

Demographic and risk analyses of spiny dogfish (*Squalus suckleyi*) in the Gulf of Alaska using age- and stage-based population models

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Abstract. Demographic models are useful tools for assessing data-limited species and may be an appropriate alternative to cohort analyses for sharks due to their long-lived, slow-growing nature. In this study, age- and stage-based demographic analyses were conducted to examine the intrinsic rebound potential (r) and potential risk of fishing for spiny dogfish (*Squalus suckleyi*) in the Gulf of Alaska. Monte Carlo simulations were conducted to incorporate input parameter uncertainty. For an unfished population, r was estimated to be $0.02\text{--}0.03\text{ year}^{-1}$. Fishing mortalities (F) of $F = 0.04$ and 0.03 (age- and stage-based models respectively), resulted in $r = 0$, indicating that populations fished at higher F are not sustainable. Harvest strategies targeting juveniles (age-based model) and subadults (stage-based model) caused the highest risk of the population falling below defined thresholds (B_{MSY} , $B_{40\%}$ and $B_{50\%}$) after 20 years. The age- and stage-based models provided similar estimates of r and sustainable fishing mortality, suggesting that the stage-based model is an appropriate substitute for the age-based model in this case. *S. suckleyi* and the closely related *S. acanthias* are often harvested around the world and this modelling approach could be useful to the management of these species and other sharks where data is limited.

Additional keywords: elasmobranch, Leslie models, model comparison, shark.

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Introduction

Classic demographic models are used often in lieu of or to strengthen stock assessments. In the case of elasmobranchs, demographic models are generally based only on fundamental biological information (i.e. vital rates) about a species, such as natural mortality and fecundity schedules, to estimate population growth rate or growth potential, along with age distributions, reproductive potential and generation times (Caughley 1977; Caswell 2001). These types of models became popular for modelling elasmobranch populations in the 1990s when data to perform more complex population dynamics models was lacking (Cailliet 1992; Cortés 1998; Simpfendorfer *et al.* 2005). These models can also be used to examine how a population reacts to fishing pressure (Cortés 1998; Smith *et al.* 1998; Beerkircher *et al.* 2003) and can include regional distribution and migration parameters (Heifetz and Quinn 1998). Although demographic models can be complex, including migration rates and regional abundances (e.g. Heifetz and Quinn 1998), they are also ideal for populations with data limitations, such as fishery-dependent data and are well suited for simulations of hypothetical scenarios when vital rates are poorly known (Cortés 2002).

Compared with other approaches, demographic models have several advantages and disadvantages. In terms of advantages, modelling results can be compared between models as biological reference points or indicators of a population's status, they allow for examination of constraints imposed by life history traits and they permit examination of fishing effects and migration on a species (Heifetz and Quinn 1998; Smith *et al.* 1998; Gallucci *et al.* 2006). Unfortunately, most examples of demographic population models provide only a static species-specific assessment, because vital rates are assumed to be constant over time (Cortés 1998). Thus, they do not account for dynamics owing to density dependence, migration or a changing environment (Gedamke *et al.* 2007). If the parameters for density dependence or migration rates are known, they can be incorporated into the model to correct this drawback (Heifetz and Quinn 1998; Caswell 2001). Moreover, because these models can be run with minimal data (only requiring fecundity and natural mortality at a minimum), they can overlook the influences of migration when estimating a population's potential for growth or ability to rebound from exploitation. Nonetheless, demographic models can be powerful tools for strategic management advice.

