A Comparison of Linear Demographic Models and Fraction of Lifetime Egg Production for Assessing Sustainability in Sharks

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Abstract: *Conventional methods for management of data-rich fisheries maintain sustainable populations by assuring that lifetime reproduction is adequate for individuals to replace themselves and accounting for density-dependent recruitment. Fishing is not allowed to reduce relative lifetime reproduction, the fraction of current egg production relative to unfished egg production (FLEP), below a sustainable level. Because most shark fisheries are data poor, other representations of persistence status have been used, including linear demographic models, which incorporate life-history characteristics in age-structured models with no density dependence. We tested how well measures of sustainability from 3 linear demographic methods (rebound potential, stochastic growth rate, and potential population increase) reflect actual population persistence by comparing values of these measures with FLEP for 26 shark species. We also calculated the value of fishing mortality (F) that would allow all 26 species to maintain an accepted precautionary threshold for sharks of FLEP = 60%, expressing F as a fraction of natural mortality (M). Values of stochastic growth rate and potential population growth did not covary in rank order with FLEP (p = 0.057 and p = 0.077, respectively) and neither was significantly correlated with FLEP. Ordinal ranking of rebound potential positively covaried with FLEP (p = 0.00013), but the relative rankings of some species were substantially out of order. Adopting a sustainable limit of F = 0.16M would maintain all 26 species above the precautionary minimum value of FLEP (60%). We concluded that shark-fishery and conservation policies should rely on calculation of replacement (i.e., FLEP), and that sharks should be fished at a precautionary level that would protect all stocks (i.e., F< 0.16M).*

Keywords: FLEP, rebound potential, replacement, sustainability

Comparación entre Modelos Demográficos Lineales y la Fracción de Producción de Huevos a lo Largo de la Vida para Estudiar la Sustentabilidad en Tiburones Resumen

Resumen: *Los métodos convencionales para el manejo de pesquerías ricas en datos mantienen poblaciones sustentables al asegurar que la reproducción a lo largo de la vida es adecuada para que los individuos se reemplacen y respondan por el reclutamiento dependiente de la densidad. No está permitido que la pesca reduzca la reproducción relativa, que es la fracción de la producción actual de huevos relativa a la producción interrumpida de huevos (FLEP), debajo de un nivel sustentable. Ya que la mayoría de las pesquerías de tiburón tienen pocos datos, se han utilizado otras representaciones del estado de persistencia, incluyendo modelos demográficos lineales que incorporan características de la historia de vida en modelos estructurados por edad y sin dependencia de la densidad. Probamos que tan bien las medidas de 3 modelos demográficos lineales (potencial de recuperación, tasa de crecimiento estocástica e incremento potencial de la población) reflejan la persistencia poblacional actual al comparar los valores de estas medidas con el FLEP de 26 especies de tiburón. También calculamos el valor de la mortandad pesquera (F) que permitiría a las 26 especies mantener un umbral de precaución aceptable para tiburones con FLEP=60%, expresando F como una fracción de la mortandad natural (M). Los valores del crecimiento estocástico y el crecimiento potencial de la población no covariaron en orden de rango con FLEP (p = 0.057 y p = 0.077, respectivamente) y ninguno*

estuvo correlacionado significativamente con FLEP. El rango ordinal del potencial de recuperación covarió positivamente con FLEP (p = 0.00013), pero el rango relativo de algunas especies estuvo sustancialmente fuera de orden. La adopción de un límite sustentable de F = 0.16M *mantenía a las 26 especies por encima del valor mínimo de precaución de FLEP (60%). Concluimos que la pesca de tiburones y las políticas de conservación deberían depender del cálculo de reemplazos (p.ej.: FLEP) y que los tiburones deberían ser pescados a un nivel de precaución que proteja toda la mercancía (p.ej.:* F < 0.16M*).*

Palabras Clave: FLEP, potencial de recouperación, reemplazo, sustentabilidad

Introduction

Commercial and recreational harvest of sharks has led to the overexploitation of many species (Stevens et al. 2000). Because they are often taken as bycatch in other fisheries (Stevens et al. 2000; Smith & Aseltine-Neilson 2001) or landed in countries without sufficient fisheries documentation and infrastructure (Bonfil 1994), data on shark species that can be used in rigorous assessments and management are lacking. Managers of shark fisheries and researchers have sought reliable indicators of the persistence status of shark populations (Stevens et al. 2000). In general, these indicators are based on life-history characteristics, not on current population-level data. Some linear demographic models have been used to determine the persistence status of shark populations with only minimal current fishery data and no estimates of current fishing mortality (F) (i.e., rebound potential of Smith et al. [1998] and calculations of geometric growth rate by Cortés [2002]). These linear models are based on life tables or Leslie matrices, which rely on age-specific mortality, fecundity, age of maturity, and lifespan, but they do not empirically account for density dependence.

