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SOME POSSIBLE BIASES IN SWORDFISH VPAs DUE TO SEXUALLY DIMORPHIC GROWTH

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SUMMARY

The purpose of this study is to identify possible biases in the VPA methodology applied for swordfish that can result from using the Gompertz curve (both sexes combined) to age the catch of a swordfish population hypothesized to exhibit sexually dimorphic growth. For analysis, hypothetical populations of swordfish were simulated using trends in recruitment and mortality loosely based on the 1989 ICCAT assessment. The range of dimorphic growth hypotheses defined was based on the analysis of Berkeley and Houde and that of Erhardt.

RESUME

L'objectif de cette étude est de définir les biais éventuels de la méthodologie VPA appliquée à l'espadon qui peuvent surgir du fait d'employer la courbe de Gompertz (les deux sexes combinés) pour déterminer l'âge d'une population d'espadon dont on suppose qu'elle présente un dimorphisme sexuel de la croissance. Pour l'analyse, les populations hypothétiques d'espadon ont été simulées en utilisant des tendances de recrutement et de mortalité basées dans les grandes lignes sur l'évaluation de 1989 de l'ICCAT. La gamme des hypothèses d'une croissance dimorphique se base sur l'analyse de Berkeley & Houde et sur celle d'Erhardt.

RESUMEN

El objeto de este estudio es identificar los posibles sesgos en la metodología del VPA aplicado al pez espada que podrían resultar del empleo de la curva de Gompertz (ambos sexos combinados), para hallar la edad en la captura de una población de pez espada hipotética, con el fin de obtener el crecimiento sexual dimórfico. En el análisis, se hizo una simulación con poblaciones hipotéticas de pez espada, aplicando tendencias del reclutamiento y la mortalidad basadas, hasta cierto punto, en las evaluaciones realizadas por ICCAT en 1989. La gama de hipótesis sobre crecimiento dimórfico que se definen se basó en los análisis de Berkeley y Houde y en el de Erhardt.

INTRODUCTION

Currently, swordfish assessments carried out by ICCAT are conducted with virtual population analyses (VPAs) which require estimates of a catch-at-age matrix, and of CPUE indices used to calibrate the VPA. The raw data used to estimate the catch matrix is mostly in the form of numbers caught by dressed-weight category. These weights are transformed to lengths (LJFL) which are, in turn, assigned ages via a Gompertz growth equation that was estimated from tagging data (Table 1). Most landed fish are not sexed and a single growth curve is used to assign ages to the fish, regardless of their sex.

There is concern that if sexually dimorphic growth occurs in this species, previous assessments may have led to positively biased fishing mortality estimates (Suzuki and Miyabe 1989). Berkeley and Houde (1983) and later Ehrhardt (1989) analyzed samples of anal fin spine sections with the purpose of obtaining precise growth rates for each sex. The samples examined in both studies were essentially the same (Ehrhardt's analyses included a few more small fish in the sample) but the methods used to backcalculate lengths and the fitted functions differed (Table 1). As a result, the growth functions obtained in each study were quite different, particularly for older fish (Figure 1). The growth rates estimated by Berkeley and Houde (1983) suggest a greater degree of dimorphism than do those estimated by Ehrhardt (1989).

The work of Suzuki and Miyabe (1989) focused on re-examining the available data by performing cohort analyses for each sex separately, given information about the likely pattern of sex ratios at size. The purpose of this paper is to further investigate possible consequences of sexually dimorphic growth with respect to VPAs, from a different perspective. The possible biases are investigated using simulated data of known characteristics, as opposed to using existing data.

METHODS

The analyses that follow rely on simulations of hypothetical populations that grow according to either Berkeley and Houde's (1983) or Ehrhardt's (1989) formulations. In this paper, these are referred to as Berkeley-Houde or Ehrhardt-type growth, respectively; the growth curve used by ICCAT is referred to as Gompertz-type. Note that the latter growth curve is based upon tagging data, while the Ehrhardt and Berkeley-Houde curves are based upon anal fin spine sections.

