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"A Comparison of the Relationship Between Optimal Harvesting Strategies & Reproductive Values in Four Marine Species With Different Life History Characteristics"

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Abstract

The relationships between reproductive value and optimal harvesting strategies in four species with different life history characteristics were examined in light of MacArthur's (1960) work which suggested that harvesting should be inversely related to reproductive value. Linear programming and geometric programming were used to solve the optimal harvesting problems. Optimal yields were found to reflect a species specific reproductive value distribution. Optimal yields always involved partial harvesting of the age class with the smallest reproductive value. These results are in agreement with MacArthur's original hypothesis. Some implications for the management of different species groups are discussed.

NOTE

This manuscript has been submitted to the "Transactions of the American Fisheries Society" for publication. It represents some initial applications of geometric and linear programming approaches to harvest optimization, and it is being disseminated for comment and information to all interested collaborators in the fisheries stock assessment CRSP prior to publication

To us one of the interesting implications of this work is that for some short-lived and highly fecund species (such as occur in the tropics), it may be advantageous to partially harvest all age (size) classes rather than imposing restrictive size regulations which involve heavier exploitation of the remaining age (size) groups. However, this remains to be examined in further detail with empirical data.

The dynamics of exploited populations are dependent on individual growth, reproductive and mortality rates. However, most models used in fisheries management and in the analysis of optimal harvesting strategies do not include these vital rates. For example, the yield model of Beverton and Holt (1957), is used to estimate sustainable yield solely as a function of fishing effort and gear selectivity-at-age under the assumption of a stable age distribution. Methods based on the logistic growth function also do not explicitly include individual growth, reproductive and mortality rates (Botsford 1981). MacArthur (1960) stated that harvesting should be inversely related to the expectation of future progeny. This relationship is given by Fisher's (1956) reproductive value and is a function of individual survivorship and reproductive rates.

The purpose of this study is to examine the relationship between optimal harvesting strategies and reproductive value in some fisheries. This work represents a portion of a larger study directed toward developing assessment and management techniques for tropical species. In these species it is believed that data on survival and fecundity may be more readily obtained than growth data. Four diverse species were utilized in this study : 1) Atlantic menhaden (Brevoortia tyrrannus), 2) cunner (Tautogolabrus adspersus), 3) ray (Raja clavata), and 4) blue whale (Balaenoptera musculus)). These species were chosen in order to cover a wide range of life history characteristics and because suitable data were available. The Atlantic menhaden is an example of a relatively short-lived pelagic spawner with high

reproductive and low survivorship rates. The cunner is less fecund and survivorship rates are high compared to the menhaden. The ray species produces relatively few young in egg cases, has a longevity three times that of the other two species and higher survivorship rates. The blue whale is an example of a very long-lived species with extremely low reproductive rates and high survivorship rates.

The dynamics of these species were modeled using a Leslie matrix. While the restricted applicability and inadequacy of the density indepedent Leslie model is recognized (Mendelsohn 1976), it was considered suitable for comparing the selected species under similar assumptions. This exploratory study was aimed at testing MacArthur's theory with some real data with a view toward acquiring a better understanding of reproductive value and it's implications to optimal harvesting and management. In particular, it was thought that reproductive value might shed some light on the potential effects of additional mortality which could be of value as a criterion in the establishment of minimum size regulations and other measures aimed at enhancing population egg production. To date there has been little application of the concept of reproductive value in fisheries. However, some studies have recognized it's potential usefulness. Jensen (1981) suggested that the best description of the impact of fishing mortality on reproduction may be given by reproductive value and Ware (1985) showed that resilience and compensatory ability in Pacific herring (*Clupea harrengus*) were functions of reproductive value.

The specific objectives of this study were: 1) to determine how optimal harvesting strategies vary for species with different life history characteristics, 2) to examine the relationship between the

reproductive value distributions and optimal harvesting strategies, and 3) to compare different harvesting strategies where the characteristics of the yield to be maximized were numbers, weight, and the inverse of reproductive value (minimizing yield in terms of reproductive value).

Methods

Leslie models for the Atlantic menhaden, cunner and blue whale were taken directly from the literature (Horst 1977; Doubleday 1975). In the case of the blue whale, the time interval was two years because of the length of the gestation and weaning periods (Cullen 1986). In all others the interval was one year. Reproductive and survivorship rates for the ray were constructed using data from Holden (1975) and Ryland and Ajayi (1984). For comparative purposes, all four matrices were adjusted to have a maximum eigenvalue (λ) of approximately 1.002 1.003 using a program in BASIC from Poole and Borchers (1977) to calculate λ. The reproductive and survivorship rates used in this study are given in Table 1. The reproductive value distributions are given in Figures 1a - c and were calculated using the discrete time formula:

$$v_{(x)} = \frac{e^{r(x-1)}}{l_{(x)}} \sum_{j=x}^{\omega} e^{-rj}\, l_{(j)}\, m_{(j)}$$

where r is the intrinsic growth rate, ω is the oldest age class, $m_{(j)}$ is the survivorship function and $l_{(j)}$ is the proportion of a cohort surviving at time j (Goodman, 1982). Weight-at-age values for the menhaden and the ray were taken from Reintjes (1969) and Ryland and

Ajayi (1984) respectively.

Following Beddington and Taylor (1973), Doubleday (1975) and Rorres (1976), a harvesting strategy was considered in which the excess in each class is harvested so that the yield is sustainable. In matrix notation, if A is the Leslie matrix and x is an age distribution vector with $1'x=1$, $1'Ax$ is the total amount of the resource prior to each harvest. Considering a harvesting matrix Θ of the form:

$$\Theta = \begin{vmatrix} \Theta_1 & 0 & . & . & 0 \\ . & \Theta_2 & & & . \\ . & & . & & . \\ . & & & . & . \\ 0 & . & . & . & \Theta_n \end{vmatrix}$$

where the diagonal elements represent the proportion of each class remaining after harvesting, the problem is to maximize $c'(I - \Theta)Ax$. c' is a column vector of weights corresponding to the particular aspect of the harvest which is to be maximized and I is the identity matrix. For harvesting after reproduction, $\Theta Ax = x$ is the requirement that the initial age structure be restored following harvesting. Therefore, maximizing $c'(I - \Theta)Ax$ is equivalent to maximizing $c'(Ax - x)$ over x subject to:

$$\begin{aligned} x_{(i)} &>= 0 \\ Ax &>= x \\ 1'Ax &= 1 \\ 1'x &= 1 \end{aligned}$$

Theta (Θ) can then be calculated from the relationship $\Theta Ax = x$. The quantity $c'(Ax - x)$ represents the yield per unit amount of resource prior to each harvest. This is a standard linear programming problem. For each species, the optimal yield, age structure and harvesting matrix for various harvesting strategies were calculated using a program by Juha and Converse (1968). For all the species, yield in terms of numbers of individuals and in terms of the inverse of reproductive value (v^{-1}) were maximized for different age-at-first-capture policies. In addition, yield in terms of weight was also maximized for the Atlantic menhaden and the ray. To illustrate the difference between the harvesting strategies, yields in numbers and in weight were converted to yields in v^{-1} (the inverse of reproductive value).