Rebound potential is determined using a linear demographic model that artificially includes an arbitrary compensatory response in the survival of juvenile individuals (Au & Smith 1997; Smith et al. 1998, 2001). In this approach, Euler's equation is applied to a population, and one assumes a natural value of mortality (M), determined from Hoenig's (1983) regression on maximum observed age. It is further assumed that $F = M$. Euler's equation is then solved for the value of early survival (S_0) that is required to produce a stable population (growth rate = 0). Fishing pressure is then removed (by setting $F = 0$) with S_0 held at the enhanced level. Finally, Euler's equation is solved to determine the intrinsic rate of increase if the fishery were removed, a value termed the rebound potential (r_{2M}) (Au & Smith 1997).

Smith et al. (1998) applied this method with life-history parameters obtained from the literature to determine the value of r_{2M} for 26 species of sharks (including 2 stocks of dogfish). These values of r_{2M} have been represented in the elasmobranch fisheries literature as relative current risks to populations of overexploitation from fisheries (e.g., Xiao & Walker 2000; Francis et al. 2001; Campana et al. 2006), empirical values of intrinsic growth

(e.g., Beerkircher et al. 2003; Pacific Fishery Management Council 2007; Jiao et al. 2011), species turnover rates (Bornatowski et al. 2011), and doubling times of populations (Braccini et al. 2006). Cortés (2002) suggests these values should be used as a means to prioritize research and conservation efforts in sharks. The Pacific Fisheries Management Council has extended use of r_{2M} beyond sharks and uses it as an estimate of relative productivity of sharks, billfish, and tunas (Pacific Fishery Management Council 2011). However, there has been no validation of the actual relation between the values of r_{2M} and the true intrinsic rate of increase (Gedamke et al. 2007). In addition, although r_{2M} is considered an indicator of persistence status, it is not related empirically to the current state of a population (i.e., it does not depend on current F or the current age structure). Instead, it describes a rate of potential population growth under specific assumed static conditions.

A second approach to representing the persistence status of sharks is the calculation of stochastic growth (λ) (Cortés 2002). Cortés used age-structured life tables and Leslie matrices to model the demography and elasticities of females in 38 species of sharks (24 of these species were also examined by Smith et al. [1998]). He used Monte Carlo simulation to incorporate uncertainty in the estimates of demographic traits. Cortés concluded these values of λ provide a relative index of population growth over time.

A third approach to persistence status for sharks is to calculate a potential rate of population increase (r') from existing relations among life-history parameters (Frisk et al. 2001). The quantity r' is defined as the natural log of fecundity at the size at which half the individuals are mature divided by age at maturity (Jennings et al. 1998). High values of this variable were found to be associated with declining abundance in a study of 18 fish stocks in the northeast Atlantic. However, this method does not consider density dependence, which limits its value.

Because the nature of density dependence is a key determinant of population persistence and yield with fishing pressure, its omission limits these depictions of persistence. A few models of shark populations include density dependent recruitment. For example, Wood et al. (1979) incorporated several types of density dependence, and Punt and Walker (1998) included density-dependent pup production. There are few instances in
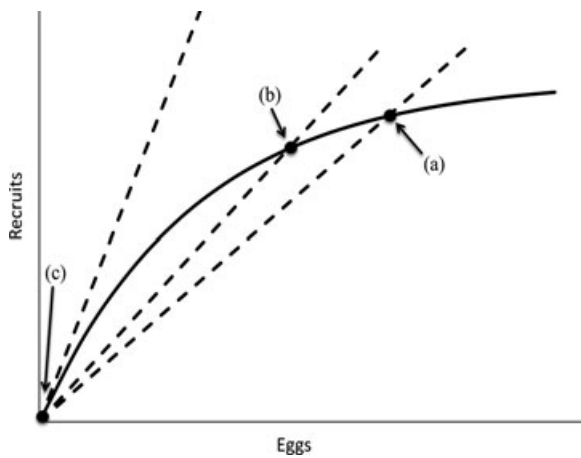
Figure 1. The graphical solution for shark population equilibrium of an age-structured model with density-dependent recruitment (solid black line, egg-recruit relation; dashed lines, recruitment line with a slope of the inverse of fraction of lifetime egg production [FLEP]; filled circles, population equilibrium values, where the recruitment line and egg-recruit line cross where there is [a] no fishing pressure, [b] fishing pressure such that eggs and recruits decline, and [c] excessive fishing pressure such that egg and recruits decline substantially and cause population collapse.

shark fisheries where estimates of the parameters of density dependence are included (e.g., Gedamke et al. 2009; Forrest & Walters 2009).