The simulated populations reflect recruitment trends and fishing mortalities such as those obtained for the North Atlantic stock during the last ICCAT Meeting (1989). The "true" populations consisted of 15 age classes that were subjected to exploitation

during 11 years, from 1978 to 1988. For each sex, the number of recruits to age 1 during this time period was set to
187500, 200000, 205000, 210000, 250000, 265000, 290000, 290000, 325000, 445000 and 595000;
the population sizes for ages 2 to 15 in 1978 were set to
130000, 97500, 70750, 44750, 24000, 15000, 7500, 4250, 2250, 1250, 750, 400, 250 and 250.

Natural mortality was fixed at 0.2 $year^{-1}$ and full-selection fishing mortality for the 11 years was set to
0.39, 0.36, 0.47, 0.39, 0.46, 0.53, 0.48, 0.45, 0.54, 0.66, 0.70.

In the simulations, selectivity was assumed to be a logistic function of size, L (LJFL in cm), and independent of time:

$$S_L = \frac{1}{1 + \exp(8.7706 - 0.06362\ L)} .$$

This selectivity curve roughly coincides with the selection-at-age pattern used for the terminal year in the last ICCAT swordfish assessment.

Every simulation year was divided into 30 time steps and in each step the expected catch in numbers was computed for each sex. These catches (by age, year, time-step and sex) were stored in parallel to a similar array of lengths obtained assuming that growth followed either of the two growth functions used. The choice of 30 time steps was made in order to ensure a sufficient diversity of lengths. The "true" catch-at-length data by sex simulated with either set of growth formulations was then converted to biased annual catch-at-age estimates (C_{ay}) by pooling both sexes with the Gompertz curve.

The resulting catch-at-age matrices, grouped at age 9, were used as inputs to program ADAPT which performs the VPAs. In order to make the available data resemble that used by ICCAT, five CPUE indices were used to calibrate the VPAs (ages 1, 2, 3, 4 and 5+) assuming that the errors made in assigning ages to the catches would also be made in assigning ages to the indices. Accordingly, the index for a particular age, a, in a given year, y, was obtained by dividing the *apparent* catch at age by the true fishing mortality of fully-recruited fish in that year and then multiplying this result by an arbitrary constant:

$$CPUE_{ay} = C_{ay} / F_y * 0.001.$$

RESULTS AND DISCUSSION

Hoey (1986) and Garcia and Mejuto (1988) presented evidence that the sex ratios of catch at size data deviate from a 1:1 value, particularly for larger fish in which the ratio favors females. The results of the simulations in this work indicate that sexually-dimorphic growth is indeed a sufficient cause to observe such deviations (Figure 2). However, size and sex-specific natural mortality rates and/or availabilities could also account for the observed sex ratios. Figure 2 gives the pooled sex ratios at size, expressed as the percentage of females, for the simulated populations that follow either Ehrhardt (solid line) or Berkeley-Houde (dashed line) growth. The symbols represent 3,487 records collected from various places in the North Atlantic between 1978 and 1989 (including those reported by Hoey, 1986, and by Garcia and Mejuto, 1988).

The VPA biases examined in this study arise from what can be considered misageing of the catches. That is, an "erroneous" growth curve is used to assign ages to both sexes combined, when in fact fish follow different sex-specific functions. The simulations were structured such that no other errors would introduce additional biases. For instance, growth was assumed to be deterministic, as ageing is actually carried out assuming deterministic growth. Also, the only errors introduced in the indices were those due to use of the incorrect growth formulation.

The degree of misageing of the catches by use of the Gompertz formulation when in fact fish follow another growth function is presented in Table 2. This table presents the percent bias in estimated catch at age, relative to the "true" catches. If swordfish follow Ehrhardt-type growth then the catch-at-age matrix estimated via the Gompertz curve is unbiased for ages 1 to 4, and positively biased for all ages except age 7 (Case I, Table 2). On the other hand, if they follow Berkeley-Houde type growth, then only the estimated catches for the first two age groups are unbiased; most catch estimates are negatively biased (Case II, Table 2). These differences should also be considered in terms of the CPUE indices used for calibration: If no sources of error other than misageing affect the indices then 4 out of the 5 indices used for tuning the VPAs in CASE I are unbiased, while 2 of the 5 indices are unbiased in Case II.

