

REVIEW

Perspectives on the intrinsic rate of population growth

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Summary

1. The intrinsic rate of population increase (r_{\max}) is a fundamental metric in ecology and evolution of immediate practical application in conservation and wildlife management. I examine the interpretation of r_{\max} by revisiting the theory behind the density-independent and density-dependent paradigms. The criticism that density-independent approaches underestimate r_{\max} *per se*, often expressed in the field of fisheries, is shown to be theoretically unfounded. The difficulty in estimating r_{\max} is due to lack of knowledge on the depletion level of the population rather than theory.
2. I reviewed a method commonly used to estimate extinction risk of marine and terrestrial populations and show that it has been used incorrectly. I also examined five other methods to calculate r_{\max} , the Euler–Lotka equation, and four other methods derived from it.
3. I used the same data inputs for a suite of 65 shark populations with a broad range of life histories as an example to show that the incorrectly used extinction risk method overestimates r_{\max} . I compared the r_{\max} values for sharks obtained with the incorrectly applied extinction risk method to published values for other vertebrate taxa to further show that this method generates implausible values for this group of predators.
4. I advocate focusing on obtaining estimates of all required vital rates simultaneously when possible while taking into consideration the exploitation history of the population under study as a pragmatic way to provide plausible estimates of r_{\max} .
5. The Euler–Lotka equation and its derivations are recommended for different degrees of data availability, particularly for slow- and medium-growing populations, to provide sensible advice for conservation and management of living vertebrates in situations where a series of credible abundance estimates are not available as is often the case in marine systems. Methods that combine allometry and demography should also be further explored.

Key-words: conservation, density dependence, density independence, Euler–Lotka equation, extinction risk, sharks, wildlife management

Introduction

The intrinsic rate of population growth, denoted as r_m (Caughley & Birch 1971) or r_{\max} (Skalski, Ryding & Millspaugh 2005) when referring to the continuous time formulation, is a fundamental metric of population vigour in ecology and evolution, and of direct practical importance in the conservation, wildlife and fisheries fields. Indeed, r_{\max} is used to quantify extinction risk in conservation contexts or to assess the dynamics of terrestrial and aquatic animal populations. While population growth rates can be estimated with a variety of direct methods, including visual surveys, transects or regression-based approaches among others (Skalski, Ryding & Millspaugh 2005), series of abundance estimates are notoriously difficult to obtain for aquatic organisms, especially for long-lived, late-maturing marine species (Dillingham *et al.* 2016). For these species, population growth rates are instead typically derived from models based on survival and fecundity schedules, which

may not necessarily reflect optimal conditions and thus not represent the maximum, or intrinsic, growth rate. Lotka (1907) based on Euler (1760) was the first to derive λ , the finite form of the population rate of increase, from age-specific demographic parameters, and Leslie (1945) generalized the approach using matrix algebra introducing the age-based Leslie matrix, where λ is calculated as the dominant eigenvalue of a projection matrix. Both of these formulations generally assume exponential growth (density independence), but they can also incorporate terms for density dependence or logistic growth (Skalski, Ryding & Millspaugh 2005).

Alternative derivations of the Euler–Lotka equation are essentially simplifications that assume constant rates of adult mortality and fecundity and even omit life span (Skalski, Millspaugh & Ryding 2008). Interestingly, the main equation used to assess extinction risk in marine organisms was derived from the Euler–Lotka equation by Myers, Mertz & Fowlow (1997) assuming constant adult survival and fecundity. This formulation also invoked density dependence by defining a quantity, $\tilde{\alpha}$, which is the number of spawners (individuals at a reproducing age) produced by each spawner each year at very low spawner

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abundance. Another derivation of the Euler–Lotka equation that has been used to calculate the ‘rebound’ productivity or potential of fish, notably elasmobranch (sharks, skates, and rays) populations, was derived by Smith, Au & Show (1998). This expression also incorporates concepts of density dependence by assuming a compensatory response to population reduction that is elicited through increased pre-adult survival.

In this perspective, I address two main issues relevant to the population growth rate especially in the context of conservation of aquatic animals, particularly sharks, from which I draw examples. First, I address the criticism often expressed in the field of fisheries (see, e.g., Walker 1998; Gedamke *et al.* 2007; Zhou *et al.* 2012) that population rates of increase obtained through density-independent demographic methods such as the Euler–Lotka equation and analogous methods underestimate r_{\max} because they do not consider density dependence. Secondly, I examine the application of the Myers, Mertz & Fowlow (1997) equation to calculate extinction risk and contend that multiple published studies have overestimated r_{\max} and therefore underestimated extinction risk because the method was used incorrectly. I used several common methods to calculate r_{\max} for a suite of shark populations spanning a wide range of life-history traits to illustrate the point and put results in a more general context by comparing values obtained with the incorrectly applied method with values reported in the literature for different vertebrate taxa.

Issue 1: density-independent vs. density-dependent frameworks

The basic expression for estimating r_{\max} , the Euler–Lotka equation, and associated formulations such as life tables and the Leslie matrix assume no resource limitations and therefore density independence. This has often been used as a criticism of these methods on the grounds that they do not generate a maximum value of population growth (r_{\max}) because they do not take into account density dependence and r_{\max} can only be attained at very low levels of population abundance. For example, Walker (1998:563) argued that demographic analyses consistently produced pessimistic prognoses of population status because these methods do not allow for density-dependent compensation and Zhou *et al.* (2012:1299) stated that demographic modelling cannot estimate intrinsic r without additional information and that estimates of r for chondrichthyan fishes (sharks, skates, rays and chimaeras) seem to be biased low by a factor of 0.5, which would be consistent with these estimates being derived from populations that are at about half carrying capacity rather than from highly depleted populations.