We based our evaluation of population status directly on the condition for the equilibrium of an age-structured population with density dependent recruitment. Equilibrium condition can be portrayed graphically by a straight line through the origin of the egg-recruit function with a slope equal to the inverse of lifetime egg production (LEP) (also known as eggs per recruit) (Sissenwine & Shepherd 1987) (Fig. 1). Population equilibrium occurs at the intersection of this straight line with the egg-recruit curve. As fishing increases, LEP declines and the equilibrium moves to the left, ultimately to low values of recruitment. When LEP is less than the inverse of the slope at the origin of the egg-recruit relation, the population collapses to zero recruitment. Thus, maintaining the fishing mortality rate at levels low enough that LEP will remain sufficiently high for individuals in the population to replace themselves will assure a sustainable fishery. For the sake of uniformity among species, LEP is normalized to express its value as a fraction of the value with no fishing (fraction of unfished lifetime egg production [FLEP], also known as spawning potential ratio), and it is assumed that maintaining an FLEP greater than a certain precautionary fraction will maintain a sustainable population. Thus, FLEP is a measure of the relative remaining capacity for replacement

as mortality due to fishing increases. Researchers have sought both the values of slopes at the origin of egg-recruit relations for different species (Myers et al. 1997) and the associated values of FLEP that lead to population collapse (e.g., Mace & Sissenwine 1993).

Following this framework the current value of FLEP can be computed as a measure of persistence currently inherent in the age structure of a population and compared to the critical value of FLEP below which the population will collapse, a constraint of the egg-recruit relation. In species for which there are sufficient data on egg production and recruitment at low abundance to estimate the slope of the egg-recruit relation, initial safe values of FLEP are estimated to be 35–40% (Mace & Sissenwine 1993). Some species, however, require larger values, for example, 50% for groundfish on the west coast of North America (Ralston 2002).

A problem for sharks is that the data sufficient to determine empirically the egg-recruit relations for elasmobranchs at low abundance are seldom available. In such instances, current values of FLEP can still be calculated from the dependence of fecundity and survival on age and fishing mortality rate. However, these values of FLEP cannot be compared with the steepness or slope of the egg-recruit relation at low abundance. But, even if the egg-recruit relationship is unknown, replacement is still a meaningful, direct metric of relative persistence (Fig. 1). Because the consequences of values of FLEP at low abundances for sharks are unknown, a minimum precautionary value of FLEP = 60% has been recommended for elasmobranchs (Restrepo et al. 1998). This value was established on the basis of qualitative considerations that long-lived species require an additional precautionary buffer above the value of 35% used for bony fishes. Comparison of the current value of FLEP of the fishery to the general threshold of FLEP = 60% yields a direct measure of the persistence status of a population at specific levels of fishing.

We compared the calculated relative persistence of sharks as determined from FLEP with status indicators obtained from 3 linear demographic models that were based on known life-history data. We summarized the implications of replacement for age-structured populations with density-dependent recruitment and examined the linear models currently being used for sharks. We then determined a level of F, as a fraction of M, that can maintain sharks above a precautionary value of FLEP.

Methods

To test how well methods for assessing conservation status that are based on linear models compare with measures of persistence that are based on the population-dynamic point of view used in conventional fisheries management, we compared values of r_{2M}, λ, and r' with

values of FLEP for 26 species of sharks (only 24 species could be compared for λ). We used the same assumptions regarding F and life-history parameter values as Smith et al. (1998) to determine the value of FLEP for these sharks. The values of FLEP calculated under the assumption $F = M$ are indicated by $FLEP_{F = M}$. We evaluated 26 species of sharks (including 2 stocks of dogfish) assuming the values of age at 50% female maturity (α), maximum age (ω), fecundity (m), and M compiled by Smith et al. (1998).

