

Protecting the Reproductive Value of Swordfish, *Xiphias gladius*, and Other Billfishes

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ABSTRACT

The intrinsic rate of population growth (r) and the reproductive value of females at given age (v_x) are estimated for swordfish, *Xiphias gladius*, and other billfishes to determine how protecting reproductive value affects population sustainability. The procedure involves the standard demographic equations and standard assumptions regarding density-dependent changes in vital rates from basic deterministic population dynamics. It appears that to ensure population sustainability of swordfish and blue marlin, age at first capture should be high enough to protect the first 1–2 mature age classes, but need not protect the most reproductively valuable, older females. For striped marlin and sailfish, however, the most valuable females may need protection.

Introduction

An argument frequently raised regarding the management of billfishes is that large, mature individuals, especially females, should be protected for their valuable reproductive capability. That very large and fecund females are valuable to their populations is intuitively obvious, and especially so if they are scarce or solitary, as adult billfishes usually are. In addition, female billfishes grow rapidly to sizes that are larger than males of the same age (see Boggs, 1989) and tend to be outnumbered by males on the spawning grounds (Hopper, 1990); this suggests they constitute a particularly valuable reproductive resource. Some protection of these females would obviously be beneficial—but to what extent?

The purpose of this paper is to estimate the reproductive value of billfish females to their populations, using the demographic formulae of Lotka (1907) and Fisher (1958). How a population's potential for increase is affected by protecting females below the most reproductively valuable age will be examined. This involves first estimating the population's intrinsic rate of increase when it is near the size that produces maximum sustainable yield, and then using that estimate to determine reproductive value and the effects of protection. The focus will be on the commercially important

swordfish, *Xiphias gladius*, but the cases for blue marlin, *Makaira mazara*, striped marlin, *Tetrapturus audax*, and sailfish, *Istiophorus platypterus*, will also be evaluated for perspective.

Classical demographic analyses are not much used in studying the dynamics of fishes other than sharks (e.g. Cailliet, 1992; Cailliet et al., 1992; Cortes, 1995), because most teleosts have extremely low larval and juvenile survival rates which are very difficult to measure. Proposed survival schedules are therefore not very convincing for these fishes. However, the demographic relationships allow this difficulty to be circumvented, as will be shown.

Methods

Estimating Life History Parameters

Estimates of age at maturity (α), maximum age of reproduction (w), and instantaneous natural mortality (M) are basic for a demographic analysis. These parameters were estimated from the biological characteristics of billfishes taken in the eastern Pacific. Age at 50% maturity (α) was estimated as the age at which a species' gonad index increased rapidly to values greater than 3 (see Eldridge and Wares, 1974; Miyabe and

Bayliff, 1987; Nakano and Bayliff, 1992). Maximum reproductive age (w) was obtained from converting maximum sizes observed historically in the longline fisheries (Shingu et al., 1974; Miyabe and Bayliff, 1987; Nakano and Bayliff, 1992) to age (von Bertalanffy growth parameters as listed by Boggs, 1989; Table 1). Maximum age w is difficult to estimate from growth relationships without underestimation, and very old fish are expected to be rare, especially in an exploited population; therefore the calculated maximum ages were arbitrarily increased by 10% to estimate unexploited w for this analysis. Natural mortality was obtained from this age, w , using Hoenig's (1983) relationship for fishes ($\ln M = 1.46 - 1.01 \ln w$).

To estimate fecundity (m_x), size at age was converted to weight at age using length-weight relationships as given by Kume and Joseph (1969) for swordfish and by Wares and Sakagawa (1974) for the other billfishes. Fecundity-weight relationships are best known for swordfish (10^6 advanced mode ova = $2.725 + 0.015 \cdot$ adult weight in kg; Uchiyama and Shomura, 1974); that relationship, which is nearly identical to one reported for sailfish (Eldridge and Wares, 1974), was used for all species considered here. There is no quantitative information on batch frequency of spawning among the billfishes. The final fecundities calculated were divided by 2 to obtain age-specific estimates of female newborn per adult female, i.e. m_x .