Obviously, potential biases in the VPA estimates of F and population sizes are largely dependent on the true growth function that the population follows. In the case of Ehrhardt-type growth, full F is estimated with a modest positive bias for the last few years in the simulated data series (Figure 3). The estimates converge towards the true values for the earlier years of data. When the growth of males and females differs as much as suggested by the Berkeley-Houde estimates, VPA overestimates of F can be large, almost by a factor of 2 (Figure 3). However, the *trends* in mortality rate are quite similar.

Similar results are obtained for the estimates of population sizes. When the "true" growth is Ehrhardt-type, the VPA estimates of population sizes for ages 5 and above correspond closely to the true total population sizes of males and females (Figure 4). If the "true" growth is Berkeley-Houde type, the VPA estimates do not reflect the true stock sizes of old males and females. Instead, the estimates are closer to the population size of females alone (Figure 5). Once again, the trends in abundance are similar between the "true" and the estimated populations.

An examination of Figure 1 provides guidance as to the reason for these results. Catches of old males and females that follow Ehrhardt-type growth will be assigned to the oldest age group when ages are assigned via the Gompertz curve. Old males that follow the curves estimated by Berkeley and Houde will not be assigned to the oldest age groups. Conversely, old females will. As a consequence, the VPA estimates of Berkeley-Houde growing populations mostly reflect the population size of females.

The results presented thus far refer to likely biases in the VPA estimates. An additional (and crucial) question is how these likely biases may affect management criteria used to compare the estimated current status of the stock (i.e., in the terminal year) against reference points such as $F_{0.1}$ or F_{max} or some measure of spawning potential. In order to address this question, yield-per-recruit computations were made for each sex and growth type using the "true" F vector corresponding to the last simulated year of data. These computations were then compared to those obtained using the terminal F vectors from the VPAs for both sexes combined (Figures 6 and 7, Table 3). When the true growth curve is as described by Ehrhardt, the shape of the VPA-based yield curve is quite similar to the true curve for either males or females (Figure 6). If growth is as described by Berkeley and Houde, the shape and location of the VPA-based yield curve is closer to the "true" curve for females (Figure 7).

Table 3 gives, for each of the above scenarios, the reduction that would be required from the current F to reach $F_{0.1}$ or F_{max}, expressed as a multiplier of the terminal year's F vector. Given that growth is Ehrhardt-type, F should be reduced to 27% or 29% of its current value in order to reach $F_{0.1}$ for females or males, respectively (Table 3). An analysis based on the VPA results for both sexes combined would suggest that F should be reduced to 25% of its current value (Table 3). If growth follows Berkeley-Houde then the analyses based on the VPA would suggest a reduction to 18% of the current F value, compared with reductions to 25% or 35% for females or males in the "true" case (Table 3).

Thus, for either growth scenario, analyses based on the VPAs call for slightly greater reductions in F that would be chosen if the "true" status of the stock were known. Because lower F values are associated with the maintenance of greater spawning potential, decisions based on analyses stemming from the VPAs can be considered as conservative from the point of view of the reproductive capacity of the stock.

In terms of the VPA estimates of N and F, the most biased scenario identified in this study occurs when the population grows as suggested by Berkeley-Houde but ageing is made via the Gompertz formulation. It is encouraging to note that despite the large overestimation of F (Figure 2) and underestimation of N (Figure 4), management advice based on yield-per-recruit considerations does not appear to be severely affected (Table 3). Nor are trends in mortality and abundance greatly affected (Figures 2 and 4). That is not to say that decisive evidence in support of sexually dimorphic growth should be ignored in favor of assessments that pool together catches of both sexes with a single growth curve. Rather, as suggested by Suzuki and Miyabe (1989), more conclusive studies on swordfish growth that can lead to more appropriate assessments should be encouraged.

ACKNOWLEDGMENTS

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Table 1. Equations used in the simulations.