The real issue does not lie in the conceptual model used, but rather in the biological information used to estimate r_{\max} . Theory predicts that the per capita growth rate (r_{\max}) is maximized at *any* population size when assuming exponential growth, whereas it is only maximized at a population size close to zero when assuming logistic growth (Fig. 1 top). An exponential model can thus be thought of as an approximation of a logistic model at low densities. When using a density-independent

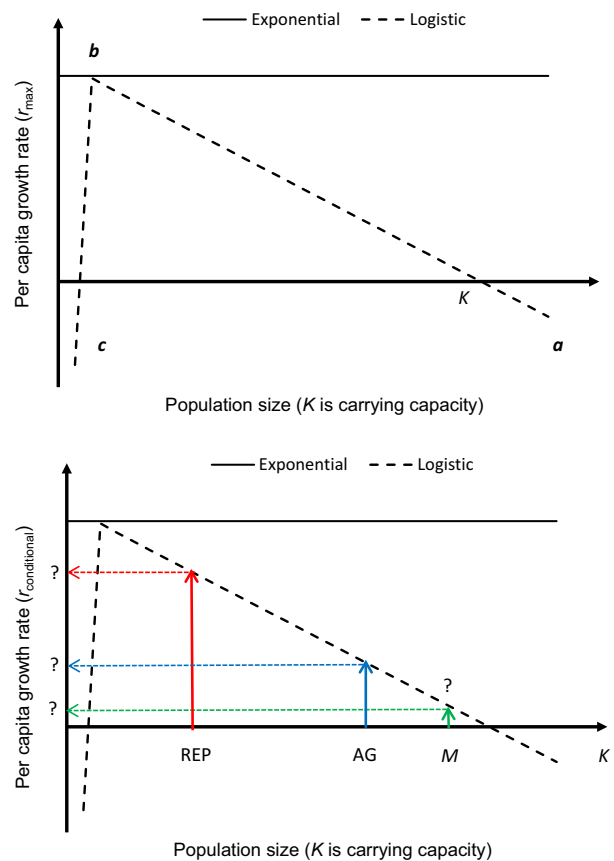


Fig. 1. Top panel: per capita growth rate (r_{\max}) for populations exposed to exponential or logistic growth. The exponential growth model results in constant (density-independent) growth, whereas the logistic growth model results in a linear (density-dependent) increase with decreasing population size. Label K is carrying capacity, a shows that the per capita growth rate can become negative if it exceeds carrying capacity (a stable equilibrium), and b shows that the maximum per capita growth rate is reached at a low population size, after which an Allee effect comes into play and the per capita growth rate abruptly declines and can become negative at very low population size (c , an unstable equilibrium). Modified from Skalski, Ryding & Millsbaugh (2005). Bottom panel: Example showing a hypothetical case where the reproductive information (label REP) used to generate the reproduction schedules of a population was collected when the population was already heavily exploited ($N/K = 0.3$), the age and growth information (label AG) used to estimate age at first breeding and life span and generate the survival schedules was collected when the population was less exploited ($N/K = 0.7$), and the life-history invariant methods typically used to estimate M for chondrichthyans and generate the survival schedules do not explicitly state the conditions under which the biological values of the populations used to derive those very methods were collected (label M). This makes $r_{\text{conditional}}$ (r_{real}) a moving target and prevents estimation of the ‘true’ r_{\max} .

model such as the Euler–Lotka equation, one must recognize that if the survival and fecundity schedules used to generate r_{\max} do not represent maximum values that could be achieved under ideal conditions (which may not be those under which these biological traits were collected), then r_{\max} will indeed be underestimated. In a density-dependent framework, the observed values of population growth rate should be augmented by a factor proportional to the level of depletion (reduction in abundance) of the population with respect to

virgin level or carrying capacity, or $r_{\text{real}} = r_{\text{max}}(1 - N/K)$ using Skalski, Ryding & Millspaugh (2005)'s notation or $r_{\text{conditional}} = r_{\text{intrinsic}}(1 - N/K)$ using Gedamke *et al.*'s (2007) notation. Gedamke *et al.* (2007) further defined $r_{\text{predicted}} = r_{\text{conditional}} - F$, where F is the instantaneous rate of fishing (harvesting) mortality. The expressions by Gedamke *et al.* (2007), for example, provide an explicit way to obtain r_{max} , but in most real-life situations the schedules of survival and reproduction are obtained from populations that are subject to some degree of exploitation and F is typically unknown unless it has been estimated through a catch curve or tag–recapture experiment, for example, or obtained from a stock (population) assessment. Similarly, the degree of population depletion ($1 - N/K$) is obviously unknown unless it has been obtained from a series of abundance estimates, which are seldom available for fishes, in particular chondrichthyans, or from a stock assessment. Additionally, the level of depletion corresponding to a given estimate of $r_{\text{conditional}}$ (r_{real}) will vary according to the prevailing demographic and environmental conditions present when the biological information used to generate the survival and reproduction schedules was collected (Skalski, Ryding & Millspaugh 2005). For example, one can envision a case where the reproductive information used to generate the reproduction schedules of a given population was collected when the population was already heavily exploited ($N/K = 0.3$), the age and growth information used to estimate the age at first breeding and life span and generate the survival schedules was collected when the population was less exploited ($N/K = 0.7$), and the life-history invariant methods that are typically used to estimate M (instantaneous rate of natural mortality) for chondrichthyan and many fish stocks and generate the survival schedules do not explicitly state the conditions under which the biological values of the populations used to derive those very methods were collected (see, e.g., Kenchington 2014). Gedamke *et al.* (2007) also argued that some of these life-history invariant M estimators were derived for conditions close to an unexploited state and thus overestimate M and underestimate the ‘true’ r_{max} . This uncertainty in the level of depletion can lead to different predictions of $r_{\text{conditional}}$ (r_{real}) effectively turning it into a moving target and thus preventing estimation of the ‘true’ r_{max} (Fig. 1 bottom).