Estimating Intrinsic Rate of Increase

The intrinsic rate of population increase (r) is estimated here by incorporating the standard concept that

density-dependent compensation occurs in a population as a response to reduction by fishing. Lotka's equation (more correctly, the Euler-Lotka equation) expresses the fundamental relation between survival from birth to age x (i.e. l_x), m_x , α , and w , and rate of population growth, r , of a stable-aged population. The term stable-aged means that all population segments (e.g. age classes) are growing at the same rate, the abundance ratio of any one segment relative to another remaining the same. Lotka's equation may be written (e.g. Stearns, 1992, Chapter 2, p. 20–38)

$$\sum_{x=\alpha}^w l_x e^{-rx} m_x = 1.0. \quad (1)$$

It states that recruitment into a population must come from offspring, with contributions from older females discounted at rate r relative to those from younger females because they have less time to contribute to population growth. In terms of survival to maturity (l_α), l_x equals $l_\alpha (l_x/l_\alpha) = l_\alpha e^{-M(x-\alpha)}$ for $x \geq \alpha$. Thus Equation (1) becomes

$$l_\alpha \sum_{x=\alpha}^w e^{-M(x-\alpha)} e^{-rx} m_x = 1.0 \quad (2)$$

which can be solved for r if m_x , M , and l_α are known.

Our interest is finding r when the population is most productive, i.e. at the size that produces maximum sustainable yield (MSY). Theory and experience (e.g. Shepherd, 1982; Kimura, 1988; Clark, 1991) suggest

Table 1
Growth and life history parameters of billfishes.

Species	Sex ²	Von Bertalanffy growth parameters ¹			Life history parameters		
		L_∞ (cm)	K (yr ⁻¹)	t_0 (yr)	α^3 (yr)	w^6 (yr)	M^7 (yr ⁻¹)
Swordfish	U	309	0.124	-1.169	5	20	0.21
Blue marlin	F	487 ^{3,4}	0.116	-0.161	4	11	0.38
Striped marlin	U	275	0.264		4	9	0.47
Sailfish	U	232	0.472		3	8	0.53

¹ From Boggs (1989).

² U = Unidentified/unreported sex; F = female. U growth rate used for striped marlin because F growth rate did not accommodate the largest size observed.

³ Corrected from value listed by Boggs (1989).

⁴ After age 8, size at age was based on a freehand-drawn curve rather than predictions from growth parameters, because the largest blue marlin in the E. Pacific longline catch (332 cm) was much smaller than the reported maximum size (about 389 cm).

⁵ Age at 50% maturity.

⁶ Maximum reproductive age.

⁷ Natural mortality derived from $\ln M = 1.46 - 1.01 \ln w$ (Hoenig, 1983).

that MSY usually occurs in teleosts at population sizes between 1/2 and 1/5 of initial biomass, usually closer to the smaller fraction. A fishing mortality (F) with values between M and $2M$ (total mortality $Z = (F + M) = 2M$ to $3M$) would reduce an exploited population to approximately between 1/2 and 1/3 of its initial numerical size. In terms of biomass the reduction would be greater (Beverton and Holt, 1957), though it may not be if growth is density-dependent (Beverton¹). Therefore, this range of F should conservatively bracket the MSY population size and will be used here for that purpose.

With this fishing mortality emplaced, total reproductive output would be reduced and the population would decline. If, however, the decline ends at a level that is sustainable, there must be density-dependent compensation such that Equation (2) describing the smaller, now stationary ($r = 0$) population is satisfied. Under total mortality $Z (= 2M$ or $3M)$ this compensation is assumed here to result from an increase in the survival of immature fish, to (say) survival $l_{\alpha,Z}$

Equation (2) then becomes, with $r = 0$,

$$l_{\alpha,Z} \sum_{x=\alpha}^w e^{-Z(x-\alpha)} m_x = 1.0 \tag{3}$$

from which $l_{\alpha,Z}$ can be estimated as the reciprocal of the summation term, given that the other parameters are specified. Estimation of $l_{\alpha,Z}$ enables specification of the particular adult survival schedule of a population at its Z -reduced size. The actual, age-specific survival rates of pre-adult fish need not be of concern.

