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NOAA Technical Memorandum NMFS

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ESTIMATING DOLPHIN JUVENILE SURVIVAL RATES FROM THE PROPORTION OF CALVES NURSING

Tom Polacheck

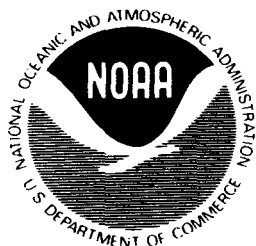NOAA Technical Memorandum NMFS

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CONTENTS

LIST OF TABLES

LIST OF FIGURES

ESTIMATING DOLPHIN JUVENILE SURVIVAL
RATES FROM THE PROPORTION OF CALVES NURSING

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INTRODUCTION

Information on the age structure of a population is often used to estimate survival by comparing the number of individuals in successive age classes. Techniques for determining the age of individuals in a population may not be available or may be prohibitively costly or time consuming. In contrast, classification of individuals into reproduction categories is often easier. If some of the reproductive states are of relatively constant duration and data exist on the time spent in these states, classification according to these states can provide a sorting of individuals into disjoint age groupings and, thus, provide information on the age structure of the population. The accuracy of determining the actual age structure of a population from reproductive classifications depends upon the variability of the duration of the various categories being used. Biases may exist in such classification if reproduction is seasonal or if sampling is non-uniform. However, in the absence of other data, the use of reproductive-state classification may be the only source of information on survival rates.

Anytime a sample can be divided into disjoint age groupings, these age groupings have a potential to provide information on survival rates. As with any survival estimate based on the age structure of a population, it is necessary to assume a stable age distribution, a net rate of increase, and some form of functional relationship for the survival rate within an age interval. (Note, the net rate of increase is usually assumed equal to zero while the relationship for the survival rate within an interval is assumed constant.)

In Polacheck (1984), I discuss how the reproductive classification into immature and mature females, along with an estimate of the fecundity rate and the age of maturity, can be used to provide estimates of survival rates during these two stages, and I apply this method to data from samples of dolphins

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killed incidentally in tuna purse seine fishery in the eastern tropical Pacific. In the present paper, general equations are presented for estimating the survival rates in two successive age groupings in which the number of age classes in each group differs. These equations are then applied to the reproductive data on dolphins in the eastern tropical Pacific to provide information on survival rates for nursing and non-nursing immature females.

METHODS

Two equations were used to estimate the survival rates; one is based on a continuous model of population growth, and the other on a discrete model. For a continuous model of population growth, the ratio, R_c, of the number of individuals in two successive age groupings which span different lengths of time can be expressed as:

$$R_c = \frac{(r + q_m) \, (1 - e^{-(r+q_w)\,w})}{(r+q_w) \, e^{-(r+q_w)w} \, (1-e^{-(r+q_m)m})} \tag{1}$$

where w = the duration of the first stage
   m = the duration of the second stage
   q_w = the instantaneous mortality rate during w
   q_m = the instantaneous mortality rate during m
   r = the instantaneous net rate of increase

A derivation of this expression is provided in the appendix. A similar expression for a discrete model of population growth is

$$R_d = \frac{\displaystyle\sum_{i=0}^{w} \frac{S_w^{\,i}}{\lambda^{\,i}}}{\dfrac{S_w^{\,w}}{\lambda^{\,w}} \displaystyle\sum_{i=i}^{m} \frac{S_m^{\,i}}{\lambda^{\,i}}} \tag{2}$$

where w and m are as above and

   S_w = the survival rate per unit time during w
   S_m = the survival rate per unit time during m
   λ = the finite rate of increase per unit time.

Derivation of equation 2 follows from expressing the stable age vector for a Leslie matrix as successive products of S_i/λ, where S_i is the survival rate at age i (e.g. Pielou, 1977).