The analysis described so far assumes that harvesting can focus on particular age classes. However, in reality this is seldom possible. A more realistic approach is that of harvesting all age classes above a certain age class at a constant rate. In this case the harvesting matrix takes the form:

$$\Theta_k = \begin{vmatrix} 1 & 0 & . & . & 0 \\ . & \Theta & & & . \\ . & . & \Theta & & . \\ . & & & . & . \\ 0 & . & . & . & \Theta \end{vmatrix}$$

where $\Theta = 1$ for age classes not harvested. This more realistic fisheries

problem cannot be solved with linear programming; Doubleday (1975) showed that if $Ax >= x >= 0$, $\Theta_k Ax = x$ has at most n-k+1 solutions since Θ_k must satisfy a polynomial of degree n-k+1. Geometric programming was therefore used to solve this harvesting problem (BLAU program (Kuester and Mize 1973), implemented in BASICA). The interested reader is referred to Rao (1984) for details concerning geometric programming. The objective function to maximize is either $c'(Ax - x)$ or $c'(I - \Theta_k)Ax$ over x and Θ_k subject to:

$$1'Ax = 1$$

$$1'x = 1$$

$$\Theta_k Ax = x$$

where $\Theta_k Ax = x$ are nonlinear constraints. As with the linear programming problem, optimal harvesting strategies were calculated over a range of age-at-first-capture policies and for different weighting factors ($c' = 1, v^{-1}$, weight).

Results

The results solving this more realistic problem by geometric programming showed that for a given age-at-first-capture, optimal age structure and Θ were not affected by the value of the weighting factor c'. This is because when all harvestable age classes are harvested at the same rate, differential weighting of the ages makes no difference and the optimal age structure and Θ are a function solely of the Leslie matrix. Optimal yields and values of Θ for the four species are given in

Tables 2a - d. The value of Θ decreased with increasing age-at-first-capture. The decrease was initially gradual for all species, but increased rapidly when relatively few age classes were harvested. The rate of decrease of Θ appeared to be greatest for the Atlantic menhaden when compared to the cunner, which had the same number of age classes. Comparing the ray with the blue whale is more difficult but it seems that the rate of decrease was greatest for the ray. In general, with increasing age-at-first-capture, optimal age structures were characterized by decreasing numerical importance of the older age classes. For all species, there was an age-at-first-capture (the highest) for which there were no feasible solutions. All individuals would be harvested and the constraint conditions would still not be satisfied in this case.

To illustrate the trends in the yields with increasing age-at-first-capture, the $\log_{10}$ transformations of the yields were plotted (Figures 2a - d). For the three fish, the highest yields by far with $c' = 1$ and $c' = v^{-1}$ occurred when all age classes in the population were harvestable (0 - N). For the blue whale this was also true for $c' = 1$. However, when yield in terms of v^{-1} was maximized the yield for "age classes" 13 - 19 harvestable was almost equal to that of 0 - 19 harvestable. For the fish species the decrease in yield in numbers and in v^{-1} from age 0 at-first-capture to age 1 at-first-capture was dramatic, especially for menhaden. From age 1 at-first-capture and above, the yield ($c' = 1$, v^{-1}) for Atlantic menhaden and cunner decreased gradually. For the ray, yield decreased initially and then stabilized. However, a decrease in yield ($c' = v^{-1}$) for age classes 18 22 harvested can be seen. The results for the blue whale were quite

different. Yield in terms of numbers and in terms of v^{-1} reached a minimum at age classes 3 - 19 harvested and subsequently increased with age-at-first-capture. As with the ray, there was a decrease in yield ($c' = v^{-1}$) for the last harvesting policy for which there was a solution.

When the objective was to maximize yield in weight, results for the menhaden showed a large drop in yield ranging from all age classes harvestable to age class 1+ harvested, with a gradual decrease thereafter with increasing age-at-first-capture. For the ray, there was an initial decrease in yield followed by an increase with a peak for age classes 13 - 22 harvested.

When specific age classes were considered for harvesting (the linear programming problem), the weighting factor c' influenced the optimal age structure. For menhaden with $c' = 1$ and $c' = v^{-1}$, the optimal fishing strategy in all cases was to harvest the youngest available age class partially, and in some cases, all of the oldest age class (Tables 3a - b). Greatest yields were obtained by fishing all age classes, with a significant drop in yield when the first age class was not fished. For yield in weight there was a similar trend. However, when age classes 1 - 7 were fished, the optimal harvesting strategy was not to partially fish age class 1 but to fish age class 2 (Table 3c). With increasing age-at-first-capture, optimal yields for menhaden decreased gradually (Tables 3a - c).

In contrast, optimal harvesting of the blue whale always involved the partial harvest of one age class and the complete harvesting of the oldest age class (Tables 4a - b). As with the fish, optimal yields were greatest when all "age classes" were subject to

harvesting. However, the decrease in yield associated with the increase in age-at-first-capture from 0 to 1 was insignificant compared to that for the fish species. For $c' = 1$ and $c' = v^{-1}$, yield stabilized at age class 3 and above at-first-capture. Partial harvest of the youngest age class available was not the best strategy in many cases. For example, for $c' = 1$ and age classes 3 to 13 and above at-first-capture, the optimal yield was obtained by partially harvesting age class 16 ($\Theta_{15} = .49$) in all cases.

Optimal yields in numbers converted to equivalent yields in v^{-1} show that for species such as menhaden where the first age class is numerically by far the most important and where reproductive value reaches a peak late in life, there is little if any difference between maximizing yield in numbers or in terms of v^{-1}. However, for a species such as the blue whale, optimal yields in numbers coverted to yields in v^{-1} are sigificantly inferior to yields where the strategy was to maximize v^{-1}.

Discussion

The results of this study support MacArthur's (1960) contention that harvesting should be scaled in units of reproductive value. In all the cases examined, the greatest yield involved partially harvesting the youngest age class (0) alone or age 0 and one or more other age classes. For the fish species, age 0 had the smallest reproductive value. Although the youngest age class does not have the smallest reproductive value, this is still the case for the blue whale because the constraints could not be satisfied by harvesting those other

older age classes with reproductive value less than 1. Going across the continuum from short-lived species with high reproductive and mortality rates to long-lived species with high survivorship and low fecundity there is a definite trend in the reproductive value distribution. For species in the first category, reproductive value increases with age; reaching a peak late in life. For intermediate species reproductive value is more equally distributed; with a peak reached approximately at mid-life. At the other extreme of high survivorship and low fecundity, maximum reproductive value is reached early in life.

