Abstract.–Dynamic pool models were originally developed to evaluate the effect of exploitation on gonochoristic species of fishes. Consequently, application of these models to hermaphroditic species may lead to erroneous conclusions. The objective of our analysis was to develop an alternative method for estimation of yield-per-recruit and spawning stock biomass-per-recruit that incorporates the effect of sex transformation. Life-history characteristics such as the rate of sex change, growth, and mortality are size-specific; therefore, a length-based model was produced using a series of time-invariant distributed delays. The model incorporates a sequence of length-stages through which the cohort moves, at rates determined from empirical length data. At each length-interval, fish may die, move to the next interval, or switch sex according to a probability distribution of transformation. The model tracks the cohort through time and length categories as an aggregation of individuals rather than a representative average. The estimate of yield-per-recruit for a protogynous hermaphrodite, black sea bass *Centropristis striata*, differed little from traditional models. The distributed delay model with a sex-transformation phase produced considerably lower estimates of spawning stock biomass-per-recruit than the model with traditional assumptions. Potentially erroneous estimates of biological reference points using standard methods for hermaphroditic species may be overcome with use of a distributed delay model, which can incorporate size-specific life-history dynamics.

Length-based analyses of yield and spawning biomass per recruit for black sea bass *Centropristis striata*, a protogynous hermaphrodite

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Analytical models describing the potential yield of a fisheries resource consist of three basic dynamic elements: population growth, recruitment, and mortality (Russell 1931). Dynamic pool models (e.g., Thompson & Bell 1934, Ricker 1954, Beverton & Holt 1957) are traditionally used to evaluate potential yield-per-recruit (Y/R) and spawning stock biomass-per-recruit (SSB/R) relative to fishing mortality and size-at-recruitment. Potential yield and spawning biomass of a cohort are typically calculated as a summation across discrete age-increments, under specified conditions of growth and natural mortality. Within each age-interval, growth and fishing mortality rates are assumed to apply uniformly to all members of the cohort (Gulland 1977). Not all individuals follow the same growth trajectory, however, and the susceptibility of individual fish to mortality is often a size—rather than age-dependent phenomena (Kirkpatrick 1984). Consequently, length-based models can provide a more precise and accurate depiction of cohort dynamics, in addition to using directly measurable variables that are often linked to management measures.

Traditional age-based models of Y/R and SSB/R may be particularly inappropriate for species with unusual and/or complex life histories. This may be true for hermaphroditic species that have unique reproductive stages that change as a function of fish size. For example, significant growth and mortality changes that occur following sexual transformation would not be accounted for in conventional Y/R models.

Hermaphroditism will also influence estimation of sex-specific mortalities. For example, as transformations occur in a protogynous hermaphrodite, females are lost from the cohort, creating the same effect as increased female mortality. The transformations increase the number of males in the cohort, reducing the apparent mortality of males. Consequently, the mortality estimates for each sex are not independent, and a potential bias may exist in estimating Y/R and SSB/R when sex-specific characteristics are not considered.

Black sea bass *Centropristis striata* is a protogynous hermaphrodite common along the continental shelf of the northwest Atlantic between Massachusetts and Florida. Growth in black sea bass is sexually dimorphic, with faster growth but lower maximum age in females (Lavenda 1949, Mercer 1978, Alexander 1981). Females commonly reach sizes of 38 cm and age 8 yr (Lavenda 1949); however, at sizes of 8–35 cm females may transform into males and enter the male growth regime. Males may grow

to 60 cm and age 20 yr (Lavenda 1949) with greater variability in size-at-age than females. Consequently, a black sea bass has three possible growth rates: female, male, and transitional. These differences in growth rates and variability in size-at-age between the sexes will influence the potential yield from a cohort.

An alternative approach for modeling changes in a cohort over time is use of delay models. Delay models were first developed in the field of industrial dynamics as a technique to monitor movement of individuals through a system of substages (Forrester 1961), and have since been modified to incorporate effects of attrition (mortality) and variability in timing of movements (Manetsch 1976, Vansickle 1977). The subclass of distributed delay models can be a useful tool to describe the movement of any item through a process or, in a biological context, through developmental stages (Manetsch 1976). Extending the model to include a series of consecutive processes, it has been used to simulate growth dynamics in marine crustaceans (Idoine & Finn 1984), insects (Ravlin et al. 1978, Schaub & Baumgartner 1989), and agricultural crops (Gutierrez et al. 1984, 1988). The major advantage of this model type is its focus on the aggregated behavior of individuals rather than a representative mean.

To estimate Y/R and SSB/R in black sea bass, we modeled the growth and mortality of a cohort as a series of distributed delays with an associated mortality, using length categories as individual developmental stages. This approach allowed us to simulate the decline of the cohort while retaining information about variation in size composition and size-specific mortality in the cohort. In addition, we were able to evaluate the influence of additional mortality on the population dynamics of a species with an hermaphroditic life history.