We calculated the value of $FLEP_{F = M}$ by integrating egg production over all mature ages (a) from α to ω with natural mortality from Hoenig's (1983) expression (ln[M] = 1.44–0.982ln[ω]) and setting F equal to M (i.e., total mortality, $Z = 2M$), as in Smith et al. (1998). Fishing began with knife-edge selection at α and continued until ω. The value of FLEP was thus

$$\text{FLEP} = \frac{\int_{a=\alpha}^{\omega} me^{-(M+F)a}da}{\int_{a=\alpha}^{\omega} me^{-Ma}da}, \quad (1)$$

where m is independent of age as in Smith et al. (1998). We then integrated Eq. (1)

$$\text{FLEP} = \frac{\dfrac{e^{-(M+F)\omega} - e^{-(M+F)\alpha}}{F + M}}{\dfrac{e^{-M\omega} - e^{-M\alpha}}{M}}. \quad (2)$$

Because fecundity is not assumed to be age or density dependent and is therefore the same in the fished and unfished terms (i.e., the numerator and the denominator), fecundity plays no role in determining the value of FLEP in Eq. (2). This results from the assumption described above, that sustainability depends on the fraction of unfished LEP to which fishing has reduced the population.

We ranked each species according to its value of $FLEP_{F = M}$, r_{2M}, λ, and r'. Species with lower relative resilience to overexploitation were assigned lower ranks. Species with the same rank score were given the average ranking between the values. We compared the values in terms of their order, with Spearman rank correlation, and in terms of their numerical values, with Pearson product-moment correlation coefficient.

With the values of F and parameter values we used from Smith et al. (1998), all the species we evaluated had an $FLEP_{F = M}$ less than the recommended precautionary value of 60%. To determine precautionary values of F, we used these life-history data to determine the threshold values of F that would allow the value of FLEP for each shark species to be >60%. Use of these life-history data to calculate FLEP provided a relative index of how intensively different species can be fished. We also applied the same value of F to all shark species and plotted the fraction of species for which FLEP remained above 60% at different values of F. Because F can be expressed either directly (F_{direct}) or as a proportion of M (μ, where $F = \mu M$), we also expressed fishing mortality of each species in terms of a fraction of its corresponding natural mortality (i.e., we plotted the percentage of populations remaining above FLEP = 60% vs. F_{direct} and FLEP = 60% vs. μ). For comparison we included in the same plots values for FLEP = 35%, a nominal value for most teleost species. To determine relative restrictiveness of each approach, we compared the distribution of Fs computed from μM with the value of F_{direct} that allowed all species to be above FLEP = 60%.

Results

Our null hypothesis of the Spearman rank correlation test was that the rankings do not covary. The rankings of λ and r' did not covary significantly with values of $FLEP_{F = M}$ (Table 1) (Spearman's $\rho = 0.32$, $p = 0.057$; $\rho = 0.28$, $p = 0.077$, respectively). The Pearson product-moment correlation coefficient indicated λ and r' had slightly positive correlation with $FLEP_{F = M}$ ($R = 0.013$ and $R = 0.34$, respectively), although neither were significant at $p = 0.05$ (Fig. 2).

The ordinal rankings of r_{2M} were not significantly different than the rankings of $FLEP_{F = M}$ (Spearman's $\rho = 0.65$, $p = 0.00013$), which indicates the order of $FLEP_{F = M}$ and r_{2M} covaried significantly. The Pearson product-moment correlation coefficient indicated there was positive covariability ($R = 0.68$, significant at $p = 0.05$), but some species had substantially different relative numerical values (Fig. 2). For example, the numerical values of r_{2M} for the whitetip reef (*Carcharhinus longimanus*) and sand tiger (*Carcharias taurus*) sharks suggest similar levels of vulnerability to exploitation ($r_{2M} = 0.048$ and 0.052, respectively) (Fig. 2c), yet $FLEP_{F = M}$ values indicated the whitetip reef shark is 4 times more vulnerable than the sand tiger shark ($FLEP_{F = M} = 0.060$ and 0.24, respectively). Similarly, r_{2M} values indicated the sand tiger shark is nearly 3 times more vulnerable to exploitation than the gray smoothhound (*Mustelus californicus*) ($r_{2M} = 0.052$ and 0.14, respectively) (Fig. 2c), whereas the $FLEP_{F = M}$ values for sand tiger and gray smoothhound were nearly equal ($FLEP_{F = M} = 0.24$ and 0.25, respectively).

The value of μ (where $F = \mu M$) that maintained FLEP above 60% (precautionary level for sharks) or 35% (conventional level for bony fishes) was <1.0. This indicates the values of F used in the calculation of r_{2M} (i.e., $F = M$) resulted in values of FLEP that exceeded both precautionary values (Fig. 3). Setting μ to 0.16 led to all 26 species having an FLEP value greater than the precautionary value for sharks. Precautionary levels were also achieved by specifying a value of $F = 0.014$/year (Fig. 4), but far more species could be fished at greater rates when the level of F was specified in terms of the fraction (μ) of the natural mortality of each species (Fig. 5).