These differences are reflected in optimal harvesting strategies. Realistic fisheries optimization using geometric programming showed that trends in optimal yield are opposite to those in reproductive value. The trend in optimal yield ranges from a decrease with increasing age-at-first-capture to relative stability and later increases in the ray and the blue whale. The implication for fisheries is that for short-lived, relatively highly fecund and fast growing species, such as small pelagics and many tropical species of fish, it may be of greater benefit to fish all age classes including age 0 at a slightly lower rate than to impose measures to protect age 0 fish and other young age classes while fishing at a higher rate the older age classes. The significance of the youngest age class is seen in the dramatic decreases in yield going from age 0 at-first-capture to age 1 at-first-capture. This is true for the maximization of yield in numbers, weight and for v^{-1} (minimizing yield in reproductive value units). It therefore seems that establishing a minimum age-at-first capture only becomes useful for species at the other end of the spectrum where we see that yield in numbers, weight and v^{-1} may increase with age

at-first-capture, assuming, in all cases that only surplus production is harvested.

The age class reproductive distribution also has a sigificant trend. In fish, the age distribution is dominated numerically by age class 0. Thus, the first few age classes account for most of the population reproductive value. With greater longevity, survivorship and lower reproductive rates, population reproductive value is more equally distributed. The implications for management here is that a shift in age-at-first-capture in the latter type species will have much less significance in terms of what proportion of the population reproductive value is harvested. In other words, there is greater stability associated with more equal distribution of reproductive value across the lifespan. This is of relevance to management by minimum size regulations for species such as the striped bass (Morone saxatilis). As Jensen (1981) pointed out, reproductive value may be the best descriptor of the effect of increased fishing mortality on population reproduction. These analyses are in agreement with Jensen (1981). Management decisions based in part on knowledge of a population's reproductive value distribution may be more appropriate than decisions based on age-at-maturity.

The limitations of the Leslie model are recognized. In real populations density dependent changes in fecundity and survivorship will result in changes in the reproductive value distribution. Nevertheless, it is believed that knowledge of a species reproductive value distribution may be of considerable utility in helping us to understand potential effects of additional mortality and in making better management decisions.

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Table 1. Survivorship and reproductive rates for Atlantic menhaden, cunner, ray and blue whale.

	Menhaden		Cunner		Ray		Blue whale	
Age Class	P_i	F_i	P_i	F_i	P_i	F_i	P_i	F_i
0	0.000077	0	0.0002121	0	0.0086	0	0.77	0
1	0.2015	7597	0.6252	85	0.77	0	0.77	0
2	0.2015	19597	0.6252	698	0.77	0	0.77	0.19
3	0.2015	29567	0.6252	2029	0.77	0	0.77	0.44
4	0.2015	37647	0.6252	3967	0.77	50	0.77	0.50
5	0.2015	43537	0.6252	6294	0.77	54	0.77	0.50
6	0.2015	47617	0.6252	8796	0.77	58	0.77	0.45
7		51355		11303	0.77	61	0.77	0.45
8					0.77	64	0.77	0.45
9					0.77	67	0.77	0.45
10					0.77	69	0.77	0.45
11					0.77	71	0.77	0.45
12					0.77	73	0.77	0.45
13					0.77	75	0.77	0.45
14					0.77	77	0.77	0.45
15					0.77	79	0.77	0.45
16					0.77	80	0.77	0.45
17					0.77	81	0.77	0.45
18					0.77	83	0.77	0.45
19					0.77	84		0.45
20					0.77	85		
21					0.77	86		
22						87		

Table 2. Optimal Θ and yield in numbers (c' = 1), in weight (c' = weight), and in the inverse of reproductive value ($c' = v^{-1}$) for different age-at-first-capture policies for: a) Atlantic menhaden, b) cunner, c) ray, and d) blue whale.

a) Atlantic menhaden

Age Classes Fished	Θ	Yield c'=1	c'=1/v	c'=weights(k)
0 - 7	.9983	1.73E-03	1.73E-03	6.58E-05
1 - 7	.9972	2.71E-07	1.85E-11	5.08E-08
2 - 7	.9924	1.47E-07	5.00E-12	5.77E-08
3 - 7	.9722	1.05E-07	2.58E-12	5.22E-08
4 - 7	.8826	7.93E-08	1.61E-12	4.73E-08
5 - 7	.4147	3.36E-08	6.36E-13	2.20E-08
6 - 7*				

* No solution possible.

b) Cunner

Age Classes Fished	Θ	Yield c'=1	c'=1/v
0 - 7	.9983	1.74E-03	1.74E-03
1 - 7	.9979	1.15E-06	1.94E-10
2 - 7	.9973	8.96E-07	1.07E-10
3 - 7	.9963	7.42E-07	6.97E-11
4 - 7	.9943	6.60E-07	5.44E-11
5 - 7*			

* Did not converge.

c) Ray

Age Classes Fished	θ	Yield c'=1	c'=1/v	c'=weights(k)
0 - 22	.9978	2.20E-03	2.09E-03	3.97E-04
1 - 22	.9975	8.75E-05	4.81E-07	1.69E-04
2 - 22	.9972	7.72E-05	3.53E-07	1.87E-04
3 - 22	.9967	6.97E-05	2.75E-07	2.07E-04
4 - 22	.9960	6.49E-05	2.34E-07	2.32E-04
5 - 22	.9949	6.32E-05	2.22E-07	2.67E-04
6 - 22	.9934	6.20E-05	2.14E-07	3.03E-04
7 - 22	.9915	6.10E-05	2.09E-07	3.40E-04
8 - 22	.9890	6.05E-05	2.05E-07	3.77E-04
9 - 22	.9855	6.03E-05	2.04E-07	4.15E-04
10 - 22	.9808	6.03E-05	2.06E-07	4.52E-04
11 - 22	.9742	6.07E-05	2.09E-07	4.90E-04
12 - 22	.9649	6.14E-05	2.15E-07	5.26E-04
13 - 22	.9514	6.25E-05	2.22E-07	5.62E-04
14 - 22	.9312	6.41E-05	2.32E-07	5.94E-04
15 - 22	.8994	6.62E-05	2.43E-07	6.21E-04
16 - 22	.8466	6.88E-05	2.52E-07	6.33E-04
17 - 22	.7512	7.18E-05	2.49E-07	6.10E-04
18 - 22	.5511	7.50E-05	2.04E-07	4.86E-04
19 - 22*				

d) Blue whale

Age Classes Fished	θ	Yield c'=1	c'=1/v
0 - 19	.9967	1.43E-02	2.31E-03
1 - 19	.9962	2.95E-03	1.79E-03
2 - 19	.9953	2.75E-03	1.53E-03
3 - 19	.9940	2.69E-03	1.46E-03
4 - 19	.9921	2.73E-03	1.51E-03
5 - 19	.9893	2.79E-03	1.58E-03
6 - 19	.9856	2.85E-03	1.66E-03
7 - 19	.9806	2.90E-03	1.73E-03
8 - 19	.9735	2.96E-03	1.81E-03
9 - 19	.9633	3.04E-03	1.91E-03
10 - 19	.9484	3.13E-03	2.02E-03
11 - 19	.9258	3.25E-03	2.15E-03
12 - 19	.8899	3.38E-03	2.27E-03
13 - 19	.8292	3.54E-03	2.35E-03
14 - 19	.7161	3.71E-03	2.26E-03
15 - 19*			

* No solution possible.

