturity and slower growth of various species (Sutherland 1990). Our simulations indicated the larger average size of early born (May) versus late-born (August) subcohorts caused early born fish to mature and become vulnerable to fishing sooner and to have lower survivorship. Thus, selection would be expected to favor spawning later in the season (creating more August-born fish with their smaller size at age). However, greater lifetime survivorship does not necessarily translate into the most eggs. Under the baseline fishing regime the May subcohort had the greatest lifetime fecundity, because of the relatively low fishing mortality during the first year's spawning season, allowing May fish to produce more eggs, because they matured earlier and had a larger size.

We based our subcohort mean size at age 1 on the assumption that the duration of the first growth season was the predominant factor affecting size at age 1. We did this because of a lack of data and because weakfish spawn primarily in the summer, when temperatures are warm and growth is relatively fast. This is similar to the bluegill sunfish, *Lepomis macrochirus*, which spawn primarily in June and July and showed a clear relationship between birth date and

Fig. 5. Annual mean ($n = 30$ runs) egg production, yield, and number of fish caught (± 1 SD) under the baseline fishing regime, with equal-sized subcohorts and seasonal growth, with and without individual variability in growth.



yearling body size (Cargnelli and Gross 1996). However, a fall spawning season such as that of the Atlantic croaker might greatly decrease the importance of duration of the first growth season.

Because of a lack of data, we had to base important parameters such as subcohort-specific L_1 s, time of peak seasonal growth and monthly F on general assumptions and historical data. To fully assess the impact of these assump-

Table 1. Mean ($n = 30$ runs) yield, number and average weight (g) of fish caught by year, when subcohorts were modeled as equal, increasing, and decreasing.

Year	Equal subcohort size			Decreasing subcohort size			Increasing subcohort size		
	Yield (kg)	No. caught	Average weight	Yield (kg)	No. caught	Average weight	Yield (kg)	No. caught	Average weight
1	136	528	257	193	657	294	84	410	204
2	589	1415	417	702	1475	476	475	1335	356
3	460	595	774	471	504	936	439	686	639
4	219	168	1302	226	143	1580	218	198	1099
5	93	47	1963	93	41	2259	93	56	1648
6	34	13	2661	34	11	3040	35	15	2294
Total caught	2766			2831			2700		

Table 2. Mean, range, and standard error of egg production ($n = 30$ runs) for a virgin and fished stock of weakfish, *Cynoscion regalis*, when subcohort size was modeled as equal, increasing and decreasing.

Statistic	Equal subcohort size		Decreasing subcohort size		Increasing subcohort size	
	Virgin	Fished	Virgin	Fished	Virgin	Fished
Mean	358	24	383	26	333	22
Range	346–379	23–26	369–403	25–28	348–319	22–24
SE	1.78	0.11	1.61	0.13	1.43	0.10

Note: Egg production is in billions.

Table 3. Mean ($n = 30$ runs) spawning biomass (in kg) and egg production (in billions) of a fished stock by year, when subcohorts were modeled as equal, increasing, and decreasing.

Year	Equal subcohort size			Decreasing subcohort size			Increasing subcohort size		
	Spawning biomass	No. alive	Eggs	Spawning biomass	No. alive	Eggs	Spawning biomass	No. alive	Eggs
1	330.8	2757	4.7	443.4	2634	6.1	218.0	2865	3.4
2	670.5	983	10.3	729.5	835	11.2	608.1	1147	9.3
3	434.6	276	5.9	451.0	237	5.8	418.6	327	6.1
4	201.7	77	2.3	211.0	66	2.2	203.6	91	2.5
5	84.1	21	0.8	85.4	19	0.8	83.0	25	0.9
6	29.4	6	0.3	29.6	5	0.2	30.9	7	0.3

tions we will need to do further sensitivity analysis. However, important aspects of our simulation results were similar to those from the field. As already mentioned, simulated L_1 and maximum size ranges were reasonable, given what has been reported for the field. In addition, maximum age in our simulations was age 8, the same as that from general Chesapeake Bay commercial samples from 1989 to 1992 (Lowerre-Barbieri et al. 1995). Our simulations indicated ages 2 and 3 contributed the most to egg production as did our field studies (Lowerre-Barbieri et al. 1996b). Also the simulated differential maturity closely followed that reported from the field, with early born fish maturing earlier the following year than later born (Lowerre-Barbieri et al. 1996b).

