Conservation and management of exploited shark populations based on reproductive value

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Abstract: Several life history traits of sharks result in juveniles being particularly vulnerable to exploitation. However, population level impacts of harvests on juvenile sharks have not been well quantified. This paper examines a range of harvest strategies, including those targeting juveniles. Reproductive value and yield per recruit are used to compare the harvests, which are represented by Leslie matrix models with a harvest matrix. Two species are used as examples: the short-lived *Rhizoprionodon taylori* and the long-lived *Squalus acanthias*. Harvests that maintain a stationary population size cause reproductive values to change in opposing ways, but they remove equal fractions of the population's reproductive potential. A new theorem gives population growth as a function of the fraction of reproductive potential removed by a harvest, a relationship useful for comparing harvests on juveniles and adults. Stochastic projections indicate that the risk of depletion is associated with the fraction of reproductive potential removed annually, a measure which encompasses the information in both the selectivity and the rate of fishing mortality. These results indicate the value of focusing conservation efforts on preserving reproductive potential.

Résumé : Plusieurs caractéristiques du cycle biologique des requins rendent les jeunes particulièrement vulnérables à l'exploitation. Cependant, les impacts démographiques des récoltes des jeunes n'ont pas été bien mesurés quantitativement. Notre étude examine une gamme de stratégies de récolte, y compris celles qui ciblent les jeunes. La valeur reproductive et le rendement par recrue sont les variables qui nous servent à comparer les récoltes qui sont représentées par des modèles matriciels de Leslie avec un matrice de récolte. Deux espèces servent d'exemple, *Rhizoprionodon taylori*, une espèce à vie courte, et *Squalus acanthias*, une espèce à vie longue. Les récoltes qui maintiennent la taille de la population stationnaire changent les valeurs reproductives de façon opposée chez les deux espèces, mais elles retirent des fractions semblables du potentiel reproductif de la population. Un nouveau théorème présente la croissance de la population comme une fonction de la fraction du potentiel reproductif retirée par une récolte donnée, une relation utile pour comparer les récoltes faites sur les jeunes et les adultes. Des projections stochastiques indiquent que le risque de déplétion est associé à la fraction du potentiel reproductif retirée chaque année, une mesure qui englobe à la fois l'information relative à la sélectivité et aux taux de mortalité due à la pêche. Ces résultats démontrent l'intérêt qu'il y a à concentrer les efforts de conservation sur le maintien du potentiel reproductif.

[Traduit par la Rédaction]

Introduction

It is generally agreed that shark populations are particularly vulnerable to overexploitation because of the limited number of offspring they bear and the long period of time before they are sexually mature (Musick 1999). Merging this line of thought with the standard methodologies applied in fisheries stock assessment leads to a number of inconsistencies. Methods of analysis based on the use of compensatory models such as the Schaefer stock-production model (McAllister et al. 2001) assume that almost all of the life history parameters fundamental to modeling the dynamics can be represented by the two-parameter logistic model. In contrast, age-structured models (Cailliet 1992; Cortés 1998; Punt and Walker 1998) allow the explicit use of the same life history parameters central to understanding why shark populations are easily overexploited. This paper builds on the use of life history parameters by the simultaneous use of the reproductive value of a given species, which is associated with Leslie matrix models (Caswell 2001), and the application of the mathematical methodology of the Beverton and Holt (1957) yield-per-recruit (Y/R) model formulated as a function of reproductive potential removed.

This research was motivated by earlier work on multi-mesh-size artisanal fisheries where juveniles of larger species were captured in mesh sizes designed for smaller species (Lai et al. 1993; Gallucci et al. 1996). In the present case, our initial interest was in sharks that use tropical bays as nurseries (V. Gallucci, personal observation), where artisanal fishermen harvested prereproductive sizes as part of their fishing

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932

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operation. Even if not targeted, sharks were a bycatch item in drift gillnet and seine gear and were either marketed or simply discarded. These harvests of juvenile sharks, which have been noted in other artisanal fisheries (Castillo-Géniz et al. 1998; Kroese and Sauer 1998), led to research into new methods for estimating the impacts of the capture of prereproductive animals in a more generalized context. The traditional approach in stock assessment would attempt to estimate a biological reference point (Gabriel and Mace 1999), which would be an age- or size-specific rate of instantaneous fishing mortality, such as F_{max}, $F_{0.1}$, or F_{MSY}. Occasionally these reference points are based on the spawning stock biomass of the population. The alternative approach we considered was to use reproductive value and the fraction of the reproductive potential of the population removed by harvesting any subset of the ages. This led to the derivation of a new theorem, presented herein.

Reproductive value (RV) has its roots with Fisher (1930) as a part of human demographic analysis and as a part of the ecological literature with MacArthur (1960), who considered fisheries harvests as a special case of optimal foraging theory. He phrased the predator's problem in two ways: when it knows, and does not know, the age of the prey. RV was used in the first case, which also applies to our interest as a fishery typically designs its capture gear to correspond to an initial age of capture. Our work diverges from MacArthur's, but his initial results are a basis for our approach. RV, which can be interpreted as the relative contribution of individuals at each age to the long-term growth of the population, has become a part of demographic analyses like those frequently employed for shark populations (Cailliet 1992; Cortés 1999; Frisk et al. 2002). Reproductive potential (RP) extends RV to the population level. RP is defined here as the sum of RVs of all individuals in a population. This measure, also called "total reproductive value" (Leaman 1987, 1991), was also developed by Fisher (1930) and has been considered as an alternative to spawning stock biomass (Leaman 1987, 1991; Katsukawa et al. 2002). Leaman (1987, 1991) concludes that RP should be incorporated into monitoring programs for decision-making. Taylor and Gallucci (2005) found that the connection between RP and biomass of a species was an indicator of the degree to which surplus production models could fit biomass trends for that species.

Representing the contribution of a shark of a given age to the whole population by its RV allows the quantification of harvest strategies in terms of the removals of these contributions. This approach, used along with Y/R analysis for different exploitation strategies, allows the exploration of the long-term consequences of these harvest policies. By extension, this allows investigation of the balancing of yield, selection of juveniles, and harvest sustainability. Deterministic analyses of the type described above do not provide information on the influence of variability in life history parameters on the results, and so Monte Carlo simulations are used in a risk analysis to supplement deterministic projections.

In this paper, the comparison between short- and long-lived species allows a demonstration of the utility of RV-based measures. The above methodologies are applied to a number of practical situations representing different exploitation scenarios for sharks of two basic types: those that grow to great ages and those that do not. These short- and long-lived types are represented here by the Australian sharpnose shark (*Rhizoprionodon taylori*) and the spiny dogfish (*Squalus acanthias*), respectively. These methodologies allow quantification of the consequences of harvesting prereproductive sharks from nurseries and facilitate tracking the subsequent population wave across the age structure. This analysis demonstrates the potential value of different management approaches for these two archetypes. The RP framework developed here is a valuable new tool for identifying patterns of harvest impacts across life histories and harvest strategies.

Materials and methods

Matrix formulation for harvested populations

Deterministic population dynamics were modeled using age-structured female-only Leslie matrix models (definitions of terms are provided in Table 1). Parameter values (Table 2) were taken from available published information on the Australian sharpnose shark (Simpfendorfer 1999a) and the Northeast Pacific population of spiny dogfish (Ketchen 1972, 1975; Saunders and McFarlane 1993). These species were chosen as representative of short- and long-lived species, respectively.

Natural mortality rates for the two species were assumed constant over all ages with $M = 0.561$ for the sharpnose shark (Simpfendorfer 1999a). The method of Hoenig (1983) was applied for the dogfish assuming a maximum age of 80 years (McFarlane and King 2003) to get a value of $M = 0.0515$. The annual survivorship terms in the subdiagonal of the Leslie matrix were calculated as $s_x = e^{-M}$.