Table 3. Atlantic menhaden optimal yields ($c' = 1$, v^{-1}, and weight) and Θ_1 for different age-at-first-capture policies. Individuals of different ages can be harvested at different rates (linear programming problem).

a) $c' = 1$

Age Classes Fished	Θ 1	2	3	4	5	6	7	8	Yield
0 - 7	.9952	1	1	1	1	1	1	1	4.88E-03
1 - 7	1	.9955	1	1	1	1	1	1	3.44E-07
2 - 7	1	1	.9895	1	1	1	1	1	1.63E-07
3 - 7	1	1	1	.9636	1	1	1	1	1.14E-07
4 - 7	1	1	1	1	.8539	1	1	1	9.20E-08
5 - 7	1	1	1	1	1	.3736	1	0	8.14E-08
6 - 7	1	1	1	1	1	1	.000081	0	2.54E-08

b) $c' = v^{-1}$

Age Classes Fished	Θ 1	2	3	4	5	6	7	8	Yield
0 - 7	.9952	1	1	1	1	1	1	1	.999904
1 - 7	1	.9955	1	1	1	1	1	1	2.64E-11
2 - 7	1	1	.9894	1	1	1	1	1	5.93E-12
3 - 7	1	1	1	.9636	1	1	1	1	2.89E-12
4 - 7	1	1	1	1	.8539	1	1	0	1.89E-12
5 - 7	1	1	1	1	1	.3736	1	0	1.48E-12

c) c' = weight

Age Classes Fished	Θ 1	2	3	4	5	6	7	8	Yield
0 - 7	.9954	1	1	1	1	1	1	1	1.16E-04
1 - 7*	1	1	.9901	1	1	1	1	0	6.01E-08
2 - 7									
3 - 7	1	1	1	.9656	1	1	1	0	5.59E-08
4 - 7	1	1	1	1	.8613	1	1	0	5.43E-08

* Did not converge.

Table 4. Blue whale optimal yields ($c' = 1$ and v^{-1}) and θ_1 for different age-at-first-capture policies. Individuals of different ages can be harvested at different rates (linear programming problem).

a) $c' = 1$

Age Classes Harvested	θ 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Yield
0-19	.98	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	5.96E-03
1-19	1	.98	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	4.94E-03
2-19	1	1	.98	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	4.16E-03
3-19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	.49	1	1	1	1	0	3.87E-03
4-19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	.49	1	1	1	1	0	3.87E-03
5-19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	.49	1	1	1	1	0	3.87E-03
6-19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	.49	1	1	1	1	0	3.87E-03
7-19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	.49	1	1	1	1	0	3.87E-03
8-19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	.49	1	1	1	1	0	3.87E-03
9-19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	.49	1	1	1	1	0	3.87E-03
10-19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	.49	1	1	1	1	0	3.87E-03
11-19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	.49	1	1	1	1	0	3.87E-03
12-19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	.49	1	1	1	1	0	3.87E-03
13-19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	.49	1	1	1	1	0	3.87E-03
14-19	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	.25	1	1	1	0	3.87E-03
15-19*																					

b) $c' = v^{-1}$

Age Classes Harvested	θ 1	2	3	4	5	6	7	8	9	10	11	12	13	14	15	16	17	18	19	20	Yield
0-19	.99	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	8.19E-03
1-19	1	.99	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	6.39E-03
2-19	1	1	.99	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	1	0	5.23E-03
3-19	1	1	1	1	1	1	.96	1	1	1	1	1	1	1	1	1	1	1	1	0	4.76E-03
4-19	1	1	1	1	1	1	.96	1	1	1	1	1	1	1	1	1	1	1	1	0	4.75E-03
5-19	1	1	1	1	1	1	.96	1	1	1	1	1	1	1	1	1	1	1	1	0	4.78E-03
6-19	1	1	1	1	1	1	.96	1	1	1	1	1	1	1	1	1	1	1	1	0	4.75E-03
7-19	1	1	1	1	1	1	1	.95	1	1	1	1	1	1	1	1	1	1	1	0	4.71E-03
8-19	1	1	1	1	1	1	1	1	.93	1	1	1	1	1	1	1	1	1	1	0	4.65E-03
9-19	1	1	1	1	1	1	1	1	1	.91	1	1	1	1	1	1	1	1	1	0	4.58E-03
10-19	1	1	1	1	1	1	1	1	1	1	.88	1	1	1	1	1	1	1	1	0	4.51E-03
11-19	1	1	1	1	1	1	1	1	1	1	1	.81	1	1	1	1	1	1	1	0	4.40E-03
12-19	1	1	1	1	1	1	1	1	1	1	1	1	.74	1	1	1	1	1	1	0	4.25E-03
13-19*																					

* No possible solutions.

Table 5. Yields in numbers ($c' = 1$) converted to equivalent yield in inverse of reproductive value ($c' = v^{-1}$).

a) Atlantic menhaden

Age Classes Harvested	Equivalent Yield $c'=1$	Equivalent Yield $c'=v^{-1}$
0-7	.999904	.999904
1-7	2.64E-11	2.64E-11
2-7	5.93E-12	5.93E-12
3-7	2.89E-12	2.89E-12
4-7	1.89E-12	1.89E-12
5-7	1.48E-12	1.48E-12

