Vital Rate Statistics for Billfish Stock Assessment

Christofer H. Boggs

Growth, mortality, recruitment, and migration rates are sometimes called "vital" statistics because they are "life" history parameters used in population dynamics models. Since the previous symposium (Shomura and Williams 1974, 1975) and the Pacific billfish workshop in 1977 (Shomura 1980), many studies have been conducted on billfish vital rates, concentrating mostly on age and growth rates. Analysis of hardpart markings has advanced growth rate estimation beyond the old method of following length-frequency modes through time. Billfish stock assessments making use of age and growth data have, however, been limited to western Atlantic stocks of swordfish *(Xiphias gladius)* and Atlantic sailfish *(Istiophorus albicans)* (Conser 1984, SEFC 1987). Much of the available data on billfish vital rates have not been utilized. This chapter compares some new vital rate estimates with older ones and examines their adequacy for stock assessment.

Growth Rates

Methods of Estimating Growth

All approaches to estimating growth have major limitations, as applied to billfish. These limitations must be addressed because different approaches (Table 1) have not produced similar results. Analysis of length-frequency modes has been applied to most species. This method is relatively easy, but it depends on assumptions not met for most billfish. Length-frequency modes do not represent age classes unless the spawning season is distinct, no mixing occurs for fish with different growth rates or from different spawning seasons, and the length sampling process is not selective. Each sequential length-frequency sample must be collected over a short time frame, or growth will blur the modes. When these conditions are met, growth rate estimates are specific to the size of the modes analyzed, but actual age is still not known. To construct a growth curve showing growth as a function of age (e.g., Atlantic swordfish, Fig. 1), it is necessary to assume that the mode for the smallest fish represents a given age (in this case, 1 year old). An additional problem with constructing growth models from length-frequency data is that, as growth slows with age, the modes becomes indistinguishable.

The tag-and-recapture method of estimating growth is compromised by the lack of age determinations or precise sizes of billfish at tagging. Estimates of change in size divided by time since tagging and release provide growth rates for specific sizes of fish that can be useful in verifying results from other methods (Conser 1984). Unfortunately, the weight at tagging is often estimated visually, so individual growth estimates are often wrong and frequently negative (SEFC 1987). The justification for the method is that, on average, no systematic bias exists in the estimated weight at release. As more tournaments encourage the tagging and release of billfish, promoting better methods of estimating initial size might be advantageous. Such methods could include the use of measured streamers, slipped onto the leader to trail alongside the fish, and photography. The remaining problem is that age is not known. Fitting an age-specific growth model to tag-and-recapture growth data requires assumptions about age and assumptions about how growth rate changes with age (the form of the model). For example, for Atlantic swordfish (Fig. 1), a model was used that assumed an increasing growth rate phase early in life and a diminishing growth rate phase later in life (Gompertz model: SEFC 1987). It was also assumed that age 0 fish were 1.4 kg (3 lb) dressed weight.