Length was assumed to follow the von Bertalanffy growth function (Gallucci and Quinn 1979), and average numbers of offspring per mature female was a linear function of length for both species (Table 2). The census for abundance was assumed to be postbreeding (Caswell 2001), making newborn pups the first age class (age 0). The fecundity values thus include the probability of the mother surviving to pup at the end of the year, making possible the modeling of harvests on young-of-the-year pups. A sex ratio of 1:1 was assumed for both species. All sharpnose sharks were assumed to mature at age 1 and to pup every year, whereas mature dogfish were assumed to pup every 2 years. The maturity schedule for dogfish was assumed to be a logistic function of age with 50% maturity at 35.5 years (Saunders and McFarlane 1993), so the fraction mature at age x was $(1 + e^{-0.4(x-35.5)})^{-1}$. The average number of female pups per female of age x, m_x, is the product of the function for the number of pups per mature female (Table 2), the maturity schedule, and the sex ratio. The fecundity terms which make up the first row of the Leslie matrix were calculated as $f_x = s_x m_x$.

Harvests were incorporated into the model as a diagonal matrix **H** following Lefkovitch (1967) and Caswell (2001). The elements of the harvest matrix, h_x, represent the fraction of individuals of age x surviving the harvest. Thus, the usual Leslie age-structured model (Caswell 2001)

$$(1) \qquad N_{t+1} = \mathbf{M}N_t$$

where **M** is the projection matrix and N_t is the vector of numbers at each age in year t, is modified to incorporate age-specific removals of individuals in a harvest:

Table 1. Definitions of terms.

M	Leslie matrix
H	Harvest survival matrix with diagonal elements h_x
h_x	Fraction surviving harvest at age x
H* = I − H	Diagonal matrix containing fraction harvested at each age with diagonal elements $1 − h_x$
λ	Dominant eigenvalue of **M** giving the annual multiplicative increase of the unharvested population at stable age distribution (SAD)
λ'	Dominant eigenvalue of **MH** giving the annual multiplicative increase of the harvested population at SAD
w	SAD vector for **M**, satisfying $\mathbf{M}w = \lambda w$
w'	SAD vector for **MH**, satisfying $\mathbf{MH}w' = \lambda' w'$
v	Reproductive value vector for **M**, satisfying $v^{\mathrm{T}}\mathbf{M} = \lambda v^{\mathrm{T}}$
v'	Reproductive value vector for **MH**, satisfying $v'^{\mathrm{T}}\mathbf{MH} = \lambda' v'^{\mathrm{T}}$
v_x	Reproductive value at age x
$P_t = v^{\mathrm{T}}N_t$	Reproductive potential of the population in year t
$P = v^{\mathrm{T}}w'$	Reproductive potential of the SAD vector w' corresponding to **MH**
$P_h = v^{\mathrm{T}}\mathbf{H}^*w'$	Reproductive potential of the fish harvested from w' each year
$\Phi = P_h/P$	Fraction of the reproductive potential removed by the harvest at SAD
N_t	Vector of numbers at each age in year t
$N_{x,t}$	Number of individuals of age x in year t
t_c	Age of entry into the fishery
t_ε	Maximum age selected by the fishery
t_∞	Maximum age of the species

Table 2. Parameter values used for each species.

Species	Common name	Pups per mature female (TL in cm)	Age of 50% maturity	t_∞	M	L_∞	K	t_0
Rhizoprionodon taylori	Australian sharpnose shark	0.19·TL − 7.919	1	7	0.561	73.2	1.013	−0.455
Squalus acanthias	Spiny dogfish	0.20·TL − 13.24	35.5	80	0.0515	114.94	0.0437	−3.557

Note: TL, total length; M, natural mortality; L_∞, K, t_0, standard von Bertalanffy growth function parameters. See Table 1 for other definitions.

$$(2) \quad N_{t+1} = \mathbf{MH}N_t$$

The augmented projection matrix **MH** has the same form as the Leslie matrix but fecundity and survival of the harvested ages are reduced. The dominant eigenvalue of **M**, λ, and, the dominant eigenvalue of **MH**, λ', give the asymptotic annual change in population size with and without a given harvest. Primed (′) variables are associated with a harvested population. Thus, the unharvested case (eq. 1) is a special case of eq. 2.

Two general classes of harvest strategy were evaluated: juvenile and adult. The selection of a younger portion of the population is intended to represent harvests on the juvenile population present in nursery areas or the only sizes available to artisanal fishers. The selection of the older portion of the population matches the more common pattern of minimum size limits or the use of selective gear in commercial fisheries. For juvenile harvests, the age of entry into the fishery t_c was set to 0, and for adult harvests, the maximum age in the fishery t_ε was set to the maximum age for the species, t_∞ (Fig. 1). All individuals between t_c and t_ε are considered fully recruited into the fishery.

To reduce the set of harvests considered, the fraction harvested annually from all selected ages was equal. Thus, the harvest matrix **H** has diagonal elements $h_i = h$ for $t_c \leq i \leq t_\varepsilon$, and $h_i = 1$ otherwise. The harvest rate $(1 − h)$, associated

Fig. 1. Example of juvenile and adult harvests showing that both types may include some juveniles and some adults.
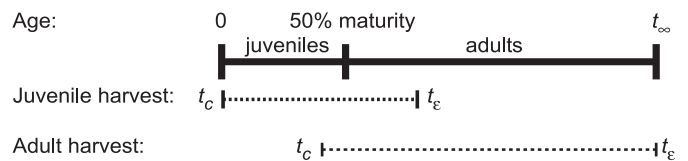
with a stationary population size, was found by iteratively searching for the constant survival fraction h, which made $\lambda' = 1$. The term "stationary harvest" will be used for all harvests that make $\lambda' = 1$. The right and left eigenvectors corresponding to these eigenvalues give the reproductive value and the stable age distribution, respectively.

RV and stable age distribution

The RV vector v was calculated as the right eigenvector of the projection matrix **M**, satisfying

$$(3) \quad v^{\mathrm{T}}\mathbf{M} = \lambda v^{\mathrm{T}}$$

where v^{T} is the transpose of the column vector v. The RV of the harvested population v' is the right eigenvector of **MH**, satisfying

(4) $v'^T \mathbf{MH} = \lambda' v'$

The resulting elements of v, which are defined by eq. 4 only up to a scalar multiplier, are proportional to those given by the discrete form of Fisher's (1930) formula:

(5) $v_x = \sum_{i \geq x} \lambda^{-(i-x)} f_i \dfrac{l_i}{l_x}$

where v_x is the RV at age x, and $l_x = \prod_{i=0}^{x-1} s_x$ is the probability of survival from birth to age x. The elements of v' can be calculated using eq. 5 by substituting λ', f'_x, and l'_x derived from the augmented projection matrix $\mathbf{MH}$.

   Evaluating eq. 5 at $x = 0$ yields a function similar to the Euler–Lotka equation (Lotka 1907). This similarity can be used to show that computing v_x using eq. 5 is equivalent to scaling the v so that $v_0 = \lambda$. Correspondingly, harvests that lead to a stationary population size have $v'_0 = \lambda' = 1$. Under such stationary harvests, eq. 5 is identical to the equation for life-time egg production of an individual of age x (Quinn and Deriso 1999):

(6) $R_x = \sum_{i \geq x} f_i \dfrac{l_i}{l_x}$

so that the net reproductive rate R_0 will equal the reproductive value at age 0: $R_0 = v'_0 = 1$. The scaling of the eigenvectors to make $v_0 = \lambda$ and $v'_0 = \lambda'$ has been used when comparing v_0 and v'_0.

   The stable age distribution (SAD) vectors of unharvested and harvested populations, w and w', are the left eigenvectors corresponding to λ and λ' (Caswell 2001), respectively, and satisfy

(7) $\mathbf{M}w = \lambda w$

and

(8) $\mathbf{MH}w' = \lambda' w'$

Reproductive potential

   RP, a scalar value, is defined here as the sum of the RVs of all individuals in the population, whether at a SAD or not. It is computed following Leslie (1948) as the vector inner product

(9) $P_t = v^T N_t = \sum_x v_x N_{x,t}$

where $N_{x,t}$ is the element of the population vector N_t corresponding to age x. RP is a measure of the potential for the population to grow in the absence of a harvest. Thus, v rather than v' is used in eq. 9.