Table 1. Twenty-six species of sharks (including 2 stocks of dogfish) ranked according to their value of fraction of lifetime egg production ($FLEP_{F=M}$), rebound potential (r_{2M}) (Smith et al. 1998), potential population increase (r') (Frisk et al. 2001), and stochastic growth rate (λ) (Cortés 2002).

Species	$FLEP_{F=M}$ rank	r_{2M} rank	r' rank	λ rank	$FLEP_{F=M}$	r_{2M}	r'	λ	$F_{direct60\%}$[d]	$F_{m=0.16}$[e]	μ[f]
Bull	1	4	4	6	0.047	0.027	0.08	.998	0.027	0.018	0.16
Dusky	2	2	3	10	0.052	0.02	0.07	1.03	0.019	0.024	0.17
Sandbar	3	5.5	6	9	0.058	0.028	0.1	1.022	0.026	0.022	0.17
Sevengill	4	3	20	X[c]	0.059	0.026	0.24	X	0.025	0.022	0.17
Whitetip reef	5	15.5	1	X	0.060	0.048	0.03	X	0.049	0.044	0.17
Lemon	6	9.5	10	12	0.064	0.034	0.13	1.064	0.032	0.029	0.18
Leopard	7	7	13	7	0.077	0.032	0.14	1.016	0.029	0.024	0.19
Scalloped hammerhead	8	5.5	16	25	0.078	0.028	0.16	1.6	0.025	0.021	0.19
Sharpnose	9	24	21	11	0.092	0.084	0.26	1.056	0.09	0.070	0.20
Gray reef	10.5	19.5	10	3	0.095	0.054	0.13	0.941	0.051	0.040	0.20
Blacktip	10.5	19.5	13	4	0.095	0.054	0.14	0.974	0.051	0.040	0.20
Spiny dogfish[a]	12	1	2	1	0.104	0.017	0.04	0.893	0.014	0.010	0.21
Silky	13	13.5	15	16	0.106	0.043	0.15	1.108	0.039	0.029	0.21
Galapagos	14	15.5	17.5	14	0.119	0.048	0.21	1.086	0.042	0.030	0.22
Tiger	15	13.5	24	22	0.124	0.043	0.3	1.246	0.037	0.026	0.23
School/soupfin	16	8	19	13	0.134	0.033	0.22	1.077	0.027	0.018	0.24
Blue	17	21	26	24	0.137	0.061	0.55	1.401	0.054	0.036	0.24
Angel	18	11	6	8	0.143	0.038	0.1	1.019	0.032	0.021	0.24
Commonthresher	19	23	13	18	0.161	0.069	0.14	1.125	0.061	0.037	0.26
White	20	12	10	15	0.168	0.04	0.13	1.098	0.034	0.02	0.26
Mako	21	17	17.5	20	0.169	0.051	0.21	1.141	0.043	0.026	0.27
Bonnethead	22	25	27	23	0.172	0.105	0.6	1.304	0.099	0.059	0.27
Oceanic whitetip	23	22	25	17	0.187	0.067	0.32	1.117	0.057	0.032	0.28
Spiny dogfish[b]	24	9.5	8	2	0.207	0.034	0.12	0.938	0.027	0.015	0.30
Sand tiger	25	18	6	5	0.236	0.052	0.1	0.978	0.042	0.021	0.32
Gray smoothhound	26	27	22.5	19	0.246	0.136	0.28	1.132	0.122	0.059	0.33
Brown smoothhound	27	26	22.5	21	0.283	0.127	0.28	1.163	0.108	0.047	0.37

[a]British Columbia.
[b]Northwestern Atlantic.
[c]Indicates species that were not evaluated by Cortés (2002).
[d]Value of fishing mortality (F) for each species that maintains FLEP = 60%.
[e]Value of F allowed for each species if F is specified by F = 0.16M.
[f]Value of μ, in F = μM, for each species that maintains FLEP = 60%.

Discussion

The goal of our comparison of the different methods was to provide quantitative values for use in ranking the persistence status of sharks to inform management actions (Smith et al. 1998). Our results show that 3 linear demographic models currently in use do not reflect the actual relative persistence status of these populations very well; they produced rankings and numerical values that were different from those based on the population dynamics of age structured populations with density-dependent recruitment (i.e., replacement, as expressed by FLEP).