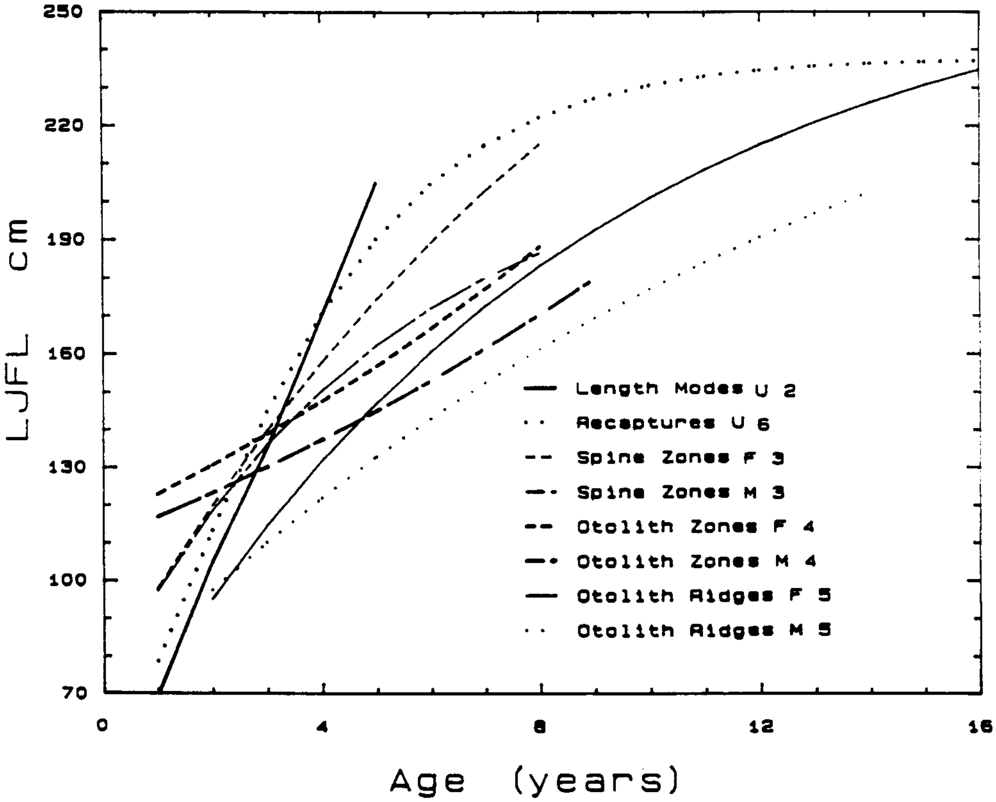

Figure 1. Length (LJFL = lower jaw to fork length) versus age curves for swordfish *(Xiphias gladius)*. Numerals in the key refer to literature in footnote 3 of Table 1. M = male, F = female, and U = unknown or unreported.

Biologists have been reluctant to use age-specific growth rate models based on billfish hardpart studies because of a lack of verification and a near absence of validation. Verification is agreement between age estimates from one method, or source of material (i.e., hard parts), and those from another. Validation is proof that a count of hardpart markings equals the measured passage of time (i.e., time since hatching or since the hard parts were chemically marked). Thorough validation is proof that, throughout the life of the animal, hardpart markings are deposited at regular intervals (i.e., one per day or per year). Marginal increment studies to establish the periodicity of growth mark formation on billfish hard parts have not yet produced definitive results (Berkeley and Houde 1983, Prince et al 1987). Failed attempts to verify billfish hardpart age estimates have usually involved counts of large-scale internal zones observed in spines compared with some other hardpart estimate (Radtke and Hurley 1983, Prince et al 1986, 1987). Spine zone counting is popular because spines are easily removed and cause little damage to marketable fish, but spines contain living tissue that can resorb inner zones. A method of estimating missing zones based on spine diameter appears to resolve this discrepancy (Hill 1986). Verification has been obtained by using fine-scale increment counts across the entire radius of otoliths for two adult swordfish, aged 6 and 9 years old based on external otolith ridge counts (Radtke and Hurley 1983). The daily addition of fine-scale increments in otoliths has been validated in many tropical species, including yellowfin tuna *(Thunnus albacares)* (Wild and Foreman 1980). So, although extremely small and difficult to remove, billfish otoliths are useful indicators of age.

A few good validations of annual marks or daily fine-scale increments in billfish hard parts could remove much of the skepticism that has kept a large amount of age and growth research (Table 1) from being applied to stock assessment. The reluctance to apply growth curves based on hardpart aging data is not appropriate, considering that growth curves based on other approaches which have been applied are equally unproven. There is a single validation of a billfish age estimate: An Atlantic sailfish recaptured 10.8 years after being tagged as a 2- to 4-year old had 13 external otolith ridges (Prince et al 1986). Validation in billfish hardpart aging

Table 1. Billfish growth and mortality rate estimates. Von Bertalanffy growth parameters were taken directly from the literature or from analyses of data therein (see Shomura 1980). Natural mortality rates (M) were calculated from K using the equation of Murphy and Sakagawa (1977).