Demographic models have not been previously developed for *Squalus suckleyi* in the Gulf of Alaska (GOA). Attempts have been made to develop biomass models for the species (e.g. Rice 2007), but because *S. suckleyi* are a non-target species catch data do not provide a good metric to build a model around and *S. suckleyi* are generally not well sampled by existing surveys (Tribuzio *et al.* 2010). Until 2010, *S. suckleyi* in the North Pacific Ocean were considered the same species as those in the North and South Atlantic Oceans, Mediterranean, North and Black Seas and the South Pacific Ocean (*S. acanthias*, Ebert *et al.* 2010). Due to the name change, all previous literature on *S. acanthias* in the North Pacific Ocean is considered as *S. suckleyi* research. Although the volume of literature regarding *S. suckleyi* is growing, very little research into the population dynamics has been published and therefore many comparisons will be made between the two similar species throughout the paper. In many other regions where *S. suckleyi* and *S. acanthias* have been commercially harvested, such as the North Atlantic and North-east Pacific Oceans (Canadian and Washington State waters), *S. suckleyi* and *S. acanthias* have either become a management concern (King and McFarlane 2009) or worse, overfished (Rago *et al.* 1998). Both species have characteristics rendering them highly susceptible to overfishing: long-lived, late-maturing, slow growth and low fecundity (Rago *et al.* 1998; King and McFarlane 2009). In the GOA, *S. suckleyi* are not commercially targeted; however, by-catch of the species can be high in some fisheries. The global demand for both *S. suckleyi* and *S. acanthias* is high and it is possible that a market for GOA *S. suckleyi* could develop. The history of *S. suckleyi* (and *S. acanthias*) fisheries in other jurisdictions, as well as the life history characteristics of the species, indicate that *S. suckleyi* fisheries in the GOA should be developed in a precautionary manner.

The primary goal of our research was to create a demographic model for the GOA *S. suckleyi* population. Our secondary goal was to determine if a stage-based demographic model would be an appropriate substitute for a fully age-structured demographic model. Using Monte Carlo simulations, we examined the effects of natural variability, variability among published life history traits and multiple harvest scenarios for the GOA population (Cortés 2002). Lastly, we conducted a risk analysis for different harvest scenarios (Burgman *et al.* 1993; Aires-da-Silva and Gallucci 2007). Although this analysis is centred on a specific population of *S. suckleyi*, we believe that the results of this study will be broadly applicable to other data-limited shark species and further to other taxa.

Materials and methods

Sampling area

The GOA is a large basin at the far north of the North Pacific Ocean, extending from Dixon Entrance (at the USA/Canadian border) to the western Aleutian Islands (Fig. 1). Catch of *Squalus suckleyi* in the Bering Sea is limited and the GOA is believed to be the far northern extent of the distribution. Studies have shown that a small number of *S. suckleyi* may migrate into or out of the GOA and suggest that subpopulations may also exist (Taylor 2008; C. A. Tribuzio, unpublished data). However, the rate of movement between groups and distinct population

boundaries are unknown. For this study, *S. suckleyi* in the GOA were considered a distinct closed population. This analysis should be considered the most conservative case and as detailed migration and movement data become available, the model can be adapted accordingly.

Age class and stage class models

Two forms of demographic models were used in this study: age-structured and stage-structured (Brewster-Geisz and Miller 2000; Caswell 2001; Frisk *et al.* 2002). These types of models are convenient and easily implemented because they require only basic life history information (Simpfendorfer 2005). Both models incorporate female data only; males are not considered in the context of the population demographics. The basic formulation for both models is:

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

where N_t is the vector of numbers of animals at each age class at time t and \mathbf{M} is the transition or projection matrix composed of survival and fecundity for each age (Caswell 2001; Simpfendorfer 2005). The models in our study ignore the possible impact of density dependence on parameters such as survival, fecundity and growth. The mechanisms of density dependence are largely theoretical at this time and it was beyond the scope of this study to examine those effects, therefore we assumed density independence (Walker 1998).

The projection matrix \mathbf{M} differs for each model (all parameters described below are summarised in Table S1, available as an Accessory Publication to this paper). For the age-based model, animals in each year class must move to the next year class (see Fig. S1, available as an Accessory Publication to this paper), thus, \mathbf{M} is a Leslie matrix of the form (Caswell 2001; Aires-da-Silva and Gallucci 2007):

$$\mathbf{M} = \begin{bmatrix} f_0 & f_1 & \cdots & f_{i-1} & f_i \\ l_0 & 0 & \cdots & 0 & 0 \\ 0 & l_1 & \cdots & 0 & 0 \\ 0 & 0 & \cdots & l_{i-1} & 0 \end{bmatrix}, \quad (2)$$

where i is the age class, l is the age-specific survivorship and f is age-specific per-capita fecundity rate (fertility). Survivorship was calculated as a function of l_{i-1} and the total mortality (Z), which is the sum of fishing (F) and natural mortality (M):

$$l_i = l_{i-1}e^{-Z}. \quad (3)$$

We assumed a birth-pulse, post-breeding census, where birth occurs at the end of the year and fertility (f_i) is given by

$$f_i = l_i b_i, \quad (4)$$

where b_i is the age-specific female fecundity (the number of female pups produced by each female each year). *S. suckleyi* have been aged to at least 100 years in the north-eastern Pacific Ocean (G. A. McFarlane, personal communication), so we included a maximum of 120 age classes depending on the random distribution for longevity (see below).

