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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 sublethall 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.

Developing demographic toxicity data: Optimizing effort for predicting population outcomes

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Abstract

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 subletahl 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.

Introduction

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

Materials and Methods

Species tested

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

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

Development of life tables

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

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

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

Statistical analysis

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

Results

C. dubia

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

D. pulex

The cutoff point for the values of *Ro*, *DT*, r_m, and $\lambda$for *D. pulex* was five weeks (Table 2). The cutoff time for *d* was four weeks while the cutoff for *b* and *T* was six weeks.

D. magna

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

Discussion

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

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

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