Given a current rate of increase and the ratio of the number in two successive age groupings, these expressions can be used to provide an estimate of the survival rate during the second interval as a function of the rate during the first. They do not provide a single estimate of the survival rate between ages w and m (as a normal age distribution would) because of the need to account for the individuals in age group w that will not survive to age m. However, in particular situations, as will be shown with the data on dolphin populations, given values for w, m, and R, the combination of meaningful solutions for the survival rates during those periods may be limited.

Data are available on the number of immature females and the number of females lactating from the samples available of dolphins from the eastern tropical Pacific for the northern off-shore spotted stock of Stenella attenuata, and the eastern spinner, and northern whitebelly spinner stocks of S. longirostris (Henderson et al., 1979 [1] and Perrin and Henderson, 1979[2] and Perrin, et al., 1976). Estimated values for these three stocks of the length of lactation (i.e. the age of weaning), the age of maturity, and the proportion of immature females which are nursing are given in Table 1 and are the values used in the analysis below. This information can be used to examine the survival rates of nursing and non-nursing calves. The estimate of the proportion of immature females that are nursing was derived as follows: If one assumes a random sample, the number of lactating females provides an estimate of the number of nursing calves in a sample as dolphins almost always have a single birth. By assuming a 50:50 sex ratio for nursing calves, the ratio of one half of the number of lactating females to the number of immature females provides an estimate of the proportion of immature females that are nursing. Note that the ratio of nursing to non-nursing calves has been expressed in terms of the proportion of immature calves which are nursing so that the results can be easily compared with an earlier sensitivity analysis of the reproductive data (Polacheck, 1983).

As indicated in Table 1, the length of lactation has been estimated in two different ways (see Henderson, et al., 1979[1] for a complete description of both methods). Method I is actually an estimate of the average length of time all females nurse, which includes the females which stop nursing because of the death of their young. Method II is a direct estimate of the age of

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[1]Henderson, J., W.F. Perrin and R.B. Miller. 1979. Gross annual production in dolphin populations (Stenella spp) in the eastern tropical Pacific, 1973-1978. NMFS-SWFC, SOPS/79/33.

[2]Perrin, W.F. and J.R. Henderson. 1979. Growth and reproductive rates in populations of spinner dolphins, (Stenella longirostris) with different histories of exploitation. NMFS-SWFC Admin. Rept. #LJ-79-29.

weaning based on an estimation of the age of the oldest individual still nursing. Method I underestimates the actual age of weaning (DeMaster personal communication). The relationship between Method I estimates of the average length of lactation and the actual age of weaning can be expressed as

ppp
$$w_I = \frac{1 - e^{-q_w w}}{q_w} \qquad (3)$$

where w_I = method I estimate of the length of lactation
w = the actual length of lactation
q_w = the instantaneous calf mortality rate before weaning

It has been suggested that q_w can be estimated by substituting Method II's estimate for the length of lactation for w in equation 3 (DeMaster, Personal communication). However, because of potential biases in both methods of estimating the length of lactation (Polacheck, 1984), separate analyses will be presented below for both Method I's and Method II's estimates of the length of the lactation period. Note that whenever results are presented for Method I estimates, the actual value for w used in solving either equation 1 or 2 is the value of w derived from solving equation 3 for w. In other words, the following expression for w was substituted into equations 1 or 2

$$w = \frac{\ln (1 - w_1 q_w)}{q_w} \,. \qquad (4)$$

When equation 4 was used in equation 2, q_w was assumed to equal $-\ln s_w$.

RESULTS AND DISCUSSION

Both equations 1 and 2 were solved for the survival rate of non-nursing calves using the parameter estimates in Table 1. Equation 2 was solved for a discrete time unit equal to one month. When converted to a common time scale, the survival rate estimate from either equation was essentially the same. Thus, only results from the continuous model (equation 1) will be presented. All rates presented below have been converted to a common finite time scale of one year.