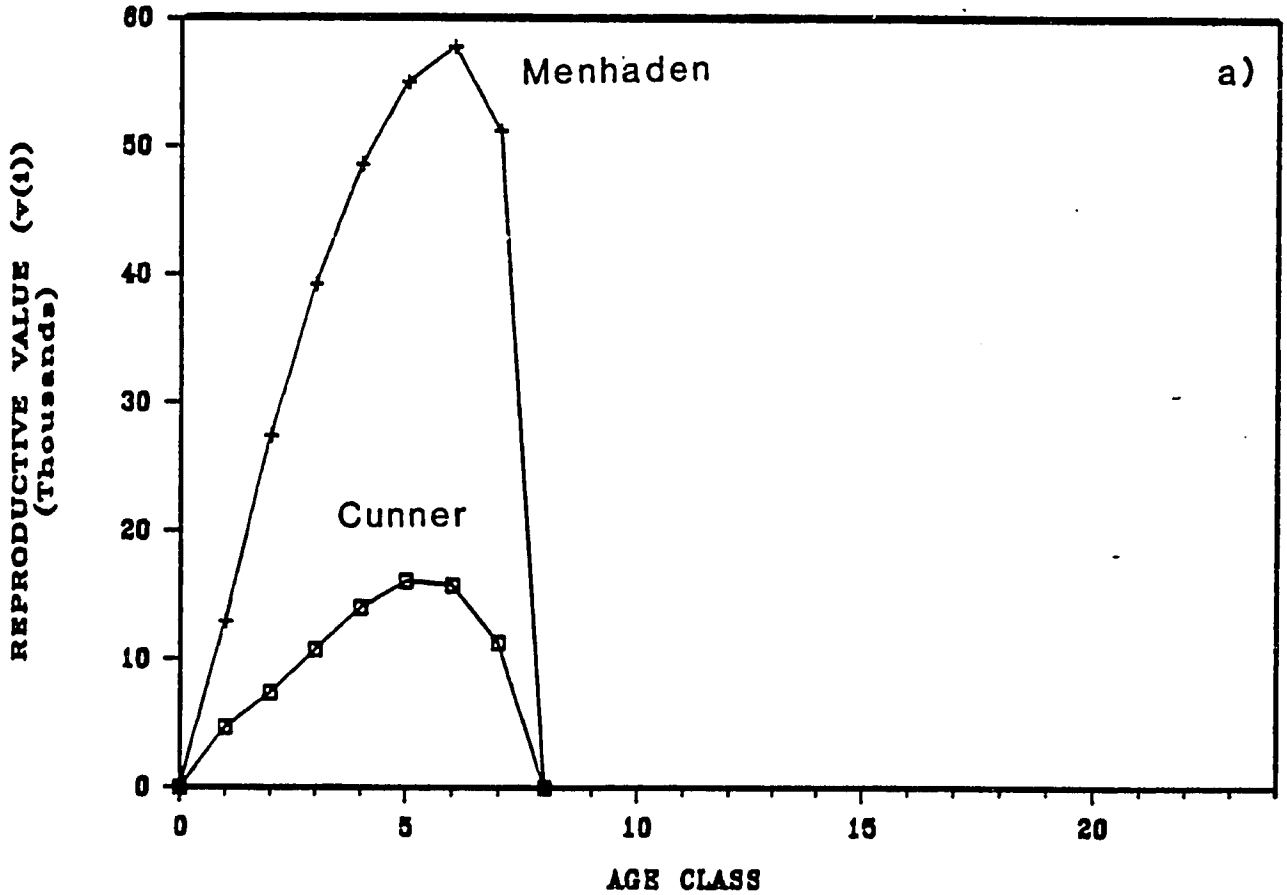
b) Blue whale

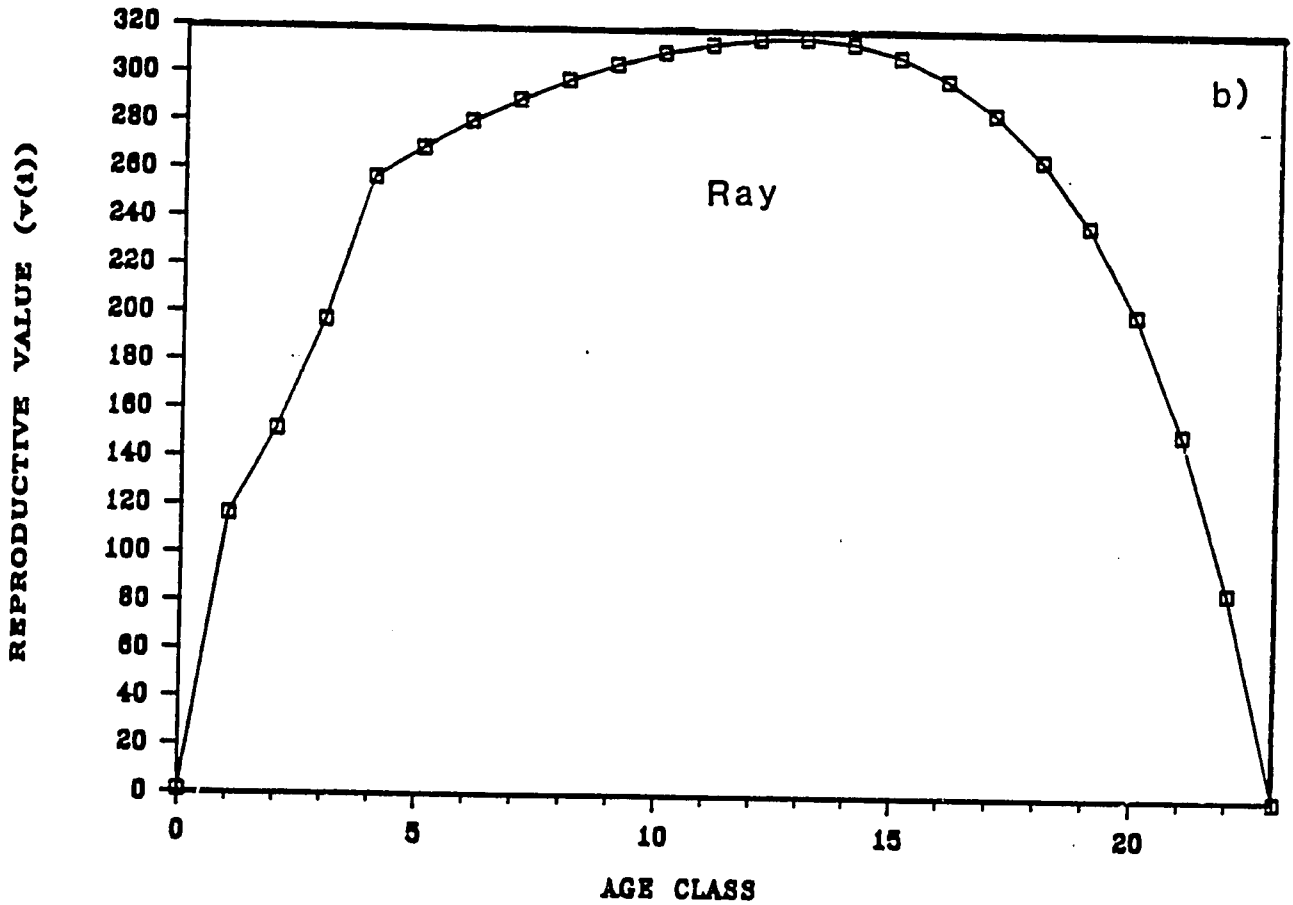
Age Classes Harvested	Equivalent Yield $c'=1$	Equivalent Yield $c'=v^{-1}$
0-19	7.35E-03	8.19E-03
1-19	6.14E-03	6.39E-03
2-19	5.08E-03	5.23E-03
3-19	3.78E-03	4.75E-03
4-19	"	"
5-19	"	"
6-19	"	"
7-19	"	4.71E-03
8-19	"	4.65E-03
9-19	"	4.58E-03
10-19	"	4.51E-03
11-19	"	4.40E-03
12-19	"	4.25E-03

