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Comparative population demography of elasmobranchs using life history tables, Leslie matrices and stage-based matrix models

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Abstract. Results of demographic analyses of four species of elasmobranchs were compared by use of life-history tables, Leslie matrices, and several stage-based matrix models. *Dasyatis violacea*, with few age classes, was used to demonstrate the basics of Leslie-matrix and stage-based matrix model calculations. The demography for *Carcharias taurus*, with a 2-year reproductive cycle, produced higher potential population growth using actual fertility rather than effective annual fertility. The demography for *Alopias pelagicus*, with continuous reproduction, produced higher potential population growth for a birth-flow than a birth-pulse population. The *Carcharodon carcharias* example demonstrated only a small difference in potential population growth between step-like and logistic fertility functions. Stage-based models with fixed stage duration produced potential population growths identical to those obtained from a life-history table or Leslie matrix, but the net reproductive rates and generation times differed. Stage-based models with few stages had different dynamics with shorter recovery to the stable age distribution; they underestimated the elasticity of juvenile survival and overestimated the elasticity of adult survival, suggesting that interpretation should be cautious. Elasticity analyses were used to estimate the number of juvenile age classes that could be fished and have the same effect on potential population growth as fishing all the adult age classes.

Introduction

Age-based (Leslie) or stage-based matrix models for elasmobranchs are becoming increasingly popular (Hoenig and Gruber 1990; Cortés 1999, in press; Heppell *et al.* 1999; Brewster-Geisz and Miller 2000). The advantages of using stage-based models had not been adequately explored for elasmobranchs before Brewster-Geisz and Miller (2000) first used a stage-based model for an elasmobranch, *Carcharhinus plumbeus* (sandbar shark). They suggested that stage-based models might provide a more realistic view of the dynamics of some populations and suggested potential problems with the application of life-history tables (LHTs) to long-lived marine species because small errors in parameter estimates can become magnified. Cortés (1999) introduced a stage-based model for *C. plumbeus* but then used a LHT for the calculation of population growth. The concept of stage-structure is more applicable to plants or animals such as parasites, crustaceans, insects, cnidarians, and perhaps turtles, which have more distinct life-history stages than do elasmobranchs. A stage-structured model based on maturity or breeding condition invokes the concept of step-like (also known as knife-edge) changes from one stage to another. This is clearly not the case for the many elasmobranchs, which mature over a wide range of lengths and presumably ages.

Assessment models developed for marine mammals rather than teleosts might be more appropriate for elasmobranchs (Anderson 1990; Walker 1998). Heppell *et al.* (1999) applied an age-based matrix model to long-lived marine species, which included *Triakis semifasciata* (leopard shark) and *Squatina californica* (Pacific angel shark). Elasticities were summed across age classes to present management options. Heppell *et al.* (2000*a*) introduced a modified age-classified model, with all the adult age classes lumped into one stage, for a perturbation analysis of species with minimal demographic data. The elasticities compared favourably with the summed elasticities of full Leslie-matrices and are useful as a qualitative guide for research and management. Brewster-Geisz and Miller (2000) used a 5-stage based matrix model for *C. plumbeus*, which included a stage for resting females (proportion of females not giving birth each year), and presented management options based on elasticity analyses. Cortés (2000) identified at least three separate life-history strategies with trade-off between fertility and neonate/juvenile mortality. Cortés (in press) incorporated uncertainty into demographic modelling and followed Heppell *et al.* (1999) to calculate stage-based elasticities from a life-history table by summing over age classes. He concluded that research, conservation and management efforts should focus on the combined results from elasticity (prospective) and correlation (retrospective) analyses.

Both Brewster-Geisz and Miller (2000) and Heppell *et al.* (2000*a*) used fixed stage duration to calculate the proportion

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of individual animals graduating to the next stage, which is most appropriate when the stages are really groups of age classes (Caswell 2001). However, Brault and Caswell (1993) used a geometric distribution for *Orcinus orca* (killer whale) with good results, although the stages were groups of age classes.

In this paper, we compare results of deterministic life-history tables and/or Leslie-matrices with those of deterministic stage-based models using four species of elasmobranchs for which a reasonable amount of life-history information was available. Our population growth rates are purely analytical projections assuming that the vital rates are reasonably accurate, the environment is constant, and that density effects are unimportant (Caswell 2001). Our elasticity results can be used to formulate and evaluate management strategies affecting the vital rates and population dynamics. This is different from a diagnosis of why vital rates varied in the past or might vary in the future, which relies on retrospective perturbation analysis using life-table response experiments, e.g. random designs based on variance decomposition (Caswell 2001).

We use *Dasyatis violacea* (pelagic stingray) to introduce the Leslie matrix because it produced a small 10×10 matrix. We then introduce several stage-based models for *D. violacea* and compare elasticities of Leslie matrix and stage-based models. We use *Carcharias taurus* (sandtiger shark) to compare the use of actual and annual effective fertility based on a reproductive cycle of two years. *Alopias pelagicus* (pelagic thresher shark) was chosen to compare birth-pulse (seasonal parturition) and birth-flow (year-round parturition) populations of sharks. *Carcharodon carcharias* (white shark) was used to explore the difference between step-like and logistic fertility functions in a life-history table and the difference between fixed-stage and variable-stage distribution in a stage-based model. We also used *C. carcharias* to explore the difference between fixed-stage and geometric distribution and then compared the results with data reported for *Orcinus orca* (Brault and Caswell 1993).

Methods

Summary of vital parameters of elasmobranchs used in calculation

We used the best available vital parameters taken from the literature for each of four elasmobranch examples (Table 1). They are age-at-first reproduction (α), longevity (ω), age-specific natural mortality rate (M) or corresponding survival probabilities (S), and maturity/fertility function (m) giving number of female offspring as a function of age or size. In demographic calculations, the relevant 'age-at-maturity' is the mean age-at-first-reproduction, which would be mean age-at-first-maturity plus gestation period. However, it is often not clear what the reported age-at-maturity was based on, and maturity functions giving fraction mature as a function of length or TL are often not available either. In all the examples, we assumed that a litter contained 50% females. The most important vital parameters are the survival probabilities, for which only rough estimates are available for most elasmobranchs. We estimated the mortality rate from estimated longevity (ω) by assuming that 1% of the individuals remain at the longevity estimate (i.e. $M = -\ln(0.01)/\omega$, e.g. Campana *et al.* 2001). For *Carcharias taurus*, we used actual fertility of 1.0 (2 pups, assumed to be 1 female and 1 male, are born every other year) and the more often used effective annual fertility of 0.5 (here it is assumed that 0.5 female pups are born every year). We used longevity of 60 years, producing survival probability of 92.6% and a reproductive cycle of 3 ($m = 8.9/(2\times3) = 1.483$), for *Carcharodon carcharias* in most calculations. We also used longevity of 36 years with survival probability of 93% and fertility of 1.2 for the comparison with the *Orcinus orca*. This allowed step-like changes of survival probability from 93% to 99% and fertility from 1.2 to 0.12, which are good approximations for *O. orca*.

Life history table and Leslie matrix

We used a standard life-history table (LHT) based on the discrete Euler–Lotka equation (Caughley 1977) to find the solution (r = instantaneous rate of population increase (year^{-1}); $e^r = \lambda$, the natural parameter in the matrix formulation, see below) and other

Table 1. Summary of life-history parameters for elasmobranchs used in this study

α, age-at-first-reproduction; ω, longevity; M, natural mortality rate (estimated as $-\ln(0.01)/\omega$); fertility (No. of female pups per litter)

Species	α (years)	ω (years)	M (year^{-1})(S)	Fertility	Reference
Dasyatis violacea	3	10	0.4604 (63.1%)	3 (6/2)	Mollet *et al.* 2002
Carcharias taurus	6	25	0.1842 (83.2%)	0.5 (2/(2×2)) (annual)	Branstetter and Musick 1994
C. taurus[A]	6	25	0.1842 (83.2%)	1.0 (2/2) (2-year cycle)	Branstetter and Musick 1994
Alopias pelagicus	8	30	0.1535 (85.8%)	1.0 (2/2)	Liu *et al.* 1999
Carcharodon carcharias	15	60	0.07675 (92.6%)	1.483 8.9/(2×3)	Cailliet *et al*. 1985; Francis 1996; Wintner and Cliff 1999; Mollet *et al*. 2000
C. carcharias[B]	15	36	(93.0%)	1.20	modified after above
Orcinus orca[B]	15	36	(99.0%)	0.12	modified after Brault and Caswell 1993 and Caswell 2001

[A]Actual female fertility (1.0 female pup every other year) rather than effective annual fertility (0.5 female pups per year).