Methods

The model structure

Time-invariant distributed delay models with a mortality term (Vansickle 1977) can be characterized as a sequence of stages, with flow through each stage i represented by a series of differential equations (Fig. 1):
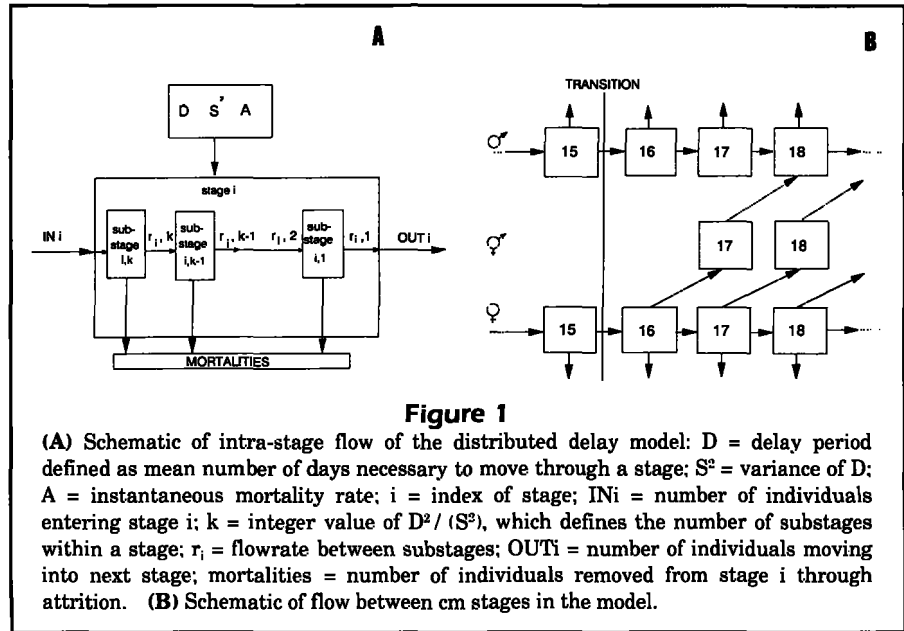

Figure 1

(A) Schematic of intra-stage flow of the distributed delay model: D = delay period defined as mean number of days necessary to move through a stage; S^2 = variance of D; A = instantaneous mortality rate; i = index of stage; INi = number of individuals entering stage i; k = integer value of $D^2/(S^2)$, which defines the number of substages within a stage; r_i = flowrate between substages; OUTi = number of individuals moving into next stage; mortalities = number of individuals removed from stage i through attrition. (B) Schematic of flow between cm stages in the model.

$$dr_{i,1}/dt = k/D[(x(t)-r_{i,1}(t))-(A(t)*D/k)]$$
$$dr_{i,2}/dt = k/D[(r_{i,1}(t)-r_{i,2}(t))-(A(t)*D/k)]$$

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.

$$dr_{i,k}/dt=k/D[(r_{i,k-1}(t)-r_{i,k}(t))-(A(t)*D/k)]$$

where $x(t)$ = input rate at time t,

k = integer value of D^2/variance of D (S^2) which defines the number of substages within a stage,

i = index of stage,

j = index of substage from 1 to k, and

$r_{i,j}$ = flowrate between substages j and j-1, stage i;

or $$r_{i,j} = (k_i / D_i) * Q_{ij}$$

where Q_{ij} = the number of individuals in substage j, stage i,

D = delay period defined as the mean number of days necessary to move through a stage (the value of D at stage i varies by sex), and

$A(t)$= mortality rate at time t.

All rates in the model are instantaneous. The model was simulated as a series of difference equations with a time step equal to 1 day. The delay model can be expressed either in terms of flows (r_{ij}) or state variables (Q_{ij}) (Vansickle 1977). For simulation purposes, this model utilizes flows within, between, and out of stages representing 1 cm length categories through which a cohort will pass. These flows were converted

Figure 2
Erlang probability density function for various values of k
and a mean t = 10.
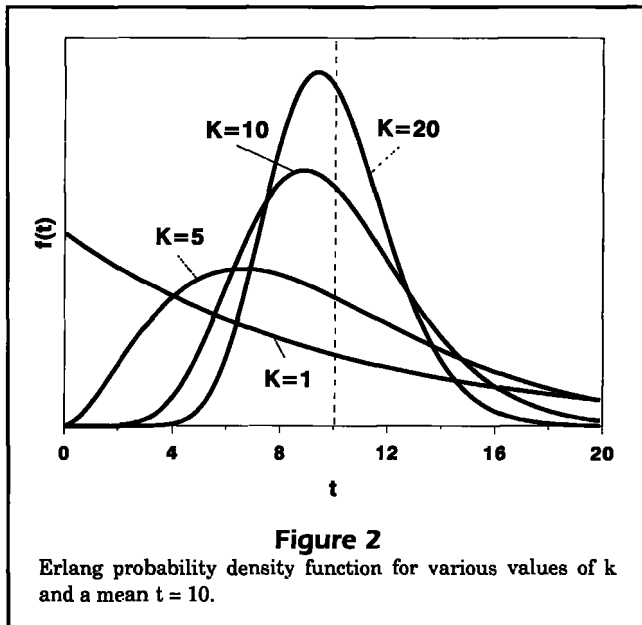
to state variables (e.g., numbers of individuals dead
due to fishing mortality at a given size) where neces-
sary for analyses. Individuals in the cohort passed
through each stage at a rate determined by an Erlang
probability density function. The shape, or the order,
of the density function was determined by the value of
k (Manetsch 1976) (Fig. 2). Transit time of an indi-
vidual through stage i was a function of the mean
delay period (D) and associated variance. The greater
the variance relative to the mean, the greater the value
of k. This continuous function was approximated, us-
ing difference equations, by a series of substages. The
number of substages within a stage was equal to the
integer value of k, since fractional substages cannot be
used in the discrete approximation necessary for the
model.