Another often overlooked consideration is that it is unclear at what level of population depletion (x -axis in Fig. 1 top) r_{max} would be obtained in species with delayed density dependence such as chondrichthyans (Cortés, Brooks & Gedamke 2012). This is because of Allee effects, also referred to as depensation or undercrowding (Skalski, Millspaugh & Ryding 2008), by which the linear increase in the per capita growth rate as population size decreases reaches a maximum at an unknown population size, which could be considerably larger than 0 when a strong Allee effect is present, and then precipitously decreases below zero (Fig. 1 top).

Given the lack of sufficient information to generate r_{max} estimates within a density-dependent framework, that is knowledge of $1 - N/K$ to correct $r_{\text{conditional}}$ (r_{real}), one partial solution proposed by Cortés (2007) for chondrichthyans is to use survival and reproduction schedules and other biological

variables that approximate maximum values that could be achieved under conditions corresponding to unlimited resources in the absence of fishing. This includes assumptions in both the density-independent paradigm and the density-dependent paradigm at low population levels.

Issue 2: Overestimation of r_{max}

MYERS, MERTZ & FOWLOW (1997): METHOD 1

Myers, Mertz & Fowlow (1997) derived an expression from the Euler–Lotka equation by assuming constant adult survival and reproduction schedules and incorporating density dependence through a quantity known as $\tilde{\alpha}$, the number of spawners produced by each spawner each year at very low spawner abundance:

$$e^{r_m a} - e^{-M}(e^{r_m})^{a-1} - \tilde{\alpha} = 0 \quad \text{eqn 1}$$

where a is age at maturity, e^{-M} is probability of adult survival from natural mortality only, $\tilde{\alpha} = ml_a$, with m being the number of age 0 fish produced per spawner and l_a the cumulative survival from age 0 to age at maturity, and r_m is the population rate of increase.

This equation, with r_m taken as r_{max} , has been used to calculate r_{max} for marine fishes and terrestrial and marine mammals (Hutchings *et al.* 2012), and is considered a standard measure of extinction risk (Dulvy *et al.* 2004). In a subsequent paper, Myers & Mertz (1998) presented another expression of $\tilde{\alpha}$ that explicitly incorporated the level of fishing that could be imposed on a stock before it went extinct, or F_t (F_{extinct} ; García, Lucifora & Myers 2008):

$$\tilde{\alpha} = e^{F_t(a-a_{\text{sel}}+1)}(1 - e^{-(M+F_t)}) \quad \text{eqn 2}$$

where a_{sel} is the selectivity age or age at which fish enter the fishery. If $a_{\text{sel}} = 1$, F_t is equivalent to r_{max} and equation (2) simplifies to equation (1). Although Myers, Mertz & Fowlow (1997) stated that $\tilde{\alpha} = ml_a$, that is the number of spawners produced by each spawner per year, it appears that multiple authors misinterpreted this to mean $\tilde{\alpha} = m$, where m is the constant number of female offspring produced per year. In other words, they left the l_a term (cumulative survival to maturity required to become a spawner) out of the equation (e.g. García, Lucifora & Myers 2008; Hutchings *et al.* 2012; Dulvy *et al.* 2014a). This obviously has the effect of increasing the estimated r_{max} value. It is unclear why this occurred, but a possible explanation is that Myers & Mertz (1998:S167) stated that the biological limit of fishing (F_t) is ‘given by the scaled slope at the origin, $\tilde{\alpha}$, or in ecological terms, the maximum annual reproductive rate’. However, both Myers, Bowen & Barrowman (1999:2405) and Myers & Worm (2005:15) restated that $\tilde{\alpha}$ is the ‘number of spawners produced by each spawner per year, after a lag of a years, where a is age at maturity’.

Other methods

I used five other methods to estimate r_{max} in addition to Method 1: three methods that assume density independence

(the Euler–Lotka equation, equivalent to a Leslie matrix; an equation by Eberhardt, Majorowicz & Wilcox (1982); and an equation by Skalski, Millspaugh & Ryding (2008)); a method by Smith, Au & Show (1998) that implicitly assumes density dependence; and a demographic invariant method (DIM; Niel & Lebreton 2005; Dillingham 2010) that combines an age-based matrix model and an allometric model. The goal of this exercise was not to include an exhaustive list of methods to estimate r_{\max} or to characterize uncertainty in the estimates through Monte Carlo simulation or other resampling methods or using Bayesian inference, which can be computationally intensive, but simply to compare the estimates of r_{\max} obtained with these additional methods with those from the Myers, Mertz & Fowlow’s (1997) method to show that it overestimates r_{\max} when used incorrectly.

EBERHARDT, MAJOROWICZ & WILCOX (1982): METHOD 2

Eberhardt, Majorowicz & Wilcox (1982) derived another expression from the Euler–Lotka equation by assuming constant adult survival and fecundity rates that can be written as (Skalski, Millspaugh & Ryding 2008):

$$e^{ra} - e^{-M}(e^r)^{a-1} - ml_a \left(1 - \left(\frac{e^{-M}}{e^r} \right)^{w-a+1} \right) = 0 \quad \text{eqn 3}$$

where a is age at first breeding, m is constant fecundity, w is maximum life expectancy and r is the population rate of increase. The Eberhardt, Majorowicz & Wilcox (1982) method has been used to calculate population growth rates of several terrestrial and marine vertebrates, including feral horses (*Equus caballus*), elk (*Cervus elaphus*), grizzly bears (*Ursus arctos horribilis*), sea otters (*Enhydra lutris*) and spotted owls (*Strix occidentalis*) (Skalski, Millspaugh & Ryding 2008).

