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U.S. DEPARTMENT OF COMMERCE
National Oceanic and Atmospheric Administration
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The major criterion used for evaluating the status of dolphin stocks involved in the eastern tropical Pacific tuna purse seine fishery has been the ratio of current population abundance to pre-exploitation abundance (NMFS, 1976¹; Smith, 1979²). Estimates of pre-exploitation abundance have been calculated using a population projection model which starts with an estimate of current abundance and adds animals killed while subtracting net recruitment of animals in a sequential manner moving backwards in time. The net recruitment or net rate of increase has been estimated by taking the difference between estimates of the gross annual reproductive rate, G.A.R. (i.e., the pregnancy rate times the proportion of females that are mature times the proportion of females in the population), in exploited and unexploited stocks. This procedure assumes 1) that survival rates are constant, over time and age, 2) that the net rate of increase is zero in unexploited stocks, and 3) that changes in G.A.R. can be directly translated into changes in the net rate of increase. Not considered in this procedure are the effects of the age structure of the population. If the age structure is unstable, then it is unlikely that changes in the G.A.R. would directly translate into changes in the net rate of increase and this procedure would produce an inaccurate estimate. Also, even when populations approach their stable age distributions, inaccurate estimates may result if survival rates are not constant with age. This latter effect is examined in this report.

One of the simplest age structured models is one in which there are two age classes, corresponding to mature and immature individuals. A simple

¹National Marine Fisheries Service. 1976. Report of the workshop on stock assessment of porpoises involved in the eastern Pacific yellowfin tuna fishery (La Jolla) July 27-31, 1976. Southwest Fisheries Center Administrative Report No. LJ-76-29.

²Smith, T. (ed). 1979. Report of the status of porpoise stocks workshop (August 27-31, 1979, La Jolla, California). Southwest Fisheries Center Administrative Report No. LJ-79-41.

Leslie matrix formulation of such a model is

$$\vec{N}(t+1) = \tilde{Q} \cdot \vec{N}, \quad (1)$$

where

$$\tilde{Q} = \begin{pmatrix} 0 & F \\ S_j & S_M \end{pmatrix}$$

$$\vec{N} = \begin{pmatrix} N_j \\ N_M \end{pmatrix}$$

F = the fecundity rate

S_j = survival rate for immature individuals

S_M = survival rate for mature individuals

N_j = the number of immature females

N_M = the number of mature females.

The time units are the number of years to sexual maturity, and the net rate of increase, assuming a stable age distribution, is the eigen value λ of the matrix \tilde{Q} ,

$$\lambda = \frac{S_M + \sqrt{S_M^2 + 4S_j F}}{2}. \quad (2)$$

If the pregnancy rate equals the fecundity rate and a sex ratio is 50:50, the gross reproductive rate is

$$G = \frac{N_M}{N_j + N_M} \cdot F = \frac{\lambda F}{F + \lambda}. \quad (3)$$

For density dependent changes in F , it can be shown that $\lambda - G$ equals a constant if and only if $S_j = S_M$ (see appendix). In other words, if adult fecundity rates are the only vital rates changing in response to density,

observed changes in G.A.R. (ΔG) will be equivalent to changes in the current rate of increase ($\Delta \lambda$) if and only if adult and juvenile survival rates are equal. Some numerical examples of the differences between $\Delta \lambda$ and ΔG are presented in Table 1. There are three points to note from this table: (1) the larger the differences between S_j and S_M , the greater the discrepancy between $\Delta \lambda$ and ΔG , (2) if $S_j < S_M$, then ΔG results in an overestimation of $\Delta \lambda$ and vice versa, and (3) the magnitude of the discrepancy between ΔG and $\Delta \lambda$ for fixed values of S_j and S_A is greatest for small values of λ .