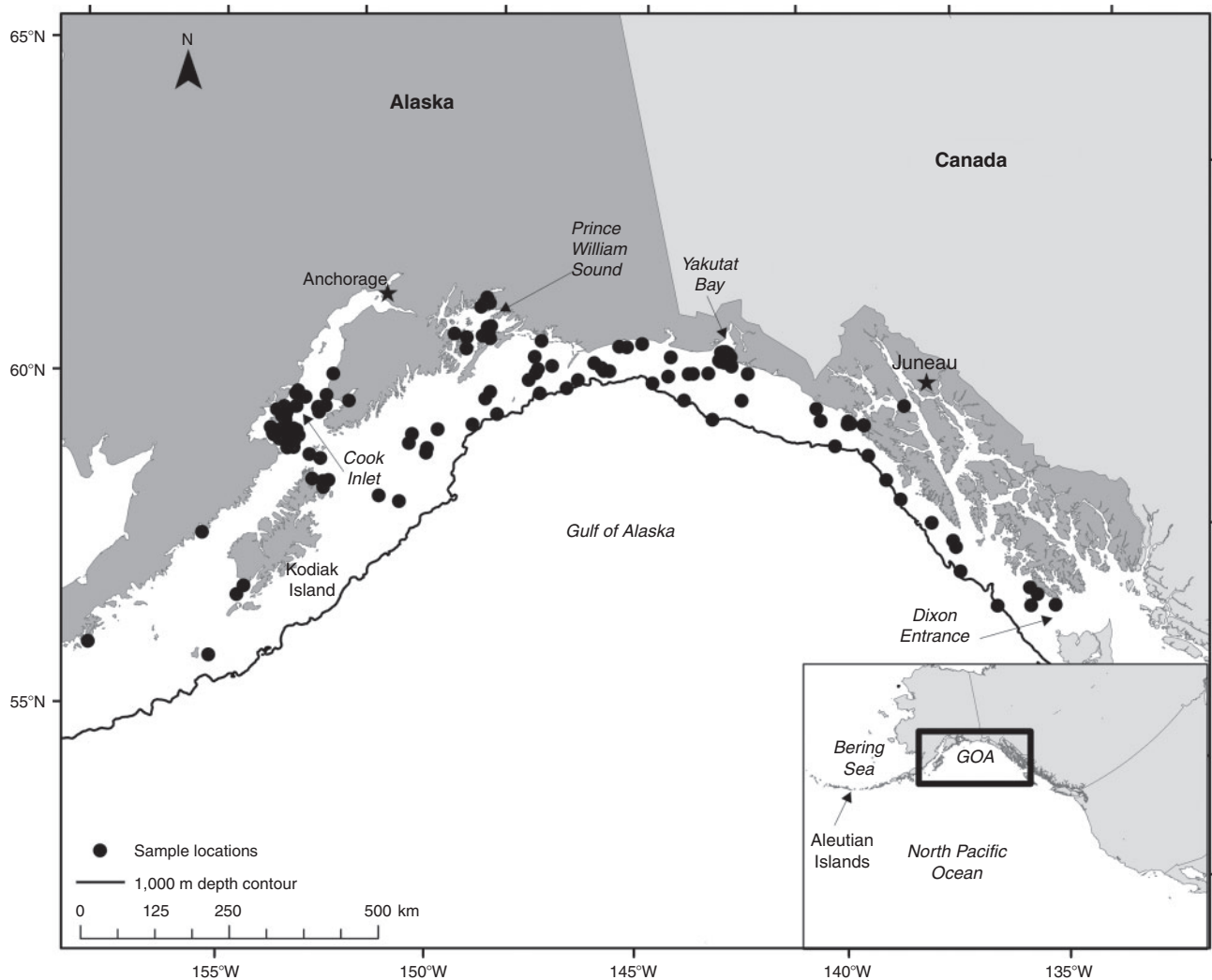


Fig. 1. Map of the Gulf of Alaska showing sampling locations.