If fishing mortality is removed ($F = 0$) and if $l_{\alpha,Z}$ holds, this stationary population will begin growing, eventually at a rate here designated r_Z . This is the r -potential at the MSY population size, and it is found by iteratively solving for r_Z from Equation (2), now written

$$l_{\alpha,Z} \sum_{x=\alpha}^w e^{-M(x-\alpha)} e^{-r_Z x} m_x = 1.0. \tag{4}$$

Estimating Reproductive Value

The reproductive value (v_x) of a female at age x from a stable-aged cohort can be written (Fisher, 1958)

$$v_x \sum_{t=x}^w e^{-r(t-x)} (l_t / l_x) m_t. \tag{5}$$

It measures that female's relative contribution to future population growth, again discounting for the lesser effect that contributions made at older ages will have.

Equation (5) is more meaningfully expressed in terms of the standing population, which is the abundance at hand and the focus of fishermen's interest. Then v_x would be a measure of the reproductive output of ages x and older in the population, normalized by the relative abundance at age x . The standing relative abundance of fish at each age x (designated S_x) in such a population is

$$S_x = l_x e^{-rx} \tag{6}$$

and similarly for S_t (e.g. Caughley, 1977). Gathering those terms and substituting S_x gives

$$v_x = 1/S_x \sum_{t=x}^w S_t m_t$$

or

$$v_x = 1/(S_x/S_\alpha) \sum_{t=x}^w (S_t/S_\alpha) m_t \tag{7}$$

i.e. reproductive value in terms of the standing abundance of age- α fish (S_α). Values of v_x can be readily calculated for any age $x \geq \alpha$ in a population with fishing mortality removed, using the abundance ratio $S_x/S_\alpha = (l_x/l_\alpha) (e^{-rx}/e^{-r\alpha}) = e^{-(M+r)(x-\alpha)}$ (and similarly for (S_t/S_α)). At the MSY population size, r is the r_Z estimated previously.

Evaluating Effects of Protection

Reproductive value in a population capable of increasing at rate r , and therefore with survival l_α (designated $l_{\alpha,r}$) and relative abundance $S_{\alpha,r}$ at age α ($S_{\alpha,r} = l_{\alpha,r} e^{-r\alpha}$), can be protected to ensure that the population's rate of increase remains at least equal to r' , where $r' \leq r$. This protection can be obtained by raising the age at first capture to compensate for reduced r' . Lotka's equation would still remain satisfied, but now by the reproductive output from the protected ages alone. Operationally, a certain r' is assumed, and then the age to which protection needs to be extended (x_c) for obtaining that r' is found.

To determine this age (x_c) for an r' less than or equal to a given r , survival $l_{\alpha,r'}$ must first be determined. From Equation (5), reproductive value at age 0 (v_0) equals 1.0, because its expression is then equivalent to Lotka's equation (since $l_0 = 1.0$). Also $S_0 = 1.0$, from Equation (6). Thus, using Equation (7), v_0 becomes

¹ Beverton, R. J. H. 1994. Montana, Old Roman Rd., Langstone, Gwent, NP6 2JU, U.K. Personal commun.

Table 2

Fecundity (m_x) schedules, in 10^6 female newborn per adult female at each age x , for four species of billfish. From age-length relationships calculated by von Bertalanffy equations (see Boggs, 1989). Length-Weight relationship for swordfish is $\log W = -4.675 + 2.961 \log L$ (Kume and Joseph, 1969). L-W for other billfishes as described by Wares and Sakagawa (1974). Fecundity-weight relationship as per Uchiyama and Shomura (1974): 10^6 advanced-mode ova = $2.725 + 0.015$ kg adult weight; m_x is the final fecundity divided by 2.