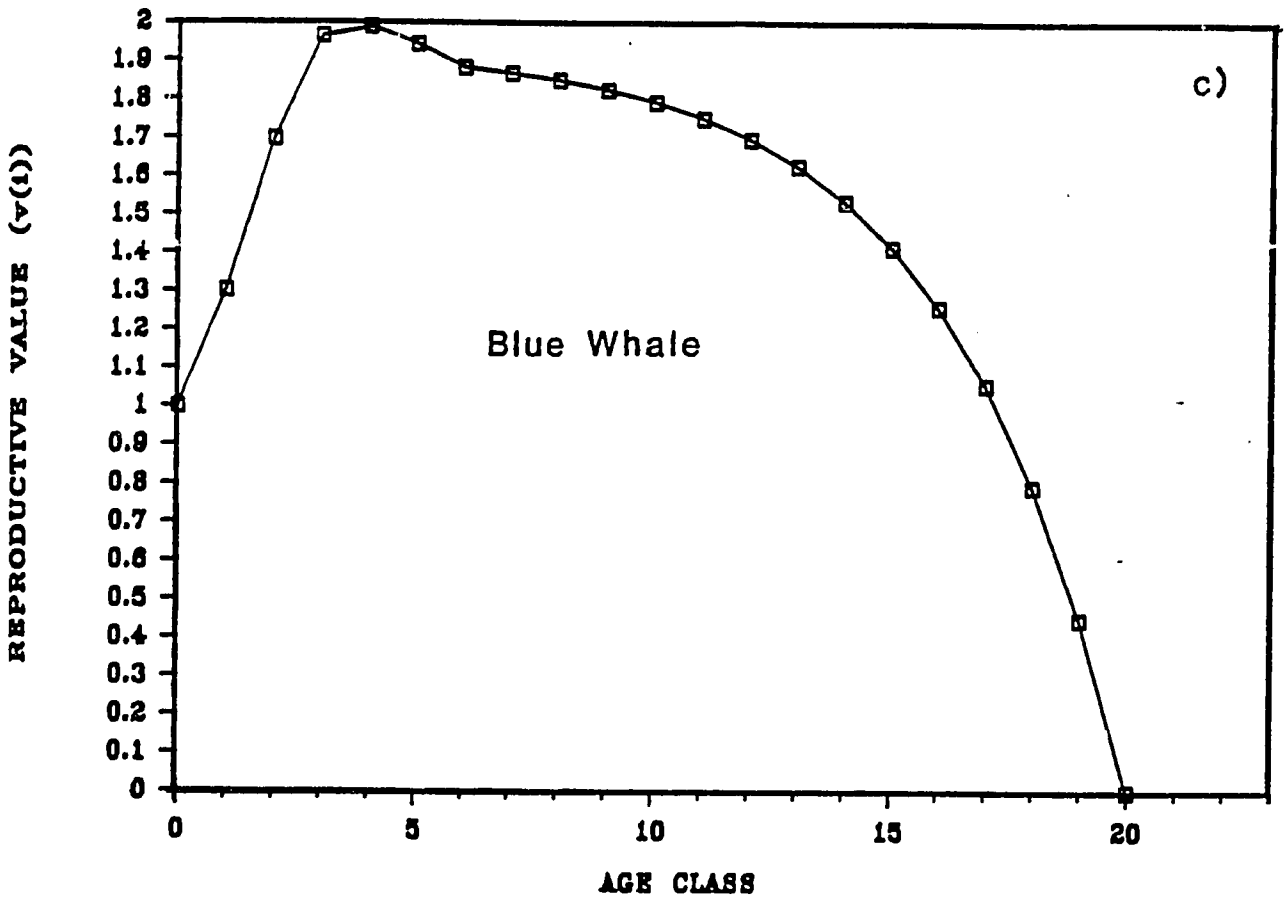
Figure Captions

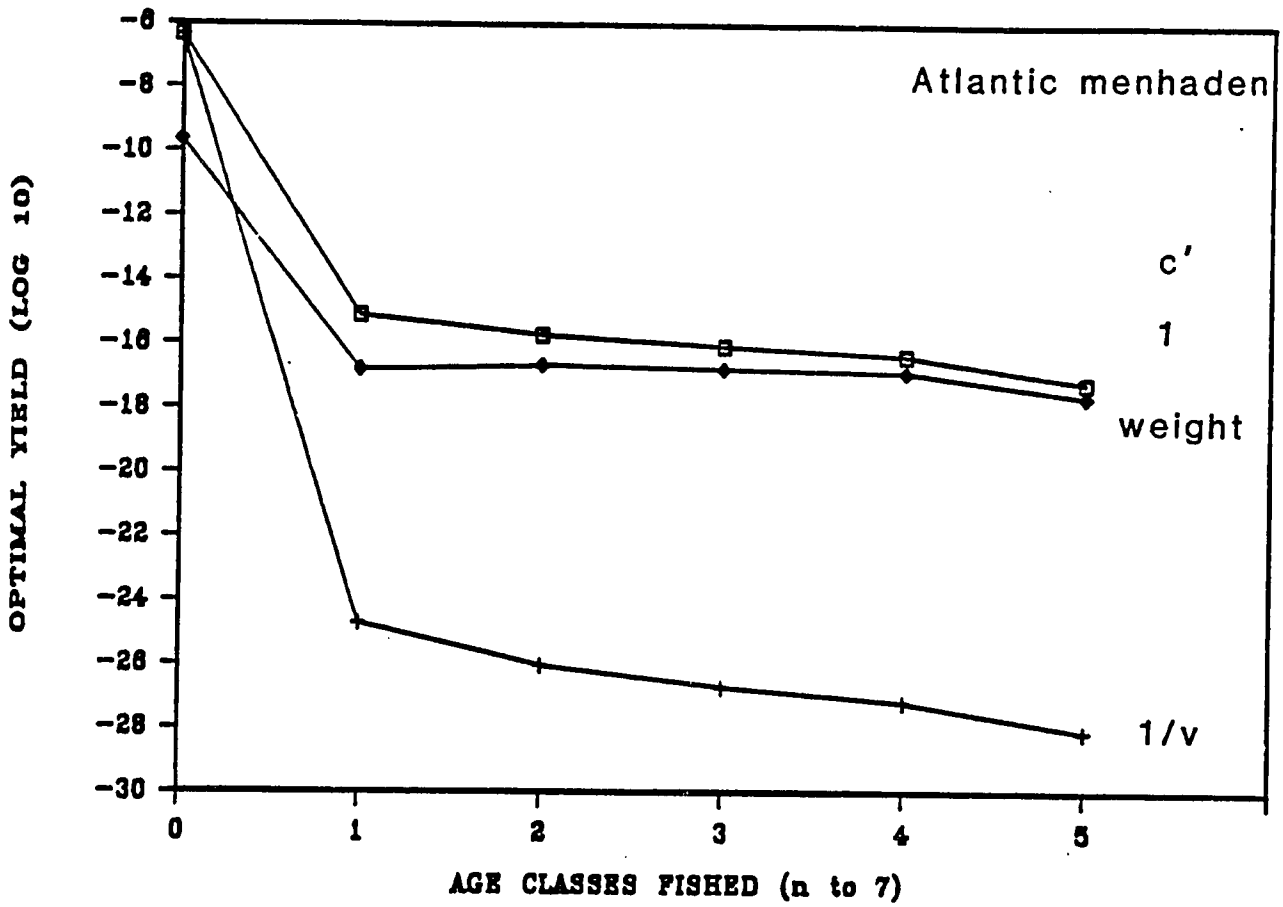
Figure 1. Derived reproductive value distributions of: a) Atlantic menhaden (*Brevoortia tyrranus*) and cunner (*Tautogolabrus adspersus*), b) ray (*Raja clavata*) and c) blue whale (*Balaenoptera musculus*).