[B]Data were modified to permit comparison calculations for *C. carcharias* and *O. orca* using fixed stage duration and geometrical distribution for stage duration.

population parameters R_0, T, μ_1, and $\bar{A}$ for all four elasmobranch examples. The net reproductive rate R_0 is the mean number of pups, by which a newborn individual will be replaced by the end of its life. The time T required for the population to increase by a factor of R_0 is given by $T = \ln R_0 / \ln \lambda = \ln R_0 / r$ (Coale 1972). Somewhat surprisingly, T is not equal to any of the several mean ages of 'pup-bearing' that can be defined (Coale 1972). There are three mean ages of reproductively active females of interest in this context (see Caswell 2001 for details):

(1) The mean age of females bearing pups in a cohort subject to no mortality, which is not a very meaningful measure in most fish;

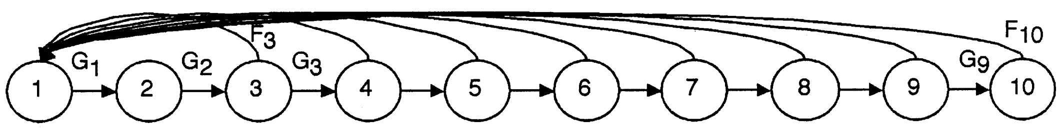
(2) The mean age (μ_1) of the females bearing pups produced by a cohort over its lifetime (also known as the mean length of a generation, and it does not require a stable age distribution)

(3) The mean age ($\bar{A}$) of the females bearing pups produced by a population at the stable age distribution.

If assumed that the survivorship curve ($l = l$ (age)) decreases linearly with time over the range of interest, then $T \sim (\bar{A} + \mu_1)/2$ (Coale 1972). In a stationary population ($\lambda = 1.0$), $\mu_1 = \bar{A}$.

We used a CSIRO program called PopTools (Greg Hood, http://www.dwe.csiro.au/vbc/poptools/) to calculate many of the life-history parameters. PopTools is an add-in to Excel and can be used to draw life-cycle graphs, carry out the basic matrix analysis, calculate sensitivity and elasticity matrices, and perform projection analysis. An age-classified matrix model (Leslie matrix) is best understood with the help of a life-cycle graph (Caswell 2001) (see Fig. 1 for heuristic example). The nodes in the life-cycle graph represent ω age classes, starting at $i = 1$. Individuals in stage i survive, with growth probability G_i to become 1 year older and create, beginning at α with fertility F_i, new individuals in the first age class ($i = 1$) after one projection interval (usually 1 year). The corresponding Leslie matrix has fertility matrix

Life cycle graph of 10 x10 Leslie matrix



Leslie matrix[A]

[A]We used G (rather than P) to get agreement with notation used in stage-based matrix models

1	2	3	4	5	6	7	8	9	10
0	0	F_3=1.8929	F_4=1.8929	F_5=1.8929	F_6=1.89329	F_7=1.8929	F_8=1.8929	F_9=1.8929	F_{10}=1.8929
G_1=0.6310	0	0	0	0	0	0	0	0	0
0	G_2=0.6310	0	0	0	0	0	0	0	0
0	0	G_3=0.6310	0	0	0	0	0	0	0
0	0	0	G_4=0.6310	0	0	0	0	0	0
0	0	0	0	G_5=0.6310	0	0	0	0	0
0	0	0	0	0	G_6=0.6310	0	0	0	0
0	0	0	0	0	0	G_7=0.6310	0	0	0
0	0	0	0	0	0	0	G_8=0.6310	0	0
0	0	0	0	0	0	0	0	G_9=0.6310	0

Eigenvalues		**Eigenvectors (right & left) of largest real eigenvalue**	
Real	Imaginary	Age struct.	Reprod value
1.1739	0	46.35%	1.00
0.4392	0.4310	24.91%	1.86
0.4392	-0.4310	13.39%	3.46
0.0406	0.6453	7.20%	3.44
0.0406	-0.6453	3.87%	3.40
-0.2941	-0.7773	2.08%	3.33
-0.2941	0.7773	1.12%	3.20
-0.4748	0.4083	0.60%	2.94
-0.4748	-0.4083	0.32%	2.48
-0.5960	0	0.17%	1.61

r = 0.1604 yr^{-1} (rate of increase)

Ro = 1.9907 (expected number of replacements)

T = 4.29 yr (generation time - time for increase of Ro)

μ_1 = 4.50 yr (mean age of parents of pups of a cohort over its lifetime)

$\rho = \lambda_1/|\lambda_6| = \lambda_1/|\lambda_7| = 1.4126$ (damping ratio)

Elasticity matrix

0	0	0.1134	0.0610	0.0328	0.0176	0.0095	0.0051	0.0027	0.0015
0.2436	0	0	0	0	0	0	0	0	0
0	0.2436	0	0	0	0	0	0	0	0
0	0	0.1301	0	0	0	0	0	0	0
0	0	0	0.0691	0	0	0	0	0	0
0	0	0	0	0.0364	0	0	0	0	0
0	0	0	0	0	0.0188	0	0	0	0
0	0	0	0	0	0	0.0093	0	0	0
0	0	0	0	0	0	0	0.0042	0	0
0	0	0	0	0	0	0	0	0.0015	0

Fig. 1. Life cycle graph and Leslie matrix using post-breeding census, birth-pulse, and fixed-stage-duration distribution of *Dasyatis violacea* with solution (G = 0.6310 (M = –ln(0.01)/10), m = 3.0, F = $m\sigma$ = mG).

elements (F_i values) on the first row starting at α and has growth/survival probabilities matrix elements (G_i values) on the first sub-diagonal. We used G rather than the standard P for the survival matrix elements in the Leslie matrix to get agreement with the notation used for stage-based models.

The Leslie matrices for our four examples, including the 10×10 Leslie matrix for *Dasyatis violacea* shown in Fig. 1, were constructed using the vital rates from Table 1 and assuming a birth-pulse population with a post-breeding census. We used a post-breeding census because the life-cycle graph is easier to understand and because we wanted to include a 2×2 matrix, the smallest possible matrix, among the stage-based models for which it is not possible to use a pre-breeding census. Following Caswell (2001), a birth-pulse population with post-breeding census has Leslie-matrix elements on the sub-diagonal and first row

$G_{\mathrm{i}} = \mathrm{l}\,(i) / \mathrm{l}\,(i+1)$ and $F_i = G_i\, m_i$ (=discounted fertility m_i), respectively.

This matrix, also known as projection matrix (A), has 10 solutions or eigenvalues. The largest positive and real solution (λ_1 = dominant eigenvalue) gives the long-term behaviour of the population with exponential population increase according to $\mathbf{n}\,(t+1) = \lambda_1\, \mathbf{n}\,(t)$. The PopTools solution provides the stable population structure (= age structure = % individuals in each age class) and the reproductive values of each age class (e.g. see Fig. 1 for *D. violacea*). PopTools also provides r, R_0, T, $\mu_{1,}$ as well as the fundamental matrix (N) and the lifetime production matrix (R). The fundamental matrix (N) is given by $\mathrm{N} = (\mathrm{I} - \mathrm{T})^{-1}$, where I is the identity matrix (1's on the diagonal, 0's elsewhere) and T is the matrix in the decomposition of A into transition matrix (T) and fertility matrix (F) (A = T + F, Cochran and Ellner 1992; Caswell 2001). The matrix elements of N give the mean time spent in each age class. We summed the column values of the fundamental matrix to provide the life expectancy of each age class.

The subdominant eigenvalues produce oscillations, which usually decrease over time as the population approaches the stable age distribution. The rate of convergence to the stable stage distribution (recovery) is governed by the other eigenvalues (complex conjugates if not real) and it will be the more rapid, the larger λ_1 is relative to the other eigenvalues. This led to the definition of the damping ratio $\rho = \lambda_1 / |\lambda_2|$. The time for the contribution of λ_1 to become 10 times as great as that of λ_2 (the second-largest eigenvalues) is $t_{10} = \ln(10)/\ln(\rho)$. The simplest way to determine convergence (recovery) is a numerical projection. Starting with a stage vector $\mathbf{n}\,(t = 0) = [1,0,0]$ (i.e. a depressed population after a catastrophic event with one pup in the first age class and zero individuals in all other age classes at time zero), one calculates $\mathbf{A}^t\, \mathbf{n}\,(0) = \mathbf{n}\,(t)$ and checks how long it takes until $\mathbf{n}\,(t)$ approaches the stable age-class distribution.