Locality	Method	No.	Sex[1]	Size range[2] (cm)	Source[3]	Growth parameters			
						K	t_0	L_∞	M
				Swordfish					
Pacific	Length modes		U	61-245	1	0.124	-1.169	309 cm	0.22
Atlantic	Length modes and vertebrae		U	50-260	2	[4]0.230		[4]365 cm	0.43
	Anal spine internal zones	275	M	70-270	3	0.19	-2.04	217 cm	0.35
		164	F			0.09	-2.59	340 cm	0.15
	Otolith internal zones	39	M	79-209	4				
		39	F	102-290					
	Otolith ridges	73	M	88-208	5	0.07	-3.94	277 cm	0.12
		195	F	80-270		0.12	-1.68	267 cm	0.21
	Tag recapture	66	U	100-270	6				
				Pacific sailfish					
Pacific	Length modes	51,000	U	140-210	7	0.472		232 cm	0.90
				Atlantic sailfish					
Atlantic	Length modes	8,630	U	1-201	8	0.901	-0.496	243 cm	1.73
	Otolith ridges	64	U	102-184	9				
	Dorsal spine internal zones	259	M	80-186	10	0.301	-1.959	184 cm	0.56
		310	F	86-198		0.159	-3.212	230 cm	0.29
	Tag recapture	59	U	100-180	11	Same as dorsal spines.[5]			
				Striped marlin					
Pacific	Length modes		U	120-235	12	0.264		275 cm	0.49
	Length modes	16,898	M	108-171	13	0.417	-0.521	206 cm	0.79
		13,532	F	108-175		0.696	0.136	186 cm	1.33
				Pacific blue marlin					
Pacific	Length modes	1,327	M	93-212	13	0.285	0.106	276 cm	0.53
		1,757	F	78-289		0.116	-0.161	505 cm	0.21
	Otolith ridges	7	M	165-191	14				
		7	F	217-294					
				Atlantic blue marlin					
Atlantic	Otolith ridges	8		87-136	15				
	Otolith and dorsal spine internal zones	10	M	82-157	16				
		4	F	110-133					
		6	U	82-140					
				Black marlin					
Pacific	Length modes		U	150-250	17	0.474		282 cm	0.90

[1] M = male, F = female, and U = unknown or unreported.

[2] Atlantic swordfish and Atlantic sailfish data are given in lower jaw fork length. All other data are given in eye to fork length. Transformations between size measurements are in Royce (1957) for Pacific marlin, Lenarz and Nakamura (1974) for Atlantic marlin, and Jolley (1977) for Atlantic sailfish.

[3] Sources: 1. Yabe et al. (1959), 2. Caddy (1976, 1977), 3. Berkeley and Houde (1983), 4. Wilson and Dean (1983), 5. Radtke and Hurley (1983), 6. SEFC (1987), 7. Koto and Kodama (1962a), 8. de Silva (1957), 9. Radtke and Dean (1981), 10. Hedgepeth and Jolley (1983), 11. Conser (1984), 12. Koto (1963), 13. Skillman and Yong (1976; all age groups, model 1), 14. Radtke (1983), 15. Radtke et al. (1982), 16. Prince et al. (1987), 17. Koto and Kodama (1962b).

[4] These estimates of K and L_∞, from Caddy (1977) do not match the size at age groups given in Caddy (1976). Midpoints of the age groups in Caddy (1976) were used to plot the curve in Figure 1.

[5] Conser (1984) refit the data of Hedgepeth and Jolley (1983) using nonlinear regression, and the results were much more similar between males ($K=0.1947$, $t_0=-3.168$, $L_\infty=199.4$ cm, $M=0.358$), and females ($K=0.1967$, $t_0=-2.842$, $L_\infty=210.4$ cm, $M=0.362$).

studies is extremely difficult because maintaining billfish of any age in the laboratory is not possible and injecting chemicals for marking hard parts is difficult during tagging. Newly available methods for injecting chemical markers into billfish from a distance with dart guns or syringes on the ends of sticks should help solve this problem.

Comparison of Growth Estimates

A difference in billfish growth rate by sex is usually seen when both sex and age are determined. Unfortunately, a lack of sex data for the catches makes it impossible to apply sex-specific growth curves in stock assessments (Conser 1984, SEFC 1987). The faster growth of females compared with males is clear in hardpart estimates for swordfish (Fig. 1) and Pacific blue marlin *(Makaira mazara)* (Fig. 2) but less distinct in Atlantic sailfish and in length-frequency mode estimates for Pacific blue marlin and striped marlin *(Tetrapturus audax)* (Table 1).