In Figures 1-3, the survival rate of non-nursing calves (S_m) has been plotted as a function of the survival rate of nursing calves (S_w) for a range of values for the net rate of population growth for the three dolphin populations. The estimates of S_m are a decreasing function of S_w and the net rate of increase. S_m is a lot more sensitive to changes in S_w for Method I estimates of the length of lactation than for Method II estimates due to the interaction between S_w and w for Method I (i.e. Equation 4). (Note in figure 3 no results are shown for Method I estimates because no biologically possible

solutions exist for the combination of input parameters.)

When w is not a function of S_w but is held constant, as with Method II estimates, the overall survival rate from birth to age m appears almost insensitive to any particular combination of values for S_m and S_w which are used to solve equation 1. This insensitivity is illustrated in Table 2 where the range of overall average annual survival rates has been tabulated for the three stocks using Method II's estimate of the length of lactation when S_m is allowed to range from 0.70 to 0.98. The estimate of overall average annual survival rate varies by at most 0.019 for a given value of net rate of increase. This means that estimating survival rates by this method is useful because only the overall survival rate from birth to maturity and not the age specific rates within this period affect the overall dynamics of the population model.

Using the ratios in Table 2 as estimates of the overall survival rate from birth to age of maturity, the results appear not to be consistent with a hypothesis of density dependent changes in juvenile survival rates given current understanding of the level of exploitations for these three stocks (Smith, 1979[3]). Thus, the least exploited stock, the northern whitebelly spinner, has the highest estimated survival rates; the most exploited stock, the eastern spinner, has intermediate estimates.

These estimates, however, may be more of an indication of sampling biases and inconsistency in the data than of evidence for or against density dependent changes in juvenile survival rates. Thus, the results for the northern whitebelly spinner suggest that the overall juvenile survival rates must be extremely high, approaching absolute biological limits, if the population is not declining. A similar conclusion was reached from an examination of the estimates of the sexually mature proportion and the pregnancy rate for this stock (Polacheck, 1983[4]).

For the eastern spinner stock, Method II estimates of the length of lactation provide biologically plausible survival estimates. The survival estimates derived from Method I are not biologically possible unless the population was rapidly declining. The two methods of estimating the length of lactation are only partially independent as both are dependent upon the actual number of lactating females sampled. Thus, a rejection of the juvenile survival estimates based on Method I estimates of the length of lactation because they are biologically unreasonable brings into question the juvenile

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[3]Smith, T. (ed.) 1979. Report of the status of porpoise stocks workshop (August 27-31, 1979, La Jolla, California). NMFS-SWFC Admin. Report No. LJ-79-41.

[4]Polacheck, T. 1983. Estimating current rates of increase and survival rates from reproductive data for dolphin populations in the eastern tropical Pacific NMFS-SWFC Admin. Report LJ-83-11. 25 pp.

survival estimates from Method II. The difficulties with the estimates from Method I suggest a possible bias in sampling towards juveniles. Such a bias would affect both the estimate of the mature proportion and Method II estimation of the length of lactation (Polacheck, 1983). The source of the problem in the estimates for Method I most likely is affecting the estimates of Method II. Similar difficulties in obtaining juvenile survival rate estimates that were biologically possible in a population which was not rapidly declining were also encountered for this stock when analyzing the estimates of the sexually mature proportion and the pregnancy rates (Polacheck, 1983[4]) which further suggests sampling problems.

For the northern offshore spotted stocks, the survival estimates from both Methods I and II estimates of the length of lactation are consistent with a wide range of potential rates of increase and suggest that a reasonable estimate for the average overall juvenile survival rate for this stock may be in the range of 0.80-0.90. While this range of rates is somewhat lower than the range of juvenile survival rates for this stock suggested by an examination of the estimate of the sexually mature proportion and the pregnancy rate (Polacheck, 1983[4]), the two sets of estimates do not appear highly inconsistent given the possible sampling variabilities in the input parameters.

