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Developing demographic toxicity data: Optimizing effort for predicting population outcomes

John D. Stark, John E. Banks

Mounting evidence suggests that population endpoints in risk assessment are far more accurate than static assessments. Complete demographic toxicity data based on full life tables are eminently useful in predicting population outcomes in many applications as they capture both lethal and sublethal effects; however, developing these data is extremely costly. In this study we investigated the efficacy of partial life cycle tests as a substitute for full life cycles in parameterizing population models. Life table data were developed for three species of Daphniids, *Ceriodaphnia dubia*, *Daphnia magna*, and *D. pulex*, weekly throughout the life span of these species. Population growth rates (λ) and a series of other demographic parameters generated from the complete life cycle were compared to those calculated from cumulative weeks of the life cycle in order to determine the minimum number of weeks needed to generate an accurate population projection. Results showed that for *C. dubia* and *D. pulex*, λ values developed at > 5 weeks (55.6% of the life cycle) were not significantly different from λ developed for the full life cycle (9 weeks) of each species. For *D. magna*, λ values developed at > 7 weeks (70% of the life cycle) were not significantly different from λ developed for the full life cycle (10 weeks). Furthermore, these statistically significant cutoff points for λ were not the same for other demographic parameters, with no clear pattern emerging. Our results indicate that for *C. dubia*, *D. magna*, and *D. pulex*, partial life tables can be used to generate population growth rates in lieu of full life tables. However, the implications of differences in cutoff points for different demographic parameters need to be investigated further.

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Developing demographic toxicity data: Optimizing effort for predicting population outcomes

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25 Abstract

26 ~~Mounting~~ evidence suggests that population endpoints in risk assessment are ~~far~~ more accurate
27 than static assessments. Complete demographic toxicity data based on full life tables are
28 ~~eminently~~ useful in predicting population outcomes in many applications as they capture both
29 lethal and sublethal effects; however, developing these data is extremely costly. In this study we
30 investigated the efficacy of partial life cycle tests as a substitute for full life cycles in
31 parameterizing population models. Life table data were developed for three species of Daphniids,
32 *Ceriodaphnia dubia*, *Daphnia magna*, and *D. pulex*, weekly throughout the life span of these
33 species. Population growth rates (λ) and a series of other demographic parameters generated
34 from the complete life cycle were compared to those calculated from cumulative weeks of the
35 life cycle ~~in order~~ to determine the minimum number of weeks needed to generate an accurate
36 population projection. Results showed that for *C. dubia* and *D. pulex*, λ values developed at ≥ 5
37 weeks (55.6% of the life cycle) were not significantly different from λ developed for the full life
38 cycle (9 weeks) of each species. For *D. magna*, λ values developed at ≥ 7 weeks (70% of the
39 life cycle) were not significantly different from λ developed for the full life cycle (10 weeks).
40 Furthermore, these statistically significant cutoff points for λ were not the same for other
41 demographic parameters, with no clear pattern emerging. Our results indicate that for *C. dubia*,
42 *D. magna*, and *D. pulex*, partial life tables can be used to generate population growth rates in lieu
43 of full life tables. However, the implications of differences in cutoff points for different
44 demographic parameters need to be investigated further.

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Introduction

47 A growing body of literature suggests that demography-based approaches are ~~far~~ more effective
48 in determining what happens to populations subjected to stressors or disturbance than short-term
49 acute mortality estimates (e.g., LC₅₀) (Van Straalen et al. 1989, Forbes & Calow 1999, Sibly
50 1999, Calow et al. 2001, Pastorok et al. 2002, Stark & Banks 2003, Akçakaya et al. 2008,
51 Bartnhouse et al. 2008). In particular, demography-based approaches can address issues such as
52 sub-lethal effects, stage- or age-specific life history rates, and time-varying demographic
53 processes ~~far~~ better than more static methods (Stark & Banks 2003, Banks et al. 2008). However,
54 the development of demographic data is costly and time-consuming. In some cases, such as
55 recent  toxicological risk assessments, researchers have attempted to use partial life table data
56 instead to predict population outcomes (Laskowski & Hopkin 1996, Preston & Snell 2001,
57 Ducrot et al. 2010). However, it is not clear how predictions from these studies incorporating
58 reduced datasets compare with studies using complete life tables. In particular, little attention has
59 been paid to the tradeoff between accuracy and experimental effort when comparing partial vs.
60 full life table studies. We offer here ~~just~~ such an approach, in which population outcomes from
61 complete life tables are compared with those developed from partial life tables for three
62  ~~D~~aphniid species. We address the issue of whether ~~or not~~ partial demographic data can be used
63 in lieu of complete demographic data without loss of accuracy in projecting population
64 outcomes. We focus in particular on whether ~~or not~~ we can explain differences in the accuracy of
65 population responses based on reduced datasets by comparing proportional differences in life
66 spans of the three ~~D~~aphniid species. Finally, we compare outcomes for lambda  vs. other
67 demographic parameters across all species, and assess the overall potential for using reduced
68 datasets to generate reliable population projections.