SKALSKI, MILLSPAUGH & RYDING (2008): METHOD 3

Skalski, Millspaugh & Ryding (2008) proposed a further modification of the above equation that explicitly allows w to go to infinity and thus does not require estimates of longevity, which are often uncertain or unknown:

$$e^{ra} - e^{-M}(e^r)^{a-1} - ml_a = 0. \quad \text{eqn 4}$$

This equation is identical to that originally proposed by Myers, Mertz & Fowlow (1997), with the exception that Myers, Mertz & Fowlow (1997) defined a as age at maturity, and thus provides supporting evidence that the Myers, Mertz & Fowlow (1997) equation has been misapplied in the literature. The Skalski, Millspaugh & Ryding (2008) method has been used to calculate population growth rates of terrestrial vertebrates (Skalski, Millspaugh & Ryding 2008) and humpback whales (*Megaptera novaeangliae*; Zerbini, Clapham & Wade 2010), for example.

REBOUND POTENTIALS: METHOD 4

This method was developed by Smith, Au & Show (1998) and is also a modification of the Euler–Lotka equation that

incorporates concepts of density dependence by assuming a compensatory response to population reduction elicited through increased pre-adult survival. The method has been applied to sharks and pelagic teleosts. The premise of this method is that the growth potential of each species can be approximated for a given level of exploitation, which then becomes its potential population growth rate after harvest is removed, or its ‘rebound’ potential. The density-dependent compensation is assumed to be manifested in pre-adult survival as a result of increased mortality in the adult ages. Starting from the Euler–Lotka equation:

$$\sum_{x=a}^w l_x m_x e^{-rx} - 1 = 0 \quad \text{eqn 5}$$

if l_x is expressed in terms of survival to age at maturity $l_a e^{-M(x-a)}$ and m_x is replaced with a constant fecundity m (average number of female pups per female), completing the summation term yields:

$$e^{-(M+r)} + l_a m e^{-ra} \left(1 - e^{-(M+r)(w-a+1)} \right) - 1 = 0. \quad \text{eqn 6}$$

Pre-adult survival $l_a = l_{a,Z}$ that makes increased mortality Z ($=M + F$) sustainable ($r = 0$) is calculated from the following equation by setting $M = Z$ and $r = 0$:

$$e^{-Z} + l_{a,Z} m \left(1 - e^{-(Z)(w-a+1)} \right) - 1 = 0. \quad \text{eqn 7}$$

If F is then removed ($Z = M$), the population under survival $l_{a,Z}$ will rebound at a productivity rate of r_z , which is found by substituting $l_{a,Z}$ into equation (6) and solving equation (6) iteratively (Au & Smith 1997). The rebound potential r_z thus represents the population growth rate at maximum sustainable yield (MSY).

Smith, Au & Show (1998) multiplied the fecundity term m in equation (6) by 1.25 to allow for an arbitrary 25% increase which they felt was appropriate because, even if fecundity was constant with age, the average m value of a population would increase as it expands under reduced mortality because there would be more, older and larger fish that would survive. They also acknowledged that, based on density-dependent theory under a logistic function, $r_{\max} = 2r_z$, or in other words that their rebound potentials should be doubled to obtain r_{\max} . Au, Smith & Show (2008) later arrived at the conclusion that $Z_{\text{MSY}} = 1.5M$ is a more appropriate level of MSY for determining the intrinsic rebound potential of sharks compared to pelagic teleosts (for which $Z_{\text{MSY}} = 2M$) by linking stock–recruitment and abundance-per-recruit relationships via the Euler–Lotka equation; thus, the rebound potential for sharks should be $r_z = r_{1.5M}$ and $r_{\max} = 2r_{1.5M}$.

DIM: METHOD 5

Niel & Lebreton (2005) developed a method that combines an age-based matrix model with an allometric model. The age-based matrix model assumes constant adult survival ($s = e^{-M}$) and fecundity and a mean generation time $T = a + s/(\lambda - s)$, where a is age at first breeding, is also derived. The allometric

model is based on relationships between r_{\max} and T and body mass (M), such that $r_{\max} = a_r M^{-0.25}$ and $T = a_T M^{-0.25}$, which when multiplied yield the dimensionless maximum rate of increase per generation or $r_{\max} T = a_r a_T = a_{rT}$. When combined with the matrix model, the allometric model provides an equation for the DIM (Niel & Lebreton; Dillingham 2010) which can be written as:

$$e^r = e^{\left(a_{rT} \frac{1}{\left(a + \frac{e^{-M}}{e^r - e^{-M}} \right)} \right)} \quad \text{eqn 8}$$

and can be solved iteratively. Niel & Lebreton (2005) found that $a_{rT} \approx 1$ for birds and Dillingham *et al.* (2016) recently found that $a_{rT} \approx 1$ for several vertebrate taxa (birds, mammals and elasmobranchs); thus, r_{\max} can be obtained from knowledge of a and s only.

EULER–LOTKA EQUATION: METHOD 6

This method is simply the traditional Euler–Lotka equation (eqn 5).