Our results also show that if the data used in the linear population methods are available, they can be used to calculate the relative values of replacement (FLEP). Calculations of FLEP are based on population dynamics and would likely express relative risk better than linear demographic models. The FLEP approach would be more consistent with management of other data-rich species (e.g., groundfish in the case of the Pacific Fisheries Management Council). Moreover, shark managers could choose the value of μ below, which all sharks evaluated here would have a value of FLEP >60% (i.e., $\mu = 0.16$). Or, if the species of concern is on the list in Table 1, they could choose the value of $F_{direct60\%}$. For species we did not consider, F could be calculated directly. Empirically based values of F depend on the specific nature of the fishery. For example, we assumed, for reasons of comparability, that fishing selection is knife-edged and equal across individuals. However, it is likely that fishing pressure in sharks is size selective rather than age selective and both mature and immature individuals may be available to the fisheries. Actual selectivity would likely be more dome shaped than knife-edged. However, these specific variations could be easily included.

The manner in which F is assumed to affect the structure of a population is different among the 3 linear demographic models and FLEP, which likely led to the differences in rankings and numerical values among the models. For example, with r_{2M} fishing pressure results in a compensatory increase in S_o, but there is no guarantee that this level of S_o is attainable or even realistic. At best, the level of growth explained by r_{2M} is an upper
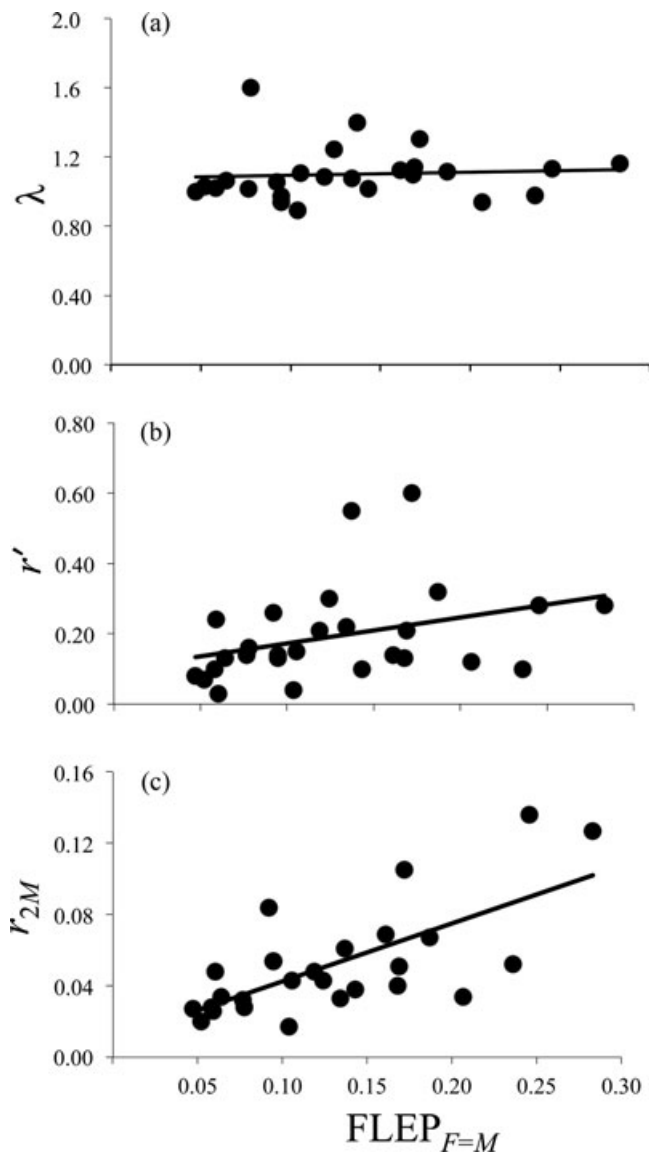
Figure 2. *Regression of 3 linear demographic models versus fraction of lifetime egg production (FLEP$_{F=M}$) in 26 species of sharks: ordinal rank relation of FLEP$_{F=M}$ to (a) stochastic growth rate (λ) (Cortés 2002), (b) potential population increase (r$'$) (Frisk et al. 2001), and (c) rebound potential (r$_{2M}$) (Smith et al. 1998).*

theoretical threshold, resulting from arbitrary compensation in S_o when fishing pressure is removed. Conversely, FLEP is a measure of how the age structure of the population will change with fishing pressure. The shape of a population's age structure is a direct measure of the capacity of an individual to replace itself, as summarized in FLEP (Fig. 1).