Growth rate differences between stocks within a species are not evident in a casual comparison of swordfish growth curves estimated from length-frequency mode data. After eye to fork length curves from the Pacific (Yabe et al 1959) and tropical Atlantic (Ovchinnikov et al 1980) are converted to lower jaw to fork length curves, they appear similiar to the data from the western Atlantic (Caddy 1976). Blue marlin age data from the Pacific, based on otolith ridge counts, barely overlap with data from the Atlantic (Fig. 2). Making comparisons between single growth parameters such as *K*, t_o and L_{oo} can be misleading since they are not independent. The parameters are listed (Table 1) to update a previous summary (Shomura 1980), but comparisons are made between actual length at age estimates from the models (i.e., Figs. 1 and 2).

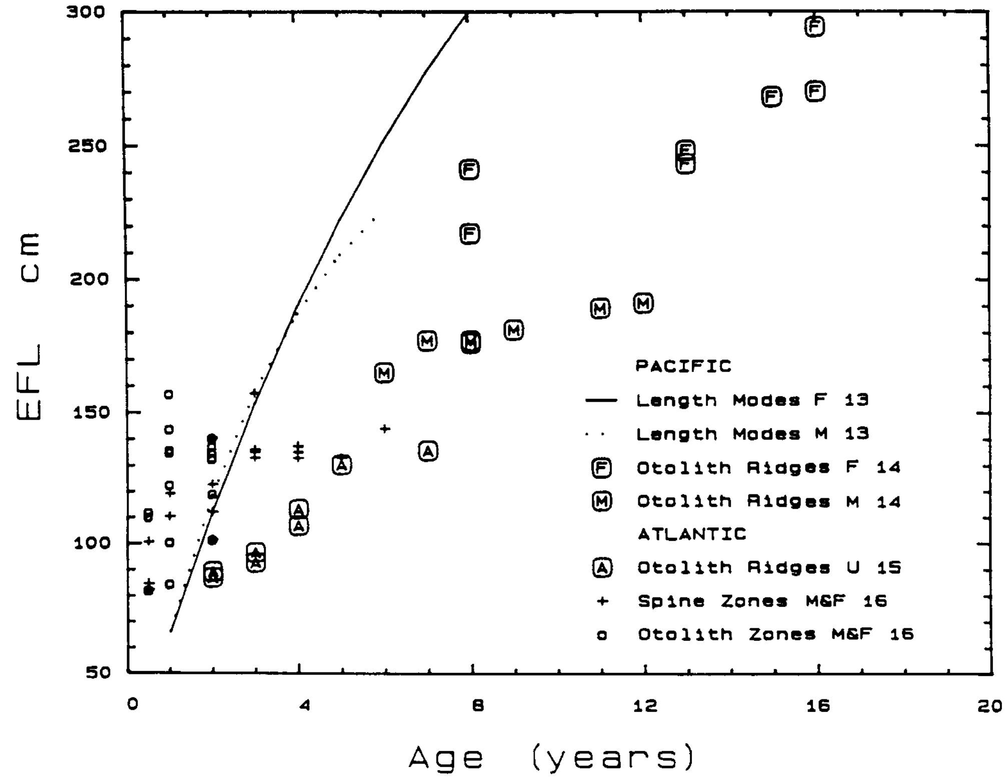

Figure 2. Length (EFL = eye to fork length) versus age data for Pacific blue marlin *(Makaira mazara)* and Atlantic blue marlin *(M. nigricans)*. Numerals in the key refer to literature in footnote 3 of Table 1. M = male, F = female, and U = unknown or unreported.

A comparison between Atlantic blue marlin *(M. nigricans)* and Pacific blue marlin is not a "stock" comparison since two separate species are now recognized (Nakamura 1985). Age-at-size estimates from Atlantic blue marlin otolith ridge counts barely overlap with those from Pacific blue marlin (Fig. 2).

Some of the discrepancies resulting from different approaches to estimating growth are too consistent to be due to true variation in the growth of the species caused by environmental and physiological variables (e.g., feeding, temperature, activity). Adult growth rates estimated from length-frequency mode analysis are always the fastest, and those from hard parts are always the slowest (Table 1), with tag-and-recapture estimates matching the length-frequency estimates in one case (swordfish; Fig. 1) and matching the hardpart estimates in another (Atlantic sailfish; Conser 1984). The slowest growth rates in adult swordfish (Fig. 1), Atlantic sailfish (Table 1), and Pacific blue marlin (Fig. 2) have been estimated from hard parts. The only validated datum (an Atlantic sailfish; Prince et al 1986) and the only study verified with complete fine-scale otolith increment counts (swordfish; Radtke and Hurley 1983) indicate that adult billfish are much older than estimated from other methods. In contrast to the slow growth in adult billfish indicated by hardpart studies, hardpart age estimates suggest that very young billfish grow much faster than indicated by other methods (Figs. 1 and 2).