COMPARISON OF METHODS WITH A SUITE OF SHARK POPULATIONS

I used life-history inputs for a suite of shark populations (Table S1, Supporting information) to estimate growth rates (assumed to be r_{\max}) through the methods described above using common notation for variables for clarity: (1) Myers, Mertz & Fowlow's (1997) extinction risk equation intentionally misspecified as $\tilde{\alpha} = m$ instead of $\tilde{\alpha} = ml_a$, (2) Eberhardt, Majorowicz & Wilcox's (1982) equation, (3) Skalski, Millspaugh & Ryding's (2008) equation (identical to Myers, Mertz & Fowlow's (1997) original equation with $\tilde{\alpha} = ml_a$), (4) Smith, Au & Show's (1998) rebound potentials increased by a factor of two to represent r_{\max} (i.e. $r_{\max} = 2r_{1.5M}$) and with m set to $1.25m$, (5) the DIM method and (6) the Euler–Lotka equation (equivalent to a Leslie matrix) (Table 1). Although I used life-history information from published studies, the purpose of this exercise was to compare the values obtained with the different methods and not necessarily to arrive at the 'real' values of r_{\max} for the suite of populations considered. Population growth rates can be calculated with a variety of software; an R script is included here as an example (Appendix S1; R Development Core Team 2015).

I included life-history (age, growth and reproduction) information for 65 shark populations with a wide range of life histories (Table S1). To estimate survivorship for Method 6, I used the maximum age-specific value (from ages 0 to maximum), or minimum age-specific value of M , from seven life-history invariant methods: a modified longevity-based Hoenig (1983) estimator (Then *et al.* 2015); a modified growth-based Pauly (1980) estimator (Then *et al.* 2015); two Jensen (1996) estimators based on age at maturity and k , the rate constant from the von Bertalanffy growth curve (VBGC); the Chen & Watanabe (1989) estimator also based on the VBGC; and two mass-based

estimators, Peterson & Wroblewski's (1984) and Lorenzen's (1996). The last three estimators provide age-specific values and I used published length–mass conversions to transform lengths into mass for the two mass-based estimators. Constant adult survivorship for methods 1–5 was the mean of the age-specific values for adults.

For reproductive rates, a was taken as the age at first breeding, except for methods 1 and 4, which defined it as age at maturity. To obtain age at first breeding, I adopted the convention of adding 1 year to the age at maturity to account for the length of the gestation period. The annual fecundity rate (m) consists of the mean reported litter size (ls) and reproductive frequency (f), such that $m = ls/f/2$ to account for female pups only. All methods assume a constant m , except Method 6, in which m may increase with age and can also be modulated by the proportion of mature females at age through a maturity ogive, if one exists. Method 6 also differs from the remaining four methods in that it uses age-specific values of survivorship (Table 1).

I found that the median estimates of r_{\max} obtained with Method 1 (Myers, Mertz & Fowlow's extinction risk equation with $\tilde{\alpha} = m$) exceeded those obtained with all other methods by a factor of 2.2 to 3.6 (Table 1). Median estimates of r_{\max} for Method 1 were 0.236 (2.5th and 97.5th percentiles = 0.104, 0.877) whereas those for the other five methods ranged from 0.066 to 0.106 (Table 2; Figs 2 and 3). The medians for methods 2 (Eberhardt, Majorowicz & Wilcox's equation), 3 (Skalski, Millspaugh & Ryding's equation) and 6 (Euler–Lotka equation) were similar, ranging from 0.092 to 0.106, but estimates from methods 2 and 6 were a little lower than those from Method 3, suggesting that the values of maximum age used in the computation of these two methods were not the asymptotic values (Skalski, Millspaugh & Ryding 2008). Surprisingly, methods 4 (Smith, Au & Show's (1998) rebound potentials) and 5 (DIM) yielded almost identical median values and very similar results overall despite the substantially different data requirements and assumptions of these two methods (Tables 1 and 2, Table S1). These two methods generated lower estimates (medians = 0.066–0.067) than methods 2, 3 and 6 (medians = 0.092–0.106).

I further divided the 65 populations into three arbitrary subgroups based on values obtained with the traditional Euler–Lotka equation (Method 6): slow-growing ($r_{\max} \leq 0.05$; $n = 7$), medium-growing ($0.05 < r_{\max} \leq 0.15$, $n = 37$) and fast-growing ($r_{\max} > 0.15$, $n = 21$) to explore whether differences among methods were influenced by different life histories. Method 1 still produced higher estimates than all other methods by an order of 1.7–5.7. The differences between Method 1 and methods 4 and 5 intensified, whereas those with methods 2, 3 and 6 generally decreased, the faster the life histories (Table 2). Methods 2 and 6, which only differ in that Method 6 is age-structured, introducing subtle changes in the survivorship and fecundity schedules, produced very close estimates, except for fast-growing populations, whereas methods 2 and 3 yielded the closest estimates for fast-growing populations, presumably because of a reduced influence of maximum age. Estimates for methods 4 and 5 were closest for slow-growing populations.