The linear demographic methods we evaluated omit direct consideration of density dependence. Density dependence likely plays a key role in elasmobranch resilience,
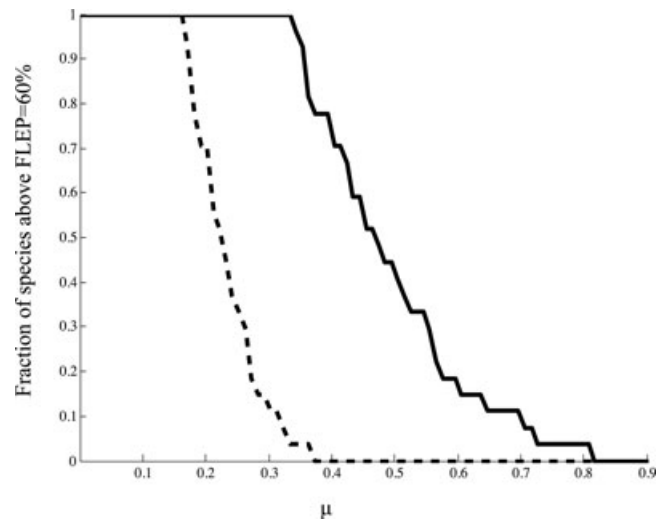

Figure 3. *Fraction of 26 species of sharks that would be persistent at fraction of lifetime egg production (FLEP) of 35% (solid line), recommended for teleosts, and FLEP = 60% (dashed line), recommended for elasmobranchs (Restrepo et al. 1998), as fishing mortality increases. Fishing mortality (F) is given as a fraction (μ) of natural mortality (M), where F = μM.*

but it is poorly known (Stevens et al. 2000; Carlson & Baremore 2003). Because they do not include density dependence, these linear population models characterize populations as growing exponentially. Although exponential growth may occur in shark populations at low abundance, in most real populations the growth rate will decline as the population abundance increases then
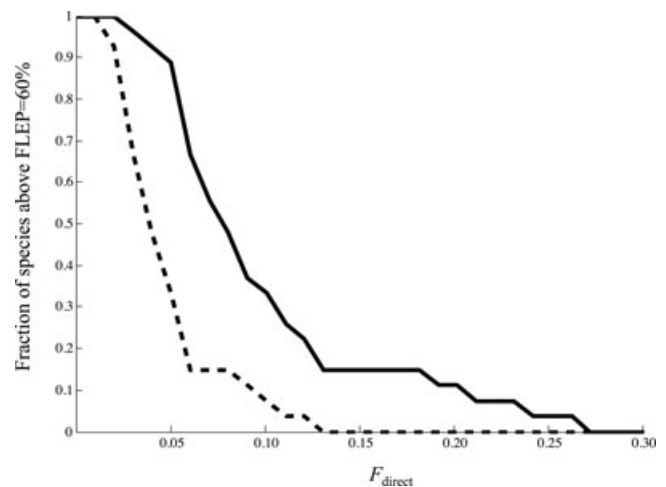

Figure 4. *The fraction of 26 species of sharks that persist at fraction of lifetime egg production (FLEP) of 35% (solid line), recommended for teleosts, and FLEP = 60% (dashed line), recommended for elasmobranchs (Restrepo et al. 1998), as a direct measure of fishing mortality (F$_{direct}$) increases.*
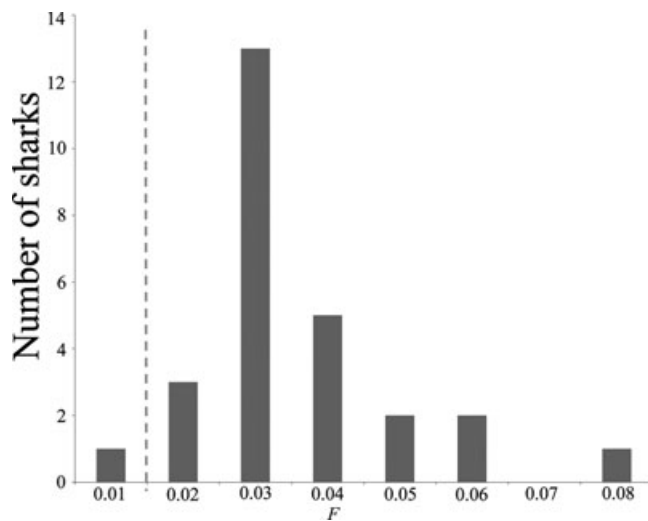
Figure 5. Number of sharks that could be fished at each value of fishing mortality (F) binned in increments of 0.01 when the largest standard proportion of natural mortality (M) ($\mu = 0.16$, where $F = \mu M$) is used to specify the value of F that maintains fraction of lifetime egg production (FLEP) >60% for all sharks included in this study (dashed line, the maximum directly calculated value of $F_{[direct]}$ that would maintain all species in this study above 60%).