The sensitivity matrix, with matrix elements $s_{ij} = \delta\lambda/\delta a_{ij}$, is the matrix comprising the first partial derivative of λ with respect to the matrix elements a_{ij} of A, while all the other matrix elements are held constant (i = row number, j = column number). The elasticity matrix has matrix elements ($e_{ij} = a_{ij}/\lambda\ \delta\lambda/\delta a_{ij} = \delta \ln(\lambda)/\delta \ln a_{ij}$,), which give the relative change of λ with respect to the relative change of the matrix elements of A. We used the symbols E_1, E_2 and E_3 for the sum of the elasticities of fertility, juvenile survival (including pup age class) and adult survival, respectively. We note that E_1 equals the elasticity of each juvenile age class (Heppell *et al.* 1999; Caswell 2001). The sum of the elasticities E_1, E_2 and E_3 in a post-breeding census is $1 + E_1$ rather than 1.0, because the adult survival probabilities appear as a lower-level parameter in the fertilities (Caswell 2001). We defined the elasticity ratios $ER_2 \equiv E_2/E_1$ $(=\alpha - 1)$ and $ER_3 \equiv E_3/E_1$ $(=1/E_1 - \alpha + 1)$ (modified from ratios used by Heppell et al. (1999) and Cortés (in press), who used a pre-breeding census). We propose that the elasticity ratio of fertility to adult survival (ER_3) can be interpreted in management terms as the number of juvenile age classes that, if fished ([Fish] = instantaneous fishing mortality rate), will reduce population growth (λ) by the same amount as fishing all the adult age classes. Since elasticities give the proportional changes of λ for proportional changes of the survival probabilities and $S = e^{-(M+[\mathrm{Fish}])}$ (M = instantaneous natural mortality rate), it follows that elasticities give the proportional change of λ for absolute changes of added fishing mortality. If all age classes/stages are fished, the maximum amount of fishing allowed before population declines is $[\mathrm{Fish}] \leq \lambda - 1$ according to Caswell (2001). We suggest that zero population growth is reached when [Fish] = r (instantaneous growth rate) rather than at $\lambda - 1$ (Caughley 1977).

Stage-based matrix models

We used a variety of stage-based models to evaluate the influence of different stage numbers and stage durations on demographic parameters for all four elasmobranch examples. First, we used the simplified age-structured model introduced by Heppell *et al.* (2000*a*) in which all the adult age classes are combined into one stage, but we used a post-breeding census. For *Dasyatis violacea* with $\alpha = 3$ (i.e. only two juvenile age classes), the Heppell-matrix was a 3×3 matrix with stage durations 1–1–8 years (Fig. 2). The Heppell model for our three shark examples had more juvenile age classes and produced the following transition matrices (A) and (stage durations): 6×6-matrix (1–4×1–20) for *Carcharias taurus* ($\alpha = 6$ and $\omega = 25$); 8×8-matrix (1–6×1–23) for *Alopias pelagicus* ($\alpha = 8$ and $\omega = 30$); 15×15-matrix (1–13×1–46) for *Carcharodon carcharias* ($\alpha = 15$ and $\omega = 60$).

The nodes in the life-cycle graph represent the juvenile age classes and one adult stage (Fig. 2 with only two juvenile age classes for *D. violacea*). The straight arrows G_1 and G_2 represent the probability of age-classes 1 and 2 growing to age-class 2 and adult stage3, respectively. The probability of growing to the next stage (i.e. post-reproductive stage or death) would be G_3 and is not needed. The in-stage probability (self-loop) of the adult stage is P_3. The reproductive output of the adult stage is F_3 and is called the fertility coefficient. We first had to calculate the probabilities P_i and G_i for each stage. Caswell (2001) separated the processes of survival and growth and introduced

σ_i = probability of survival of an individual in stage i and

γ_i = fraction of the individuals in stage i that graduate to the next stage.

In terms of these parameters

$$G_{\mathrm{i}} = \sigma_i\, \gamma_i \text{ and}$$

$$P_i = \sigma_i\,(1 - \gamma_i).$$

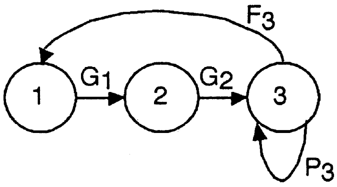
A fixed-stage-duration distribution for both juvenile and adult stages is most suitable for elasmobranchs because the stages are really groups of age classes (Heppell *et al.* 2000*a*; Brewster-Geisz and Miller 2000; Caswell 2001). The proportion of individuals in the last age class of a stage that graduate to the first age class of the next stage is given by

$$\gamma_i = ((\sigma_i/\lambda)^{T(i)} - (\sigma_i/\lambda)^{T(i)-1)}) / ((\sigma_i/\lambda)^{T(i)} - 1).$$

The calculation of the γ values and λ is an iterative process. One starts with a suitable λ (say 1.0) and calculates γ_i, G_i and P_i, and then solves the matrix for λ. The process is continued until the assumed λ agrees with the calculated λ and is easily implemented in an Excel spreadsheet using the Solver tool. The fertility coefficient F_α represents discounted fertility (m) and is given by $F_3 = \sigma_3 m$ in a post-breeding census.

Second, for our three shark examples we used a 3-stage model comprising a first-year age class (pups), a juvenile stage and an adult stage. This produced 3×3-matrices with stage durations of 1–4–20 for *Carcharias taurus* ($\alpha = 6$, $\omega = 25$), 1–6–23 for *Alopias pelagicus* ($\alpha = 8$, $\omega = 30$), and 1–13–46 for *Carcharodon carcharias* ($\alpha = 15$, $\omega = 60$).

Third, for all four species, we used a 2×2-matrix model comprising one juvenile stage and one adult stage (Fig. 3 for *D. violacea*). This



Stage durations:
T_1 = 1 yr
T_2 = 1 yr
T_3 = 8 yr

A-matrix

1	2	3
0	0	F_3=1.8929
G_1=0.6310	0	0
0	G_2=0.6310	P_3=0.6272

Eigenvalues Real	Imaginary	Eigenvectors (R&L) Stage struct	Reprod value
1.1739	0	46.35%	1.00
-0.2734	-0.7531	24.91%	1.86
-0.2734	0.7531	28.74%	3.46

r = 0.1604 yr-1
Ro = 2.0211
T = 4.39 yr
μ_1 = 4.68 yr

N (fundamental matrix)

1.0000	0	0
0.6310	1.0000	0
1.0677	1.6923	2.6820

Life expectancy

2.6987	2.6923	2.6820

R (expected lifetime production)

2.0211	3.2032	5.0768
0	0	0
0	0	0

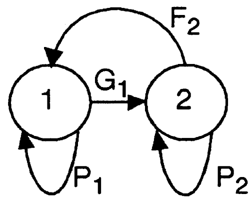
Sensitivity matrix

		0.1496
0.4487		
	0.4487	0.5177

Elasticity matrix

0	0	0.2411
0.2411	0	0
0	0.2411	0.2766

Fig. 2. Life cycle graph, transition matrix (A) of 3-stage model for *Dasyatis violacea* and matrix solution.



Stage durations:
T_1 = 2 yr
T_2 = 8 yr

A-matrix

1	2
P_1=0.4104	F_2=1.8929
G_2=0.2206	P_2=0.6272

Eigenvalues Real	Imaginary	Eigenvectors (R&L) Stage struct	Reprod val
1.1739	0	71.26%	1.00
-0.1364	0	28.74%	3.46

r = 0.1604 yr-1
Ro = 1.8992
T = 4.00 yr
μ_1 = 4.38 yr

N (fundamental matrix)

1.6960	0
1.0033	2.6820

Life expectancy

2.6994	2.6820

R (expected lifetime production)

1.8992	5.0768
0	0

Sensitivity matrix

0.4173	0.1683
1.4446	0.5827

Elasticity matrix

0.1459	0.2714
0.2714	0.3113

Fig. 3. Life cycle graph, transition matrix (A) of 2-stage model for *Dasyatis violacea* and matrix solution.

model lumped the first year class with the rest of the juvenile age classes. The model is similar to the 3-stage model but has two self-loops (P_1 and P_2). We wanted to include a 2×2 matrix model that required the use of a post-breeding census. Therefore we used a post-breeding census throughout, although the elasticities of fertility, juvenile survival and adult survival do not sum to one.