Individual variability in growth

In fishes, important life-history parameters such as survivorship, age-at-maturity, and fecundity are more closely linked to size than age (Kirkpatrick 1984), and many fish demonstrate a large range of sizes at age. Yet traditional fishery models are highly aggregated, assuming all fish of a

given age are the same size. By decreasing our level of aggregation, first to subcohorts and then to the individual, fish matured and became vulnerable to the fishery in a more realistic fashion. Thus, larger fish (due to birth date and individual growth differences) matured earlier and on average produced more eggs and died earlier, significantly affecting both yield and egg production. Had all fish been modeled to mature at the beginning of the first spawning season, egg production would have peaked in year 1 rather than year 2. In addition, earlier born fish would not have produced the most eggs, counteracting their lower survivorship. Instead, the July subcohort would have had the greatest lifetime egg production.

Growth model

Although most temperate water fish demonstrate seasonal growth (Moreau 1987), traditional age-based models rarely incorporate it. Our simulations, however, indicate it can have a significant impact on egg production estimates. Peak seasonal growth in June corresponded with the middle of the weakfish spawning season and thus increased egg produc-

tion. However, this would differ for other species depending on how the time of peak growth corresponded to their spawning seasons. With the fall-spawning Atlantic croaker, one would expect peak growth in June to have either little effect or to lower egg production estimates compared with estimates based on the traditional von Bertalanffy growth model.

We assumed growth peaked in June based on a trade-off between water temperature and spawning energetics. Water temperature at our Chesapeake Bay sampling site peaked in July at the same time that weakfish condition was at its lowest (Lowerre-Barbieri et al. 1996b), presumably because of the demands of multiple spawning. Because of the complicated weakfish migrational pattern, better defining weakfish seasonal growth from field data is virtually impossible, although it could be studied in captivity.

Subcohorts and survivorship

Ages 1 and 2 drove subcohort egg production and YPR results. Intuitively, given that the species we modeled does not reach asymptotic growth until age 6, it would seem the regime with the greatest survivorship would have the greatest YPR and egg production. However, this was not the case. In the first 2 years when numbers of fish were relatively high, the larger size of fish in the decreasing subcohort regime (more early born fish) had a greater effect on egg production and YPR than the larger number of fish surviving to older ages with the increasing subcohort regime. Obviously, these results depend on a number of factors such as size at maturity, minimum size limit, age at which growth becomes asymptotic, and mortality rate. However, they do indicate that potential differences in reproductive output over an extended season can affect adult population dynamics. They also underline the importance of young fish to egg production and yield for fish heavily exploited and with a life history similar to that of weakfish.

Summary

It has become increasingly clear that it is essential to model not only the effects of fishing on yield but also on the reproductive capacity of a stock (Norris 1991; Schirripa and Goodyear 1994). However, little attention has been paid to how a multiple-spawning strategy might affect population dynamics. A multiple spawner typically produces eggs over an extended period, while total spawners produce all their eggs at one time within a spawning season. The most obvious advantage for multiple spawners is that their fecundity is not restricted by body cavity size, and thus, they can greatly increase their egg production (Garrod and Horwood 1984). Because of this increased egg production, the number of individuals will have a greater effect on egg production than spawning biomass, as was demonstrated in our simulations by the fact that egg production peaked in year 1 when all fish matured before their first spawning season, even though spawning biomass continued to peak in year 2 (Fig. 1).