Previous papers have suggested that the average annual survival rate for all ages for these dolphin populations is ~0.90 (NMFS, 1976[5]; Smith, 1979[3]). This rate was derived from the comparison of estimates of the gross annual rates of reproduction in different dolphin populations and the assumption that these populations are not declining. However, this previous figure cannot be considered a direct estimate and provides no basis for evaluating the juvenile survival estimates in the present paper.

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[5]NMFS. 1976. Report of the workshop on stock assessment of porpoises involved in the eastern Pacific yellowfin tuna fishery. NMFS-SWFC Admin. Report. LJ-76-29. 52 pp.

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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.

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Table 1. Estimates of the values of the parameters used in the analysis of survival rates.

	Proportion of immature females nursing [1]	Age of maturity (years)	Length of Lactation Method I (months)[4]	Method II (months)[4]
Northern off-shore spotted	0.337	8[2]	16.7	18.7
Northern white-belly spinner	0.261	6[3]	16.0	17.5
Eastern spinner	0.210	5[3]	19.3	10.3

[1]Calculated from the pooled data for 1975-1979 as given in Henderson, et al. (1979) (see text footnote 1). Mature females whose reproductive state was undetermined were prorated to the various reproductive states according to the percentages in the various states.

[2]Based on estimates in Perrin, et al., 1976.

[3]Based on estimates in Perrin and Henderson, 1979 (see text footnote 2).

[4]Based on estimates in Henderson et al., 1979 (see text footnote 1).

Table 2. The range of estimates for the average annual survival rate from birth to maturity based on Method II estimate of the length of lactation when S_W was varied between 0.70 and 0.98.

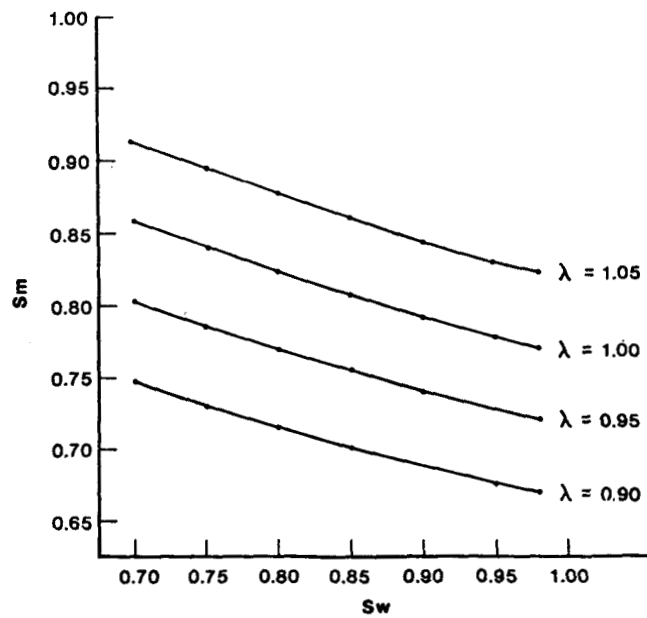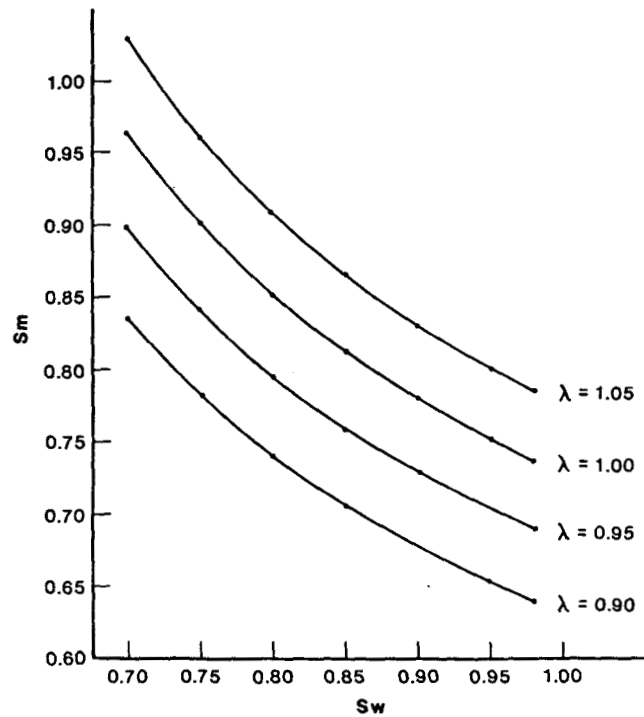| Stock	Annual Net Rate of Increase	Average Annual Survival Rate From Birth to Maturity
Northern off-shore spotted	0.90	0.721 - 0.738
	0.95	0.764 - 0.781
	1.00	0.807 - 0.825
	1.05	0.850 - 0.869
Northern white-belly spinner	0.90	0.871 - 0.873
	0.95	0.920 - 0.922
	1.00	0.968 - 0.971
	1.05	1.017 - 1.020
Eastern spinner	0.90	0.810 - 0.815
	0.95	0.856 - 0.861
	1.00	0.902 - 0.907
	1.05	0.948 - 0.953