Age	Swordfish	Blue marlin	Striped marlin	Sailfish
0				
1				
2				
3				1.67
4		2.07	1.89	1.74
5	2.04	2.49	2.07	1.80
6	2.24	2.99	2.24	1.82
7	2.45	3.50	2.38	1.85
8	2.65	4.01	2.50	1.87
9	2.89	4.54	2.60	
10	3.05	5.01		
11	3.24	5.42		
12	3.41			
13	3.58			
14	3.72			
15	3.86			
16	3.99			
17	4.11			
18	4.22			
19	4.31			
20	4.40			

Table 3

Estimates of intrinsic rate of increase (r_z) for several species of billfishes. $l_{\alpha,Z}$ is survival to maturity at age α , where $Z = 2M$ or $3M$ (to bracket the mortality level at which MSY likely occurs); r_{2M} and r_{3M} are the corresponding r estimates.

Species	α (yr)	w (yr)	M (yr^{-1})	$l_{\alpha,2M}$ ($\times 10^{-6}$)	$l_{\alpha,3M}$ ($\times 10^{-6}$)	r_{2M} (yr^{-1})	r_{3M} (yr^{-1})
Swordfish	5	20	0.21	0.142	0.201	0.076	0.118
Blue marlin	4	11	0.38	0.216	0.298	0.104	0.159
Striped marlin	4	9	0.47	0.306	0.388	0.090	0.135
Sailfish	3	8	0.53	0.385	0.472	0.107	0.158

If all fish are taken above age x_n , the population would still increase at rate r' since Lotka's equation is still satisfied for rate r' ; if no fish are taken (all ages are protected) the population would increase at its native rate r , which is here estimated by r_z . In the analysis to follow, r' is set to zero to investigate the protection needed to ensure that the population is at least stationary at the MSY level.

Results

Life History Parameters

Age at maturity α was estimated as 5, 4, 4, and 3 yr and maximum reproductive age w as 20, 11, 9, and 8 yr for swordfish, blue marlin, striped marlin, and sailfish respectively (Table 1). The natural mortality M estimates were 0.21, 0.38, 0.47, and 0.53 respectively for these same billfishes. Fecundity m_x estimates are as listed in Table 2.

$$v_0 = S_{\alpha,r} \sum_{t=\alpha}^w (S_t/S_\alpha) m_t \tag{8}$$

$$= S_{\alpha,r} \sum_{t=\alpha}^w e^{-(M+r)(t-\alpha)} m_t = 1.0$$

and $S_{\alpha,r}$ can now be found as the reciprocal of the above summation term. Finally, $l_{\alpha,r}$ is found from $S_{\alpha,r}$ using Equation (6).

With $l_{\alpha,r}$ determined, and additionally assuming that r' is to be ensured, v_0 or Lotka's equation (Equation 8) is written

$$S_{\alpha,r'} \sum_{t=\alpha}^{x_i} e^{-(M+r')(t-\alpha)} m_t = 1.0 \tag{9}$$

where $S_{\alpha,r'} = l_{\alpha,r'} e^{-r'\alpha}$ and x_i is the upper summation age to be found that satisfies the equation. The condition described is thus that of a population capable of increasing at rate r but now increasing at rate r' .

Intrinsic Rate of Increase (r)

Values for survival to maturity which bracket the likely range for the MSY condition, i.e. $l_{\alpha,Z}$ with $Z = 2M$ or $3M$ from Equation (3), are listed in Table 3 along with the resulting r estimates. The latter, which are the r_z from Equation (4) using the $l_{\alpha,Z}$ survival values, are 0.08–0.12, 0.10–0.16, 0.09–0.14, and 0.11–0.16 per yr for swordfish, blue marlin, striped marlin, and sailfish respectively. These ranges correspond to the $Z = 2M$ and $Z = 3M$ estimates. An example of this computation for r , as well as for reproductive value and age to protect (described next), is given in Table 4.

Reproductive Value (v_x)

The above estimates of r suggest that it would be useful to examine reproductive value for populations at the

MSY size that are assumed to have native rates of r in the range of the values estimated. Accordingly, v_x was calculated from Equation (7) with $r = 0.07-0.13$ for swordfish, and with $r = 0.08-0.16$ for the other billfishes.