Table 1. Six methods used to estimate the intrinsic rate of population growth. All equations are expressed using common notation for clarity. r is the instantaneous rate of population increase or r_{\max} , a is age at maturity or age at first breeding; M is the instantaneous rate of natural mortality; m is constant fecundity (expressed as annual females per female); l_a is cumulative survival to age a at maturity or age at first breeding; w is maximum age; $a_{r,T}$ is the product of the constants in the allometric equations for intrinsic growth rate and generation time (≈ 1); l_x is cumulative survival to age x ; and m_x is age-specific fecundity

Method	Equation	Difference evaluated	Median result (scalar) of Method 1 compared to this method	References
1. Myers, Mertz & Fowlow's (1997) misspecified with $\tilde{\alpha} = m$	$e^{ra} - e^{-M}(e^r)^{a-1} - m = 0$	Vital rates not age specific; no maximum age; a is age at maturity; omits l_a ; implicit density dependence		Several authors
2. Eberhardt, Majorowicz & Wilcox's (1982)	$e^{ra} - e^{-M}(e^r)^{a-1} - ml_a \left(1 - \left(\frac{e^{-M}}{e^r} \right)^{w-a+1} \right) = 0$	a is age at first breeding; includes maximum age; does not omit l_a ; density dependence not implicit	2.58	Eberhardt, Majorowicz & Wilcox (1982)
3. Skalski, Millspaugh & Ryding's (2008) (=Method 1 correctly specified with $\tilde{\alpha} = ml_a$)*	$e^{ra} - e^{-M}(e^r)^{a-1} - ml_a = 0$	a is age at first breeding; does not omit l_a ; density dependence not implicit	2.22	Skalski, Millspaugh & Ryding (2008); Myers, Mertz & Fowlow (1997)
4. Smith, Au & Show's (1998)	$e^{-(M+r)} + l_a \cdot 2.5me^{-ra} \left(1 - e^{-(M+r)(w-a+1)} \right) - 1 = 0$	omit l_a ; density dependence not implicit	3.60	Smith, Au & Show (1998)
5. Demographic invariant method	$e^r = e \left(\frac{a_{r,T}}{a + \frac{e^{-M}}{e^r - e^{-M}}} \right)$	m multiplied by 1.25; includes maximum age; does not omit l_a ; a is age at first breeding; no m ; density dependence not implicit; includes allometric relationship	3.55	Niel & Lebreton (2005); Dillingham (2010)
6. Euler-Lotka	$\sum_{x=d}^w l_x m_x e^{-rx} - 1 = 0$	Vital rates age-specific; a is age at first breeding; includes maximum age; density dependence not implicit	2.39	Euler (1760); Lotka (1907)

*The Myers, Mertz & Fowlow's (1997) equation differs from that of Skalski, Millspaugh & Ryding's (2008) only in that a is defined as age at maturity.

Table 2. Summary statistics of the intrinsic rate of population growth for 65 shark populations obtained with six different methods: Method 1: Myers, Mertz & Fowlow’s (1997) extinction risk equation with $\tilde{\alpha} = m$; Method 2: Eberhardt, Majorowicz & Wilcox’s (1982) equation; Method 3: Skalski, Millspaugh & Ryding’s (2008) equation (identical to Myers, Mertz & Fowlow’s (1997) original equation with $\tilde{\alpha} = ml_d$); Method 4: Smith, Au & Show’s (1998) rebound potentials increased by a factor of two; Method 5: the demographic invariant method; and Method 6: the Euler–Lotka equation

Method	Median	2.5th pctl	97.5th pctl	Mean	Minimum	Maximum
1	0.236	0.104	0.877	0.320	0.077	1.098
2	0.092	0.008	0.411	0.145	0.003	0.423
3	0.106	0.039	0.418	0.162	0.033	0.423
4	0.066	0.027	0.276	0.088	0.021	0.353
5	0.067	0.027	0.258	0.084	0.019	0.311
6	0.099	0.022	0.413	0.137	0.002	0.461

Populations	Method					
	1	2	3	4	5	6
All	0.236	0.092	0.106	0.066	0.067	0.099
Slow-growing	0.125	0.037	0.055	0.047	0.049	0.035
Medium-growing	0.207	0.075	0.088	0.060	0.051	0.074
Fast-growing	0.507	0.284	0.293	0.093	0.088	0.237

pctl, percentile.

The lower panel shows results (medians) split into slow-growing ($r_{max} \leq 0.05$), medium-growing ($0.05 < r_{max} \leq 0.15$) and fast-growing ($r_{max} > 0.15$) populations.