Unfortunately, if the age of maturity is not equal to one in the time units in which fecundity and survival have been measured, the conversion of fecundity rates into time units equal to the age of maturity is nontrivial even if one assumes fecundity rates are constant with age. This is because the net fecundity rate over an extended time interval is a complex function of both the survival and fecundity rates during that interval (Keyfitz, 1972). Thus, the above model cannot easily be applied to dolphin populations as estimates for the age of maturity range between 5 and 9 years (Perrin and Henderson, 1979³; Perrin et al., 1976) while fecundity (pregnancy) rates have been estimated on an annual basis (e.g., Henderson et al., 1979⁴).

To obtain an idea of how large the discrepancy between ΔG and $\Delta \lambda$ may be for the dolphin estimates, a model was explored similar to equation 1 but in which \tilde{Q} and \tilde{N} were defined as

$$\tilde{Q} = \begin{pmatrix} 0 & . & . & . & . & 0 & F \\ S_1 & 0 & . & . & . & 0 & 0 \\ 0 & S_2 & 0 & . & . & 0 & . \\ . & 0 & . & . & . & . & . \\ . & . & . & . & . & 0 & 0 \\ 0 & 0 & . & . & 0 & S_M & S_A \end{pmatrix}$$

³Perrin, W. F. and J. R. Henderson. 1979. Growth and reproduction rates in two populations of spinner dolphins, *Stenella longirostris*, with different histories of exploitation. Southwest Fisheries Center Administrative Report No. LJ-79-29.

⁴Henderson, J. R., W. F. Perrin, and R. B. Miller. 1979. Gross annual production in dolphin populations (*Stenella* spp.) in the eastern tropical Pacific 1973-1976, working paper SOPS/79/3, for status of porpoise stock workshop.

Table 1. Comparisons of $\Delta\lambda$ and ΔG for changes in F for model 1. Note $\Delta\lambda$ and ΔG are calculated as the difference between adjacent rows.

S_M	S_j	F	λ	G	$\Delta\lambda$	ΔG	$\Delta\lambda/\Delta G$
.9	.9	.25	1.1038	.2038			
		.50	1.2578	.3577	.1540	.1539	1.000
		.75	1.3867	.4867	.1289	.1290	1.000
.9	.5	.25	1.0222	.2008			
		.50	1.1226	.3459	.1004	.1451	.692
		.75	1.2099	.4630	.0873	.1171	.745
		1.00	1.2882	.5630	.0783	.1000	.783
.9	.25	.25	.9648	.1986			
		.50	1.0223	.3358	.0575	.1372	.419
		.75	1.0745	.4417	.0522	.1059	.493
		1.00	1.1227	.5289	.0482	.0872	.553
.25	.90	.25	.6155	.1778			
		.50	.8074	.3086	.1919	.1310	1.465
		.75	.9560	.4203	.1486	.1115	1.333
		1.00	1.0519	.5197	.1259	.0994	1.267

\vec{N} = vector of the number of females in each age
1 to M and the M+1 element equals the number of
mature females,

where M = age of maturity
 S_A = adult survival rate
 S_j = age specific survival
F = adult fecundity rate.

By placing S_A in the lower right hand corner of \vec{Q} , survival rates are assumed to be constant past the age of maturity, M. Again assuming a 50:50 sex ratio and that fecundity rates equal the estimated pregnancy rates, the gross reproductive rate for this model is

$$G = \frac{F N_{M+1}}{\sum_{i=1}^{M+1} N_i} . \quad (4)$$

Explicit expressions for λ in terms of F and S_j and for the relationship between ΔG and $\Delta \lambda$, given changes in F, are not possible. However, numerically it appears that $\Delta G = \Delta \lambda$ if and only if $S_j = S_A$. Similarly, the same general conclusions for the first, simpler, model hold. Some numerical results are presented in Table 2, for an age of maturity equal to 7 years, and for estimates of vital rates which span current ranges for dolphin populations. The results indicate that with the generally accepted assumption for dolphins, of $S_j < S_A$, $\Delta \lambda$ could be equal to 60 to 100% of ΔG . This demonstrates the need for caution in assuming changes in G.A.R. are equal to net rates of increase. While the direction of the change is the same for both rates, there is no simple relationship between changes in their magnitudes, even when populations are tracking their stable age distribution.