Fourth, we used a 4-stage model with stage durations 1–4–1–1 for *Alopias pelagicus* in order to be able to include a resting period for adult females (Brewster-Geisz and Miller 2000). This produces a matrix element in the 4th column above the diagonal and gives the probability of a resting female growing to become again a pregnant female. In the life-cycle graph, this is represented by an arced arrow from stage 4 back to stage 3. The corresponding simplified age-classified model following Heppell *et al.* (2000*a*) yields a 7×7 matrix with stage durations 1–4×1–1–1. The Brewster-Geisz matrix has no termination, and the individuals are potentially immortal (Kirkwood 1985). Therefore, the life expectancies will be the same for all stages if the survival probabilities are the same.

Parturition is seasonal for many elasmobranchs and the birth-pulse approximation was used therefore in most of our examples. However, some elasmobranchs have no distinct seasonal parturition, and birth is spread out throughout the year; birth-flow should be used in such cases. We chose *Alopias pelagicus*, with aseasonal parturition to explore the difference between birth-pulse and birth-flow. In addition, we used birth-flow with decreasing projection intervals of 6 months (1/2 year), 3 months (1/4 year), and 1 month (1/12 year) to simulate intermediate steps between birth-pulse and birth-flow. Such intermediate steps would be appropriate in cases where parturition is spread out over an extended period but not throughout the year. When projection intervals other than 1 year were used, mortality and fertility in the corresponding units had to be used. To allow easy comparison of the results, we reported the results as annualized parameters. This was not possible for the unit-less λ, which had to be calculated from the annualized intrinsic rate of increase (*r*).

We used a step-like maturity function in our LHTs, Leslie-matrices, and stage-based matrix models for most of our examples. In the 3-stage model of *C. carcharias* we considered the effects of using *(a)* a logistic maturity function in a life-history table and *(b)* a variable juvenile stage distribution in the 3-stage model. The fraction of individuals graduating in the juvenile stage is given by

$$\gamma_2 \approx (1/T_2)\ e^{(-a\,(T_2/2\,-\,V\,(T_2)/2)}\ \text{(Caswell 2001)},$$

where $a = \ln(\lambda/\sigma_2)$ and $T_2 = 13$ years is the mean duration of the second stage with variance $V(T_2) = 3$ year^2. The variance was estimated from standard deviation of the logistic maturity function reported for the shortfin mako (Mollet *et al.* 2000).

Brault and Caswell (1993) and Caswell (2001) used the geometric distribution for *Orcinus orca* with good results, although the stages are, as in elasmobranchs, groups of age classes. Therefore, we explored the use of a geometric stage distribution for *Carcharodon carcharias* because the durations of its juvenile and adult stages are similar to those in *O. orca*. The geometric distribution for the stage duration assumes that the probability of growing from stage i to stage i+1 is independent of the time spent in stage i. The fraction of individuals graduating to the next stage (γ_i) is then given by $\gamma_i = 1/T_i$, where T_i is the mean stage duration of stage i (Caswell 2001).

Results

Dasyatis violacea

The LHT and the corresponding Leslie matrix for *D. violacea* produced identical results and indicated a large potential annual population growth of 17.4% (λ = 1.1739, r = 0.1604 year^{-1}; Table 2). A fishing mortality of 0.1604 year^{-1} across all age classes or stages would produce a stationary population (λ = 1.0). The damping ratio was 1.4 and the estimated convergence time was 6.6 years. The net reproductive rate (R_0) was 1.99, the generation time (T) was 4.29 year, and the mean age of mature females in a cohort (μ_1) was 4.5 years. The stable age distribution decreased from 46.4% for the first age class (1) to 0.17% for the last age class (10), and the reproductive value peaked at 3.46 (12.95%) in the first adult age class (Fig. 1). The fertility, juvenile survival and adult survival elasticities were 0.244, 0.482 (ER_2 = 2.00) and 0.513 (ER_3 = 2.11), respectively. Juvenile and adult survival had similar effects on population growth, whereas the effect of fertility was about half as large. A 10% decrease in juvenile or adult survival due to fishing would require, respectively, a 20% or 21% increase in fertility to return the population to its original growth rate. Fishing of both juvenile age classes would have the same effect as fishing all the adult age classes because $ER_3 \sim 2$.

Our stage-based models produced identical population growth (17.4% year^{-1}) but the net reproductive rates (R_0) were slightly different (1.87–2.02) because the time spent in the adult stage was different (Table 2, Figs 2 and 3). The changes in R_0 reflect different adult lifetimes in the various models because the fertilities (F_i values) remain the same (3 × 0.631 = 1.893). For example, the mean time spent as an adult was 1.068 years in the 3-stage model ($N_{3,1}$ in 3×3 N-matrix), 1.003 years in the 2-stage model ($N_{2,1}$ in 2×2 N-matrix), and 1.052 years in the Leslie matrix (N-matrix not included in Fig. 1).

The stable stage distribution in the 3-stage model (46.4%, 24.9%, and 28.7%) agreed with the summed age distribution of the corresponding age classes in the Leslie matrix (Fig. 2). The reproductive values (1.0, 1.86 and 3.46) agreed with the reproductive values at the beginning age (in the Leslie matrix) of the corresponding stage (in the 3-stage matrix model). Similarly, the age distribution (71.3%, 28.7%) and reproductive values (1.00, 3.46) of the 2-stage model were as expected.

In the 3-stage model, a *D. violacea* pup spent, on average, 1 year as a pup, 0.63 year as a 2nd-year juvenile, and 1.07 years as a reproductive adult on the basis of the matrix elements of N, which give the mean time spent in each stage (Figs 2 and 3). A mature adult, in contrast, spent an average of 2.68 years in that stage. The sums of the columns produce the mean time to death (i.e. the life expectancy) and these were 2.70, 2.69 and 2.68 years for pups, 2nd-year juveniles and adults, respectively. Summing the N-matrix columns produces the mean times to death (i.e. the life expectancies)

Table 2. Summary of demographic results for *Dasyatis violacea* using life-history table (LHT), Leslie (L) matrix, and stage-based matrix models

Age-at-first-maturity 3 years; fertility 3 females per year; longevity 10 years; natural mortality rate -ln (0.01)/10 = 0.4604 year^{-1} (S = 63.10%) for all ages/stages. For complete results of 2B, 2D, and 2E see Figs 1, 2, and 3, respectively. ρ, damping ratio; E_1, Elasticity of fertility term (sum if more than one term); E_2, Elasticities of juvenile survival; ER_2, E_2/E_1; E_3, Elasticity of adult survival; ER_3, E_3/E_1

Case	Model	Stage duration	λ_1 (ρ)	r^A (year^{-1})	$R_0{}^A$	T (years)	μ_1 (years)	E_1	E_2 (ER_2)	E_3 (ER_3)
				Life history table to age 10 and 10×10 Leslie matrix						
2A	LHT	Age-based	1.1739	0.1604	1.9907	4.29	4.50			
2B	L 10×10	Age-based	1.1739 (1.4)	0.1604	1.9907	4.29	4.50	0.244	0.487 (2.00)	0.513 (2.11)
				Stage-based models with fixed stage duration						
2C	9×9	2–(8×1) years	1.1739 (1.9)	0.1604 (1.00)	1.8706 (0.94)	3.91	4.20	0.275	0.422 (1.54)	0.578 (2.11)
2D	3×3[B]	1–1–8 years	1.1739 (1.5)	0.1604 (1.00)	2.0211 (1.02)	4.39	4.68	0.241	0.482 (2.00)	0.518 (2.15)
2E	2×2	2–8 years	1.1739 (8.6)	0.1604 (1.00)	1.8892 (0.95)	4.00	4.38	0.271	0.417 (1.54)	0.583 (2.15)

[A]In parenthesis: ratio compared to LHT/L-matrix results.

[B]For *Dasyatis violacea* the simplified age classified model (Heppell *et al.* 2000*a*) is identical to a 3-stage model because there are only 2 juvenile age classes.

for pups, 2nd-year juveniles and adults of 2.70, 2.69 and 2.68 years, respectively. In the 2-stage model, a juvenile spent on average 1.70 years as a juvenile and 1.00 year as an adult. An adult, in contrast, spent on average 2.68 years in that stage. The life expectancies for juveniles and adults were 2.70 and 2.68 years, respectively.

The elasticities of the 3-stage model (= Heppell model) for *D. violacea* were similar to that of the Leslie matrix model (Table 2, No. 2D). The stage-based models, in which the juvenile age classes were combined in the same stage, yielded different elasticities and elasticity ratios (Table 2, Nos 2C, 2E). The elasticity ratio ER_2 was smaller than the elasticity ratio ER_3, which suggested that juvenile survival elasticity is underestimated at the expense of fertility elasticity and adult survival elasticity. The stage-based models 2C and 2E also had larger damping ratios of 1.9 and 8.6, respectively. The corresponding recovery times of 3.6 and 1.1 years were much shorter compared with the value of 6.6 years from the Leslie matrix and suggested that these models are not suitable for this type of analysis.