A cohort entered length stage i at time t and moved
through the substages at stage-specific rates. At time
t+1, fish either moved into length stage i+1, remained
in length stage i (at some substage), or were removed
from the system at a defined rate of mortality due to
fishing and/or natural mortality. At time t+2, some
fish were still in stage i, some in i+1, and possibly
some in i+2, etc. The biomass of the cohort and mean
size changed as the distribution moved through the
series of length stages until all individuals reached a
maximum size or the cohort was eliminated through
mortality. Any individuals moving to a size beyond the
maximum were assumed to undergo senescence and
were removed from the system at that maximum size.
Yield was calculated from the number of individuals
removed at each length stage ≥ the size of recruitment
to the fishery × the ratio of fishing mortality/total

mortality (F/Z). The biomass of fish removed via fishing
mortality was calculated using the appropriate sex-
specific length-weight equations. Spawning stock was
calculated as the sum of the number of females per
length remaining in the system at the time of spawn-
ing (1 June) × the probability of female maturity-
at-length. The number of mature females-at-length was
converted to biomass using a length-weight equation.

With this model, hermaphroditism was included by
splitting the cohort into three growth regimes and us-
ing a size-specific probability of sex transformation. At
the initial stage, the cohort was divided into an appro-
priate number of males and females, then passed
through length stages at sex-specific rates. At a desig-
nated length-interval, females began transformation
by passing through an intermediate transitional stage
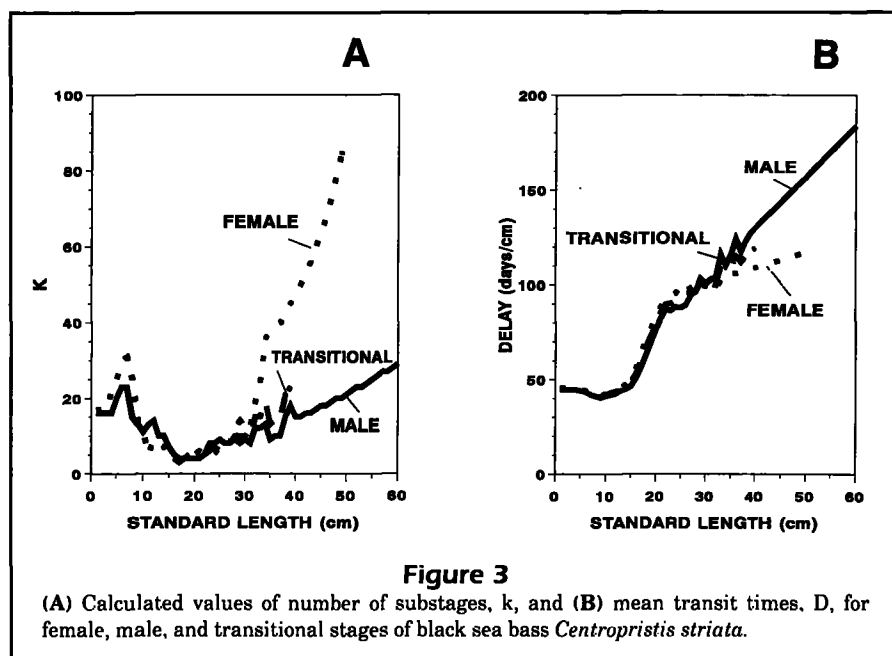prior to entering the male growth sequence (Fig. 1).

Input parameters

Input parameters required in the model were mean
transit time (D) and its associated variance (S^2) per
1 cm length-category in days and days^2 respectively,
by sex; maximum potential length for each sex in the
population; probability of sex transformation-at-length
for females; a range of lengths-at-recruitment (L_c) to
the fishery; instantaneous natural mortality rate (spe-
cific to length groups and sex if appropriate); a range
of instantaneous fishing mortality rates; and the per-
centage of females mature-at-length. In addition,
length-weight equations by sex were necessary for con-
version of numbers-at-length to biomass.