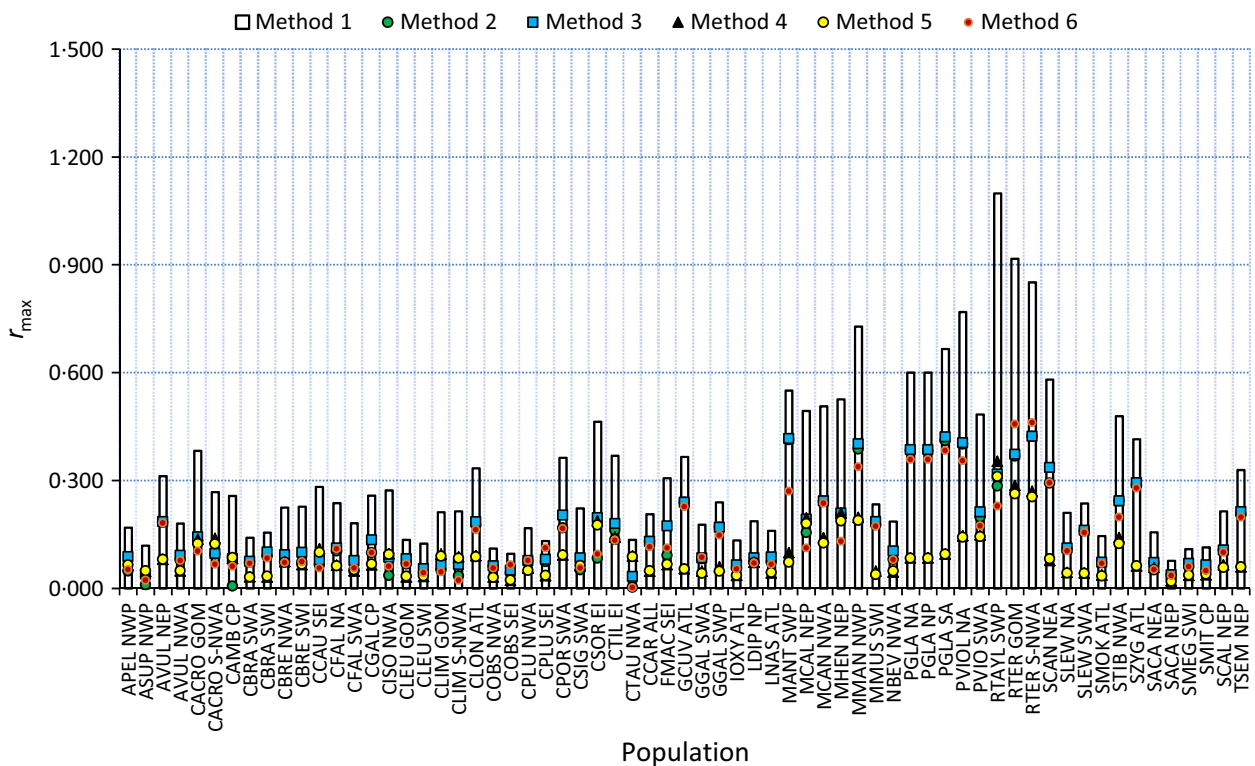


Fig. 2. Intrinsic rate of population growth for 65 shark populations obtained with six different methods: (1) Myers, Mertz & Fowlow’s (1997) extinction risk equation intentionally misspecified as $\tilde{\alpha} = m$ (denoted by bars), (2) Eberhardt, Majorowicz & Wilcox’s (1982) equation, (3) Skalski, Millspaugh & Ryding’s (2008) equation (identical to Myers, Mertz & Fowlow’s (1997) original equation with $\tilde{\alpha} = ml_d$), (4) Smith, Au & Show’s (1998) rebound potentials increased by a factor of 2, (5) the demographic invariant method and (6) the Euler–Lotka equation. See Table S1 for population code values.

COMPARISON TO OTHER VERTEBRATE TAXA

By using the same data inputs for the six methods considered, I showed that the incorrectly used Myers, Mertz & Fowlow’s

(1997) equation clearly overestimates r_{max} . The median value of 0.24 for the 65 populations analysed (2.5th and 97.5th percentiles = 0.10, 0.88) seems disproportionately high and inconsistent with the life history of a group of vertebrates that are

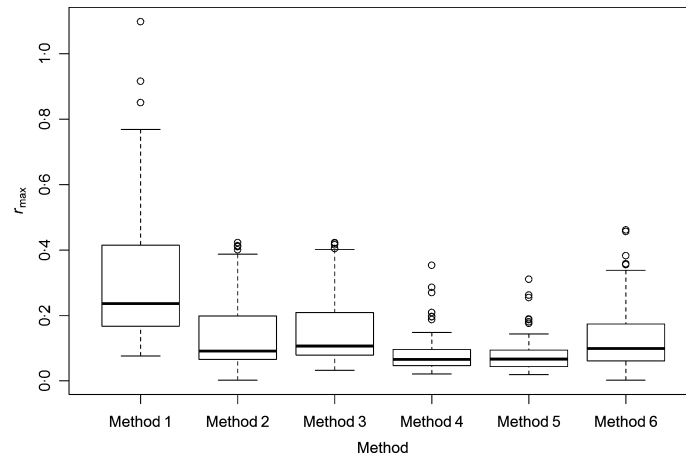


Fig. 3. Box plot of the intrinsic rate of population growth for 65 shark populations obtained with six different methods: Method 1: Myers, Mertz & Fowlow’s (1997) extinction risk equation with $\tilde{\alpha} = m$; Method 2: Eberhardt, Majorowicz & Wilcox’s (1982) equation; Method 3: Skalski, Millspaugh & Ryding’s (2008) equation (identical to Myers, Mertz & Fowlow’s (1997) original equation with $\tilde{\alpha} = ml_e$); Method 4: Smith, Au & Show’s (1998) rebound potentials increased by a factor of 2; Method 5: the demographic invariant method; and Method 6: the Euler–Lotka equation. Horizontal lines are medians, bottom and top of the boxes denote 25th and 75th percentiles, vertical dashed lines show approximately 2 SDs, and circles are outliers.

reputed to have very low population growth rates (e.g. Baum *et al.* 2003; Dulvy *et al.* 2014b) and consequently a high risk of extinction (e.g. Dulvy & Forrest 2010; Kyne, Bax & Dulvy 2015). With the same misapplied method, García, Lucifora & Myers (2008) found that mean F_{extinct} (r_{max}) was 0.149 for deepwater, 0.250 for oceanic and 0.368 for continental shelf chondrichthyans, respectively. Hutchings *et al.* (2012) also used this method and reported median values of r_{max} of 0.71 ($n = 54$) for terrestrial mammals, 0.43 for teleost fishes ($n = 47$), 0.26 for chondrichthyans ($n = 82$) and 0.07 for marine mammals ($n = 16$). The high values obtained by Hutchings *et al.* (2012) for terrestrial mammals and especially chondrichthyans are not the result of including very productive species in their analysis, but to the misapplication of the extinction risk equation, also amplified by their use of the maximum reported litter size, not the average, for fecundity.