Mortality Rates

Using Age and Growth Data

With growth curves (age-length relationships) and population length-frequency distributions, age-structured models can be used to estimate the proportion of fish being harvested, the annual variation in this proportion, and the effect on yield of changing the size of fish caught. However, even if growth curves are available, the inadequacy of data on length frequency, catch, and effort can prevent adequate stock assessments. Without vital rate statistics, analysis of catch and effort data can indicate only the level at which increasing fishing effort begins to produce a decrease in catch.

The most important application of growth models is the estimation of mortality rates which, in turn, are useful in determining sustainable yield. Total mortality (Z), which is the rate of removal of fish from a population through fishing mortality (F) and natural mortality (M) combined $(F+M=Z)$, can be estimated from the age distribution in the population, as determined from the length-frequency distribution and a growth curve. With additional data on the catch, or with independent estimates of M, it is possible to separate F from M (Gulland 1983). As a rule of thumb,the level of catch may be sustainable if $F<M$, but the stock may be overexploited if F is $\gg M$. Together or individually, fishing and natural mortality can remove more fish from the population in a year than are present at any given time. (F, M, or Z can be >1.0) if the population is constantly replacing biomass through recruitment and growth. In other words, a Z estimate of 1.5 means that 1.5 times the standing stock of fish die or are caught each year (under certain equilibrium conditions).

Estimating the average age of fish in the population is the simplest way to estimate Z, because the older all the fish are, the lower the mortality rate must be. The average age can be estimated from average age of the catch, adjusted by the age at first capture. Thus, Z can be estimated from the average length caught, adjusted by the size at first capture, using a growth curve to translate length into age. Other more complex procedures for estimating Z are based on the same idea (Gulland 1983). It is also possible to estimate Z from length-specific growth curves obtained from tag-recapture data and length-frequency data, without actually knowing true age (Wetherall et al 1987).

Adequate Accuracy and Precision

The accuracy of billfish age-length relationships is in doubt. How accurate do they need to be, and how much random error is acceptable? According to Powers (1983), who simulated the effects of bias and random error in assigning ages to length data, increasing lack of precision (random error) of up to 1 to 5% in assigning ages increases the standard error of Z estimates (in simulation), whereas increasing lack of precision in assigning age beyond 1 to 5% has only a slight effect on the standard error of Z estimates. Sample size (number of fish aged) has a much greater effect on the standard error of Z. Bias (inaccuracy) in assigning ages leads to a roughly equivalent opposite bias in Z.

The yield-per-recruit analysis for Atlantic sailfish by Conser (1984) is an example of the state of the art in age-structured billfish stock assessment: His Z estimates are from a variety of analytical methods applied to the same age and size-frequency data and cover a range equal to about 25% of the mean. This suggests biases no larger than those inherent in various analytical methods (25%) may be achieved with biases of up to about 25% in assigning ages, based on simulations in Powers (1983). Unfortunately, the disparity between ages given by various growth curves for billfish is often much greater than 100% (Table 1; Figs. 1 and 2). Thus, it is important to determine which growth models are correct.

Using Deterministic Growth Curves

Using a growth curve to assign ages by size results in assigning a single nonvariable age to a given length whereas, in reality, the ages of fish of a given size always vary. A biased age distribution results (Bartoo and Parker 1983). The worst case results when fish approach the asymptotic size given in the growth curve. In these slow-growing, older fish, size changes very little with age but does vary between individuals, so that many fish are actually larger than the theoretical maximum. These fish cannot be assigned an age by using a deterministic growth curve. Bartoo and Parker (1983) addressed this problem and recommended a stochastic method using estimated probabilities of various lengths at age. Unfortunately, this method was not used for either of the age-structured billfish stock assessments conducted to date.