Carcharias taurus

Carcharias taurus has a reproductive cycle of two years and the demographic results depend on the implementation of this reproductive cycle (Table 3). Only the Brewster-Geisz and Miller (2000) model can closely model a reproductive cycle with a resting period. Use of their model with actual fertility (1 litter every two years with a resting period in between) gave a net reproductive rate R_0 9% higher (at a value slightly above 1.0) than that obtained using effective annual fertility (1/2 litter every year). It produced a slightly increasing population (λ >1.0), whereas effective annual fertility produced a slightly decreasing population (λ <1.0). Generation time (T), μ_1 and all the elasticities and their ratios were similar when the results between the two implementations were compared, although $T < \mu_1$ when $\lambda < 1.0$.

When we used effective annual fertility, population growth of LHT, Leslie-matrix, and three stage-based models were all the same (Table 3, Nos 3A–3E). The net reproductive rate (R_0), and the generation times (T, μ_1) of the stage-based model were slightly different. The elasticities of the simplified age-classified Heppell model (3C) were similar to those of the Leslie matrix, whereas the 3-stage (3D) and 2 stage (3E) models underestimated the elasticity of juvenile survival.

When we used actual fertility, population growth and net reproductive rate of LHT or Leslie matrix were apparently slightly lower than those in the stage-based models (Table 3, Nos 3F–3J). The LHT or Leslie matrix were terminated at age 25, whereas the stage-based models (following Brewster-Geisz and Miller 2000) have no termination and therefore produced slightly larger R_0 and λ. Generation times (T) and μ_1 of the stage-based model were slightly different

Table 3. Summary of demographic results for *Carcharias taurus* using life history table (LHT), Leslie (L) matrix, and stage-based matrix models

Age-at-first-reproduction, 6 years; fertility, 2/2 = 1 female per litter; longevity, 25 years; natural mortality rate, -ln (0.01)/25 = 0.1842 year^{-1} (S = 0.8318%) for all ages/stages. ρ, damping ratio; E_1, elasticity of fertility (sum if more than one term); E_2, elasticity of juvenile survival; $ER_2 = E_2/E_1$; E_3, Elasticity of adult survival; $ER_3 = E_3/E_1$

Case	Model	Stage durations	λ_1 (ρ)	r[A] (year–[1])	R_0[A]	T (years)	μ_1 (years)	E_1	E_2 (ER_2)	E_3 (ER_3)
				Life-history table and stage-based models using annual effective fecundity						
3A	LHT to 25	Age-based	0.9960	–0.003960	0.9594	10.47	10.43			
3B	L 25×25	Age-based	0.9960 (1.2)	–0.003960	0.9594	10.47	10.43	0.095	0.476 (5.0)	0.524 (5.5)
3C	6×6[C]	1–(4×1)–20	0.9960 (1.3)	–0.003960 (1.0)	0.9580 (0.999)	10.84	10.79	0.092	0.459 (5.0)	0.541 (5.9)
3D	3×3	1–4–20	0.9960 (2.8)	–0.003960 (1.0)	0.9613 (1.002)	9.94	9.88	0.100	0.411 (4.1)	0.589 (5.9)
3E	2×2	5–20	0.9960 (1.8)	–0.003960 (1.0)	0.9634 (1.004)	9.42	9.35	0.105	0.379 (3.6)	0.621 (5.9)
				Life-history table and stage-based models using actual fecundity (c)						
3F	LHT to 25	Age-based	1.0047[D]	0.004675 (–1.18)	1.0475 (1.09)	9.93	9.97			
3G	L 25×25	Age-based	1.0047 (1.0[E])	0.004675 (–1.18)	1.0475 (1.09)	9.93	9.97	0.101	0.506 (5.0)	0.494 (4.9)
3H	7×7[BC]	1–(4×1)–1–1	1.0069 (1.0[E]))	0.006916 (–1.75)	1.0745 (1.12)	10.39	10.49	0.097	0.486 (5.0)	0.514 (5.3)
3I	4×4	1–4–1–1	1.0069 (1.3)	0.006916 (–1.75)	1.0678 (1.11)	9.49	9.61	0.107	0.435 (4.1)	0.565 (5.3)
3J	3×3	5–1–1	1.0069 (1.2)	0.006916 (–1.75)	1.0639 (1.11)	8.96	9.09	0.115	0.400 (3.5)	0.600 (5.3)

[A]In parenthesis: ratio compared to LHT/L-matrix results. [B]Simplified age-classified model (Heppell *et al.* 2000*a*).
[C]With resting period (Brewster and Miller 2000).
[D]The stage-based models (H–J) following Brewster-Geisz and Miller (2000) have no termination. Therefore the corresponding LHT/Leslie-matrix with termination at age 25 yield smaller λ and R_0. If maximum age is increased to 60 years, λ = 1.0069 and R_0 = 1.0745 (rather than 1.0475, no typos). We cannot use a LHT/Leslie-matrix with maximum age of 60 in this table, because it would be no longer be clear that the increase of λ is due to use of actual fecundity and not due to increased maximum age.
[E]Damping ratio 1.0 for these matrices because they are imprimitive. Population still increases exponentially but age structure oscillates and rate of convergence is not given by the damping ratio, and all subdominant eigenvalues have to be considered (Caswell 2001).

compared with those in the LHT or Leslie matrix. The elasticities of the simplified age-classified Heppell model (3H) were similar to those of the Leslie matrix (3G; ER_2 = 5.0, ER_3 = 4.9). A 10% decrease in juvenile or adult survival because of fishing would require a ~50% increase in fertility to return the population to its original growth rate. Fishing of ~ 5 (i.e. all) juvenile age classes would have the same effect as fishing all the adult age classes because ER_3 = 4.9. The elasticities from the 3-stage (No. 3I) and 2-stage (No. 3J) models underestimated the effect of juvenile survival compared with fertility and adult survival.

Alopias pelagicus

The demographic results of *A. pelagicus* from LHT, Leslie-matrix, and stage-based models using the birth-pulse approximation produced the same potential population growth (5.6% year^{-1}; Table 4, Nos 4A–4D). A fishing mortality of 0.0545 year^{-1} across all age classes or stages would produce a stationary population (λ = 1.0). The net reproductive rate (R_0) of the simplified age-classified Heppell model was a little higher (2.03), and R_0 of the 3-stage model was lower (1.84 *v.* 2.00). The generation times T = 11.2–12.7 years and μ_1 = 12.5–13.3 years were similar. From the elasticity ratios ER_2 = 7.00 and ER_3 = 5.1, we concluded that a 10% decrease in juvenile or adult survival because of fishing would require unrealistic large increases of fertility by 70% or 51% to return the population to its original growth rate. Fishing of ~5 out of 7 juvenile age classes would have the same effect as fishing all the adult age classes. The elasticities of the 3-stage model (4D) underestimated the elasticity of juvenile survival compared with fertility and adult survival.

Alopias pelagicus has no distinct parturition season, and a birth-flow population was expected to produce better demographic results. Annual population growth increased from 5.6% to 6.6%, when we used a birth-flow rather than a birth-pulse population (Table 4, Nos 4D–4H). Our calculations using progressively smaller projection intervals of $\frac{1}{2}$, $\frac{1}{4}$, and $\frac{1}{12}$, years indicated, as expected, a steady increase of λ between the extremes of birth-pulse and birth-flow populations.

Carcharodon carcharias

Population growth of *C. carcharias* decreased slightly from 8.2% to 7.8% year^{-1} when we used a logistic fertility function (10% mature at age 13, 50% mature at age 15) rather than a step-like fertility function (100% mature at age 15) in our LHT results (Table 5, Nos 5A, 5B). It suggested that the use of a step-like maturity function produced slightly biased results. Our calculations indicated that the anticipated increase of population growth required a logistical function so spread out (10% mature at age 8) that it was unreasonable. Population growth increased from 8.2% to 8.7% year^{-1} when we used variable stage duration with V_2 = 3 in the 3-stage model (Table 5, Nos 5C, 5D). This was as expected, but additional calculations indicated that V_2 values between 1 and 5 all produced about the same population growth rate (8.6–8.8% year^{-1}).