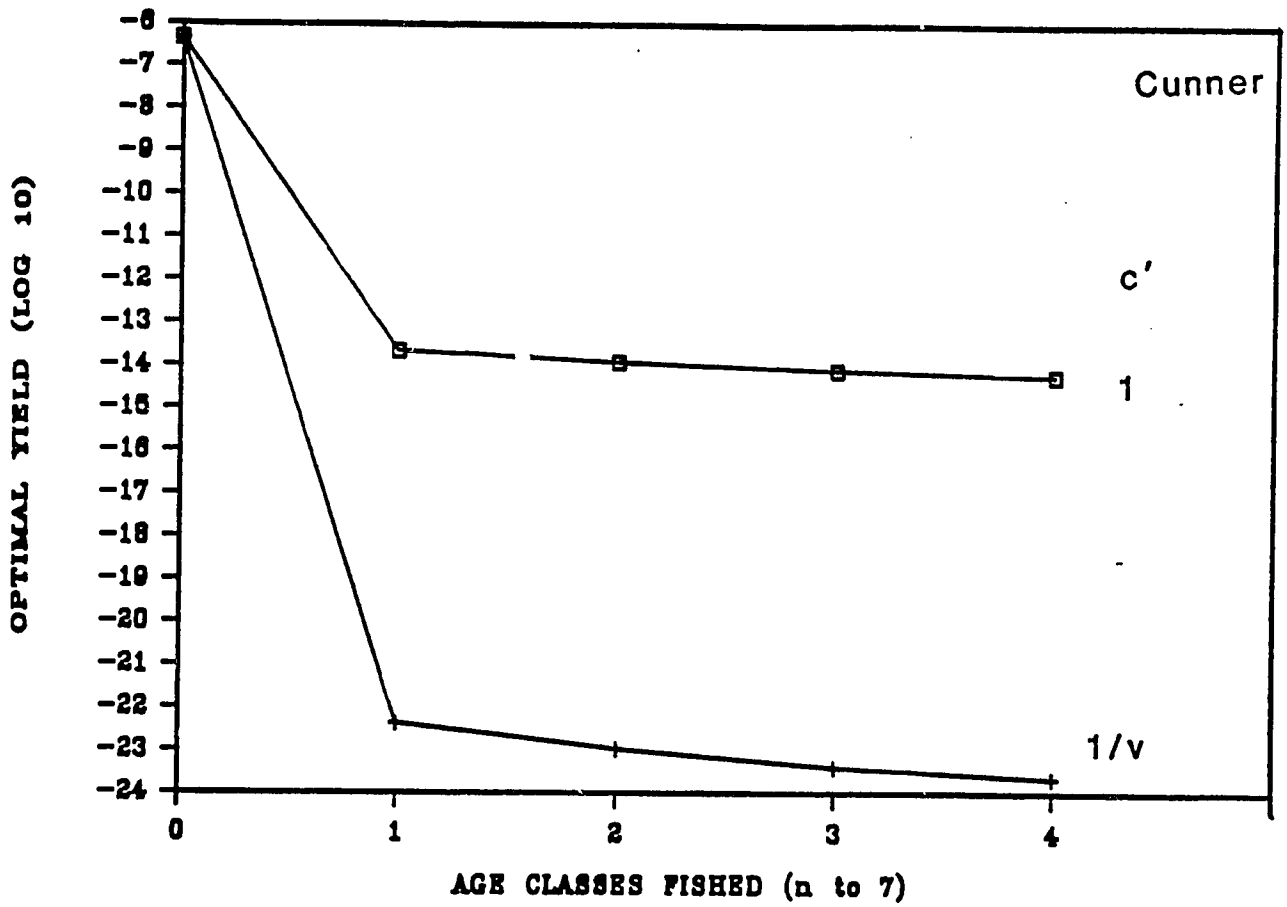
Figure 2. Optimal yields ($\log_{10}$) in numbers ($c' = 1$), the inverse of reproductive value ($c' = v^{-1}$) and in weight (c' = weight) for different age-at-first-capture policies: a) Atlantic menhaden, b) cunner, c) ray and d) blue whale.