   The RP of the SAD vector w' is given by

(10) $P = v^T w'$

and the RP of the portion of this population that is removed by the harvest in each year is

(11) $P_h = v^T \mathbf{H}^* w'$

where $\mathbf{H}^* = (\mathbf{I} - \mathbf{H})$, with $\mathbf{I}$ the identity matrix, is the diagonal matrix containing the fraction of each age removed by

the harvest. The ratio of these two quantities gives the fraction of the reproductive potential removed by a stationary harvest at SAD:

(12) $\Phi = P_h/P$

Yield per recruit

   Y/R was calculated for a range of harvest strategies as

(13) $\text{Y/R} = \sum_{x=0}^{t_\infty} (1 - h_x) l'_x W_x$

where $(1 - h_x)$ is the probability of being harvested at age x, $l'_x = \prod_{i=0}^{x-1} s_i h_i$ is the fraction of the cohort surviving to age x under the harvest, and W_x is the weight at age x given by the von Bertalanffy growth equation. The fraction surviving the harvest was also converted to a rate $F = -\ln(h)$, which was used in the Beverton–Holt Y/R model (Beverton and Holt 1957). A comparison between eq. 13 and the Beverton–Holt model found similar results, with small differences resulting from the alternative treatments of growth and mortality as discrete or continuous processes.

   Y/R was calculated for adult harvests over a two-dimensional grid of the fraction of RP removed by the harvest each year (Φ) vs. age of entry (t_c) values with the maximum age in the fishery (t_ε) fixed at the maximum age of the species (t_∞). The parameters in the grid for juvenile harvests were Φ and t_ε, with $t_c = 0$. The value of $h_x = h$ for a given range of ages $t_c \leq x \leq t_\varepsilon$ that corresponded to Φ was found using an iterative search.

Stochastic projections and risk

   The augmented projection matrix $\mathbf{MH}$ is a deterministic model of population dynamics under given fecundity and survival parameters, along with harvests of selected ages. The risk of depletion per harvest strategy was evaluated by including stochasticity in the survival, fecundity, and harvest parameters. Fecundity was assumed to have a lognormal distribution around a mean, f_x. The instantaneous rates $M = -\ln(s_x)$ and $F = -\ln(h)$, were also assumed lognormal. Use of the lognormal distribution for the instantaneous rates is convenient because the resulting fractions for survival and harvest will be between 0 and 1. The stochastic elements of the projection and harvest matrices for age x in year t were calculated as $\tilde{f}_{x,t} = f_x \varepsilon_t$, $\tilde{s}_{x,t} = e^{-M\delta_t}$, and $\tilde{h}_t = e^{-F\gamma_t}$, where ε_t, δ_t, and γ_t are all lognormal random variables with mean = 1 and coefficient of variation (CV) = 0.2. The same random variables were applied to all ages under the assumption that environmental effects will have similar impacts on all ages. Conditions that increased fecundity were assumed to decrease natural mortality, on average, so ε_t and δ_t were negatively correlated, with coefficient $\rho = -0.5$.

   A harvest strategy is defined by specification of t_c, t_ε, and either the fraction of the total RP removed in each year, Φ, or the fraction of the total biomass removed each year, β. The harvest survival parameter h corresponding to Φ or β was calculated in each year as

$$(14) \quad h = \begin{cases} 1 - \Phi \dfrac{\displaystyle\sum_{x=0}^{t_\infty} N_{x,t} v_x}{\displaystyle\sum_{x=t_c}^{t_e} N_{x,t} v_x} & \text{when } \Phi \text{ is specified} \\[2em] 1 - \beta \dfrac{\displaystyle\sum_{x=0}^{t_\infty} N_{x,t} W_x}{\displaystyle\sum_{x=t_c}^{t_e} N_{x,t} W_x} & \text{when } \beta \text{ is specified} \end{cases}$$

For each harvest strategy, 1000 stochastic projections were made in which an initial population at SAD, with biomass B_0, was projected forward 50 years to determine a final biomass B_{50}. The probability that a projection ended below 20% of the initial biomass, $P(B_{50} < 0.2B_0)$, was used as an estimate of the risk of depletion associated with each harvest strategy.

Results

Changes in reproductive value

Changes in RV differed under juvenile and adult harvests and between species (Fig. 2). These RVs may be interpreted as the relative contribution of individuals at each age to the long-term growth of the population under different harvest conditions. The bold lines in Fig. 2 refer to the RVs of the unharvested population of each species. All harvests are designed to maintain a stationary population size by constraining the removal of the selected ages so that $\lambda' = 1$. Under these harvests, the population may exhibit dampened oscillations as it approaches the SAD associated with the projection matrix **MH**, but at that SAD, the population size will be constant, regardless of the initial age distribution and population size.

The changes in RV under harvests on different segments of the population were unexpected: harvests that target juveniles can increase RV above the level corresponding to no harvest. Although unexpected, an explanation is available. In all cases, harvests reduce survival of the harvested ages. Any harvest will reduce λ' below λ, but when only juveniles are selected into the fishery, survival and fecundity of adults are unaffected. Thus, if λ', f'_x, and l'_x are substituted into the summation equation for RV (eq. 5), the negative exponent on λ' will result in an increase in RV at all ages older than those selected into the fishery because the ratio l'_i/l'_x will be unaffected by the harvest on younger ages. The RV of some juvenile ages selected into the fishery decreases because the impact of the harvest on survival and fecundity is more influential than the changes in λ'. In general, the adult ages that are unaffected by a harvest on juveniles and are already producing offspring are relatively more valuable to the population than the juveniles being harvested.

Harvests on adults, in contrast, reduce the RV of all ages in the population. The eigenvalue λ' is again reduced, but unlike harvests on juveniles, harvests that reduce the survival and fecundity of adults will impact the RV of all ages. Larger reductions occurred at the ages selected into the harvest, but because RV is a sum over all expected future offspring, the impact of a harvest on the last age in the population will re-

Fig. 2. Reproductive value vs. age for (*a*) *Squalus acanthias* and (*b*) *Rhizoprionodon taylori* under harvests that maintain a stationary population size and under no harvest. Labels denote the range of ages selected into the harvest for each curve.
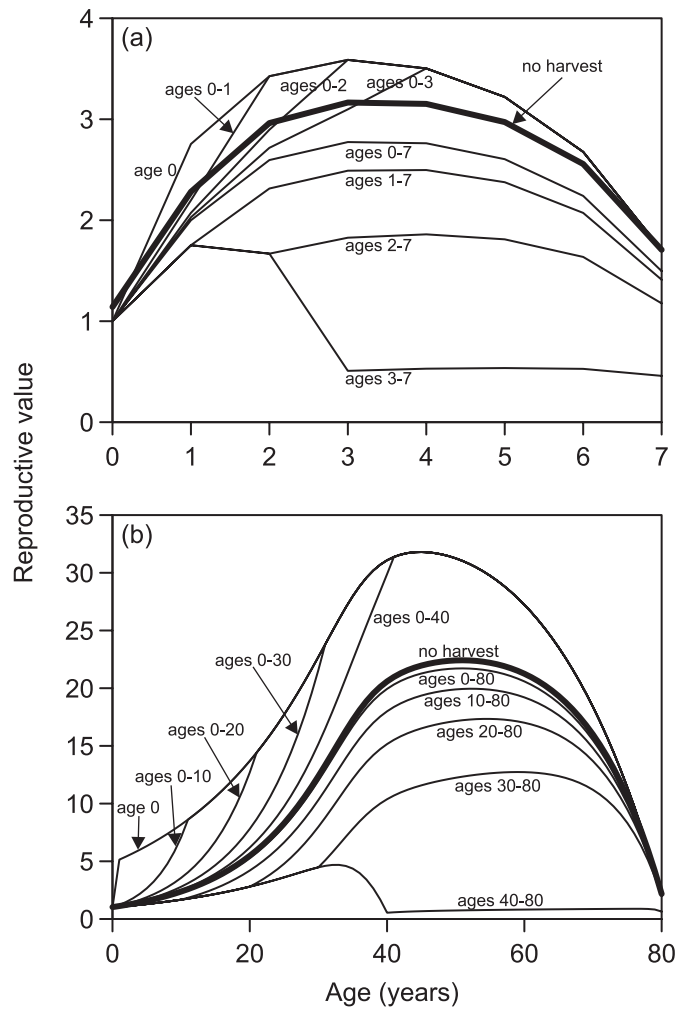
duce RV of all prior ages as well. The harvests associated with the greatest reductions in RV for both species considered were those targeting the smallest number of adult ages. The harvest rates associated with these harvest strategies (Tables 3 and 4) are the highest among the strategies considered under the constraint $\lambda' = 1$. Thus, the low RV associated with harvests on the oldest segment of the population may be interpreted as a measure of the high harvest rates, which may be applied to the oldest fish while maintaining a stationary population size.