The resulting reproductive value curves for billfishes peak at the age of maturity α or later, as v_x curves always do. But the age of maximum v_x is much larger than α if fecundity increases greatly with further age, as with the long-lived swordfish, and also blue marlin. The v_x curves begin with a value of 1.0 at age 0 ($v_0 = 1.0$ as previously explained) and end at zero after age w . They are shown only after age α in Figure 1. Among the billfish species, the high-fecundity swordfish has the highest levels of v_x , and sailfish the lowest. Within any species, v_x is seen to be reduced and to peak later as r increases. This is because increased r means higher survival to maturity, and this depreciates v_x and slows its rise with age. The correct v_x curve for a species may be considered as lying approximately midway between the curves depicted.

Protection Age

The ages (x_r) up to which protection would ensure an r' rate of increase (from Eq. 9) are shown in Figure 1 by the ages at which dashed x_0 lines cross appropriate v_x curves (here, $r' = 0$, so $x_r = x_0$ for ensuring a just-sustainable population). Thus the protection age or age at first capture is 7-8 yr for swordfish, considerably short of the peak v_x age at 13-14 yr. But for the shorter-lived, apparently higher- r sailfish, x_0 is between 4 and 5 yr, approximately the same age that gives peak v_x .

Discussion

Strictly speaking, the demographic analyses presented here pertain to populations that have become stable-aged, although any real population probably never achieves that state. Even so, the demographic approach is useful, because Lotka's equation captures robust features of demography and thus predicts long-term, underlying effects that are at least qualitatively correct (Stearns, 1992, chapter 2, p. 20-38). Vandermeer (1968), who also derived Equation (7) through a more involved argument, concluded the same. In defense of

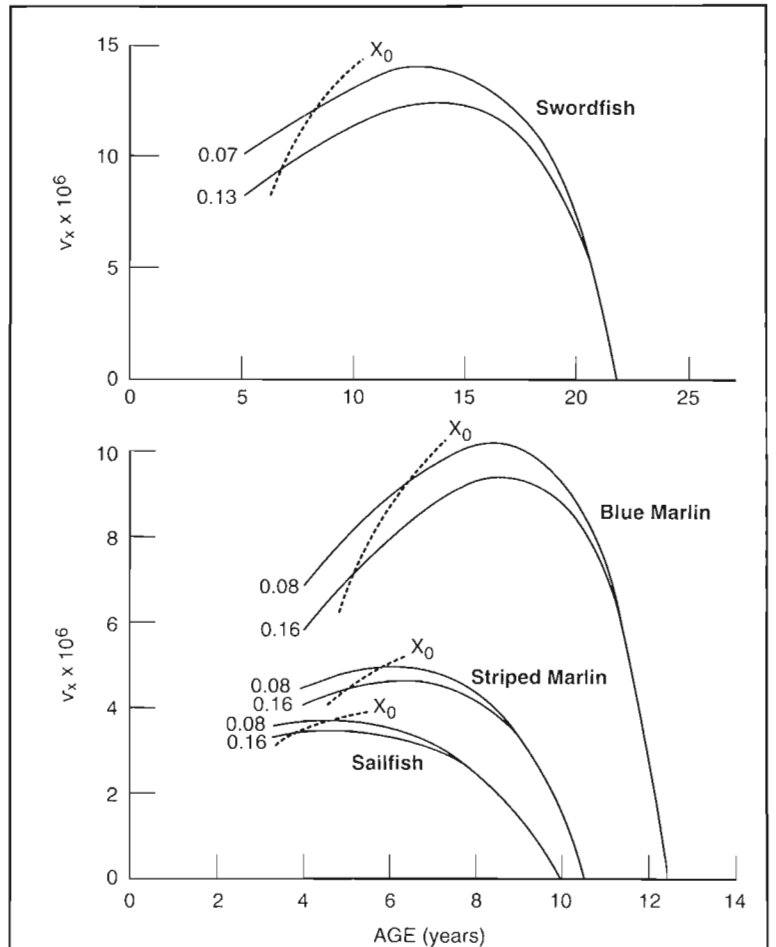


Figure 1
Intersection of protection age (x_0) curves (dashed) with reproductive value (v_x) curves (solid). Each v_x curve is for the specified assumed level of population, r . The x_0 curves specify the age at first capture that would ensure the $r = 0$ condition (population at least stationary). Note the change of scales in comparing swordfish with the other billfishes.

the demographic approach in fisheries work, it is worth noting that Murphy's (1967) sardine study is one of the better known demographic analyses in the ecological literature.