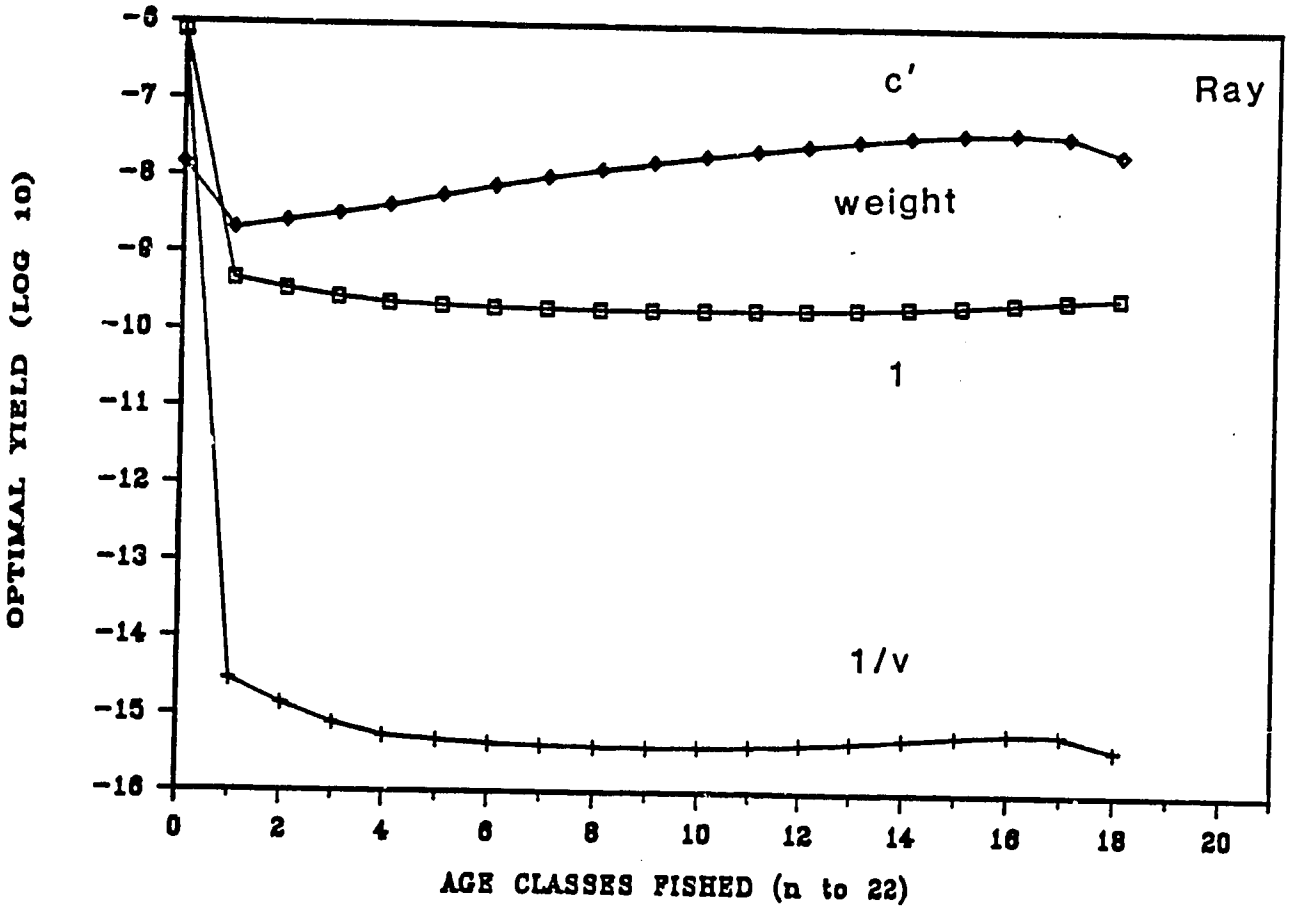

Menhaden
a)
Cunner
REPRODUCTIVE VALUE (v(i))
(Thousands)
AGE CLASS
0
10
20
30
40
50
60
0
5
10
15
20

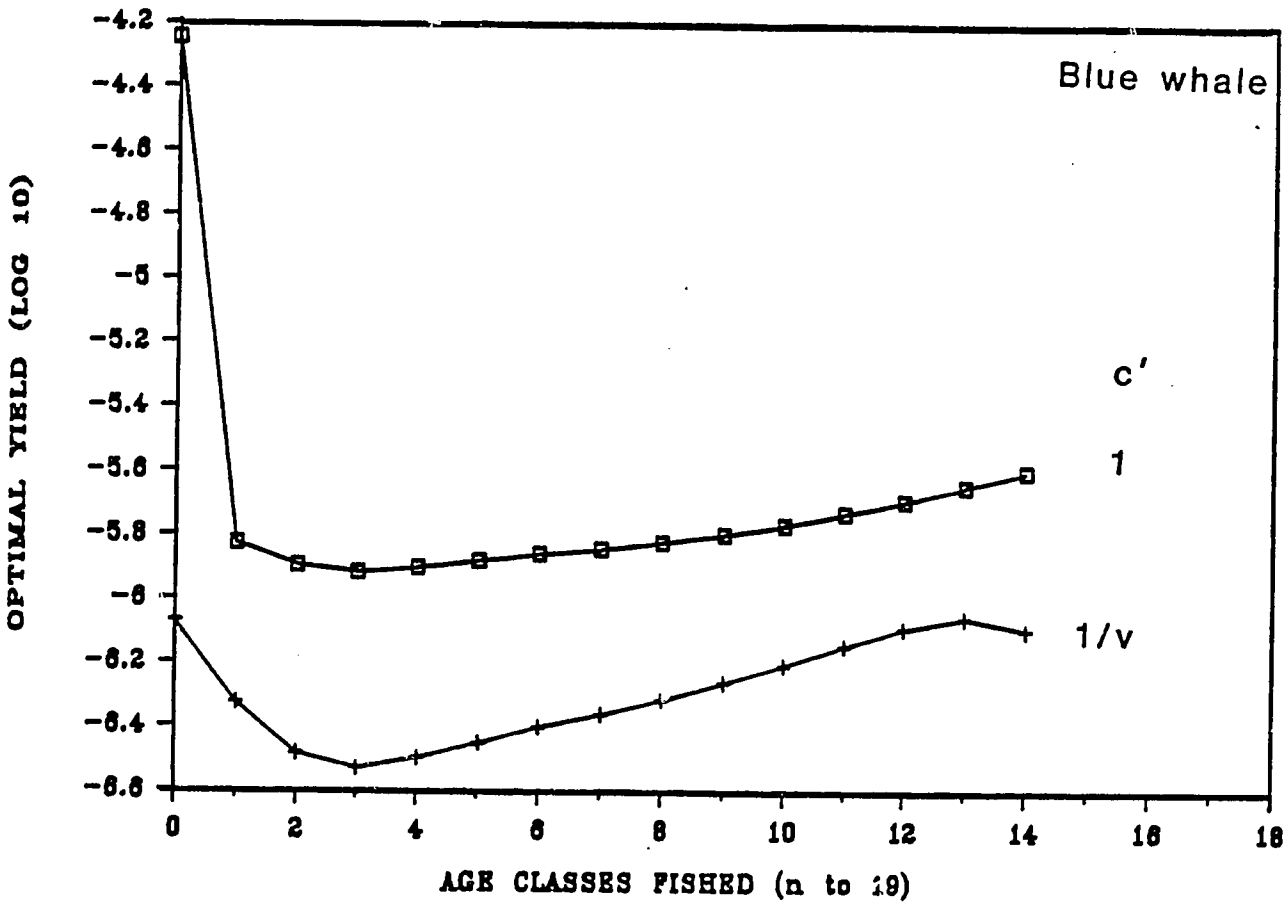

b)
Ray
REPRODUCTIVE VALUE (v(i))
AGE CLASS
320
300
280
260
240
220
200
180
160
140
120
100
80
60
40
20
0
0
5
10
15
20


c)
Blue Whale
REPRODUCTIVE VALUE (v(i))
AGE CLASS
2
1.9
1.8
1.7
1.6
1.5
1.4
1.3
1.2
1.1
1
0.9
0.8
0.7
0.6
0.5
0.4
0.3
0.2
0.1
0
0
5
10
15
20


Atlantic menhaden
c'
1
weight
1/v
OPTIMAL YIELD (LOG 10)
-6
-8
-10
-12
-14
-16
-18
-20
-22
-24
-26
-28
-30
0
1
2
3
4
5
AGE CLASSES FISHED (n to 7)


Cunner
c'
1
1/v
OPTIMAL YIELD (LOG 10)
-6
-7
-8
-9
-10
-11
-12
-13
-14
-15
-16
-17
-18
-19
-20
-21
-22
-23
-24
0
1
2
3
4
AGE CLASSES FISHED (n to 7)


Ray
c'
weight
1
1/v
OPTIMAL YIELD (LOG 10)
-6
-7
-8
-9
-10
-11
-12
-13
-14
-15
-16
0
2
4
6
8
10
12
14
16
18
20
AGE CLASSES FISHED (n to 22)


Blue whale
c'
1
1/v
OPTIMAL YIELD (LOG 10)
-4.2
-4.4
-4.6
-4.8
-5
-5.2
-5.4
-5.6
-5.8
-6
-6.2
-6.4
-6.6
0
2
4
6
8
10
12
14
16
18
AGE CLASSES FISHED (n to 19)