Population growth

Details are given of the harvests considered under the constraint that they will lead to a stationary population size ($\lambda' = 1$) (Tables 3, 4). Harvests on adults may target more ages or remove a greater fraction ($1 - h_x$) of each targeted age while maintaining a stationary population size. The differences in sustainable harvest rates between strategies are an indication of the interdependence between selectivity and sustainable harvests. The fraction of a population's biomass that may be sustainably removed each year is a function of

Table 3. Details of stationary harvests for *Rhizoprionodon taylori*.

Type of harvest	t_c	t_ϵ	Harvest fraction $(1 - h_x)$	F	λ'	R_0	Y/R	Φ	β	Fraction of numbers harvested
No harvest	—	—	0	0	1.141	1.572	0	0	0	0
Juvenile	0	0	0.364	0.452	1	1	0.018	0.124	0.029	0.199
Juvenile	0	1	0.202	0.226	1	1	0.052	0.124	0.079	0.153
Juvenile	0	2	0.155	0.168	1	1	0.070	0.124	0.102	0.135
Juvenile	0	3	0.137	0.147	1	1	0.078	0.124	0.113	0.128
All ages	0	7	0.124	0.132	1	1	0.087	0.124	0.124	0.124
Adult	1	7	0.174	0.191	1	1	0.120	0.124	0.162	0.090
Adult	2	7	0.311	0.372	1	1	0.139	0.124	0.183	0.079
Adult	3	7	0.731	1.313	1	1	0.148	0.124	0.193	0.076

Note: F, fishing mortality; R_0, net reproductive rate; Y/R, yield per recruit; β, fraction of the total biomass removed each year. See Table 1 for other definitions.

Table 4. Details of stationary harvests for *Squalus acanthias*.

Type of harvest	t_c	t_ϵ	Harvest fraction $(1 - h_x)$	F	λ'	R_0	Y/R	Φ	β	Fraction of numbers harvested
No harvest	—	—	0	0	1.032	4.892	0	0	0	0
Juvenile	0	0	0.7956	1.588	1	1	0.019	0.0314	0.0026	0.1656
Juvenile	0	10	0.1344	0.144	1	1	0.117	0.0314	0.0149	0.0926
Juvenile	0	20	0.0728	0.076	1	1	0.239	0.0314	0.0267	0.0623
Juvenile	0	30	0.0500	0.051	1	1	0.328	0.0314	0.0309	0.0464
Juvenile	0	40	0.0389	0.040	1	1	0.378	0.0314	0.0309	0.0375
All ages	0	80	0.0314	0.032	1	1	0.432	0.0314	0.0314	0.0314
Adult	10	80	0.0397	0.041	1	1	0.533	0.0314	0.0353	0.0182
Adult	20	80	0.0547	0.056	1	1	0.593	0.0314	0.0327	0.0117
Adult	30	80	0.0935	0.098	1	1	0.587	0.0314	0.0281	0.0083
Adult	40	80	0.7059	1.224	1	1	0.620	0.0314	0.0261	0.0071

Note: F, fishing mortality; R_0, net reproductive rate; Y/R, yield per recruit; β, fraction of the total biomass removed each year. See Table 1 for other definitions.

the ages selected by the harvest, where a greater fraction of the biomass is sustainably removed via harvests of adult ages of the two species. Unlike biomass, the fraction of a population's reproductive potential Φ that may be sustainably removed each year is independent of the ages selected by the fishery. This is demonstrated in the following theorem and lemma.

Theorem: (Taylor, Gallucci) The asymptotic annual growth of a harvested population λ' decreases linearly with the fraction of the reproductive potential harvested Φ annually:

(15) $\lambda' = \lambda(1 - \Phi)$

Proof:

$\lambda' = \lambda' \boldsymbol{v}^{\mathrm{T}} \boldsymbol{w}'/P$	multiplying λ' by a fraction equal to 1, using eq. 10
$\quad = \boldsymbol{v}^{\mathrm{T}} \lambda' \boldsymbol{w}'/P$	λ' is commutative under multiplication with $\boldsymbol{v}^{\mathrm{T}}$
$\quad = \boldsymbol{v}^{\mathrm{T}} \mathbf{MH} \boldsymbol{w}'/P$	substitution using eq. 8
$\quad = \lambda \boldsymbol{v}^{\mathrm{T}} \mathbf{H} \boldsymbol{w}'/P$	substitution using eq. 3
$\quad = \lambda(\boldsymbol{v}^{\mathrm{T}} \boldsymbol{w}' - \boldsymbol{v}^{\mathrm{T}} \mathbf{H}^* \boldsymbol{w}')/P$	substituting $\mathbf{H}^* = (\mathbf{I} - \mathbf{H})$ and distributing
$\quad = \lambda(P - P_h)/P$	definitions of P and P_h
$\quad = \lambda(1 - \Phi)$	distributing $1/P$ and substituting $\Phi = P_h/P$

Lemma: If the fraction of reproductive potential annually removed by the harvest is $(\lambda - 1)/\lambda$, then the population size will be stationary when it reaches SAD.

Proof: Substituting $\Phi = (\lambda - 1)/\lambda$ into eq. 15 gives

$\lambda' = \lambda(1 - \Phi)$
$\quad = \lambda(1 - (\lambda - 1)/\lambda)$
$\quad = 1$

If the Perron–Frobenius theorem (Caswell 2001) applies to $\mathbf{M}$, then under ordinary harvests (no removal of 100% of any age class), it will apply to $\mathbf{MH}$ and the population will approach a SAD. Having $\lambda' = 1$ will result in a stationary population size when the population reaches SAD. The linear relationship between λ' and Φ is shown (Fig. 3).

The results of both the theorem and lemma are independent of the ages selected by the harvest. The only effect of the selectivity pattern is that there may be a maximum Φ associated with harvests on adults. The value $\Phi = (\lambda - 1)/\lambda$, which leads to a stationary population size for a given set of demographic parameters, will be denoted $\Phi_{\text{stationary}}$. The values corresponding to the two species are $\Phi_{\text{stationary}} = 0.124$ for the sharpnose shark and $\Phi_{\text{stationary}} = 0.031$ for the dogfish. The lower level of removals that can be sustained by the dogfish are characteristic of long-lived elasmobranchs (Hoenig and Gruber 1990). Although the increase in population size per generation of dogfish is actually higher, their long generation time results in a very low annual increase in

Fig. 3. The relationship between λ' and Φ as given by the theorem and lemma. Pop., population; RP, reproductive potential.
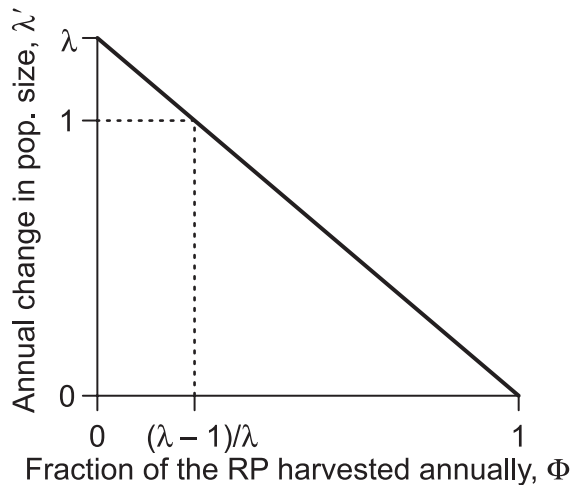
population size ($\lambda = 1.032$). Although it is intuitive that sustainable levels of fishing pressure are related to a population's growth rate, this theorem provides a quantitative framework for calculating the fraction of a population's reproductive potential that may be sustainably harvested each year.