Estimating Natural Mortality

Natural mortality *(M)* can be estimated from length-frequency data by using growth curves to assign age, as described above, but the length-frequency data must be from an unexploited population, i.e., when *F* is negligible and *Z* equals *M*. It is also possible to estimate *F* and *M* from tag-and-recapture data. However, data from unexploited populations or adequate tagging data are rarely available, so that models have been developed to estimate *M* directly from growth curve parameters (Murphy and Sakagawa 1977, Pauly 1980). The ideas supporting these models are that each species (or population or sex) has evolved growth and reproductive characteristics that balance a given *M*, providing the maximum possible reproductive success. Faster growth and reproduction have evolved in tandem with a high *M*. Slower growth and reproduction are more efficient when *M* is low. One model has included environmental temperature as a factor that increases *M* (Pauly 1980).

These models are poor substitutes for real information on natural mortality, which is almost completely lacking. However, Conser (1984) used both models (Murphy and Sakagawa 1977, Pauly 1980) and preexploitation length-frequency data on Atlantic sailfish to estimate *M* and found that all three were remarkably similar. I calculated a model estimate of *M* for each available von Bertalanffy *K* estimate (Table 1) using the model of Murphy and Sakagawa (1977). Pauly's (1980) method requires an estimate of asymptotic size (i.e., L_∞). Since length measures are problematic for billfish, the best choice would be asymptotic weight W_∞. Some estimate of the mean environmental temperature for each species would also be required.

Mortality Estimates and Stock Assessment

More age-structured billfish stock assessments are needed, and the two that were done should be reexamined in light of new growth rate estimates. For western Atlantic sailfish, Conser (1984) concluded that fishing mortality ($F = 0.338$), estimated from the difference between *Z* and *M*, was moderate and that the exploitation rate was sustainable. His yield-per-recruit analysis demonstrated that the size of fish being caught was larger than necessary to prevent growth overfishing. Conser (1984) used a growth curve based on dorsal spines (Hedgepeth and Jolley 1983) to estimate *Z* (0.674 from length-frequency distribution of the exploited stock) and *M* (0.336 from the pre-exploitation length-frequency distribution of the stock). Conser (1984) did not use an available growth curve based on otolith ridge counts (Radtke and Dean 1981). The otolith growth curve was not significantly different from the spine-based growth curve. The implications of the much greater estimate of Prince et al (1986) for sailfish longevity, however, based on a validated otolith ridge count, need to be examined.

Estimates of total mortality *(Z)* from tag recaptures can be used to check estimates derived from growth curves and length-frequency data. Decline in tag recovery rates over elapsed time since tagging is caused by *Z*. Tag-recovery *Z* estimates for western Atlantic sailfish (Conser 1984) ranged from 0.688 (corrected for tag shedding) to 1.11 (assuming no tag shedding). The corrected estimate was almost identical to the estimate used in the stock assessment (Conser 1984). Total mortality *(Z)* was estimated from tag recovery rate data on white marlin *(Tetrapturus albidus)* by Mather et al (1974), but no growth parameter estimates exist for comparison.

Age-structured stock assessments for marlins are nonexistent. Estimates of Z and M for striped marlin were given in Shomura (1980), who estimated $Z = 1.94$ (males) and $Z = 1.38$ (females) based on growth curves from Skillman and Yong (1976) and size-frequency data from the Hawaii longline fishery (Yoshida 1974). Assuming theoretical values for M (Table 1), I calculated F values of 1.15 (males) and 0.05 (females). These values seem unrealistic. The only mortality estimates for black marlin *(Makaira indica)*, or Atlantic or Pacific blue marlin are theoretical M estimates (Table 1).

The most elaborate age-structured billfish stock assessment to date was done on western Atlantic swordfish (SEFC 1987). "Virtual population analysis" (VPA) was used to estimate the number of fish present in past years, annual fishing mortality from the annual catch, and the annual number of survivors. The annual number of survivors can be estimated by working backwards, using an assumed constant M to estimate the fraction that died of natural causes each year and knowing the number caught each year. One must start with an estimate of the total number in the population, which can be calculated from M and the most recent catch by guessing the most recent annual value of F (terminal F). One also has to know the age distribution of the fish caught each year. Two "reasonable" estimates of M (0.1 and 0.2) used by SEFC (1987) were similar to theoretical M estimates based on K parameters from the otolith ridge count growth curves (Table 1). The growth curve used to age the catch was based on tag-and-recapture data and an assumed size at age 0 (Fig. 1).