Estimates of mean transit times and their associ-
ated variances for black sea bass were determined from
back-calculation of scale data. Sea bass scales were
collected in coastal Long Island during 1979–80, aged,
and length-at-age back-calculated (Mark Alexander,
Conn. Dep. Environ. Prot., Old Lyme, CT, pers. commun.).
Daily time-increments of growth were chosen to pro-
vide estimates of k. Transit time (D) by cm-intervals
was calculated as

$$D = \frac{365 / [(S_n - S_{n-1}) * SL]}{S}$$

where S_n = scale annulus n,
       S_{n-1} = scale annulus n-1,
       S   = total scale size,
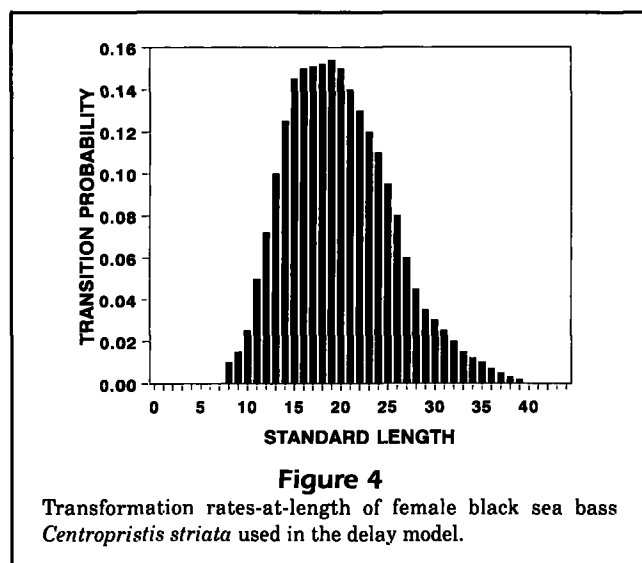   SL   = standard length of fish,

with the assumption of linear growth between annuli
(i.e., D equal between cm-intervals $(S_{n-1}/S)*SL$ and
$(S_n/S)*SL$). Thus, each individual scale provided esti-
mates of transit times (D) by cm, up to the maximum
length of the fish (SL). The means of D and S^2 were

Figure 3

(A) Calculated values of number of substages, k, and (B) mean transit times, D, for female, male, and transitional stages of black sea bass *Centropristis striata*.

Figure 4

Transformation rates-at-length of female black sea bass *Centropristis striata* used in the delay model.

estimated per length category for each sex, with sex determined at the time of capture. Delay and variance estimates were extrapolated with a linear regression between the largest length categories in the dataset and maximum potential length (Fig. 3). Maximum lengths were 49 cm SL for females, 39 cm SL for transitionals, and 60 cm SL for males. D and S^2 for each length-interval in the transitional category were estimated by using the mean values of females and males. Transformation rates-at-length were estimated from a composite of the frequency of transitional-stage fish recorded in field observations (Fig. 4) (Mercer 1978, Low 1981, Wenner et al. 1986). Transformations be-

gan at 8 cm, and individual fish were allowed to exist in a transitional state for 1 cm. Sex-specific length-weight equations (Mercer 1978) used to convert standard length (cm) to weight in grams were

males: wt=0.01773 SL [3.1525]
females: wt=0.02810 SL [3.0104]
transitional: wt=0.02120 SL [3.0991.]

Annual instantaneous natural mortality (M) for both the Y/R and SSB/R calculations was modeled as a length-dependent rate equal to 0.3 at lengths 1–10 cm and 0.2 at 11 cm–max. length. Instantaneous fishing mortality (F) was varied between 0.0 and 1.50 in both calculations. Mortality rates were applied over time-intervals of 1d (t=1/365).

Length-at-first-capture (L_c), which was modeled as knife-edge recruitment, varied between 16 and 32 cm SL. Increments were equivalent to annual mean lengths at successive ages, as determined from the delay model. The effect of harvesting was examined by incorporating an additional mortality term at each length category beyond the size-at-recruitment. Maturity-at-length data were collected during NEFSC bottom-trawl surveys between 1982 and 1990 (O'Brien et al. 1993). The initial cohort in the model consisted of 2000 fish divided according to a sex ratio of 99:1 female to male (Mercer 1978, Wenner et al. 1986). Precision of rounded values in the computer program resulted in the net loss of some individuals; therefore, the number of recruits used in the per-recruit calculations was the sum of individuals accounted for at the end of the run rather than the initial input value. The yield model was run for 25 yr or until the number of remaining fish in the cohort was <1; and the spawning biomass model (females only) was run for 11 yr or until the cohort was reduced to <1 fish. The Y/R and SSB/R models were developed as separate computer programs written in ANSI standard FORTRAN.

The Y/R estimates from the distributed delay model were compared with results from a Thompson-Bell (T-B) Y/R model. Lengths-at-annual-intervals for males and females were derived from execution of the delay model without a transitional phase and converted to grams using the appropriate length-weight equations. The mean of the male and female weights-at-age served as input to the T-B Y/R model. M was set equal to 0.3 for age 1, and 0.2 thereafter. The traditional SSB/R

model is a simple extension of the T-B Y/R model (Gabriel et al. 1989) and, consequently, the relationship to the delay models was similar. To avoid redundancy, only the relationship between the T-B Y/R model and the delay models was represented.

The sensitivity of the delay model to changes in the transition rates was examined. The transitional size-range was divided into 8 cm length-intervals and the transition rates within each interval were doubled. Spawning stock biomass-per-recruit was estimated for each interval of increased transition rates over a range of fishing mortalities and a constant size-at-first-capture of 16 cm.

Table 1

Mean length-at-age (cm) and variance from distributed delay model and mean back-calculated lengths-at-age (Mercer 1978) for black sea bass *Centropristis striata*.