Reproductive value (v_x) and its protection is naturally of interest in conservation considerations. Fisher (1958) first noted in 1930 that natural selection acts through v_x , and reproductive value has since been the subject of numerous discussions of long-term evolutionary dynamics, e.g. Goodman's (1982) explanation of how optimal life histories maximize v_x . In terms of reproductive value, an optimal predator or fishery should avoid or protect the most valuable v_x ages and harvest mainly juveniles (MacArthur 1960), notwithstanding the loss from taking individuals before they

Table 4

Example of a computation to determine r , v_x , and age to protect, x_p , for swordfish when total mortality Z equals $2M$. Swordfish population parameters are $\alpha = 5$ yr, $w = 20$ yr, $M = 0.21/\text{yr}$, and $Z = 2M = 0.42/\text{yr}$.

x (yr)	Determining r			Determining v_x when $r = 0.07$				Determining x_p for $r' = 0$ when $r = 0.07^{10}$		
	l_x/l_α (2)	l_x ($\times 10^{-6}$) (3)	m_x ($\times 10^6$) (4)	S_x/S_α (5)	$(S_x/S_\alpha)m_x$ ($\times 10^6$) (6)	$\Sigma(S_x/S_\alpha)m_x$ (7)	v_x ($\times 10^6$) (8)	S_x/S_α (9)	$l_\alpha(S_x/S_\alpha)m_x$ (10)	Cumul (11)
5	1.0000	0.1420	2.04	1.0000	2.0400	10.5500	10.5500	1.0000	0.2744	0.2744
6	0.6570	0.1151	2.24	0.7558	1.6930	8.5100	11.2596	0.8106	0.2442	0.5186
7	0.4320	0.0933	2.45	0.5712	1.3994	6.8170	11.9345	0.6570	0.2165	0.7351
8	0.2840	0.0756	2.65	0.4317	1.1440	5.4176	12.5495	0.5326	0.1898	0.9249
9	0.1860	0.0613	2.86	0.3263	0.9332	4.2736	13.0971	0.4317	0.1661	1.0900
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19	0.0028	0.0061	4.31	0.0198	0.0853	0.1513	7.6414	0.0529	0.0207	
20	0.0018	0.0000	4.40	0.0150	0.0660	0.0660	4.4000	0.0429	0.0254	

¹ Age in years.

² Relative survival is $l_x/l_\alpha = e^{-Z(x-\alpha)}$.

³ Survival to age x is $l_x = l_\alpha(l_x/l_\alpha)$, where (from Equation 3) $l_\alpha = 1/\Sigma(l_x/l_\alpha)m_x = 1/7.0425 = 0.1420 \times 10^{-6}$.

⁴ Fecundity at age x .

⁵ Relative standing abundance at age $x = S_x/S_\alpha = e^{-(M+r)(x-\alpha)}$, where $r = 0.07$ (from the estimate of $r = 0.0763$ in note 10).

⁶ Reproductive value at age x . $v_x = 1/(S_x/S_\alpha) \Sigma(S_r/S_\alpha)m_r$ = previous column / column 5 = $\Sigma_{x=5}^{20}(S_x/S_\alpha)m_x / (S_x/S_\alpha)$ (see Equation 7).

⁷ Relative standing abundance at age x when $r' = 0$ is $S_x/S_\alpha = e^{-M(x-\alpha)}$.

⁸ These are the terms of Equation 9 when $r = 0.07$ and $r' = 0$, for then (from Equation 6) $S_{\alpha,r} = l_{\alpha,r} = S_\alpha/e^{-r\alpha}$ where $S_\alpha = 1/10.550$ (from Equation 8) and $e^{-r\alpha} = e^{-0.7(5)}$. Thus $l_{\alpha,r}$ (here designated l_α) = 0.1345×10^{-6} .

⁹ Cumulative sum of previous column from age 5 to age x , according to Equation 9.