The stage-based model was developed with five classes (Fig. S1): neonates, juveniles, subadults, adults-pregnant and adults-resting. Stages and durations were determined by reviewing the species' life history (Tribuzio and Kruse in press). Neonates (*N*) are the young-of-the-year and must either die or survive to the next stage in 1 year. Juveniles (*J*) tend to inhabit shallower, inshore waters, do not mix with the adult schools and are not susceptible to the fishery. Subadults (*S*) move out of the nursery areas and do mix with the schools of larger adults and are susceptible to fishing. Mature female *S. suckleyi* could either be pregnant (*AP*, adult-pregnant) or not (*AR*, adult-resting) and can go back and forth between these two stages. Gestation is 18–22 months for *S. suckleyi*, which determines the 2 year duration for adult-pregnant. There is some evidence that females may skip a year between pregnancies in the GOA (Tribuzio and Kruse in press). However, this has not been observed in *S. suckleyi* populations at lower latitudes (Tribuzio *et al.* 2009). The resting stage was defined such that a female that proceeded to this stage must return to the pregnant stage after 1 year and a pregnant female may either return to the pregnant stage or proceed to the resting stage.

The resulting five stage projection matrix is:

$$\mathbf{M} = \begin{bmatrix} 0 & 0 & 0 & f_{AP} & 0 \\ G_N & P_J & 0 & 0 & 0 \\ 0 & G_J & P_S & 0 & 0 \\ 0 & 0 & G_S & P_{AP} & G_{AR} \\ 0 & 0 & 0 & G_{AP} & 0 \end{bmatrix}, \quad (5)$$

where G_x is the product of the probability of an individual in stage x surviving (σ) and the probability of shifting to another stage (γ), such that $G_x = \sigma_x \gamma_x$ and P_x is the probability of an individual surviving and remaining in its current stage: $P_x = \sigma_x(1 - \gamma_x)$ (Brewster-Geisz and Miller 2000; Frisk *et al.* 2002). The σ_x over a single stage can be written $\sigma_x = e^{-Z_x}$. Estimates of γ_x are calculated by:

$$\gamma_x = \frac{\left(\frac{\sigma_x}{\lambda_{init}}\right)^{t_x} - \left(\frac{\sigma_x}{\lambda_{init}}\right)^{t_x-1}}{\left(\frac{\sigma_x}{\lambda_{init}}\right)^{t_x} - 1}, \quad (6)$$

where t_x is the duration of stage x , which assumes that all individuals within a stage have equal survival (Caswell 2001). The initial population growth rate, λ_{init} , is a starting value which is determined by iteratively changing it in the stage model (before incorporating the stochastic variables) until it equals the population growth rate (λ) from the eigenvector.

Model results were calculated by solving the Euler–Lotka equation (Caughley 1977) and were the same for each model. Resultant parameters included: instantaneous rate of increase (r , also called the rebound potential), λ ($\lambda = e^r$), net reproductive rate or the total number of female offspring produced per individual in a single cohort (R_0), generation time or the time for the population to increase by R_0 ($t = \ln R_0 / \ln \lambda$), the mean age of the parents of a cohort (μ_1) and the population doubling time ($t_{x2} = \ln(2)/r$). The right eigenvector, \mathbf{w} , represents the stable age or stable stage distributions (SAD or SSD respectively) and the left eigenvector, \mathbf{v} , the reproductive values (RV) which are the proportions at age or stage and the contribution of offspring by each age class to future classes for a stable population ($r=0$) respectively. Elasticities (e_{kj}) were estimated to examine how the r is affected by changes in individual age/stage survival and fecundity using the equation (Heppell *et al.* 1999; Caswell 2001):

$$e_{kj} = \frac{m_{kj}}{\lambda} \frac{v_k w_k}{\langle \mathbf{w}, \mathbf{v} \rangle}, \quad (7)$$

where m_{kj} are the elements of \mathbf{M} , \mathbf{v} and \mathbf{w} are the left and right eigenvectors of \mathbf{M} and $\langle \mathbf{w}, \mathbf{v} \rangle$ is the scalar product of \mathbf{v} and \mathbf{w} . Elasticities are additive and the sum of the elasticities over all k and j must equal 1.