approaches equilibrium. Smith et al.'s (1998) approach artificially included a compensatory increase in juvenile survival at low abundance, but there is no empirical basis for assuming this is the true nature of compensation at low shark abundance. There is some evidence that juvenile survival of sharks increases with reduced density, but this increase is likely accompanied by increases in individual growth rates (Sminkey & Musick 1995; Stevens & West 1997; Carlson & Baremore 2003), decreases in age of maturity (Parsons 1993; Castro 1996; Carlson & Baremore 2003), or other compensatory responses.

The values we calculated for $FLEP_{F=M}$, although an improvement over r', λ, and r_{2M}, are still not based empirically on the current population age structure; hence, we did not compare them with the overfishing threshold as they would have been in conventional, data-rich fisheries-management scenarios. The values of FLEP we calculated from the shark life-history data represent the relative rank of persistence of these species as values of F vary, under the explicit assumption of particular values for life-history parameters (from Smith et al. 1998). The lower levels of F necessary to allow persistence in shark populations determined here from FLEP also depended on these specified parameters, so this F may not be appropriate if population-specific parameter values differ substantially from the ones we used.

In a few shark fisheries, it has been possible to assess species on the basis of additional parameters that reflect density dependence and thus also reflect maximum sustainable yield. For example, the stock-recruitment relation for the barndoor skate (*Dipturus laevis*) was empirically determined from trawl survey data (Gedamke et al. 2009). At the origin, the data fitted to both Ricker and Beverton–Holt stock-recruitment models indicated a slope of 4.99 and 5.26 recruits/spawner, respectively. This equates to an FLEP of nearly 20%. Although this value is much lower than 60%, the barndoor skate is thought to be unusually resilient to exploitation (Gedamke et al. 2009). Forrest and Walters (2009) were able to determine that the intrinsic rate of increase and maximum sustainable yield of deepwater dogsharks because their upper limit of sustainable yield is so low. However, in general, the data required for a formal assessment are lacking for most shark species. Therefore, most sharks are currently categorized on the basis of results of 1 of the 3 linear models described above.

The status assessment of sharks in terms of replacement can be understood in the context of the other major indicator of the status of sharks: i.e., declines in species abundance (IUCN 2011). A population's risk of collapse depends on abundance and replacement rate, but data to estimate these parameters are seldom available, and catch data are often used as a proxy. Replacement can be considered similar to population growth rate, which explains its role in determining a population's risk of collapse; the likelihood of collapse depends on current abundance and on how fast the population is growing. The International Union for Conservation of Nature's status for shark species has also been determined on the basis of linear population criteria (Dulvy et al. 2008), such as intrinsic growth (r), but should be more properly evaluated on the basis of replacement.

Use of a measure of replacement may be valuable in the conservation of age-structured species other than fishes that have poorly known density dependence in recruitment. A conventional approach is to compute probabilities of extinction from models that must include a description of survival at low abundance, even though it may be uncertain. Characterizing relative persistence as some form of replacement as we did here reflects the effect of additional mortality from anthropogenic sources in a direct way, which may be preferable to examination of calculated extinction rates that were based on assumed values. This approach would be most applicable to populations driven to low levels by mortality additional to *M* and would not apply to cases in which populations are at low levels because of a decline in habitat.

A fundamental limitation to our ability to maintain replacement high enough to prevent population collapse is uncertainty in the slope of the egg-recruit curve. For most sharks, data are lacking that could be used to determine this value (i.e., survival of the very young). The

3 linear age-structured modeling approaches we evaluated assumed the relation between eggs and recruits was known and that this relation exhibited a constant linear increase (i.e., that the relation was not density dependent). It seems inconsistent to declare data are lacking for a species and then to propose a method for population assessment that assumes this relation is known, when it is highly uncertain even for species on which there are more available data. It seems far better to base priorities in shark conservation policies on computed values of relative replacement (FLEP), which does not depend on assumed survival rates in the young because it is normalized by the value of LEP with no fishing. Therefore, we recommend that methods used to determine the persistence status of sharks should rely on direct calculations of replacement for shark species (i.e., FLEP) and sharks be fished with a precautionary approach ($F < 0.16M$, or a value of μ chosen from Table 1 if the species is listed, a value much less than the values of F currently used in calculating r_{2M}).

Acknowledgments

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