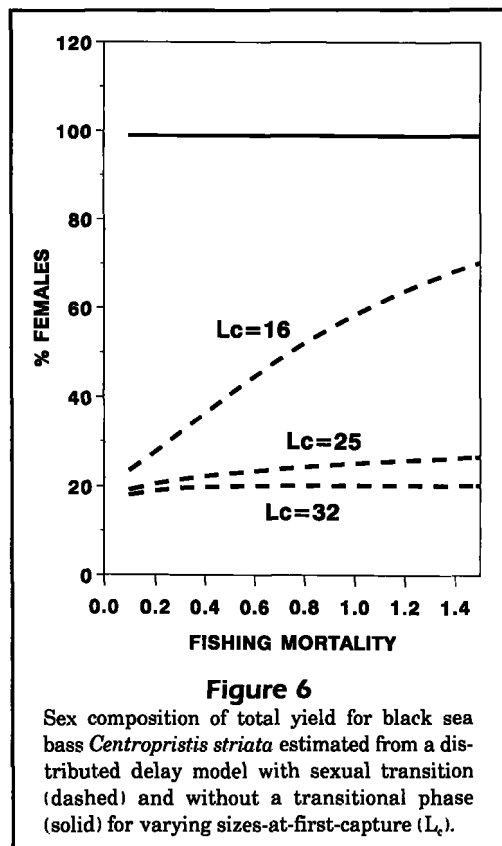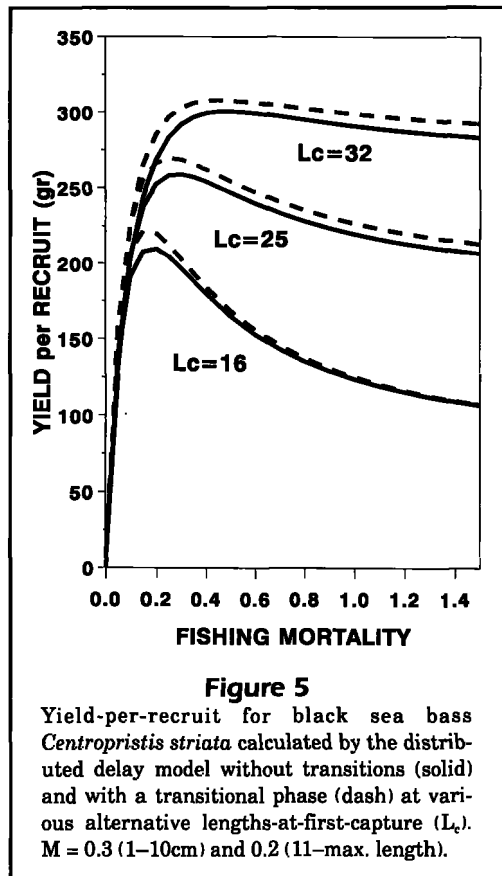| Age (yr)	Distributed delay				Back-calculated	
	Male		Female		Male	Female
1	9.6	(0.56)	9.5	(0.45)	8.7	9.0
2	17.7	(0.89)	17.2	(0.96)	16.5	16.3
3	22.5	(1.25)	21.7	(1.20)	21.1	20.4
4	26.5	(1.65)	25.4	(1.64)	24.4	23.6
5	30.1	(1.85)	29.0	(2.20)	27.6	26.1
6	33.5	(1.92)	32.8	(2.35)	31.4	27.9
7	36.6	(1.93)	36.4	(2.17)	34.6	33.6
8	39.5	(1.91)	39.9	(2.11)	36.5	
9	42.3	(1.86)	43.2	(2.02)	38.4	
10	44.9	(1.82)	46.5	(1.84)		
11	47.4	(1.79)	48.4	(0.65)		
12	49.8	(1.76)				
13	52.1	(1.72)				
14	54.3	(1.68)				
15	56.4	(1.64)				
16	58.4	(1.31)				
17	59.5	(0.54)				
18	59.8	(0.18)				

Results

To confirm that the model accurately represented growth in the absence of any harvest mortality, we calculated the mean lengths of the cohort (by sex) at successive 365d periods as generated by the model, and compared the results with independent back-calculated mean lengths-at-age (Mercer 1978) (Table 1). Growth simulated by the delay model was comparable to growth observed from back-calculations, although sizes-at-age tended to diverge in older ages, with slightly higher lengths-at-age produced by the delay model. Under the influence of natural mortality only, a cohort introduced into the delay model was reduced to 0.1% of its initial number by the time the maximum length was attained. The reduction of the cohort using only natural mortality indicated that the model provided an accurate portrayal of the black sea bass growth rate for the stated set of mortality parameters.

To evaluate the effect of harvest mortality in the absence of sex transformation, we calculated Y/R as generated by the delay model without transition and compared the results with those obtained using the T-B model. Under various L_c values, yields-per-recruit from the two models were similar, indicating the basic

Table 2

Estimates of F_{max} for black sea bass *Centropristis striata* from distributed delay model with and without transitional phase and using Thompson-Bell model. Age-at-entry in yr.