Berkeley and Houde:

$$L_t = L_\infty (1 - e^{K(t-t_0)})$$

	MALE	FEMALE
L_∞	217.36	340.04
K	0.1948	0.09465
t_0	-2.0444	-2.5912

Ehrhardt:

$$L_t = (L_\infty^a - (L_\infty^a - l_0^a)\, e^{-K a t})^{1/a}$$

	MALE	FEMALE
L_∞	281.24	325.91
a	2.02729	1.986
l_0	2.047	2.047
K	0.04541	0.03676

Gompertz (ICCAT):

$$W_t = W_\infty e^{-K e^{-g t}}$$

and

$$L_t = 44.2237\ W_t^{0.29257}$$

	MALE & FEMALE
W_∞	305.56
K	4.613907
g	0.305815

TABLE 2. Percent bias in estimated catch-at-age [100(obs-true)/true] after assigning ages to catch-at-length with the Gompertz growth curve.

CASE I: Fish grow according to Ehrhardt's growth curves.

	YEAR										
AGE	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988
1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
4	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
5	12.7	14.8	15.6	14.8	12.1	12.4	12.8	12.7	10.5	11.2	10.7
6	8.4	3.4	8.0	9.8	7.6	2.7	3.4	3.8	3.9	0.3	2.9
7	-74.9	-68.8	-73.4	-69.3	-66.8	-69.2	-74.4	-73.2	-72.6	-73.1	-77.3
8	27.5	4.4	24.3	6.9	4.3	12.7	27.3	18.3	17.3	19.4	36.5
9+	17.9	22.8	14.7	19.4	14.4	10.6	12.0	18.7	19.1	18.8	19.7

CASE II: Fish grow according to Berkeley and Houde's growth curves.

	YEAR										
AGE	1978	1979	1980	1981	1982	1983	1984	1985	1986	1987	1988
1	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
2	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0	0.0
3	28.7	27.4	23.1	24.1	24.7	24.0	20.5	22.8	21.9	23.3	19.8
4	8.7	12.8	11.1	3.7	4.1	5.4	4.5	-1.1	1.7	1.0	2.9
5	-9.3	-7.2	-1.7	-2.5	-10.8	-13.3	-12.7	-13.0	-18.8	-18.1	-19.0
6	-26.6	-27.7	-26.7	-24.1	-22.7	-27.2	-31.0	-32.5	-32.8	-35.9	-37.4
7	-59.1	-58.8	-59.1	-59.4	-57.8	-56.9	-58.6	-60.0	-60.6	-61.0	-62.7
8	-61.6	-68.9	-64.9	-68.9	-71.8	-70.5	-64.8	-65.7	-67.6	-68.2	-63.5
9+	-9.5	-5.3	-12.4	-10.1	-14.5	-19.7	-20.6	-15.2	-12.9	-12.9	-12.1

TABLE 3. Required reductions in the terminal year F to reach $F_{0.1}$ and F_{max}, expressed as a multiplier. Two cases are presented for growth: as estimated by Berkeley and Houde, or as estimated by Ehrhardt. "VPA" indicates the apparent reductions that would be suggested from a VPA estimate where data for both sexes were pooled and assigned ages with the Gompertz formulation.

	Proportion of Present F Required to Reach: $F_{0.1}$	F_{max}
CASE I: Growth follows Ehrhardt's estimates		
Females	0.27	0.53
Males	0.29	0.63
VPA	0.25	0.48
CASE II: Growth follows Berkeley-Houde's estimates		
Females	0.25	0.48
Males	0.35	0.87
VPA	0.18	0.34