Figure 1.   Estimated annual survival rate of non-nursing calves (S_m) plotted as a function of the estimated survival rate of nursing calves (S_w) for a range of values for the net rate of increase (f) for the northern off-shore spotted stock. Figure 1a is for Method I estimate of the length of lactation and Figure 1b is for Method II.
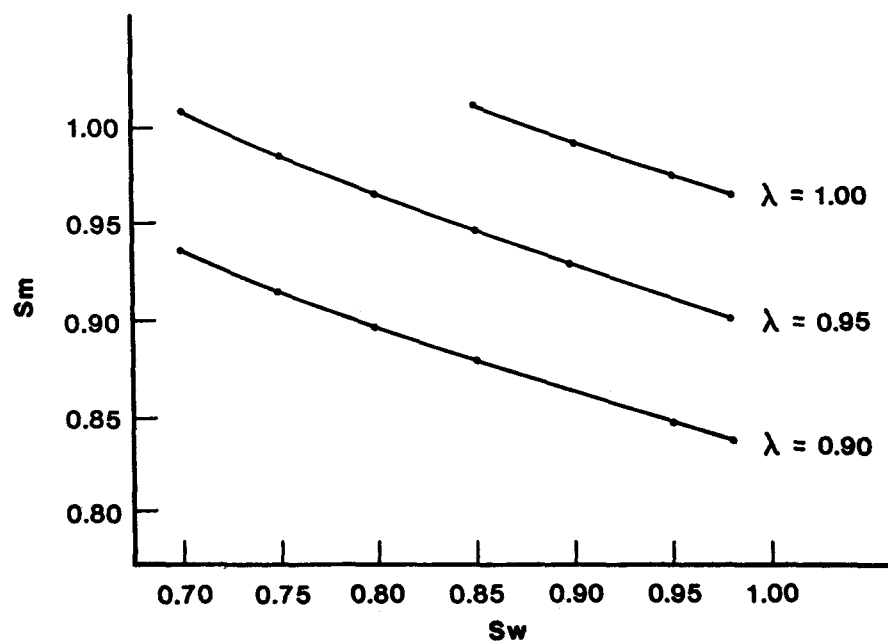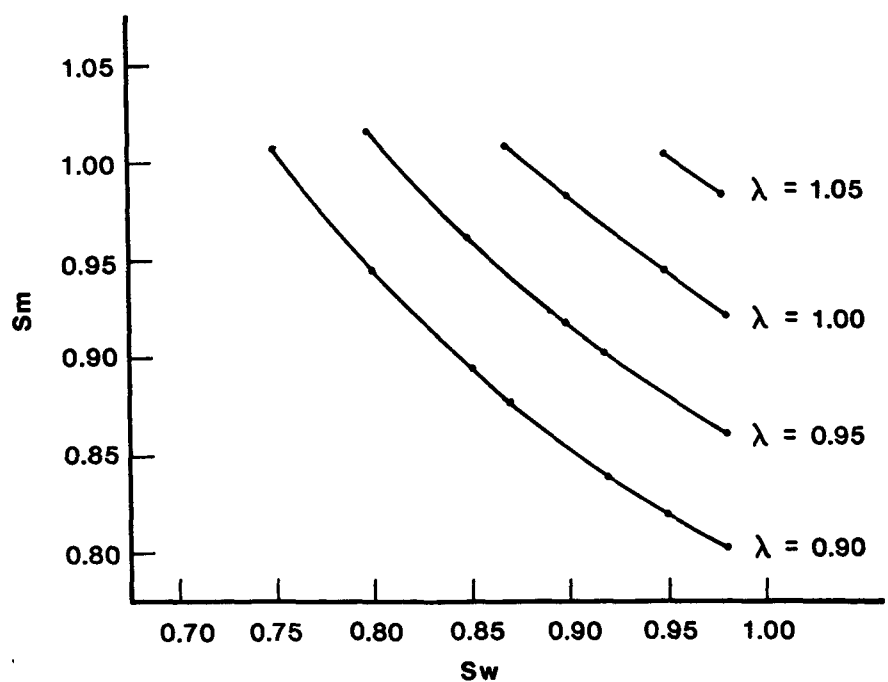
Figure 2. Estimated annual survival rate of non-nursing calves (S_m) plotted as a function of the estimated survival rate of nursing calves (S_w) for a range of values for the net annual rate of increase (λ) for the