Because multiple spawners typically have extended spawning seasons, they also produce a large range of sizes at age, which affects vulnerability to fishing and time of maturity. In our simulations, individuals maturing at different times (differential maturity) had a greater effect on egg production than survivorship, with early born fish producing the

most eggs. Thus, assuming more eggs translates into more fish, an increased number of early born fish surviving to their first year would in turn produce more early born fish the next generation and so on. In this fashion, weakfish could go into a cycle of increased abundance without any obvious cause such as a decrease in fishing pressure. However, anything increasing the survival of August-born fish over earlier born would have the opposite effect. Weakfish have gone through such cycles in abundance (Lowerre-Barbieri et al. 1995), and the timing of peak larval abundance has been reported to vary in different years (Lowerre-Barbieri et al. 1996b). The effect of differential maturity would be particularly noticeable in a highly exploited fishery like weakfish because the spawning population has been so severely restricted, increasing the importance of the first year's egg production.

These results would not have been apparent with a more highly aggregated, annual model. A monthly time step was necessary to evaluate differential maturity and recruitment to the fishery. Whereas, the individual-based approach allowed us to incorporate a large amount of detailed biological data, which the mathematics of more traditional models would have made extremely tedious. It also allowed us to compare the phenotypic traits associated with fish that were caught versus survivors (e.g., birth month, size at age 1).

Our simulations also have important management implications. The monthly time step made it easy to evaluate the effects of fishing during and outside of the spawning season. It makes it equally easy to evaluate a closed season. However, the differential maturity results indicate that the importance of protecting egg production at different points within the spawning season may vary. Our model also allowed the simulation of different fishing regimes associated with a migratory species encountering different state regulations. Although efforts are being made to standardize regulations, and in fact the North Carolina weakfish minimum size limit has recently been raised to 305 mm TL, many species continue to be exploited at different rates associated with seasonal migrations.

The model we present here also has many limitations. One of these was the same detailed input and output. This level of information is often not available. For example, with weakfish we had to estimate several important parameters based on general assumptions, as well as model theoretical subcohort regimes rather than those observed from the field. In addition, the detailed reproductive estimates such as spawning frequency and batch fecundity, are not available for many species. The current version of this model also demonstrates several of the limitations of more traditional models, such as the assumption of steady state and the estimation of an unfished cohort's biomass without incorporating compensatory mechanisms. It also does not incorporate potential changes in M associated with seasonality or age.

With any IBM there is the problem of how many individuals to use in simulations. In the present model, we were concerned with how a much larger number of fish might change the percentage of fish surviving to older ages and thus the cohort dynamics. However, differences were minimal when we compared the annual number of survivors from a deterministic version of this model run with 400 000 fish versus the IBM version with equal subcohorts and 4000

fish. The IBM on average (30 runs) had one fish survive to age 8, whereas the deterministic model had two fish survive to age 9. Annual percent survivors was actually a little higher for the IBM because all fish in a subcohort did not become vulnerable to fishing at the same time.

This model is a very simplistic representation of multiple spawning. As shown for the northern anchovy, egg production of a multiple spawner can vary in relation to food, growth, temperature, population size, and age structure. Our simulations looked at the effect of growth, population size, and age structure. Annual temperature fluctuations can be expected to affect when the spawning season begins, growth (and thus batch fecundities), and spawning frequencies. However, its effects can also be confounded by other factors affecting fish condition such as food availability. Unfortunately, studies addressing how these factors affect weakfish spawning have not yet been conducted, but we hope in the future to incorporate temperature and energetics to assess how much egg production can vary from year to year, even if population size remains constant.

Despite these limitations, our results show that IBMs can help improve our understanding of how fishing and multiple spawning interact to affect adult population dynamics. Our simulations provided insight on how various seasonal parameters can cause nonintuitive results, as well as on selective pressures of a size-based fishery on a multiple spawner with an extended spawning season. It did not, however, incorporate aspects of early life history, and there may be a number of early life history traits associated with birth date and spawning energetics that have opposite selective processes, counteracting those of the adult stages. Thus, to fully understand the factors affecting recruitment of multiple spawners it will be necessary to combine detailed information on spawning dynamics and early life history.

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