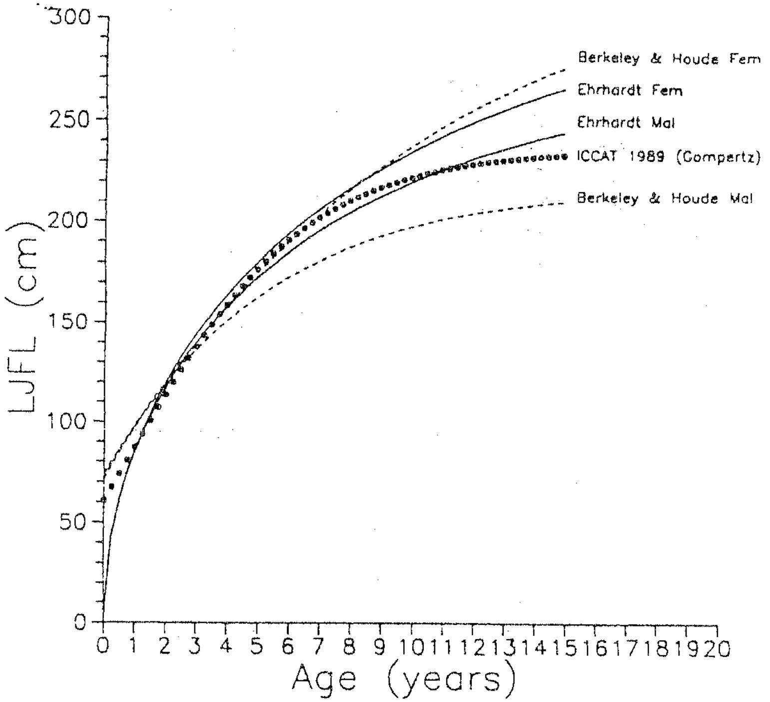

FIGURE 1. Length-age relationships derived from Berkeley and Houde models (sex-specific), from Ehrhardt models (sex-specific) and from Gompertz model (sexes pooled). The Ehrhardt and Berkeley-Houde models were derived from the same data set of anal fin spine sections; whereas, the Gompertz model was derived from mark-recapture data.

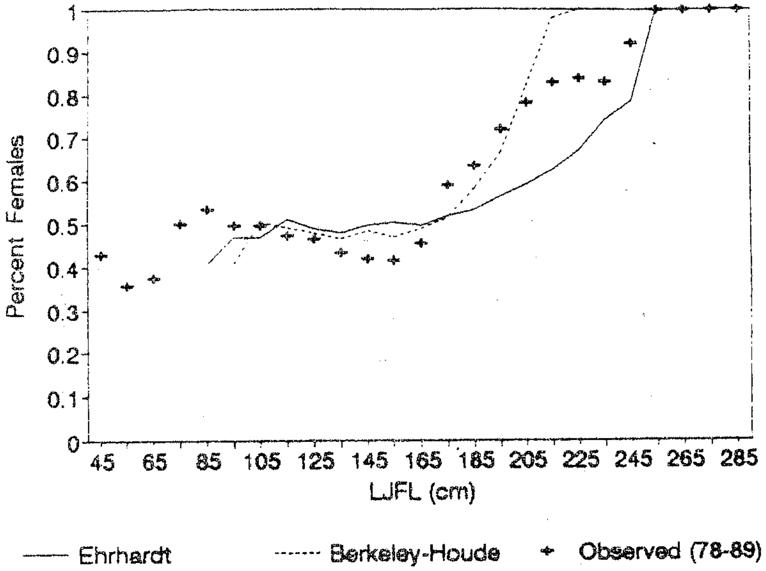

FIGURE 2. Pooled sex ratios at size, expressed as the percentage of females, for simulated populations that follow Ehrhardt-type growth (solid line) or Berkeley-Houde growth (dashed line). The symbols represent 3487 records collected in the North Atlantic between 1978 and 1989.