69

70 **Materials and Methods**

71

72 **Species tested**

73 Three species of Daphniids were evaluated in this study; *Ceriodaphnia dubia* (Richard) *Daphnia*
74 *pulex* (Leydig) and *D. magna* (Straus). Individuals used to develop life table data were obtained
75 from cultures maintained at Washington State University, Puyallup Research and Extension
76 Center. Each species was reared in reconstituted dilution water (RDW). The RDW used in this
77 study was prepared according to a method modified from a USEPA protocol (USEPA 2002)
78 resulting in a RDW with pH 7.4-7.8, conductivity 260-320 μ S, dissolved oxygen (DO) > 8.0
79 mg/l, alkalinity of 60-70 mg/l and a hardness of 80-100mg/l. Daphniids were maintained in an
80 environmental chamber set with a photoperiod of 18h: 6h light: dark, $25.0 \pm 0.1^\circ\text{C}$, and $50.0 \pm$
81 0.1% relative humidity (RH).

82

83 The Daphniids were fed a solution consisting of a 1:1.5 mixture of yeast-cereal leaves-trout
84 chow (YCT) and the algal species *Pseudokirchneriella subcapitata* (previously *Selenastrum*
85 *capricornutum*) (Charles River Co., Wilmington, MA).

86

87 **Development of life tables**

88 Individuals (<24h old) at or beyond the third filial (F3) generation were transferred into glass
89 beakers containing 25 ml RDW. Founding individuals were moved to fresh RDW every other
90 day. Three batches (replicates) of 10 individuals of each species were used to develop life tables.

91 Individual survival and the number of offspring produced were recorded daily throughout their
92 life span. Offspring ~~were~~ removed daily. Life tables were developed at weekly intervals and at the
93 end of each species life cycle. Beakers were held in an environmental chamber under the
94 conditions listed above for colony maintenance.

95
96
97 Life tables were developed following the approach outlined in Carey (1993) and Vargas et al.
98 (2002). The following demographic parameters were determined in this study: Net Reproductive
99 Rate (R_0), the per generation contribution of newborn females to the next generation, Intrinsic
100 Birth Rate (b), the per capita instantaneous rate of birth in the stable population, Intrinsic Death
101 Rate (d), the per capita instantaneous rate of death in the stable population, Mean Generation
102 Time (T), the time required for a newborn female to replace herself R_0 -fold, Doubling Time
103 (DT), the time required for the population to increase twofold, Intrinsic Rate of Increase (r_m), the
104 rate of natural increase in a closed population, and the Finite Rate of Increase (λ), the factor by
105 which a population increases in size from time t to time $t+1$

106

107 **Statistical analysis**

108 The data for all of the above-mentioned demographic parameters were analyzed with one-way
109 analysis of variance (ANOVA) (SAS Institute 2011) ~~in order~~ to test for differences among
110 means; means were separated with the Student-Newman-Keuls test. For each species, we
111 compared the value of the demographic parameter of interest for each successive week to that
112 derived from the complete life table (full life span). We thus determined the week at which the
113 demographic parameter value was not statistically significant different ($p < 0.005$) from the value

114 derived using the entire life span (complete life table), heretofore referred to as the “cutoff
115 point”.

116

117 **Results**

118

119 *C. dubia*

120 The time at which net reproductive rate (R_0) was not significantly different from the complete
121 life table for *C. dubia* was four weeks (Table 1). That is, if R_0 was the endpoint of interest for
122 this species, a life table would only have to be developed for four weeks to generate the same R_0
123 value stemming from a complete life table (nine weeks). For birth rate (b), r_m , and λ the
124 statistical cutoff point was five weeks, while it was three weeks for the death rate (d). The cutoff
125 point for both generation time (T) and doubling time (DT) for *C. dubia* was six weeks.

126

127 *D. pulex*

128 The cutoff point for the values of R_0 , DT , r_m , and λ for *D. pulex* was five weeks (Table 2). The
129 cutoff time for d was four weeks while the cutoff for b and T was six weeks.

130

131 *D. magna*


132 For *D. magna*, the cutoff times for R_0 , d , and λ were seven weeks (Table 3). The cutoff times for
133 b , T , DT , and r_m were eight weeks.