northern whitebelly spinner stock. Figure 2a is for Method I estimate of the length of lactation and Figure 2b is Method II. Note that in Figure 2b no curve has been plotted for a net rate of increase equal to 1.05 because no solutions exist in which both of the estimated survival rates are less than one.
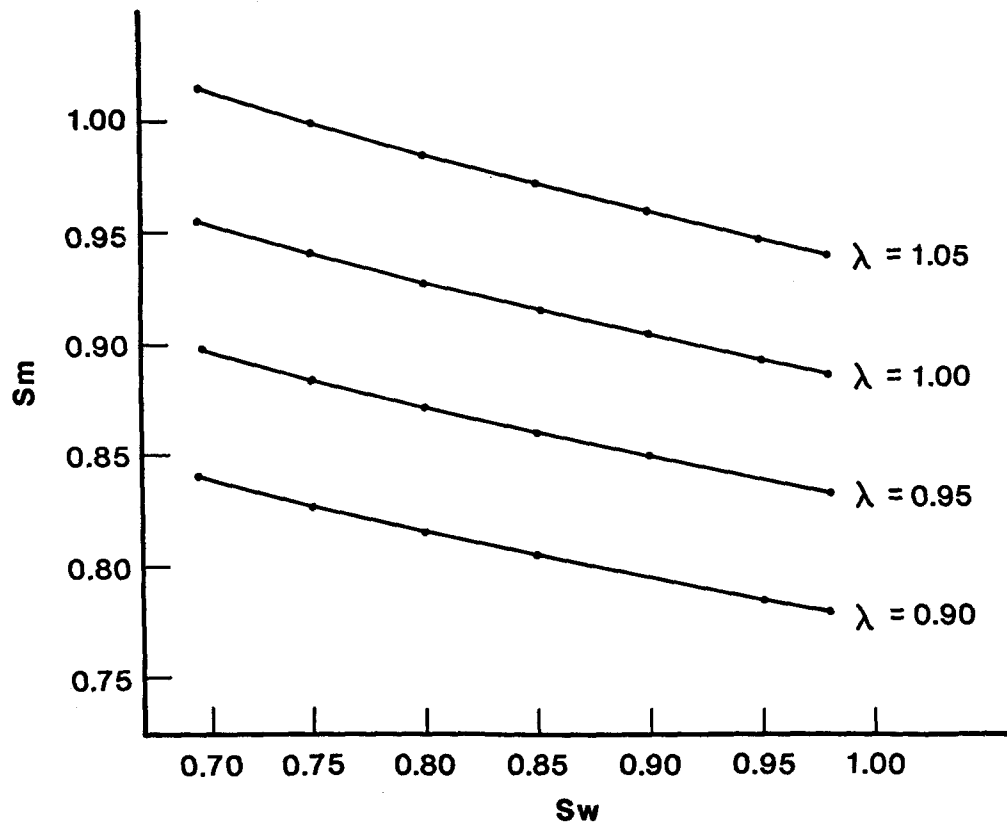
Figure 3.   Estimated annual survival rate of non-nursing calves (S_m) plotted as a function of the estimated survival rate of nursing calves (S_w) for the eastern spinner stock for a range of values for the annual net rate of increase (λ) for Method II estimate of the length of lactation.

