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Appendix 3

CLARIFICATION REGARDING POPULATION GROWTH RATE PARAMETERS USED FOR SOUTHERN HEMISPHERE HUMPBACK WHALE ANALYSES

D.S. Butterworth

Papers on the dynamics of Southern Hemisphere humpback whales have described their growth rates in different ways. To attempt a simple summary, the following have been used (sometimes with different symbols to denote them or different forms of words to describe them):

δ : instantaneous growth rate (units yr^{-1}) (sometimes indicated as r)
λ : annual growth rate (units yr^{-1})
r : intrinsic growth rate (units yr^{-1}) (sometimes indicated as r_{max})

Relationships between these parameters are as follows. The instantaneous growth rate parameter δ corresponds to the slope parameter in a log-linear regression of population estimates against time, and reflects a measure of exponential (Malthusian) growth. Computations of demographically imposed bounds on growth rates based on Leslie models assuming a steady age-structure have usually been quoted in these terms. δ is related to λ by the formula:

$$\lambda = e^{\delta} - 1$$

where λ is the proportional amount by which the population will grow over the time unit in terms of which parameter values are quoted (here one year). The Table below shows some corresponding (δ, λ) values – multiply by 100 to express either as a percentage.

δ	λ
0	0
0.01	0.0101
0.05	0.0513
0.10	0.1052
0.126	0.1343

The intrinsic growth rate (r) is (for purely compensatory population models) the highest growth rate that a population can attain, which is achieved in the limit of vanishing population size (N). It pertains to either an instantaneous or an annual growth rate depending on whether a differential or a discrete (with annual time step) equation model is used to reflect the population dynamics.

Models used for Southern Hemisphere humpback whales have been of the latter type. Parameter values for r quoted for these models therefore relate to annual growth rates (λ), rather than to instantaneous rates (δ).

Note that these models usually assume the purely compensatory density dependent formulation of the Pella-Tomlinson model:

$$r(N) = r\,[\,1 - (^{N}/_{K})^{2.39}] \quad K = \text{carrying capacity}$$

so that at any population size N greater than zero, the annual growth rate will be less than r. 'Compensatory' means that $r(N)$ is monotonically ('always') decreasing as N increases (because, if N is reduced, the population responds by increasing $r(N)$ to 'compensate'). In contrast, depensation (the 'Allee effect') reflects a situation where as N decreases, below a certain (typically rather low) level $r(N)$ starts to decrease. If below a certain level (N^*), $r(N)$ becomes negative, the situation is described as manifesting critical depensation, with N^* corresponding to the minimum viable population level.