134

135 **Discussion**



136 A number of studies have shown that incorporating demographic data into population models has
137 the potential to improve population projections, an approach that has been widely used in
138 conservation and ecological risk assessment (Stark & Banks 2003, Stark et al. 2007, Hommen et
139 al. 2010, Forbes & Calow 2002, Forbes et al. 2008, Forbes et al. 2001, Mills et al. 2015).
140 However, demographic data are expensive to develop, and it is not clear how much data is
141 needed to generate sufficiently accurate population endpoints. Past studies have empirically
142 demonstrated that partial life tables may yield accurate population projections (Van Straalen et
143 al. 1989, Oli & Zinner 2001), but none to our knowledge have attempted to quantify the cutoff
144 point beyond which adding more life history data does not improve accuracy. To this end, in this
145 study we sought to determine the minimum amount of time a life table needs to be developed to
146 get a measurement of species demographic parameters that is not statistically different from data
147 developed over the entire life span of an organism. Our results suggest that if we were only
148 interested in population growth rate (λ), commonly used in population studies, then partial life
149 tables can be used without sacrificing accuracy. However, the cutoff times varied among the
150 species we evaluated, with five weeks of data collection (instead of nine weeks) sufficient for *C.*
151 *dubia* and *D. pulex*, but seven weeks (instead of ten weeks) necessary for *D. magna*. Notably,
152 these cutoff times differed not only in real time, but also in terms of the proportion of the life
153 span of each species. That is, accurate estimates of λ were generated from data collected for
154 70%-80% of the lifespan of *D. magna*, whereas it took only 55% of the lifespan of *C. dubia* and
155 *D. pulix* to generate accurate estimates for λ . Furthermore, there were no clear patterns
156 discernible in differences among the other demographic parameters measured for the three
157 species. For instance, accurate estimates of the birth rate (b) were generated earlier than accurate
158 estimates of λ in some cases (*D. pulex*) and later or in the same time in others (*D. magna*, *C.*

159 *dubia*, respectively). Taken together, the variable responses among parameters and among
160 species suggests that simple predictions relating longevity or life history ecology patterns to the
161 amount of data we need to accurately characterize population projections may not be
162 forthcoming. 

163 We compared the values of λ in the current study, as this parameter is most commonly
164 used as a population endpoint in disciplines such as conservation science and ecotoxicology.
165 However, it is important to note that an underlying assumption of the calculation of λ in life
166 tables is that the population undergoes continuous exponential growth. This assumption may
167 yield misleading population predictions in cases of density-dependence or time-varying per
168 capita reproduction (e.g., Banks et al. 2008). More attention might be profitably paid to such
169 contingencies; here the use of more sophisticated mathematical models may elucidate differences
170 in life history that are driving differences in population outcomes.

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Table 1. *C. dubia* life table variables determined at weekly intervals

	X ± SEM								
Life table value	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9
Ro	12.17 ± 1.25a	50.43 ± 2.50b	103.17 ± 7.11c	153.83 ± 14.00d	199.67 ± 21.15d	228.90 ± 23.88d	237.90 ± 22.06d	239.40 ± 21.69d	239.80 ± 21.7d
Birth rate (b)	0.35 ± 0.016a	0.33 ± 0.007a	0.28 ± 0.003b	0.25 ± 0.003b	0.23 ± 0.002c	0.21 ± 0.000c	0.205 ± 0.002c	0.204 ± 0.002c	0.204 ± 0.002c
Death rate (d)	-0.06 ± 0.011a	-0.07 ± 0.004a	-0.05 ± 0.001b	-0.04 ± 0.000b	-0.03 ± 0.000b	-0.03 ± 0.000b	-0.02 ± 0.001b	-0.02 ± 0.001b	-0.02 ± 0.001b
Gen. time (T)	6.11 ± 0.25a	9.78 ± 0.23b	13.99 ± 0.28c	17.50 ± 0.46d	20.70 ± 0.53e	22.98 ± 0.37f	23.88 ± 0.23f	24.06 ± 0.17f	24.12 ± 0.11f
Doubling time (DT)	1.71 ± 0.12a	1.74 ± 0.06a	2.09 ± 0.03b	2.41 ± 0.03c	2.71 ± 0.02d	2.94 ± 0.02e	3.03 ± 0.05e	3.05 ± 0.05e	3.05 ± 0.05e
r _m	4.090 ± 0.027a	0.331 ± 0.007b	0.331 ± 0.004b	0.287 ± 0.004c	0.255 ± 0.002d	0.236 ± 0.001d	0.229 ± 0.004d	0.227 ± 0.004d	0.227 ± 0.004d
Lambda (λ)	1.507 ± 0.040a	1.494 ± 0.016a	1.393 ± 0.006b	1.333 ± 0.005c	1.291 ± 0.003cd	1.266 ± 0.002d	1.257 ± 0.005d	1.255 ± 0.005d	1.255 ± 0.005d