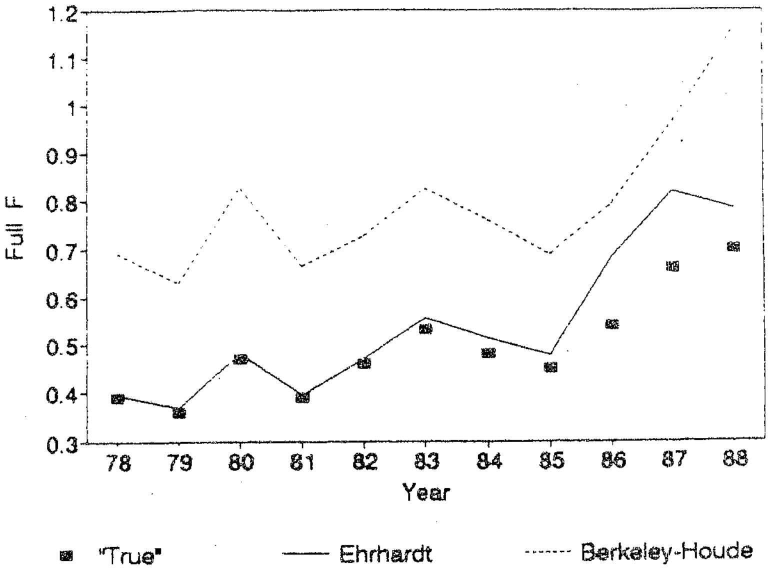

FIGURE 3. Fishing mortality rate of fully recruited fish (full F) from the simulated ("true") population versus the VPA estimates of full F obtained from ageing by the Gompertz model (sexes pooled) when, in fact, the "true" population grows sexually dimorphically like the Ehrhardt or Berkeley-Houde models.

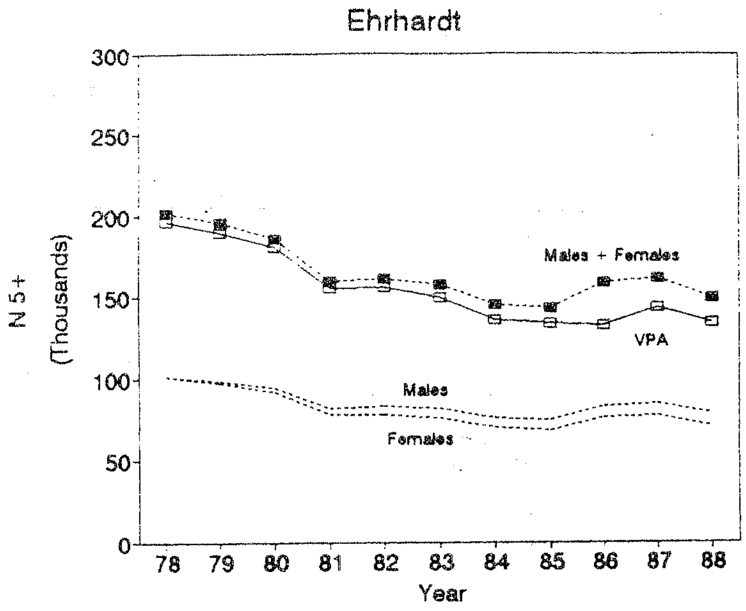

FIGURE 4. VPA estimates of the stock size of fish five years old and older (based upon the pooled-sex Gompertz ageing), when the "true" population grows sexually dimorphically like the Ehrhardt models. "True" stock sizes of males, females, and both sexes combined are shown with the dashed lines.

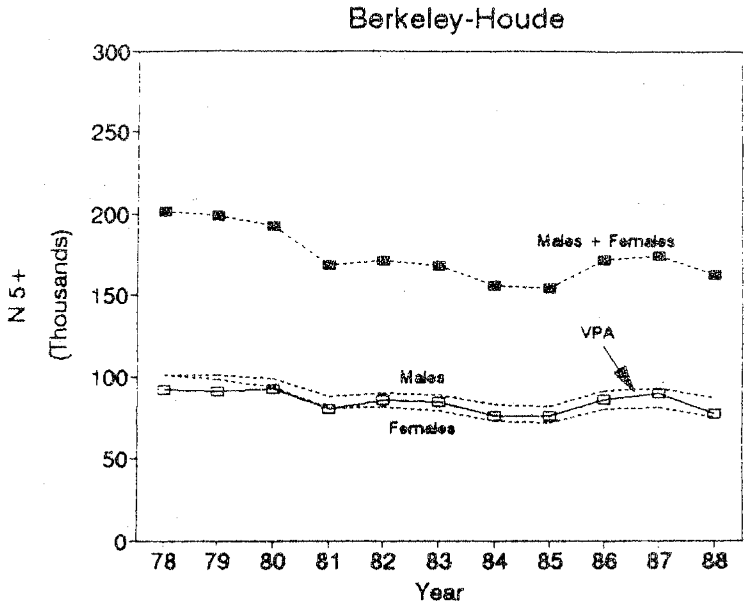

FIGURE 5. VPA estimates of the stock size of fish five years old and older (based upon the pooled-sex Gompertz ageing), when the "true" population grows sexually dimorphically like the Berkeley-Houde models. "True" stock sizes of males, females, and both sexes combined are shown with the dashed lines.