¹⁰ Summing from $x = 5$ to 20 yr. $\Sigma l_x m_x = 1.9884$; $\Sigma x l_x m_x = 18.9736$; $\Sigma(l_x/l_\alpha)m_x = 7.0425$; $\Sigma(S_x/S_\alpha)m_x = 10.5550$.

Generation length $T = \Sigma x l_x m_x / \Sigma l_x m_x = 18.9736/1.9884 = 9.5420$ yr. Thus $r = (\ln \Sigma l_x m_x) / T = (\ln 1.9884) / 9.5420 = 0.0720/\text{yr}$. Or, $r = 0.0763/\text{yr}$ by iterative solution of Lotka's equation (Eq. 1).

The age x_p to which protection must be extended to ensure $r' = 0$ is given in the last column ("Cumul") where the cumulative sum becomes 1.0 (see Equation 9). This occurs at an interpolated age of 8.4 yr (or 8.9 yr if column values are considered to occur at midpoints of age).

have realized most of their growth. For a given population r , reproductive value at any age is proportional to fecundity and inversely proportional to survival. Thus the few surviving large adult billfishes acquire high v_x .

The approach used here is simple and essentially requires solution of Lotka's equation, which is equivalent to finding the dominant eigenvalue of a population's Leslie matrix. The assumptions employed are from ordinary, deterministic population dynamics. Even the assumption that all compensation effects are through increases in l_α and that m_x is unchanged is not unusual, for any actual m_x changes can be considered as manifested through changes in l_α . Such l_α -compensation has been demonstrated in groundfish populations (Myers and Cadigan, 1993) and is implicit in constant-recruitment fishery models.

Accuracy of the v_x estimates presented here depends strongly upon the accuracy of the r and m_x estimates. The former is most sensitive to the estimates of age α , which, as here, must at least appear reasonable in terms of other life history parameters. More problematical are the m_x schedules, which are derived from rather sketchy information. There can be little doubt, however, that fecundity in-

creases rapidly with age in the fast-growing swordfish and blue marlin, thus setting those two species apart.

This analysis shows that the age to which protection should be extended to ensure a population is at least stationary ($r' = 0$) is much lower than the age of maximum v_x in the reproductively more valuable, longer-lived swordfish, more so than in the other species, especially striped marlin and sailfish. Protecting swordfish up to age $x_p = x_0$ would therefore exclude protection for the most valuable v_x ages (valuable for enabling an r rate of increase), but without endangering the population. On the other hand, the protection ages for striped marlin and sailfish do include the peak v_x ages, so those ages are needed to ensure that their populations remain sustainable. Of course if the objective were to ensure a condition of $r' > 0$, e.g. to allow stock rebuilding, then the x_p lines would cross the v_x curves to the right of the lines shown in Figure 1, i.e. the protection ages (ages at first capture) would have to increase.

The demographic analysis here is more fundamental than the similar spawning-stock biomass per recruit (SSB/R) analysis (see Gabriel et al., 1989). Both derive from the same population theory. SSB/R can be used

to determine whether present recruitment or survival to recruitment is adequate for stock rebuilding, although the findings can only be as definite as the stock-recruitment (S-R) relationship employed. That S-R relationship can be provided by demographic analysis by using an estimate of the rate of increase at the population size that produces MSY (i.e. r_Z with $Z = 2M$ or $3M$), as in this study. Noting that any such population that is stable-aged, as well as any of its segments, has potential to grow at annual rate $e^{r_Z} - 1$, it is in principle only necessary to find an S-R curve that describes an MSY exploitation rate equal to that annual rate. If recruitment (R) is defined as recruits to age at maturity α , (i.e. R_α), then this S- R_α relationship will determine the stock size produced by any mortality Z (and the converse), as established by the point on that S- R_α curve where the R_α :S survival diagonal with slope equal to $l_{\alpha,Z}$ (from Eq. 3) crosses that curve.

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NOAA Technical Report NMFS 142

A Technical Report of the *Fishery Bulletin*

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*Papers from the International Symposium on
Pacific Swordfish, Ensenada, Mexico,
11–14 December 1994*

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Cover illustration by Katherine Zecca

December 1998

U.S. Department of Commerce
Seattle, Washington