The LHT or Leslie-matrix demographic results indicated potential annual population growth of 8.2%, R_0 = 6.2, T = 23.1 years and μ_1 = 26.3 years (Table 6, Nos 6A, 6B). A fishing mortality of 0.0787 year^{-1} across all age classes would produce a stationary population (λ = 1.0). The elasticities indicated that population growth was most

Table 4. Summary of demographic results for *Alopius pelagicus* using life history table (LHT), Leslie (L) matrix, and stage-based matrix models with fixed stage distribution

Age-at-first-reproduction, 8 years; fertility, 1 female per litter and year; longevity, 30 years; natural mortality rate, -ln (0.01)/30 = 0.1535 year^{-1} (S = 85.77%) for all ages/stages. The 3-stage model shows a progression of calculation from birth pulse to birth flow. ρ, damping ratio; PI, projection interval; E_1, elasticity of fertility (sum if more than one term); E_2, elasticity of juvenile survival; ER_2, E_2/E_1; E_3, elasticity of adult survival; ER_3, E_3/E_1

Case	Model	Stage durations	λ_1 (ρ)	r^A (year^{-1})	$R_0{}^A$	T (years)	μ_1 (years)	E_1	E_2 (ER_2)	E_2 (ER_2)
			LHT, Leslie matrix, and simplified age-classified model (Heppell *et al.* 2000)							
4A	LHT to 30	Age-based	1.0560	0.05450	1.9977	12.70	13.33			
4B	L 30×30	Age-based	1.0560(1.1)	0.05450	1.9977	12.70	13.33	0.082	0.577(7.0)	0.423(5.1)
4C	8×8[B]	1–(6×1)–23	1.0560(1.2)	0.05450 (1.00)	2.0342(1.02)	13.03	13.95	0.081	0.570(7.0)	0.430(5.3)
			3-stage model with fixed stage distribution from birth-pulse to birth-flow							
4D	Birth-pulse (PI 1 year)	1–6–23	1.0560(2.3)	0.05450 (1.00)	1.8366(0.92)	11.16	12.45	0.099	0.476(4.8)	0.524(5.3)
4E	PI 1/2 year	2–12–46	1.0608[C]	0.05901 (1.08)	1.8719(0.94)	10.63	12.05			
4F	PI 1/4 year	4–24–92	1.0632[C]	0.06132 (1.13)	1.8879(0.95)	10.36	11.86			
4G	PI 1/12 year	12–72–276	1.0649[C]	0.06288 (1.15)	1.8979(0.95)	10.19	11.73			
4H	Birth-flow[D]	1–6–23	1.0656(2.1)	0.06355 (1.17)	1.9510(0.98)	10.52	12.00	0.108	0.498(4.6)	0.492(4.6)

[A]In parenthesis: ratio compared to LHT results. [B]Simplified age-classified (Heppell *et al.* 2000*a*).
[C]Calculated from annualized instantaneous rate of increase (r).
[D]Using $F_2 = l(0.5) \times (G_2\, m_3)/2$ and $F_3 = l(0.5) \times (1 + P_3)\, m_3/2$ with $l(0.5) = (P_1 + G_1)^{0.5}$ (Caswell 2001).

Table 5. Comparison of life history table (LHT) with step-like and logistic fertility function (LFF) and 3-stage model with fixed and variable stage distribution (VST) for *Carcharhinus carcharias*

Age-at-first-reproduction, 15 years; annual effective fertility, 8.9/2×3 =1.483 females per year; longevity, 60 years; natural mortality rate, ln (0.01)/60 = 0.07675 year^{-1} (S = 92.61%) for all ages/stages

Case	Model	Stage duration	λ	r^A (year^{-1})	R_0^A	T (years)	μ_1 (years)
		LHT with step-like and logistic fertility function					
5A	LHT to 60	Age-based	1.0819	0.07869 (1.00)	6.1630 (1.00)	23.11	26.15
5B	LHT to 60 with LFF	Age-based	1.0791	0.07613 (0.97)	5.9390 (0.96)	23.40	26.45
		3-stage based model with fixed stage and variable stage distribution					
5C	3×3	1–13–46	1.0819	0.07869 (1.00)	4.1884 (1.0)	18.20	24.75
5D	3×3 with VST	1–13–46	1.0869	0.08336 (1.06)	4.4289 (1.06)	17.85	24.57

[A]In parenthesis: ratio compared to LHT with step-like and 3-stage model with fixed-stage distribution results.

affected by juvenile survival (ER_2 = 14) and adult survival (ER_3 = 6.9). A 10% decrease in juvenile or adult survival due to fishing would require unrealistic large fertility increases of 140% or 69% to return the population to its original growth rate. Fishing of ~7 juvenile age classes (out of 14) would have the same effect as fishing all the adult age classes.

Our various matrix models with a fixed-stage-duration distribution produced identical population growth rates (Table 6, Nos 6C–6E). The Heppell model produced a slightly higher R_0 of 6.3, similar T and μ_1, and almost identical elasticities. The 3-stage and 2-stage model produced lower R_0 values of 4.2 and 3.9, respectively. The R_0 values were different because the average times spent as reproductive adults were different (4.49, 4.61, 3.05 and 2.87 for Leslie-matrix, Heppell, 3-stage and 2-stage model, respectively). Generation time (T) and μ_1 of the 3-stage and 2-stage models were lower but μ_1 (24.8 and 24.2 years, respectively) would provide a better estimate of generation time. The 3-stage and 2-stage models underestimated the effect of juvenile survival compared with fertility by a factor of ~ 2 (ER_2 = 7.0 and ER_2 = 6.2, respectively, instead of 14). The 3-stage (No. 6D) and 2-stage (No. 6E) models had larger damping ratios of 1.53 and 1.44, respectively. The corresponding recovery times of 5.4 and 6.3 years, respectively, were considerably shorter compared with the value of 40 years from the Leslie matrix and indicated that these models are not suitable for this type of analysis.

When we used a geometric distribution for the 3-stage and 2-stage matrix models, we obtained much larger population growth rates of 16–19% year^{-1}, similar R_0 values of 6.6–6.9, and much lower T and lower μ_1 compared with LHT or Leslie matrix (Table 6, Nos 6F, 6G). This suggested that a geometric distribution is not suitable for *C. carcharias*. In addition, the underestimation of the elasticity of juvenile survival compared with fertility was even larger (ER_2 = 4.8 and ER_2 = 3.6 for 3-stage and 2-stage model, respectively), compared with the value of 14 in the Leslie matrix.

A comparison of demographic results for *Orcinus orca* and *C. carcharias*, in a series of calculations, indicated that a fixed-stage distribution also produced better agreement with the LHT results for *O. orca* (Table 7, showing only the

Table 6. Summary of demographic results for *Carcharodon carcharias* using life history table (LHT), Leslie (L) matrix, and stage-based matrix models

Age-at-first-reproduction, 15 years; annual effective fertility, 8.9/2×3 =1.483 females per year; longevity, 60 years; natural mortality rate, -ln (0.01)/60 = 0.07675 year^{-1} (S = 92.61%) for all ages/stages. ρ, damping ratio; E_1, elasticity of fertility term (sum if more than one term); E_2, elasticity of juvenile survival; $ER_2 = E_2/E_1$; E_3, elasticity of adult survival; $ER_3 = E_3/E_1$

Case	Model	Stage duration	λ_1 (ρ)	r^A (year^{-1})	R_0^A	T (years)	μ_1 (years)	E_1	E_2 (ER_2)	E_3 (ER_3)
Life history table and Leslie matrix										
6A	LHT to 60	Age-based	1.0819	0.07869	6.1630	23.11	26.15			
6B	L 60×60	Age-based	1.0819 (1.06)	0.07869	6.1630	23.11	26.15	0.048	0.670 (14)	0.331 (6.9)
Stage-based with fixed stage distribution										
6C	15×15[B]	1–(13×1)–46	1.0819 (1.06)	0.07869 (1.00)	6.3385 (1.03)	23.47	27.51	0.048	0.669 (14)	0.331 (6.9)
6D	3×3	1–13–46	1.0819 (1.53)	0.07869 (1.00)	4.1884 (0.68)	18.20	24.75	0.072	0.503 (7.0)	0.497 (6.9)
6E	2×2	14–46	1.0819 (1.44)	0.07869 (1.00)	3.9462 (0.64)	17.44	24.17	0.073	0.470 (6.2)	0.530 (6.9)
Stage-based with geometric distribution										
6F	3×3	1–13–46	1.1610 (2.83)	0.1493 (1.90)	6.6431 (1.07)	12.68	18.53	0.107	0.513 (4.8)	0.487 (4.6)
6G	2×2	14–46	1.1853 (2.04)	0.1700 (2.16)	6.9027 (1.12)	11.36	17.78	0.127	0.462 (3.6)	0.438 (4.2)

[A]In parenthesis: ratio compared to LHT/L-matrix results. [B]Simplified age-classified (Heppell *et al.* 2000*a*).