The theorem implies that expressing effort in terms of the fraction of RP removed from the population each year is the most accurate indicator of the impact of that harvest on the growth of the population. Because λ' is directly related to Φ, a harvest that removes a greater fraction of the RP annually will have a larger impact on λ', regardless of the selectivity pattern of the fishery. Two instantaneous rates of fishing mortality can only be compared in this way when they are applied to the same selected age classes. For this reason, fishing effort in the following Y/R calculations was described in terms of the fraction of RP removed annually by the harvest.

Yield per recruit

Expressing fishing effort in the Y/R analysis in terms of Φ, the fraction of RP removed from the population each year, makes comparison of Y/R among sustainable harvests easy (Fig. 4). A vertical line at $\Phi_{stationary} = (\lambda - 1)/\lambda$ indicates those harvests that lead to a stationary population size, as shown in the lemma above. Some levels of removal were not possible for some adult harvests, in which case no Y/R was calculated. If the fraction of the RP contained within cohorts of age t_c and older is less than a given Φ, then no harvest on ages t_c and older can remove a fraction of RP equal to Φ. The t_c values for which no Φ above the stationary harvest rate can be removed are very conservative harvest strategies. In these ranges ($t_c \geq 3$ for sharpnose shark and $t_c \geq 40$ for the dogfish), the population will not be depleted under any amount of fishing pressure.

Considering changes in t_c or t_ε corresponding to $\Phi_{stationary}$, maximum Y/R from juvenile harvests occurred when the harvest included all adult ages in addition to juveniles. Maximum Y/R from stationary adult harvests was higher than Y/R from any juvenile harvest. For the sharpnose shark, this maximum occurred when the age of entry into the fishery

was as high as possible ($t_c = 3$ in Fig. 4a). With the dogfish, Y/R for stationary harvests was highest with $t_c = 24$ years (Fig. 4b). For both species, the highest Y/R at sustainable levels of Φ was about 50% higher among adult harvests than among juvenile harvests and about 100% higher among adult harvests than among juvenile harvests that included no adults.

The short-lived sharpnose shark has a high natural mortality rate ($M = 0.561$) that is unlikely to be approached by any fishing mortality rate. Therefore, within the range of Φ considered, an increase in fishing effort applied to any range of harvested ages will increase Y/R because decreases in a cohort resulting from natural mortality will be faster than increases in weight. The peak Y/R occurs at the maximum possible Φ for the harvests on adults, whereas for juveniles, the peak Y/R occurs around $\Phi = 0.4$, when the population is declining sharply already. For this species, the concern is avoiding recruitment overfishing by removing RP only from older ages that have had more time to reproduce. In contrast, natural mortality for the dogfish and other long-lived sharks is low enough that it may easily be matched or surpassed by fishing mortality. In this case, growth overfishing is also a concern. That is, especially for harvests on juveniles, increasing the fraction of RP removed from any range of ages will decrease Y/R through a shift in the mean age of harvested individuals toward the age of entry in the fishery. These younger individuals, which weigh less, would have had a high probability of surviving to an older, heavier age with less fishing pressure. For dogfish, the peak Y/R from juvenile harvests is close to the stationary harvest level. Thus, in addition to indicating the advantage of adult harvests over juvenile harvests for both species, the Y/R analysis shows that for a long-lived species, in addition to decreasing recruitment, the Y/R will be adversely impacted by overfishing.

Stochastic projections and risk

For both species, the risk of population depletion, defined as the probability that a 50-year stochastic projection will end below 20% of the initial biomass, $P(B_{50} < 0.2B_0)$, was similar for all harvest strategies at any given removal of RP, Φ (Figs. 5a, 5b), but the risk associated with a given removal of biomass, β, was highly dependent on the range of ages harvested (Figs. 5c, 5d). For the short-lived sharpnose shark (Fig. 5a), $P(B_{50} < 0.2B_0)$ rose from less than 0.05 at $\Phi = 0.11$ to greater than 0.95 at $\Phi = 0.16$. For ages 3–7, many projections resulted in a fraction of RP contained in these ages less than Φ, so the risk presented is the result of removing all individuals from these ages in some years. In contrast, when harvests are described in terms of removals of biomass (Fig. 5c), a harvest of only 5% from age 0 caused all projections to fall below $0.2B_0$, whereas three times as much biomass could be removed from ages 2–7 or ages 3–7 without causing such depletion in most of the projections.

For dogfish, the transition from low to high risk occurs over a narrower range of Φ (Fig. 5b). The late age of maturity and long lifespan of dogfish means that stochastic fecundity will impact only one or two generations in the 50-year projections, so the impact of a series of good or bad years on the variability in the projections is reduced. This lower variability in stochastic projections for the longer-lived species is also consistent with the results of Goodman (1984). None of the projections for dogfish fell below $0.2B_0$ at $\Phi = 0.05$,

938

Can. J. Fish. Aquat. Sci. Vol. 63, 2006

Fig. 4. Isopleths of yield per recruit as a function of selectivity parameters and fishing pressure expressed as Φ, the fraction of reproductive potential (RP) harvested each year. The corresponding annual change in population size λ' is shown at the top of each figure. (*a*) Adult harvests on *Rhizoprionodon taylori*; (*b*) adult harvests on *Squalus acanthias*; (*c*) juvenile harvests on *Rhizoprionodon taylori*; (*d*) juvenile harvests on *Squalus acanthias*. The vertical lines mark $\Phi_{stationary} = (\lambda - 1)/\lambda$, the value of Φ that leads to a stationary population in a deterministic projection. Shading indicates the fraction of RP in selected ages that is less than Φ.
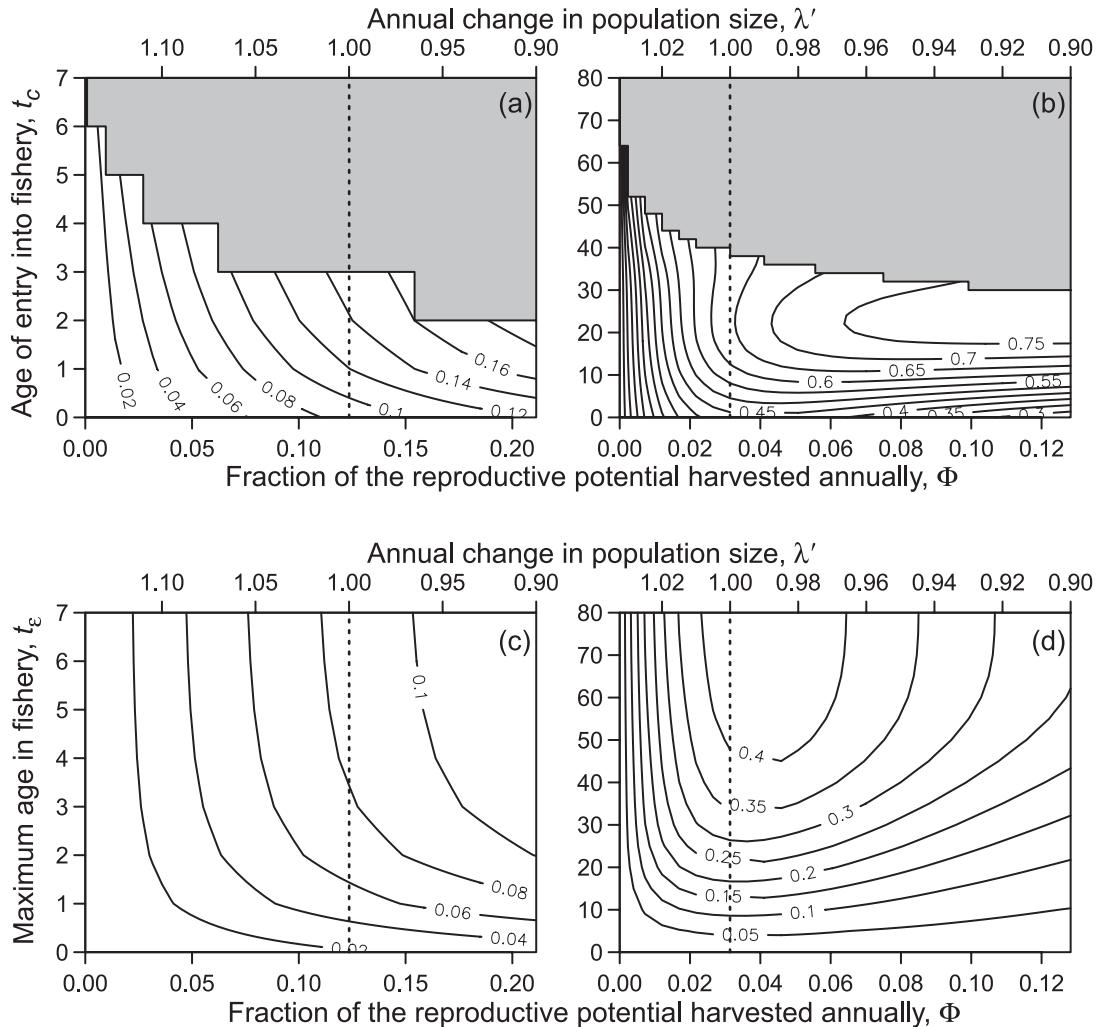
but at $\Phi = 0.08$, all projections fell below this level with the exception of strategies that led to removal of 100% of some ages.