The western Atlantic swordfish stock assessment workshop (SEFC 1987) concluded that the stock was not being overfished during 1982-1985. How would different assumptions about growth and mortality rates alter these conclusions? Recent estimates of growth rate are much slower than those used by SEFC (1987), which considered and rejected growth models based on spines (Berkeley and Houde 1983) and did not consider otolith ridge count estimates (Radtke and Hurley 1983). The growth curve based on dorsal spines was significantly different from the curve based on tag-and-recapture data. Consequently, workshop participants decided that, without validation, they could not use the spine data. What if the slower adult growth rate data (Fig. 1) are correct? Slower growth estimates produce lower theoretical M estimates (Table 1). An older population indicates a lower Z. This means the swordfish population would be replacing itself through growth and recruitment more slowly than SEFC (1987) suggests. What effect does a lower turnover rate have on estimates of F and the status of the swordfish stock? It is not necessary to wait until hardpart age estimates are validated to address this important question.

Other Vital Rate Statistics

Research on other vital rates such as migration, reproduction, and recruitment rates is extremely limited. Billfish migration rates have not been quantified, even though they confound estimates of mortality (SEFC 1987) and are critical for management. Instead, tag-and-recapture data have been used to describe qualitative movement patterns. The arrow diagram approach has been used to suggest segregation of stocks for assessment (SEFC 1987) and to explain seasonal changes in catch. However, without attention to the distribution of effort responsible for the recapture of tags, quantitative statements about movement are not possible from tagging data. Future tagging programs should make a concerted effort to monitor the fisheries involved in returning tags.

Miscellaneous information concerning size at maturity, fecundity, seasonality of reproduction, spawning areas, and larval distribution in billfish can be found in Shomura and Williams (1974,1975). The major use of such data for management purposes has been in separating stocks for assessment (e.g., SEFC 1987) rather than estimating reproductive rates or recruitment.

I was not able to find estimates of recruitment for any of the billfish except those resulting from the swordfish VPA in SEFC (1987). Such estimates result only from a concerted effort to analyze extensive size-frequency distribution data. The utility of recruitment rate estimates would be in estimating variation in productivity and in determining stock recruitment relationships in order to set minimal levels for the spawning stock. However, stock recruitment relationships are only one factor affecting recruitment. There is a need to understand the effects of environmental changes and species interactions on all of the vital rates. Current methods tend to assume that vital rates are constant.

Summary

The use of vital rate statistics such as growth and mortality rates in age-structured billfish stock assessments is a relatively recent development. Much work on growth rates has been accomplished recently, but only two age-structured billfish assessments have been made. The availability of size frequency data is a limiting factor. The implications of new estimates of growth rate based on hard parts have not been fully examined. Hardpart estimates suggest much older ages than do earlier studies based on analysis of length-frequency modes and growth of recaptured fish. Mortality estimates based on simulated length-frequency samples, using a growth curve to assign ages suggest that a large variance and considerable bias in age-at-size estimates result in acceptable levels of random error and comparable levels of bias. However, the discrepancies between results of different methods of estimating billfish growth are so large that mortality estimates based on the wrong growth model could be biased by ›100%. This level of accuracy is not acceptable. Slower growth and lower mortality rate estimates suggested by hardpart ageing studies indicate a slower turnover rate. The turnover rate is crucial in determining the amount of fishing the stock can sustain.

Age-structured stock assessment efforts have avoided using the most recent hardpart growth estimates because of a lack of validation or verification. Verification is being obtained through new techniques, but validation is extremely difficult for billfish. Increased attention to billfish tagging studies, resulting from the increased participation of sportfishermen, could help resolve the discrepancies between growth estimates. Techniques should be promoted to improve size estimation at tagging and to administer hardpart marking chemicals to validate growth rate estimates. However, it would not be wise to wait for hardpart age validation before examining the implications of much slower growth rates on the status of billfish stocks.

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Christofer H. Boggs earned the B.S. degree (biology) in 1977 at the University of Hawaii, the M.S. degree (oceanography and limnology) in 1980, and the Ph.D. (zoology) in 1984 at the University of Wisconsin. His doctoral studies on tuna bioenergetics entailed frequent trips to Hawaii for experimental work. He is now a fishery biologist at the National Marine Fisheries Service Southwest Fisheries Center's Honolulu Laboratory, leading the Pelagic Ecosystem Task in studies of tropical tunas and their relationships with the environment.