Table 7. Comparison of demographic results for *Orcinus orca* and *Carcharodon carcharias* using a 3-stage matrix model
α = 15 years; ω = 36 years; stage durations 1–13–22. *O. orca*: stage durations were close to those given by Brault and Caswell (1993); survivorship of 99% used for all stages. *C. carcharias*: longevity (ω) was reduced from 60 to 36 years; survivorship of 93% used for all stages. Fixed-stage and geometric distribution are compared with life history table (LHT) results. *S*, survivorship probability; *m*, effective female fertility per year

Species	S	m	LHT			3×3 fixed stage		3×3 geom. Distribution	
			λ	r (year^{-1})	R_0	r (year^{-1})[A]	R_0[A]	r (year^{-1})[A]	R_0[A]
O. orca	0.9900	0.12	1.0297	0.02923	2.0473	0.02923 (1.00)	2.5895 (1.26)	0.02394 (0.82)	1.8902 (0.92)
C. carcharias	0.9300	1.20	1.0734	0.07086	4.6026	0.07086 (1.00)	3.7109 (0.81)	0.1221 (1.72)	4.6724 (1.07)

[A]In parenthesis: ratios compared to values of LHT.

approximations for *O. orca* and *C. carcharias*). The fixed-stage distribution for *O. orca* produced identical λ but a R_0 that, at 2.59, was 1.26 times larger than the LHT result. The geometric distribution produced lower population growth (r-ratio 0.82) and lower R_0 (ratio 0.92), which might be considered to be acceptable. For *C. carcharias*, with lower survival probability and higher fertility, the fixed-stage distribution produced a r ratio of 1.0 (excellent) and a R_0 ratio of 0.81 (acceptable), whereas the geometric distribution produced a r ratio of 1.72 (very high and unreasonable compared with LHT result) and a R_0 ratio of 1.07 (good).

Discussion

Stage-based matrix models

Our stage-based models with a fixed stage duration distribution provided the same population growth (λ) as age-classified LHTs and Leslie matrices; this justified their use, and they have great potential to tackle more difficult problems in population analysis. For example, a 20×20 matrix could be used to obtain estimates of population growth for populations in 5 different oceans with the inclusion of both sexes. A matrix model is also more suitable to deal with stochastic models, density-dependent models, and life-table response experiments (retrospective analysis) (Caswell 2000).

Caution is necessary in interpreting R_0 and T values of stage-based models with few stages, and μ_1 provides a better estimate of generation time. Our stage-based model, using a fixed-stage-duration distribution, produced the same λ as that obtained with the corresponding Leslie matrix or LHT; however, R_0 and T were lower. To correct this, we would have to slow down the progress of individuals through the juvenile stage, which could be done by adding invisible ‘pseudo-stages’ with a negative binomial stage duration (Caswell 2001). However, this would defeat the purpose of using a small stage-based matrix, and one might as well use separate age classes for the juveniles (Heppell *et al.* 2000*a*) or the full Leslie matrix or a LHT.

The dynamics of the stage-based models with few stages are different from that of the Leslie matrix. They have larger damping ratios, which implies that the stable population is reached faster. This acceleration of individuals through the stages can also be demonstrated with projection. For example, using the 3-stage model for *C. carcharias* and starting with a state vector [1,0,0] (i.e. one pup and no juveniles nor adults), a fraction of adults are produced after only two projection intervals and pups appear after three projection intervals i.e. three years. This would take 15 years in the Leslie-matrix model. The Heppell *et al.* (2000*a*) model is much better in this respect because the juvenile age classes are left as they are, and only the adult age classes are combined into one stage. Crowder *et al.* (1994) used a 54×54 Leslie matrix, rather than their 5-stage based model, to study transient responses in *Caretta caretta* (loggerhead turtle) populations. This fast production of pups in matrix models with few stages was probably the reason that the variable-stage model with a variance of $V(T_2) = 3$ did not affect λ very much and different values of $V(T_2)$ produced almost identical results (Table 5, Nos 5C, 5D).

We suggest that a geometric distribution is not suitable for elasmobranchs because it produced different population growth rates compared with Leslie matrix or LHT. For *C. carcharias*, the annual population growth doubled from 8.2% to 16.1–18.5% year^{-1} (Table 6). We suggest that fixed stage duration is also better for *O. orca* (Table 7 based on approximate *O. orca* vital data) although the geometric distribution produced good results (Brault and Caswell 1993; Caswell 2001). When we used exactly the same data as given in Brault and Caswell (1993) and calculated the stage

Table 8. Observed and calculated stage distribution, λ, and R_0 for *Orcinus orca* using fixed stage and geometric distribution

	Observed[A]	Fixed-stage[B]	Geometric[BC]
Yearlings	3.68%	4.03%	3.69%
Juvenile	37.78%	38.75%	31.59%
Reproductive adults	36.27%	34.88%	32.27%
Post-reproductive adults	22.26%	22.34%	32.44%
Variance[D]		3.0	157.9
λ	1.0292	1.0277 (0.998)	1.0254 (0.996)
R_0	2.214	2.4042 (1.09)	2.0132 (0.91)

[A]Olesiuk *et al.* 1990 (R_0 from their table 14). [B]In parenthesis: ratios compared to observed results. [C]Brault and Caswell (1993). [D]Sum of variance of 4 stage distributions.

distribution using a geometric distribution for the stage duration (duplicating their results) and the fixed-stage distribution, the latter produced better agreement with the observed stage distribution (Table 8).

Population growth is larger if the reproductive cycle is correctly modelled with pregnant and resting stages, as was first proposed by Brewster-Geisz and Miller (2000), but this can also be modelled in a Leslie matrix or LHT. For *Alopias pelagicus*, a decreasing population became an increasing population when we used actual fertility (Table 4). We could have used actual fertility for *C. carcharias* based on the proposed 3-year reproductive cycle (Mollet *et al.* 2000), and population growth would have been 9.0% instead of the reported 8.2% year^{-1} in Table 6. Even for *Carcharhinus obscurus* (dusky shark), with α = 20 years, our calculations indicated a noticeable increase of population growth to 4.8% compared with the reported value of 4.3% year^{-1} by Simpfendorfer (1999).

It may be advantageous to keep a separate pup-age class (3-stage model) compared with inclusion of the pups with the juveniles (2-stage model), which can be done if survival probabilities are not known and assumed to be the same. A separate age class/stage provides a good relative reference point for many stage-specific traits (e.g. reproductive value). It also allows the use of a different mortality for the neonates as has been observed for *Mustelus antarcticus* (gummy shark)(Walker 1994), *Galeorhinus galeus* (school shark) (Punt and Walker 1998) and *Negaprion brevirostris* (lemon shark)(Gruber *et al.* 2001).

It is possible to calculate most of data presented here with a LHT but it would be cumbersome to calculate the matrix elements of the fundamental matrix N, the sensitivity matrix, and the elasticity matrix. Even age-structure and reproductive values are more easily calculated with a matrix model, be it stage-based or age-based Leslie matrix. This is especially true if the calculations are carried out with an easy-to-use program such as PopTools.

For elasmobranchs with year-round parturition, the birth-flow approximation is advisable, and this has not been used previously for any elasmobranch. Our results indicated a substantial increase from 5.6% to 6.6% year^{-1} for the potential annual population growth of *A. pelagicus* (Table 4). A birth-flow population would have been appropriate for the analysis of *A. superciliosus* (bigeye thresher shark) by Chen and Liu (1998). It is possible to carry out such calculations with a Leslie matrix or LHT by using a monthly projection interval but the size of the Leslie matrix might become too large.

Sensitivity and elasticity analysis

Sensitivity and elasticity analysis is a useful tool for population management but has some limitations (Benton and Grant 1999; Caswell 2000; De Kroon *et al.* 2000). Cortés (in press) concluded that research, conservation, and management efforts should focus on the combined results from elasticity (prospective) and correlation (retrospective) analyses. Caswell (2001) suggested that a prospective analysis using sensitivity or elasticity is more appropriate for management proposals than the retrospective analysis proposed by Wisdom and Mills (1997). Sensitivity and elasticity are simply first derivatives of the functions $\lambda = \lambda\ (a_{ij})$ and $\ln\lambda = \ln\lambda\ (\ln a_{ij})$, respectively. The results for our examples are as expected when compared with the results reported by Heppell *et al.* (1999) and Cortés (in press). The use of size limits or prohibition of fishing of juveniles would be most effective should a population require management. We propose that the interpretation of the elasticity ratio (ER_3), as the number of fished juvenile age classes that will have the same effect on population growth as fishing of all the adult age classes, should be useful to produce management guidelines for shark populations.