When the harvest level on dogfish was based on the fraction of biomass removed from the population (Fig. 5*d*), the risk was highly dependent on the range of ages selected by the harvest, as with the sharpnose shark. The risk of population depletion was again highest when harvests targeted only juveniles (ages 0–10, 0–20, and 0–30). The harvest targeting the old ages (ages 40–80) was again the most conservative and did not lead to any populations below $0.2B_0$, even when all individuals in these ages were harvested. Harvests on age 0 likewise did not lead to depletions, indicating that if a harvest is going to take place on juveniles, then a very narrow slot limit will reduce the risk of depletion.

In this stochastic framework, Φ is the fraction of observed RP removed in each year, rather than the fraction removed at SAD. However, the connection between risk of population depletion and Φ, independent of the ranges of ages selected by the harvest and in contrast to the more complex relation-

ship between risk of depletion and the fraction of biomass removed, further indicates the utility of using Φ as a measure of the impact of a harvest.

Discussion

RV and RP are applied to the dynamics of harvested shark populations. The argument made here is that the fraction of RP removed from a population is more representative of the impact of harvesting on a population than the traditional instantaneous rate of fishing mortality or other related management tools. This argument is supported by the results above.

MacArthur (1960) discusses RV and removals from a population in the context of optimal predation. He suggests that an optimal predator will remove individuals from the population from those ages that maximize the ratio: value to predator vs. reproductive value. Working with a continuous time model, he also considered the allowable rate of removals. This work was extended by a large body of literature on

Fig. 5. Risk of severe depletion associated with different levels of harvest, as a function of harvesting (*a*) reproductive potential from *Rhizoprionodon taylori*, (*b*) reproductive potential from *Squalus acanthias*, (*c*) biomass from *Rhizoprionodon taylori*, and (*d*) biomass from *Squalus acanthias*. Labels denote the range of ages selected into the harvest for each curve. Dashed sections of the risk curves indicate that over 90% of the projections led to complete removal of some ages classes. The vertical lines in (*a*) and (*b*) mark $\Phi_{stationary} = (\lambda - 1)/\lambda$, the value of Φ that leads to a stationary population in a deterministic projection. Arrows pointing to figure boundaries indicate risk curves that are constant at 0.
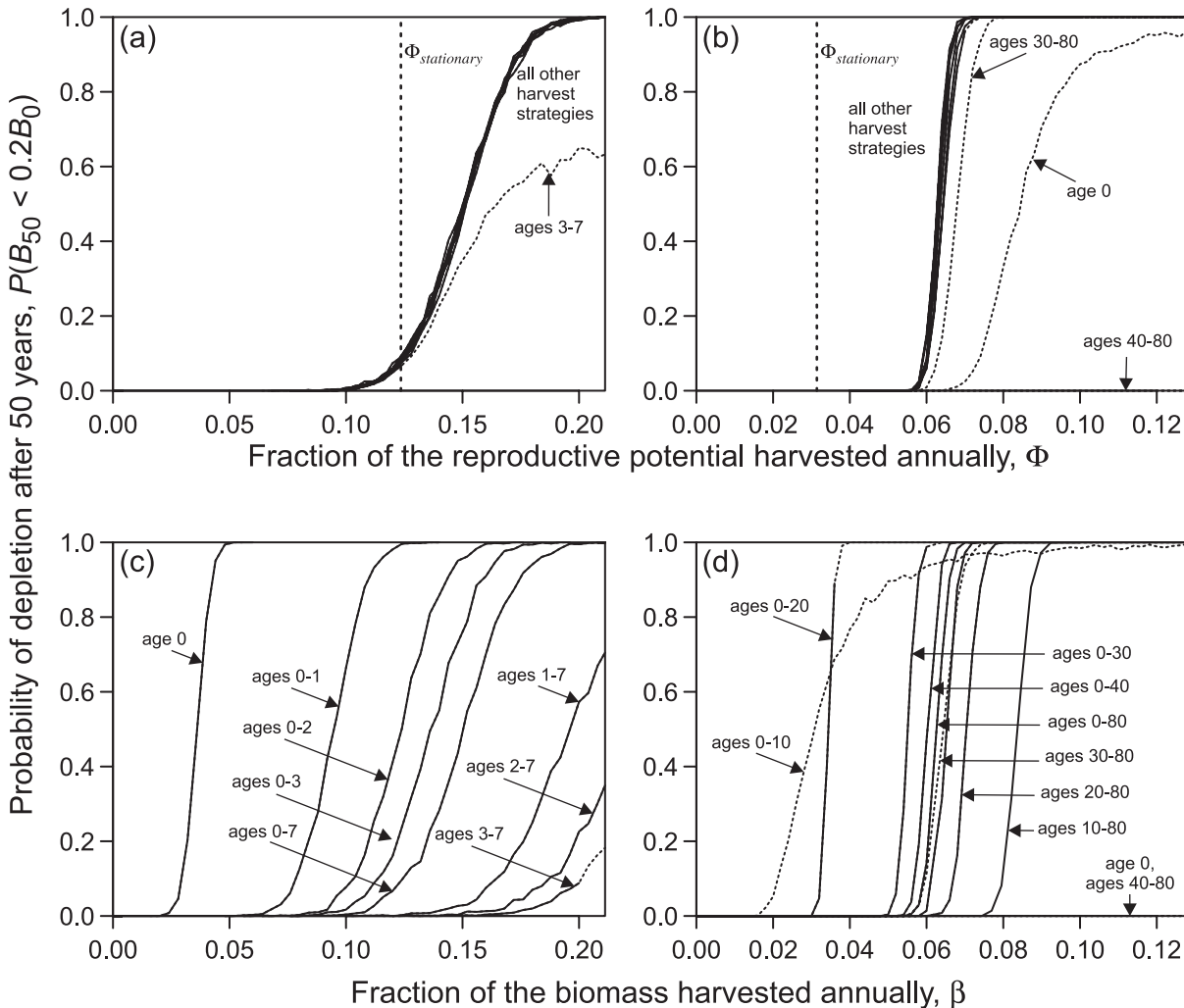
optimal harvests (Beddington and Taylor 1973; Law 1979; Brooks and Lebreton 2001). However, the gear selectivity required for optimal harvests as defined in these papers is unrealistic in most fisheries contexts. The optimal harvest in these papers involves targeting at most two age classes. In contrast, we provide no formulae for optimizing harvest, but instead provide tools for exploring the consequences of different harvest strategies. Goodman (1982) reiterated the more generally applicable idea of MacArthur (1960) that removals from a population should be measured in units of reproductive value lost. Almost a half century after MacArthur, this paper presents new uses of reproductive potential as a measure of fishing effort and a new theorem regarding the connection between the rate of population growth and removals of reproductive potential. It has also been suggested that the proof provides a rigorous foundation for MacArthur's (1960) paper.