APPENDIX

Derivation of an expression for the ratio of the number of
individuals in two successive age groupings of unequal derivation
for a continuous breeding population in a stable age distribution.

From Mertz (1971), the probability density function of an individual being age
x for a continuous breeding population with a stable age distribution is:

$$c\ (x) = be^{-r\ x}\ I(x)$$

where $\qquad I(x) = \exp\left(-\int_0^x q(y)dy\right)$

$\qquad q(y) =$ instantaneous death rate

$\qquad r \quad =$ instantaneous rate of increase for the population

$\qquad b \quad =$ asymptotic instantaneous birth rate per individual

If $q(y)$ is a constant between ages i and j and if q_j is defined as

$$q_j = q(y) \text{ for } i < y \le j$$

then for $x > i$ and $x \le j$

$$I(x) = \exp\left(-\left(\left(\int_0^i q(y)\ dy\right) + \int_i^x q_j\ dx\right)\right)$$

$$= I(i)\ e^{-q_j\ (x-i)}$$

Also note that if $q(y)$ is constant between ages i and j then for $x > i$ and $x \le j$

$$c(x) = c(i)\ e^{-r(x-i)}\ e^{-q_j(x-i)} \qquad\qquad (1)$$

$$\text{since } c(i) = b\ e^{-ri}\ I(i)$$

Thus, if f equals the lowest age of an individual in the first age grouping
and (f+w) equals the ages of the oldest individual and q_w equals the
instantaneous mortality rate during this period, the proportion of the
population between ages f and f+w is

$$\int_f^{f+w} c(x)dx = \int_f^{f+w} c(w) \, e^{-r(x-f)} \, e^{-q_w(w-f)} \, dx$$

$$= c(w) \int_0^w e^{-rx} \, e^{-q_w x} \, dx$$

$$= \frac{c(f)}{r+q_w} (1 - e^{-(r+q_w)w}) \tag{2}$$

By the exact same reasoning, the proportion of the population in the age grouping running from f+w to f+w+m is

$$\int_{f+w}^{p+w+m} c(x)dx = \frac{c(f+w)}{r+q_m} (1 - e^{-(r+q_m)m}) \tag{3}$$

From expression 1,

$$c(f+w) = c(f) \bullet e^{-rw} \bullet e^{-q_w w} \tag{4}$$

Thus by combining expression 2, 3 and 4 and then simplifying the ratio of the number of individual in the two successive age groupings can be expressed as

$$R_c = \frac{\int_f^{f+w} c(x)dx}{\int_{f+w}^{f+w+m} e(x)dx} = \frac{(r+q_m) \, (1 - e^{-(r+q_w)w})}{(r+q_w) \, e^{-rw} \, e^{-q_w w} (1-e^{-(r+q_m)m})}$$

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