We suggest that our predictions are fairly robust, despite the local nature of elasticities, because the elasticity matrix elements did not change much after we increased mortality (which can be considered fishing) until we reached a stationary population. There is a need for a comparative analysis of elasticity patterns among stage-based models for all pelagic elasmobranchs, not just the few we considered, and alternative decompositions to provide better insight into the effects of survival, growth and reproduction (Caswell 2001; Heppell *et al.* 2000*b*; Cortés in press). The importance of juvenile survival was reduced in our 3- and 2-stage-based model compared with Leslie matrix/LHT. It suggested that caution is required in interpreting elasticity results of stage-based models with few stages, and apparently it was not considered by Brewster-Geisz and Miller (2000).

Monte Carlo calculation

One flaw in our present analysis is the lack of a confidence band for our population growth estimates. Cortés (in press) incorporated uncertainty of vital rates into demographic modelling of 41 shark populations. A Monte Carlo uncertainly analysis should be carried out because available demographic data are based on estimates of fertility and few data on survival are available (Caswell 2001). The Monte Carlo calculations should be based on survivorship from model life tables of suitable species, which are re-scaled according to age-at-maturity, as was done for *Phocoena phocoena* (harbor porpoise) by Caswell *et al.* (1998). However, we cannot use a stage-based matrix model to do this, we need to use an age-based matrix model (=Leslie matrix) (Caswell *et al.* 1998).

Age-at-first-reproduction and maternity function

In demographic calculations, the relevant ‘age-at-maturity’ is the mean age-at-first reproduction (α), which is the mean age-at-maturity plus gestation period. Most reported maternity functions do not clearly state if age-at-maturity or age-at-first-reproduction is reported. For example, the determination of length-at-first-reproduction of *Isurus oxyrinchus* (shortfin mako) by Mollet *et al.* (2000) was biased high because mature females, pregnant for the first time, should have been excluded from the analysis, or their length-at-capture should have been replaced with an estimate of length-at-first-reproduction. Alternatively, the length-at-capture of females, pregnant for the first time, could have been replaced with estimated length at mating and the resulting maternity function would have given length-at-maturity. This might affect the standard deviation of the maturity function we used for *C. carcharias*. Our results for the white shark (Table 5) indicated that the use of a step-like instead of a more realistic logistic maternity function (also known as ogive) introduced little bias. However, the logistic maternity function did not include possible increases of fertility with maternal size because no data were available. Preliminary calculations for the shortfin mako (Mollet, unpublished) had indicated that population growth decreased when the entire breeding ogive was used (based on data in Mollet *et al.* 2000). Xiao and Walker (2000) stressed the importance of age-at-first-reproduction and the sex ratio at birth.

Natural mortality rate and longevity

All our suggestions for improvements are marred by the fact that we know least about the natural mortality rate (survival probabilities) of elasmobranchs, the most important parameter in most demographic analyses. No mortality data are available for our examples or of elasmobranchs in general, with the exception of *Squalus acanthias* (Wood *et al.* 1979), adult *Raja erinacea* (Johnson 1979), *Mustelus antarcticus* (Walker 1994, 1998), *Galeorhinus galeus* (Grant *et al.* 1979; Punt and Walker 1998; Punt *et al.* 2000), *Negaprion brevirostris* (Hoenig and Gruber 1990; Gruber *et al.* 2001) and *Lamna nasus* (Aasen 1963; Campana *et al.* 2001).

The Siler model, a U-shaped mortality rate *v.* age curve with 3 terms, was proposed by Gage (1998) for mammalian species. Walker (1998) discussed the need of a U-shaped natural mortality function for elasmobranchs. Xiao and Walker (2000) pointed out that relating natural mortality rate to a single quantity, such as maximum age, is overly simplistic, and that interspecific models are of limited value. Given the uncertainly of mortality rates for elasmobranchs, we used a constant mortality rate as a first approximation of the bottom of the 'U' as the best solution. If needed, the left-hand side of the 'U' can be simulated by increasing mortality of neonates and young juveniles. We propose that this is not required for our shark examples, which all have large size at birth. If pups are vulnerable, the corresponding higher mortality could be absorbed into the fertility term as was done for *Orcinus orca*, where only 57% of the calves survive to age 0.5 years (Olesiuk *et al.* 1990). The right side of the U can be approximated by increasing the mortality for older females or by termination of the life-history table at an appropriate age. Campana *et al.* (in press) reported larger mortality for adult porbeagle than for recruited juveniles.

We estimated mortality from estimated maximum age (longevity) by the simple requirement that there should be 1% of individuals left at that age. This has the drawback that mortality is now coupled to longevity, another unknown parameter and carrying large uncertainty if estimated from a von Bertalanffy growth curve. Mortality estimates based on Hoenig (1983) have the same drawback and would have provided similar estimates as those we used. The Hoenig (1983) approach applied to our examples would have yielded slightly lower mortalities with 1.3–2.1% individuals remaining at the estimated maximum age.

We have less confidence in other survivorship curves. Pauly (1980) proposed an interrelationship between natural mortality, growth parameters and mean environmental temperature in 175 fish stocks. However, Jenson (1996) showed that a simple regression without intercept of M *v.* k produced a better fit (r^2 = 0.74) than the multiple log–log regression with r^2 = 0.71 used by Pauly (1980). Peterson and Wroblewski (1984) derived a mortality rate based on dry mass of arrowworms (Phylum Chaetognatha) and larval, juvenile, and small adult fish by assuming that mortality is primarily due to predation. This has the potential advantage that no longevity estimate is needed to estimate mortality. Because plankton was included it applied to a very large range of mass magnitudes. We suggest that the model is not expected to be applicable for large pelagic sharks, which are top predators, and there is no convincing evidence that mortality of elasmobranchs, in particular large pelagic sharks, depends on mass. Cortés (in press), in an uncertainty analysis of demographic traits of 38 shark species, included mortality according to a modified Peterson and Wroblewski (1984) equation by using wet weight as a proxy for dry weight. We are also apprehensive about the mortality rates suggested by Chen and Watanabe (1989), which produced mortalities that are too large for large pelagic elasmobranchs.

Comparative life histories among species of elasmobranchs

Instead of using the exact equation to calculate intrinsic rate of population increase (r = ln (R_0)/T) (i.e. our potential population increase obtained by solving the Euler-Lotka equation) or the approximate equation ($r \sim$ ln (R_0)/μ_1), Frisk *et al.* (2001) estimated the potential population growth of elasmobranchs with r' = ln (m)/α, where m was female fertility assuming a 1-year reproductive cycle for all elasmobranchs, which unfortunately is not true, and the approximation of ln (R_0)/T with ln (m)/α might be questioned. The intrinsic rebound potential of 26 elasmobranch species reported by Smith *et al.* (1998) was fitted by us with a band defined by two equations of the same form, with an effective annual fertility of 1.35–1.57 (i.e. $r' = r_{2M} = \ln(1.37)/\alpha$ to $\ln(1.57)/\alpha$). A power regression produced an even better fit to their results ($r_{2M} = \ln(1.28)/\alpha^{0.809}$, $n = 26$, $r^2 = 0.99$), and we suggest that 1.28 can be interpreted as the effective annual fertility of their method, which would be the same for all elasmobranchs. Their intrinsic rebound potential or productivity (r_{2M}) depends only on age-at-first-production and, accordingly, blue (*Prionace glauca*) and sandtiger shark have the same productivity (0.058 year^{-1}, using our power regression, compared with the reported value of 0.061 year^{-1}) because they have the same age-at-first-maturity (6 years); in contrast, we obtained $r = -0.004$ to $r = 0.007$ year^{-1} for the sandtiger (Table 3). We suggest that potential population growth rates based on life-history tables or Leslie matrices, which provide reasonable elasticity estimates of fertility, and juvenile and adult mortalities, provide more meaningful estimates of potential population growth to serve as a basis for elasmobranch management. Cortés (in press) used a similar approach and, in addition, incorporated uncertainty into demographic modelling. Xiao and Walker (2000) introduced a generalized Lotka equation and suggested that the data in Smith *et al.* (1998) will be useful for testing alternative approaches to their dual equation for calculating intrinsic rate of increase with time and intrinsic rate of decrease with age.

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