The use of RV and RP and their applications comes from the use of the Leslie matrix and its augmented form with a harvest matrix. In our formulation, a harvested population projected with the augmented Leslie matrix will converge to a SAD. Asymptotic stationarity of the harvested population was accomplished by constraining the dominant eigenvalue of the augmented matrix (λ') to 1. With $\lambda' = 1$, populations will converge to a SAD, at which point the population size will be stationary.

The theorem in this paper states that the growth of a population projected by the augmented Leslie matrix is directly linked to the fraction of RP removed from the population, Φ. This holds regardless of the segment of a population that is harvested. A non-zero Φ corresponds to a range of yields, which are associated with a variety of harvest strategies. The reformulation of the Beverton–Holt Y/R model as a function of Φ and the age of entry into the fishery, t_c, or the maximum age in a juvenile harvest, t_ε, provides Y/R isoclines that will look familiar to a stock assessment scientist. It is easy to compare Y/R for the different strategies that lead to stationary harvests as they all correspond to the same value of Φ.

940

Can. J. Fish. Aquat. Sci. Vol. 63, 2006

The approach used here shares some properties with elasticity analysis (Caswell 2001), which has been used extensively in the elasmobranch literature (Heppell et al. 1999; Cortés 2002; Mollet and Cailliet 2002). Although mathematically related, RP differs from elasticity in important ways. Both make use of RV to identify the relative vulnerability of a population to impacts on different population segments. However, whereas elasticity is a measure of the Leslie matrix only, RP combines RV from the Leslie matrix with the numbers-at-age in the population. Therefore, RP can be used to track changes in a population over time (Leaman 1987, 1991; Katsukawa et al. 2002). Also, although elasticity can provide an approximation to the effect of a given harvest (Caswell 2001), the theorem in this paper linking population growth directly to the removal of RP allows the use of the fraction of RP removed, Φ, as an alternative measure of fishing effort.

Any application of this theorem and associated theory must rest on two different aspects of the real world: density-dependent effects and stochastic environments. Density dependence was not considered in this analysis for two reasons. First, the insight found in considering simpler models should provide a platform on which to build further research as our understanding of density dependence in elasmobranchs (Smith et al. 1998) increases. Second, a population kept at a given size will have constant survival and recruitment even in density-dependent models. Therefore, the problem of keeping the population stationary at any particular size in a density-dependent model is equivalent to the density-independent problem of maintaining a stationary population with the corresponding set of population parameters (Quinn and Szarzi 1993). That the implications of the theorem also apply outside the deterministic framework is indicated by the results of the risk analysis in which removal of RP was directly linked to the probability of population depletion. The next two sections compare the use of RV and RP.

Reproductive value

The term reproductive value has connotations of a measure that should be preserved or even maximized. Indeed, the equivalence between maximizing fitness (measured by λ) and maximizing RV has been debated in a series of papers on optimal life history strategies (Schaffer 1974; Yodzis 1981; Caswell 1982). All harvests in the density-independent model used in this paper reduce the dominant eigenvalue and thus reduce fitness as it is defined in the optimal life history literature. When a range of ages that includes juveniles is harvested from either species, the RV for some ages increases above the level associated with no harvest. However, when a single age is harvested, the RV of that one age is below the unharvested level, even if the RV of other ages is above. This is a consequence of both the constraint that all harvests result in a stationary population size and the strongly nonlinear relationship between RV and the harvest matrix parameters. These results are consistent with those of Yodzis (1981) that maximizing fitness is equivalent only to RV maximized with respect to the reproductive effort at a given age but not with respect to reproductive effort of all ages. In the results above, decreases in the eigenvalue of the augmented matrix correspond to decreases in the RV of a single harvested age, but not decreases in RV of all ages simultaneously.

The contrast between changes in RV associated with juvenile harvests and those associated with adult harvests suggests that changes in RV, especially for the older ages, are not good indicators of the effect of a harvest on the potential for growth of a population. Without more information than RV, such as the age distribution of the population, the effect of a harvest cannot be evaluated. Two harvests that are constrained to maintain stationary population sizes may lead to opposite effects on the RV of some ages. It follows that RP, as a sum of the unharvested RV over all individuals in the population, has the potential to be a better indicator of the impacts of a harvest because it includes information about the age distribution.

Reproductive potential

The framework presented in this paper is applicable to a wide variety of species. We focused on shark populations because they are harvested, they range greatly in longevity, and they are the objects of considerable conservation interest. The RP framework was used here to demonstrate that the short-lived Australian sharpnose shark was more susceptible to recruitment overfishing than growth overfishing, whereas the long-lived spiny dogfish is susceptible to both growth overfishing and recruitment overfishing, especially when juveniles are selected into the fishery. For both species, juvenile harvests lead to a greater risk of depletion than harvests that remove the same fraction of the population's biomass from adults. This pattern holds for both species and is likely to be characteristic of shark populations in general. Thus, the intuitive guideline that harvesting of juveniles endangers a population has here been given a mathematical foundation. These results also highlight one concern over the use of surplus production models, because the impacts of a suggested harvest rate may be highly dependent on the range of ages harvested.

Although only two species were considered here, and the knife-edged selectivity functions considered in the paper are only an approximation to true selectivity patterns, the benefits in yield and reduction in risk associated with harvesting the oldest possible segment of the population likely apply to many shark fisheries. Exceptions to this general rule may occur when the range of ages selected by a juvenile fishery is very narrow. In such gauntlet fisheries (Simpfendorfer 1999*b*), only high levels of effort would remove too much reproductive potential from the population. Likewise, for species where the oldest individuals are found to be the most successful spawners, the RV would reflect this, and lower fishing pressure on these oldest ages might be preferred. However, when a fishery, either artisanal or commercial, does harvest juveniles, any concurrent harvest of adults likely imperils the population.

In addition to demonstrating the benefits of avoiding harvests on juvenile sharks, the analyses in the paper have shown the utility of measures based on RP. Although survival and fecundity rates for an individual species are required to compute RV and RP, the analysis of long- and short-lived shark species identified similar trade-offs between sustainable yield and the selection of juveniles. These patterns may be used to guide the management of fisheries on species for which less information is available.

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References

Beddington, J.R., and Taylor, D.B. 1973. Optimum age specific harvesting of a population. Biometrics, **29**: 801–809.

Beverton, R.J.H., and Holt, S.J. 1957. On the dynamics of exploited fish populations. Fish. Invest. Ser. 2 Mar. Fish. G.B. Minist. Agric. Fish. Food No. 19.

Brooks, E.N., and Lebreton, J.D. 2001. Optimizing removals to control a metapopulation: application to the yellow legged herring gull (*Larus Cachinnans*). Ecol. Model. **136**: 269–284.

Cailliet, G.M. 1992. Demography of the central California population of the leopard shark (*Triakis semifasciata*). Mar. Freshw. Res. **43**: 183–193.

Castillo-Géniz, J.L., Márquez-Farias, J.F., Rodriguez de la Cruz, M.C., Cortés, E., and Cid del Prado, A. 1998. The Mexican artisanal shark fishery in the Gulf of Mexico: towards a regulated fishery. Mar. Freshw. Res. **49**: 611–620.

Caswell, H. 1982. Optimal life histories and the maximization of reproductive value: a general theorem for complex life cycles. Ecology, **63**: 1218–1222.

Caswell, H. 2001. Matrix population models: construction, analysis and interpretation. 2nd ed. Sinauer Associates, Sunderland, Mass.

Cortés, E. 1998. Demographic analysis as an aid in shark stock assessment and management. Fish. Res. **39**: 199–208.

Cortés, E. 1999. A stochastic stage-based population model of the sandbar shark in the western North Atlantic. *In* Life in the slow lane: ecology and conservation of long-lived marine animals. *Edited by* J.A. Musick. American Fisheries Society, Bethesda, Md. pp. 115–136.

Cortés, E. 2002. Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. Conserv. Biol. **16**: 1048–1062.