Size (age) at entry	Distributed delay		Thompson-Bell
	w/ transition	w/o transition	
16 cm (2)	0.16	0.17	0.17
21 cm (3)	0.20	0.21	0.21
25 cm (4)	0.25	0.27	0.26
28 cm (5)	0.31	0.33	0.33
32 cm (6)	0.45	0.47	0.45
35 cm (7)	0.63	0.64	0.63

Figure 5
Yield-per-recruit for black sea bass *Centropristis striata* calculated by the distributed delay model without transitions (solid) and with a transitional phase (dash) at various alternative lengths-at-first-capture (L_c). M = 0.3 (1–10cm) and 0.2 (11–max. length).

Figure 6
Sex composition of total yield for black sea bass *Centropristis striata* estimated from a distributed delay model with sexual transition (dashed) and without a transitional phase (solid) for varying sizes-at-first-capture (L_c).
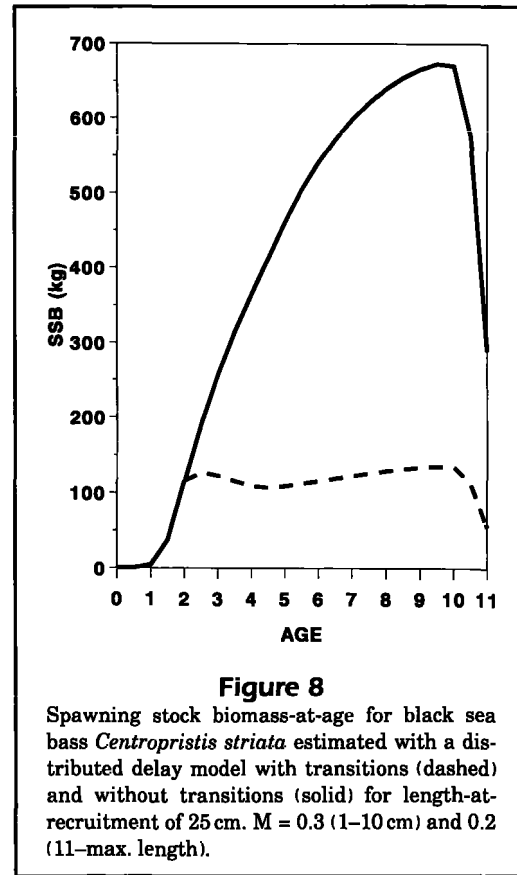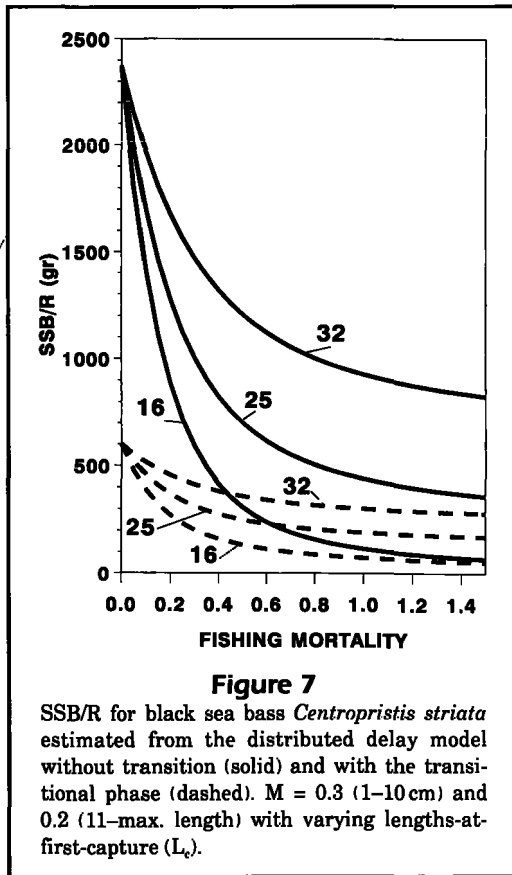
delay model was comparable to traditional methods of estimating yield-per-recruit. The calculated biological reference point of F_{max} from both models was nearly identical (Table 2).

The addition of the transitional phase into the model had little effect on the estimates of Y/R. The calculated values of Y/R and F_{max} were similar for each recruitment size and fishing mortality (Fig. 5, Table 2). Although the effect of including the transition phase on the total yield was negligible, the effect on sex composition of that total yield was substantial. With no transition phase, the proportion of females in the yield was dependent upon the initial sex ratio, in this case 99% female (Fig. 6). If the sexual transformation of females to males was included, the percentage of females to the total yield increased as a function of F and decreased as a function of size-at-first-capture (Fig. 6). At a recruitment size of 16 cm SL (age 2), the percentage of female biomass in the yield went from 21.3% at an F=0.05 to 70.4% at F=1.5, whereas a change in recruitment size to 32cm (age 6) decreased the effect of F, resulting in a percentage range of 17.3–20.3% females for F=0.05 and 1.5 respectively.

The addition of a transitional phase had a significant impact on the estimates of SSB/R from the distributed delay model and subsequent estimates of a total female spawning biomass. In the absence of any harvest mortality, maximum SSB/R for a cohort that undergoes a transition was 600.8 g/recruit as compared with 2373.3 g/recruit without transition (Fig. 7). Over the life of the cohort, the spawning biomass-at-age increases similarly for the first 2 yr regardless of the form of the delay model (Fig. 8 for size-at-recruitment of 25 cm), at which point the effect of transition begins. At age 2.5, a cohort undergoing transition approaches the maximum contribution to spawning biomass-at-age, while a cohort that does not undergo transition makes its maximum contribution at age 10.