*/ Student-Newman-Keuls test

Table 2. *D. magna* life table variables determined at weekly intervals

X ± SD										
Life table value	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9	Week 10
Ro	14.07 ± 0.78a	73.13 ± 6.21b	98.60 ± 9.37c	129.20 ± 13.58d	169.50 ± 18.65e	204.13 ± 15.07e	222.77 ± 11.81f	238.04 ± 11.76f	243.47 ± 12.33	244.34 ± 13.58f
Birth rate (b)	0.33 ± 0.005a	0.35 ± 0.006b	0.32 ± 0.003c	0.27 ± 0.003d	0.23 ± 0.003e	0.21 ± 0.006f	0.20 ± 0.008g	0.19 ± 0.007h	0.18 ± 0.007h	0.184 ± 0.006h
Death rate (d)	-0.05 ± 0.003b	-0.08 ± 0.003a	-0.06 ± 0.001b	-0.05 ± 0.001c	-0.03 ± 0.001d	-0.03 ± 0.002d	-0.02 ± 0.002e	-0.02 ± 0.002e	-0.02 ± 0.002e	-0.02 ± 0.001e
Gen. time (T)	7.00 ± 0.00a	10.09 ± 0.14b	12.08 ± 0.12c	15.22 ± 0.12d	19.24 ± 0.18e	22.58 ± 0.43f	24.54 ± 0.84g	26.35 ± 0.89h	27.11 ± 0.87h	27.25 ± 0.72h
Doubling time (DT)	1.84 ± 0.04a	1.63 ± 0.04b	1.82 ± 0.02c	2.17 ± 0.03d	2.60 ± 0.03e	2.94 ± 0.10f	3.15 ± 0.14g	3.34 ± 0.14h	3.42 ± 0.14h	3.44 ± 0.12h
r _m	0.378 ± 0.008a	0.425 ± 0.009b	0.380 ± 0.004a	0.319 ± 0.005c	0.267 ± 0.004d	0.236 ± 0.008e	0.220 ± 0.010f	0.208 ± 0.009g	0.203 ± 0.008g	0.202 ± 0.007g
Lambda (λ)	1.459 ± 0.012b	1.530 ± 0.014a	1.462 ± 0.006b	1.376 ± 0.006c	1.305 ± 0.005d	1.266 ± 0.010e	1.247 ± 0.010f	1.231 ± 0.011f	1.225 ± 0.010f	1.224 ± 0.009f

*/ Student-Newman-Keuls test

Table 3. *D. pulex* life table variables determined at weekly intervals

X ± SD									
Life table value	Week 1	Week 2	Week 3	Week 4	Week 5	Week 6	Week 7	Week 8	Week 9
Ro	8.70 ± 1.04a	69.80 ± 7.60b	122.83 ± 15.95c	169.43 ± 19.00d	201.60 ± 18.28e	223.50 ± 13.87e	231.40 ± 9.43e	234.93 ± 5.30e	237.43 ± 2.66e
Birth rate (b)	0.31 ± 0.013a	0.33 ± 0.005b	0.30 ± 0.004c	0.26 ± 0.004d	0.24 ± 0.006e	0.23 ± 0.008ef	0.22 ± 0.011f	0.22 ± 0.014f	0.22 ± 0.017f
Death rate (d)	-0.03 ± 0.009b	-0.07 ± 0.003a	-0.05 ± 0.002c	-0.04 ± 0.003d	-0.03 ± 0.003d	-0.03 ± 0.004d	-0.03 ± 0.005d	-0.03 ± 0.006d	-0.03 ± 0.007d
Gen. time (T)	6.27 ± 0.04a	10.54 ± 0.07b	13.79 ± 0.26c	16.78 ± 0.01d	19.12 ± 0.32e	21.03 ± 0.75f	21.86 ± 1.22f	22.33 ± 1.75f	22.70 ± 2.14f
Doubling time (DT)	2.02 ± 0.13a	1.72 ± 0.04a	1.99 ± 0.03a	2.23 ± 0.05ab	2.50 ± 0.08bc	2.70 ± 0.13c	2.75 ± 0.18c	2.83 ± 0.23c	2.88 ± 0.28c
r _m	0.344 ± 0.021b	0.402 ± 0.009a	0.349 ± 0.006b	0.306 ± 0.007c	0.277 ± 0.009d	0.257 ± 0.012d	0.250 ± 0.016d	0.246 ± 0.020d	0.242 ± 0.023d
Lambda (λ)	1.411 ± 0.030b	1.495 ± 0.013a	1.417 ± 0.009b	1.357 ± 0.009c	1.320 ± 0.012d	1.294 ± 0.016d	1.284 ± 0.020d	1.278 ± 0.026d	1.275 ± 0.03d

*/ Student-Newman-Keuls test