Fisher, R.A. 1930. The genetical theory of natural selection. Oxford University Press, London, UK.

Frisk, M.G., Miller, T.J., and Fogarty, M.J. 2002. The population dynamics of little skate *Leucoraja Erinacea*, winter skate *Leucoraja Ocellata*, and barndoor skate *Dipturus Laevis*: predicting exploitation limits using matrix analyses. ICES J. Mar. Sci. **59**: 576–586

Gabriel, W.L., and Mace, P.M. 1999. A review of biological reference in the context of the precautionary approach. *In* Proceedings of the Fifth National NMFS Stock Assessment Workshop. *Edited by* V.R. Restrepo. NOAA Tech. Memo. No. NMFS-F/SPO-40. pp. 34–45.

Gallucci, V.F., and Quinn, T.J. 1979. Reparameterizing, fitting, and testing a simple growth-model. Trans. Am. Fish. Soc. **108**: 14–25.

Gallucci, V.F., Saila, S.B., Gustafson, J., and Rothschild, B.J. (*Editors*). 1996. Stock assessment: quantitative methods and applications for small-scale fisheries. CRC Press, Boca Raton, Florida.

Goodman, D. 1982. Optimal life histories, optimal notation, and the value of reproductive value. Am. Nat. **119**: 803–823.

Goodman, D. 1984. Risk spreading as an adaptive strategy in iteroparous life histories. Theor. Popul. Biol. **25**: 1-20.

Heppell, S.S., Crowder, L.B., and Menzel, T.R. 1999. Life table analysis of long-lived marine species with implications for conservation and management. *In* Life in the slow lane: ecology and conservation of long-lived marine animals. *Edited by* J.A. Musick. American Fisheries Society, Bethesda, Md. pp. 137–148.

Hoenig, J.M. 1983. Empirical use of longevity data to estimate mortality rates. Fish. Bull. **81**: 898–903.

Hoenig, J.M., and Gruber, S.H. 1990. Life-history patterns in the elasmobranchs: implications for fisheries management. *In* Elasmobranchs as living resources: advances in the biology, ecology, systematics, and the status of the fisheries. *Edited by* H.L. Pratt, Jr., S.H. Gruber, and T. Taniuchi. NOAA Tech. Rep. NMFS No. 90. pp. 1–16.

Katsukawa T., Matsuda, H., and Matsumiya, Y. 2002. Population reproductive potential: evaluation of long-term stock productivity. Fish. Sci. **68**: 1106–1112

Ketchen, K.S. 1972. Size at maturity, fecundity, and embryonic growth of the spiny dogfish (*Squalus acanthias*) in British Columbia waters. J. Fish. Res. Board Can. **29**: 1717–1723.

Ketchen, K.S. 1975. Age and growth of dogfish *Squalus acanthias* in British Columbia waters. J. Fish. Res. Board Can. **32**: 43–59.

Kroese, M., and Sauer, W.H.H. 1998. Elasmobranch exploitation in Africa. Mar. Freshw. Res. **49**: 573–577.

Lai, H.L., Mug, M., and Gallucci, V.F. 1993. Management strategies for the tropical corvina reina, *Cynoscion albus*, in a multi-mesh size gillnet artisanal fishery. *In* Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations, Anchorage, Alaska, 21–24 October 1992. *Edited by* G. Kruse. University of Alaska, Fairbanks, Alaska. Alaska Sea Grant Rep. No. 93-2. pp. 21–37.

Law, R. 1979. Harvest optimization in populations with age distributions. Am. Nat. **114**: 250–259.

Leaman, B.M. 1987. Incorporating reproductive value into Pacific ocean perch management. *In* Proceedings of the International Rockfish Symposium, 20–23 October 1986, Anchorage, Alaska. *Edited by* B.R. Metleff. University of Alaska, Anchorage, Alaska. Alaska Sea Grant Rep. No. 87-2. pp. 355–368.

Leaman, B.M. 1991. Reproductive styles and life-history variables relative to exploitation and management of *Sebastes* stocks. Environ. Biol. Fishes, **30**: 253–271.

Lefkovitch, L.P. 1967. A theoretical evaluation of population growth after removing individuals from some age groups. Bull. Entomol. Res. **57**: 437–445.

Leslie, P.H. 1948. Some further notes on the use of matrices in population mathematics. Biometrika, **35**: 213–245.

Lotka, A.J. 1907. Relation between birth rates and death rates. Science (Washington, D.C.), **26**: 21–22.

MacArthur, R.H. 1960. On the relation between reproductive value and optimal predation. Proc. Nat. Acad. Sci. U.S.A. **46**: 143–145.

McAllister, M.K., Pikitch, E.K., and Babcock, E.A. 2001. Using demographic methods to construct Bayesian priors for the intrinsic rate of increase in the Schaefer model and implications for stock rebuilding. Can. J. Fish. Aquat. Sci. **58**: 1871–1890.

McFarlane, G.A., and King, J.R. 2003. Migration patterns of spiny dogfish (*Squalus acanthias*) in the North Pacific Ocean. Fish. Bull. **101**: 358–367.

Mollet, H.F., and Cailliet, G.M. 2002. Comparative population demography of elasmobranchs using life history tables, Leslie matrices and stage-based matrix models. Mar. Freshw. Res. **53**: 503–516.

Musick, J.A. (*Editor*). 1999. Ecology and conservation of long-lived marine animals. *In* Life in the slow lane: ecology and conservation of long-lived marine animals. American Fisheries Society, Bethesda, Md. pp. 1–10.

942

Can. J. Fish. Aquat. Sci. Vol. 63, 2006

Punt, A.E., and Walker, T.I. 1998. Stock assessment and risk analysis for the school shark (*Galeorhinus galeus*) resource off southern Australia. Mar. Freshw. Res. **49**: 719–731.

Quinn, T.J., II, and Deriso, R.B. 1999. Quantitative fish dynamics. Oxford University Press, New York.

Quinn, T.J., II, and Szarzi, N.J. 1993. Determination of sustained yield in Alaska's recreational fisheries. *In* Proceedings of the International Symposium on Management Strategies for Exploited Fish Populations, Anchorage, Alaska, 21–24 October 1992. *Edited by* G. Kruse. University of Alaska, Fairbanks, Alaska. Alaska Sea Grant Rep. No. 93-2. pp. 61–84.

Saunders, M.W., and McFarlane, G.A. 1993. Age and length at maturity of the female spiny dogfish, *Squalus acanthias*, in the Strait of Georgia, British Columbia, Canada. Environ. Biol. Fishes, **38**: 49–57.

Schaffer, W.M. 1974. Selection for optimal life histories: the effects of age structure. Ecology, **55**: 291–303.

Simpfendorfer, C.A. 1999*a*. Mortality estimates and demographic analysis for the Australian sharpnose shark, *Rhizoprionodon taylori*, from Northern Australia. Fish. Bull. **97**: 978–986.

Simpfendorfer, C.A. 1999*b*. Demographic analysis of the dusky shark fishery in south-western Australia. *In* Life in the slow lane: ecology and conservation of long-lived marine animals. *Edited by* J.A. Musick. American Fisheries Society, Bethesda, Md. pp. 149–160.

Smith, S.E., Au, D.W., and Show, C. 1998. Intrinsic rebound potentials of 26 species of Pacific sharks. Mar. Freshw. Res. **49**: 663–678.

Taylor, I.G., and Gallucci, V.F. 2005. Using reproductive value to evaluate surplus production models for sharks. *In* Proceedings of 21st Lowell Wakefield Fisheries Symposium: Fisheries Assessment and Management in Data-Limited Situations, Anchorage, Alaska, 22–25 October 2003. *Edited by* G. Kruse, V.F. Gallucci, D.E. Hay, R.I. Perry, R.M. Peterman, T.C. Shirley, P.D. Spencer, B. Wilson, and D. Woodby. University of Alaska, Fairbanks, Alaska. Alaska Sea Grant Rep. No. 05-2. pp. 807–829.

Yodzis, P. 1981. Concerning the sense in which maximizing fitness is equivalent to maximizing reproductive value. Ecology, **62**: 1681–1682.