The inclusion of the transitional term in the model led to lower proportional reductions in SSB/R with increasing F. In a model without the transitional form (e.g., size-at-first-capture of 25 cm [age 4] Fig. 9) at fishing mortality of 1.5, the spawning potential was reduced to 15.2% of maximum spawning potential (%MSP). In a model with the transition term, however, 28.7% of maximum spawning potential was obtained (Fig. 9). The pattern is also obtained at other sizes-at-recruitment. The transitional phase also reduced the sensitivity of SSB/R to changes in F and size-at-recruitment (L_c). Decreasing F from 0.6 to 0.2 (L_c=25) increased SSB/R by 107% in the non-transitional model, but only 60.5% in the delay model with transitions. Similarly, an increase in size-at-first-recruitment from 16 to 32 cm (with F=0.6) increased SSB/R by 201.8% in the transitional model but 368.9% in the non-transitional version. The inclusion of a transitional phase increased the natural reduction in the number of females in the system, which consequently reduced the maximum SSB/R for the cohort and the relative influence of fishing mortality on SSB/R.

The sensitivity of estimates of SSB/R to changes in transformation rates was examined. Doubling the transition rate across all lengths decreased the SSB/R by 71% from 600.8 to 174.6 g/recruit. When the transition rates were doubled over 8 cm length-increments, the impact in SSB/R varied by F and the size-range over which the transformation rate was changed (Fig. 10). Doubling the rate of

Figure 7
SSB/R for black sea bass *Centropristis striata* estimated from the distributed delay model without transition (solid) and with the transitional phase (dashed). M = 0.3 (1–10 cm) and 0.2 (11–max. length) with varying lengths-at-first-capture (L_c).

Figure 8
Spawning stock biomass-at-age for black sea bass *Centropristis striata* estimated with a distributed delay model with transitions (dashed) and without transitions (solid) for length-at-recruitment of 25 cm. M = 0.3 (1–10 cm) and 0.2 (11–max. length).

transformation in the 16–23 cm range had the greatest effect, decreasing SSB/R by 39.1% with F=0 (Table 3). Changes in transformation rates in the tails of the transformation probability distribution had little impact. In all cases, increases in F decreased the relative impact of transformation loss and, consequently, the sensitivity to changes in transformation rates decreased.

Discussion

Ignoring the unique population dynamics that may occur in hemaphroditic fishes will increase the risk of incorrectly estimating optimal exploitation levels from yield-per-recruit models (Bannerot et al. 1987). The problems can be compounded by disregarding the increased size variability within the system resulting from sexual transformations. Distributed delay models provide a mechanism for handling length-specific life-history changes, and results can be summarized as an aggregate of individuals and the associated variability rather than a simple mean estimate without error. The consequence is greater flexibility in dealing with changes between length categories without ignoring the size variability inherent within the system.

In the black sea bass example presented, the incorporation of a transitional term in the delay model had little effect on the estimate of yield-per-recruit. Since the sexes were combined to produce total yield, the growth differences between sexes were not large enough to produce significant changes in overall yield. Also, the inclusion of fishing mortality quickly removed any added yield contributed by transformed females. It is likely that the result would diverge further from a traditional model estimate as the differences in longevity or growth rate between the sexes increased.

The effect of modeling length- and sex-specific characteristics with a delay model was more apparent in spawning stock biomass-per-recruit estimates. The removal of female biomass via transformations was similar to increasing natural mortality at each length step, and consequently the spawning potential was reduced more quickly than under typical effects of fishing mortality and a constant M of 0.2. The system was more sensitive to changes in size-at-recruitment to the fishery than reduction in F at a constant size-at-recruitment.