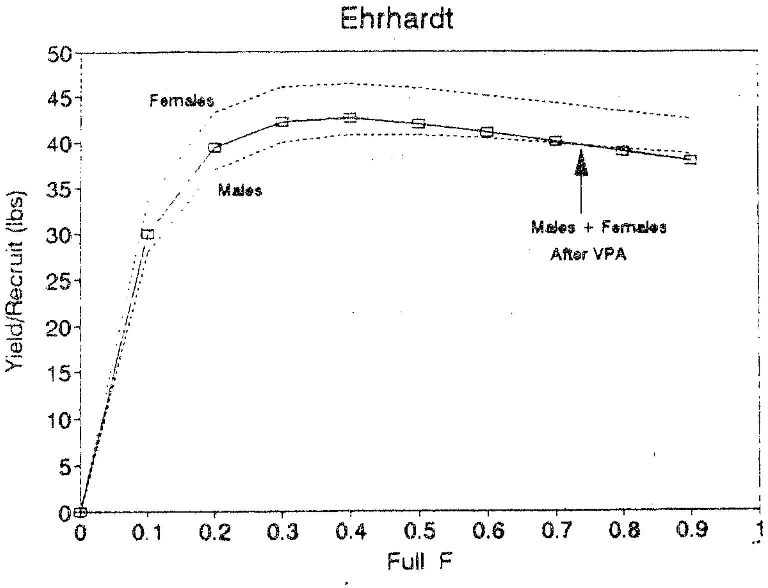

FIGURE 6. Yield per recruit relationship computed separately for males and females when the "true" population grows sexually dimorphically like the Ehrhardt models (dashed lines). These are compared to the yield per recruit calculated from VPA estimates derived from ageing using the pooled sex Gompertz model (solid line).

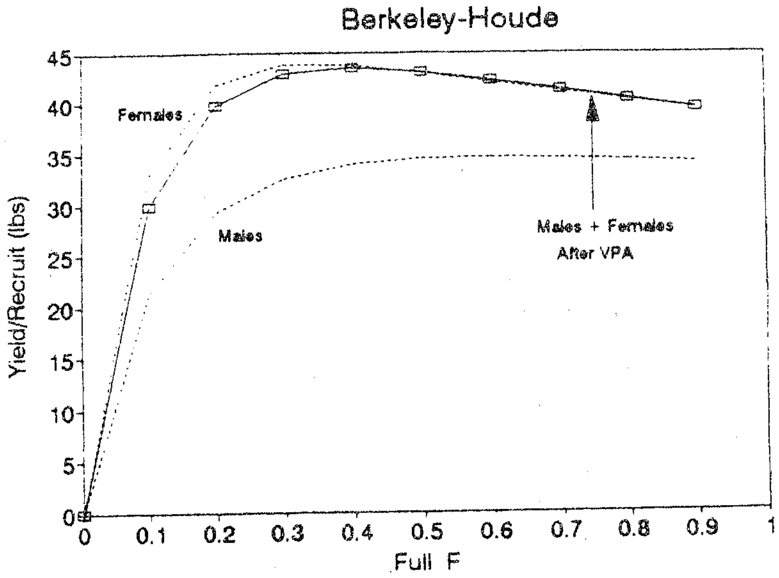

FIGURE 7. Yield per recruit relationship computed separately for males and females when the "true" population grows sexually dimorphically like the Berkeley-Houde models (dashed lines). These are compared to the yield per recruit calculated from VPA estimates derived from ageing using the pooled sex Gompertz model (solid line).