For comparison, median λ_{max} for 26 populations of seabirds was 1.051 with Method 6 ($r_{\text{max}} = 0.050$) (Russell 1999) and values of λ_{max} for marine mammals, which have fairly similar life histories to sharks, appear to range from 1.02 ($r_{\text{max}} = 0.020$) for killer whales (*Orcinus orca*) to 1.20 ($r_{\text{max}} = 0.182$) for sea otters (*Enhydra lutris*) (Wade 2009). Median λ values for 10 populations of turtles were 1.004 ($r = 0.004$) with Method 6 (Heppell 1998) and median λ for 142 populations of mammals belonging to 11 different orders was 1.002 ($r = 0.002$) using a partial life cycle model (Oli & Dobson 2003), which is analogous to Method 3, although these estimates for turtles and mammals do not represent maximum values.

I found that only Method 1 yielded r_{max} estimates in the range of 0.46–1.10 for sharks, which would confer some of these species similar demographic vigour to some very productive terrestrial mammals. As an illustrative example, the North Atlantic population of the blue shark (*Prionace glauca*) would have a productivity ($r_{\text{max}} = 0.600$) similar to that of the striped

skunk (*Mephitis mephitis*; $r = 0.583$; Casey & Webster 1975; Oli & Dobson 2003), and the South Atlantic population of the blue shark ($r_{\text{max}} = 0.666$), a productivity equal to that of the European hare (*Lepus europaeus*; $r = 0.670$; Kovacs 1983; Oli & Dobson 2003) (Table S1). Furthermore, if we use the maximum litter size (as in Hutchings *et al.* 2012) of 108 pups (Castro & Mejuto 1995) in the computation of r_{max} for the North Atlantic blue shark population, for example, the value obtained of 0.757 is <10% lower than the productivity that has been reported for the cottontail rabbit (*Sylvilagus floridanus*; $r = 0.831$; Oli & Dobson 2003).

Conclusions

Density-independent approaches do not underestimate productivity *per se*. A density-independent method can be interpreted in a more realistic way as a density-dependent model at low population size after exploitation has ceased. The problem lies in knowing the level of depletion corresponding to the vital rates used to calculate the realized or observed population growth rate to assess how representative of r_{max} that population growth rate is. Consideration should also be given to Allee effects, although this phenomenon is extremely hard to identify in marine systems, particularly for animals exhibiting delayed density dependence. In the absence of quantitative information on the level of reduction in abundance of a population in marine systems, a more pragmatic and productive approach may be to gather all biological information required to calculate population growth rates simultaneously while attempting to define its exploitation history to evaluate how far it is from theoretically optimal conditions, that is unlimited resources with no exploitation.

Maximum population growth rates obtained with the extinction rate method that omits the term for cumulative survival to maturity (Method 1) are incorrect because the original

equation developed by Myers, Mertz & Fowlow (1997) was applied incorrectly. If applied correctly, Method 1 is identical to Method 3 (Skalski, Millspaugh & Ryding's (2008) equation), which produces estimates consistent with the Euler–Lotka equation (Method 6) and a derivation that assumes constant adult survivorship and fecundity and considers the term for cumulative survival to maturity and life span (Method 2; Eberhardt, Majorowicz & Wilcox's (1982) equation). It is unclear why a method that combines demography and allometry (Method 5; DIM) and a method that has been used for fishes and implicitly assumes density dependence (Method 4; Smith, Au & Show's (1998) rebound potentials) produced very similar estimates, lower than those for the other three valid methods, despite their considerably different data requirements and assumptions. The incorrect application of the Myers, Mertz & Fowlow (1997) method ultimately undermines the widespread view that sharks are particularly prone to extinction, a view that ironically has been favoured by several of the authors that have used this method to estimate extinction risk.

With the exception of fast-growing populations, estimates from methods 2 to 6 were all within a reasonable range. For slow- and medium-growing populations, the choice of method may thus be dictated by data availability. When vital rates are well known, methods 2, 4 and 6 can be used to estimate r_{\max} , but other methods may be more appropriate for data-limited situations. Method 3, which is identical to the correctly specified Method 1, was derived for situations where maximum age is unknown or difficult to assess, in which case it is preferable to explicitly assume asymptotic survival than assuming different values of maximum age, which can influence the estimate of r_{\max} . Method 5, which additionally does not require knowledge of fecundity, still produced estimates similar to those of the other methods. Differences between methods 2, 3 and 6 and methods 4 and 5 were more accentuated for fast-growing populations, suggesting that the ad hoc treatment or omission of fecundity in methods 4 and 5, respectively, can have a large effect on estimates. It is also important to note that Method 5, which is based on allometric scaling relationships, will underestimate r_{\max} if optimal survival is overestimated, whereas Method 6 (the Euler–Lotka equation) and its derivations (methods 2 and 3) will overestimate r_{\max} if optimal survival is overestimated, which points to the fact that either of these methods (allometric vs. demographic models) should probably not be used alone (Dillingham *et al.* 2016). A recent expansion of the DIM method that draws strength from both allometric and life table models (Dillingham *et al.* 2016) has the potential to generate improved estimates and more realistic depictions of uncertainty in the population growth rate and could thus be tested across a variety of populations with different life histories to provide improved conservation and management advice.

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Data accessibility

Life-history variables and population growth rates obtained by applying the six methods referenced are provided in the supplementary information (Data S1 and Table S1).

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Supporting Information

Additional Supporting Information may be found online in the supporting information tab for this article:

Appendix S1. R code for calculating the population growth rate (r_{\max}) through the six methods described.

Data S1. Sample life history data to apply the Euler–Lotka equation for blue shark (code PGLA SA in Table S1).

Table S1. Life history variables and population growth rates obtained by applying the six referenced methods.