The differences in spawning biomass-per-recruit estimates resulting from the distributed delay model have important management implications. If management
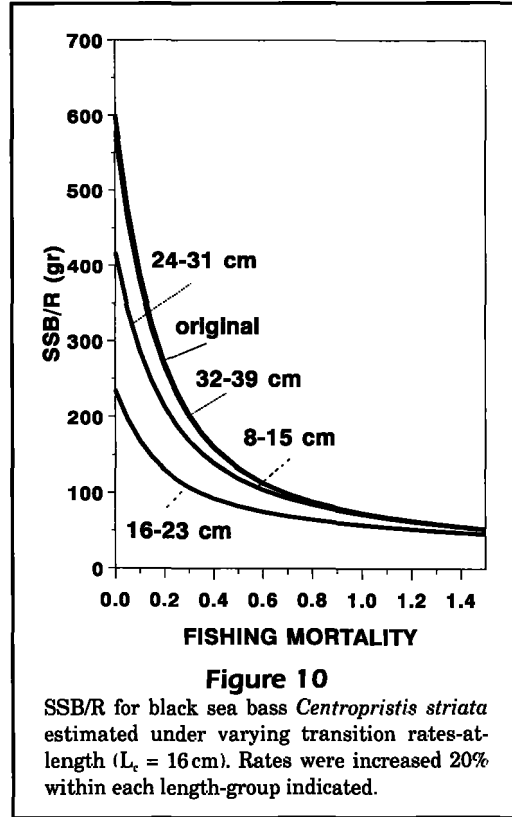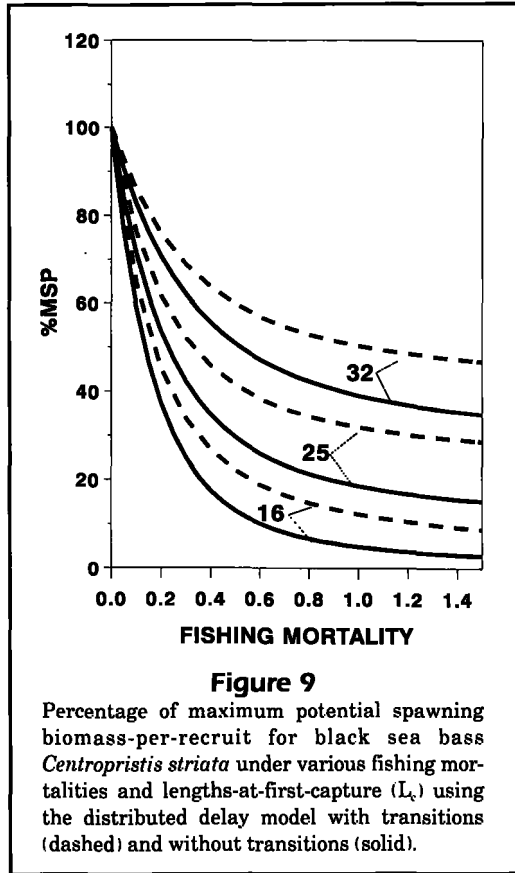
Figure 9
Percentage of maximum potential spawning biomass-per-recruit for black sea bass *Centropristis striata* under various fishing mortalities and lengths-at-first-capture (L_c) using the distributed delay model with transitions (dashed) and without transitions (solid).

Figure 10
SSB/R for black sea bass *Centropristis striata* estimated under varying transition rates-at-length (L_c = 16 cm). Rates were increased 20% within each length-group indicated.

Table 3
SSB/R for black sea bass *Centropristis striata* as percentage of original values (and L_c=16 cm), where transformation rates have been doubled in differing 8 cm intervals.

F	8–15 cm	16–23 cm	24–31 cm	32–39 cm
0	99.7	39.1	69.5	96.3
0.1	99.7	43.3	74.0	97.2
0.2	99.7	47.9	78.6	98.0
0.3	99.7	52.8	82.9	98.6
0.4	99.7	57.6	86.6	99.1
0.5	99.7	62.1	89.6	99.4
0.6	99.8	66.1	92.0	99.6
0.7	99.8	69.7	93.9	99.8
0.8	99.8	72.9	95.3	99.9
0.9	99.8	75.7	96.4	99.9
1.0	99.8	78.2	97.2	99.9
1.1	99.8	80.4	97.9	100.0
1.2	99.8	82.4	98.4	100.0
1.3	99.8	84.2	98.7	100.0
1.4	99.9	85.8	99.0	100.0
1.5	99.9	87.2	99.2	100.0

were based on a target %MSP, the presence or absence of transition terms in the model would provide dramatically different interpretations. For instance, if the target %MSP were 30% with an F=0.8, and L_c=25 cm, the non-transitional model would indicate the situation was below the target at 22%, whereas the transitional model would place the current conditions above the target at 34%. It would be critical that calculation of SSB in the stock-recruitment relationship used for development of a target SSB/R (and associated %MSP) be made using a framework similar to calculation of SSB/R.

Beyond the issue of the model structure is the appropriateness of using spawning biomass models in general for management of hermaphroditic fishes. The complex social hierarchy of reef fishes (black sea bass can be considered a temperate reef fish) during spawning implies that the number of males may be an important factor limiting reproductive potential (Smith 1982). Recent theoretical studies suggest that males are not limiting in hermaphroditic sea bass populations to the degree that non-dominant males participate in spawning ("streakers") (Peterson 1991). If streakers are abundant, there would be no benefit for a female to transform only to engage in sperm competition with other spawning males. This suggests that under limited exploitation, the reproductive potential of the population is restricted in

terms of egg production. The possibility exists that exploitation could reach a level at which males are eliminated at such a rate that females are forced to transform faster or at an earlier size. The optimal sex ratio, from a behavioral perspective, has not yet been determined for *C. straita*. As suggested by the sensitivity analysis, substantial changes in the transformation rate could significantly alter the contributions of a cohort to the spawning biomass. There is no information currently available to determine the controlling mechanism or degree of plasticity for transformation rates within a population.

Future refinements of this distributed delay model may provide a more detailed picture of the effects of harvest on species such as black sea bass. Density-dependent feedback mechanisms influencing transition rates and age-at-first-transformation will ultimately be incorporated into the model to examine theoretical implications. A time-varying distributed delay model is also possible to account for seasonal changes in growth and mortality. With a minimal amount of growth information, either from back-calculations or tagging data, and some reasonable estimates of other important life-history events, we believe the distributed delay model can provide an effective length-based alternative to traditional dynamic pool models.

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