The above results all incorporate the assumption that only pregnancy rates have changed and that survival rates have remained constant. Changes in survival also result in changes in G.A.R. and the current rate of increase. However, the effect on G will tend to be less than on λ . In some cases, it is possible to achieve rather large changes in λ with only small changes in G. This is illustrated in Table 3 for the simple model (equation 1) given above.

Positive changes in G.A.R. are evidence of positive changes in the net rate of increase (barring transitory age structure effects). A lack of significant change in G.A.R. does not necessarily mean that there has been no change in the current rate of increase. The relationship between changes in G.A.R. and changes in the current rate of increase is complex for age-structured models, but the results of changes in survival will tend to be

Table 2. Comparison of $\Delta\lambda$ and ΔC for changes in F for model II when $M = 7$. Note $\Delta\lambda$ and ΔG are calculated as the differences between adjacent rows.

S_M	S_j ¹	F	λ	G	$\Delta\lambda$	ΔG	$\Delta\lambda/\Delta G$
.95	.85	.15	1.0049	.09296			
		.20	1.0179	.11189	.0130	.0189	.684
		.25	1.0293	.12806	.0114	.0162	.705
		.30	1.0396	.1422	.0114	.0142	.806
.95	.9	.10	1.00239	.06826			
		.15	1.02055	.09041	.01817	.02215	.820
		.20	1.03598	.10878	.01543	.01837	.840
		.25	1.04945	.12454	.01347	.01576	.854
.95	.8	.10	.97966	.07186			
		.15	.99141	.09571	.0118	.0239	.410
		.20	1.00185	.11584	.0104	.0201	.517
		.25	1.0113	.13205	.0094	.0162	.580
		.30	1.01988	.14659	.0086	.0145	.591
.8	.95	.10	.9207	.0586			
		.15	.9500	.0770	.0293	.0184	1.593
		.20	.9731	.0925	.0231	.0155	1.494
		.25	.9924	.1060	.0193	.0135	1.430
		.30	1.0090	.1180	.0166	.0120	1.383

¹Survival for ages 1 to M is constant and equals S_j

Table 3. Comparison of $\Delta\lambda$ and ΔG for changes in survival rates for model 1. Note $\Delta\lambda$ and ΔG are calculated as the differences between the first row of the table and each additional row.

S_M	S_j	F	λ	G	$\Delta\lambda$	ΔG	$\Delta\lambda/\Delta G$
.90	.80	.3	1.1152	.2864			
.90	.90	.3	1.1373	.2874	.0235	.00098	23.9
.95	.80	.3	1.1578	.2824	.0426	.00184	23.5
.95	.90	.3	1.1790	.2891	.0638	.0027	23.7

underestimated by changes in G.A.R. while the results of changes in fecundity will tend to be overestimated by G.A.R. if juvenile survival is less than that of adults.

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- Perrin, W. F., J. M. Coe, and J. R. Zweifel. 1976. Growth and reproduction of the spotted porpoise, *Stenella attenuata*, in the offshore eastern tropical Pacific. Fish. Bull., U.S. 74:229-269.

APPENDIX

For model 1, to show that λ minus G equals a constant for changes in F if and only if S_j equals S_M , note that from equation 3

$$\begin{aligned} -G &= -\frac{\lambda F}{F+\lambda} \\ &= \frac{\lambda^2}{F+\lambda} \end{aligned}$$

Thus, if $-G$ equals a constant C then

$$\frac{\lambda^2}{F+\lambda} = C$$

$$\lambda^2 - C\lambda - CF = 0.$$

Thus

$$\lambda = \frac{C + \sqrt{C^2 + 4CF}}{2}, \quad (5)$$

but from equation 2

$$\lambda = \frac{S_M + \sqrt{S_M^2 + 4S_j F}}{2}. \quad (6)$$

Therefore, equation (6) to equal equation (7), S_j must equal S_M which must equal C .

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