Model scenarios and stochasticity

The purpose of these models was to examine how output parameters changed with varying input parameters, either through natural variability or hypothetical scenarios. There were three model scenarios run for each the age- and stage-based models (Table S2, available as an Accessory Publication to this paper): (1) no fishing; (2) with fishing effects; and (3) with varying entry into the fishery. Both the age- and stage-based models were run with $F=0$ (scenario 1) to determine the parameters of an assumed virgin population (i.e. $Z=M$), then F was included at varying levels (scenario 2) to examine the effects of different fixed harvest rates on the population ($Z=F+M$). We then changed the entry into the fishery to different ages or stages to examine for which combinations of time of entry and F the r was above 0, thus, sustainable (scenario 3). Fishing mortality was applied uniformly across the age or stage classes that were susceptible to fishing (i.e. knife edge selectivity).

Although many studies of *S. suckleyi* age, growth, life history and movement have been conducted, there remains a great deal of uncertainty in parameter estimates. Statistical distributions (probability density functions (pdfs) for continuous variables, or probability mass functions (pmfs) for discrete variables) were defined for input parameters to account for this uncertainty or natural variability (Cortés 2002). Monte Carlo simulations were run and involved randomly drawing each input parameter from the defined distributions and recording the model output

parameters for that ‘population’. The average of 10 000 replications was taken as the parameter value with 95% confidence intervals being the 2.5th and 97.5th percentile. Model calculations and simulations were run using Poptools (www.poptools.org, accessed 15 December 2010).

Stochasticity for l and longevity (t_{max}) was based on the distribution of M . A triangular pdf was defined for M based on Tribuzio and Kruse (in press) with the median M estimate (0.054) as the most likely value and the minimum (0.011) and maximum (0.101) estimates forming the range. The estimates of M were converted to survivorship ($l = e^{-Z}$, where $Z = F + M$) (Fig. S2a, available as an Accessory Publication to this paper). The t_{max} was calculated as $t_{\text{max}} = -\ln(0.01)/M$ (Hewitt and Hoenig 2005) and a similar triangular pmf was used with the minimum, median and maximum longevity estimates (Fig. S2b).

Age at first capture (t_c) (or age of entry into the fishery) was fixed at 4 years (the youngest age encountered in GOA dogfish sampling) for scenarios 1 and 2 and allowed to vary uniformly between zero and 60 years for scenario 3. Stage at first capture (s_c) was fixed at the subadult stage for scenarios 1 and 2 and allowed to vary between neonates and adult-pregnant for scenario 3. The pmf for the age at 50% maturity (t_m) was a normal distribution with a mean of 34 years and standard deviation of 7 years (Tribuzio and Kruse in press; Fig. S2c).

In general, b was based on the total number of pups, a 1:1 sex ratio of pups and a 2 year reproductive cycle (Tribuzio *et al.* 2009). The random normal pdfs were defined by the averages and standard deviations of b_i for each age class for the age-based model and the overall population average b and standard deviation of b (4.9 ± 1.7 female pups/female, Tribuzio and Kruse in press) for the stage-based model (Fig. S2d, e).

The durations of the juvenile and subadult classes in the stage model were also allowed to vary due to uncertainty around t_m . The t_m marked the end of the subadult stage and t_c marked the end of the juvenile stage. Thus, the juvenile stage duration was t_c minus one (for the neonate stage) and the subadult stage duration was the random t_m minus the juvenile stage duration then minus one.

Risk assessment

We conducted a risk assessment to explore the probabilities of a population declining to a threshold value at given levels of F (Burgman *et al.* 1993). Starting values were based on Rice (2007), who estimated a biomass for 2006 ($B_{2006} \sim 1.5$ million metric tonnes (t)), maximum sustainable yield ($MSY = 24\,080$ t) and biomass at which MSY can occur ($B_{MSY} \sim 0.9$ million t). In this case, $B_{MSY} = 63\%$ of B_{2006} which is $B_{63\%}$. Biomass was converted to numbers of females with an average weight and a 1:1 sex ratio. Fisheries management in the GOA is based on limit and target reference points, such as B_{MSY} or $B_{35\%}$ and $B_{40\%}$ (biomass that is 35 or 40% of the virgin biomass, the former of which is used as a proxy for B_{MSY} , respectively, and their associated fishing mortality rates (F_{MSY} , $F_{35\%}$ and $F_{40\%}$). However, inflection points ($\sim B_{MSY}$) on population growth curves for sharks tend to occur at biomass values $> B_{50\%}$ (Cortés 2007; Simpfendorfer *et al.* 2008) and it has been argued that management should strive to maintain biomass of less-productive

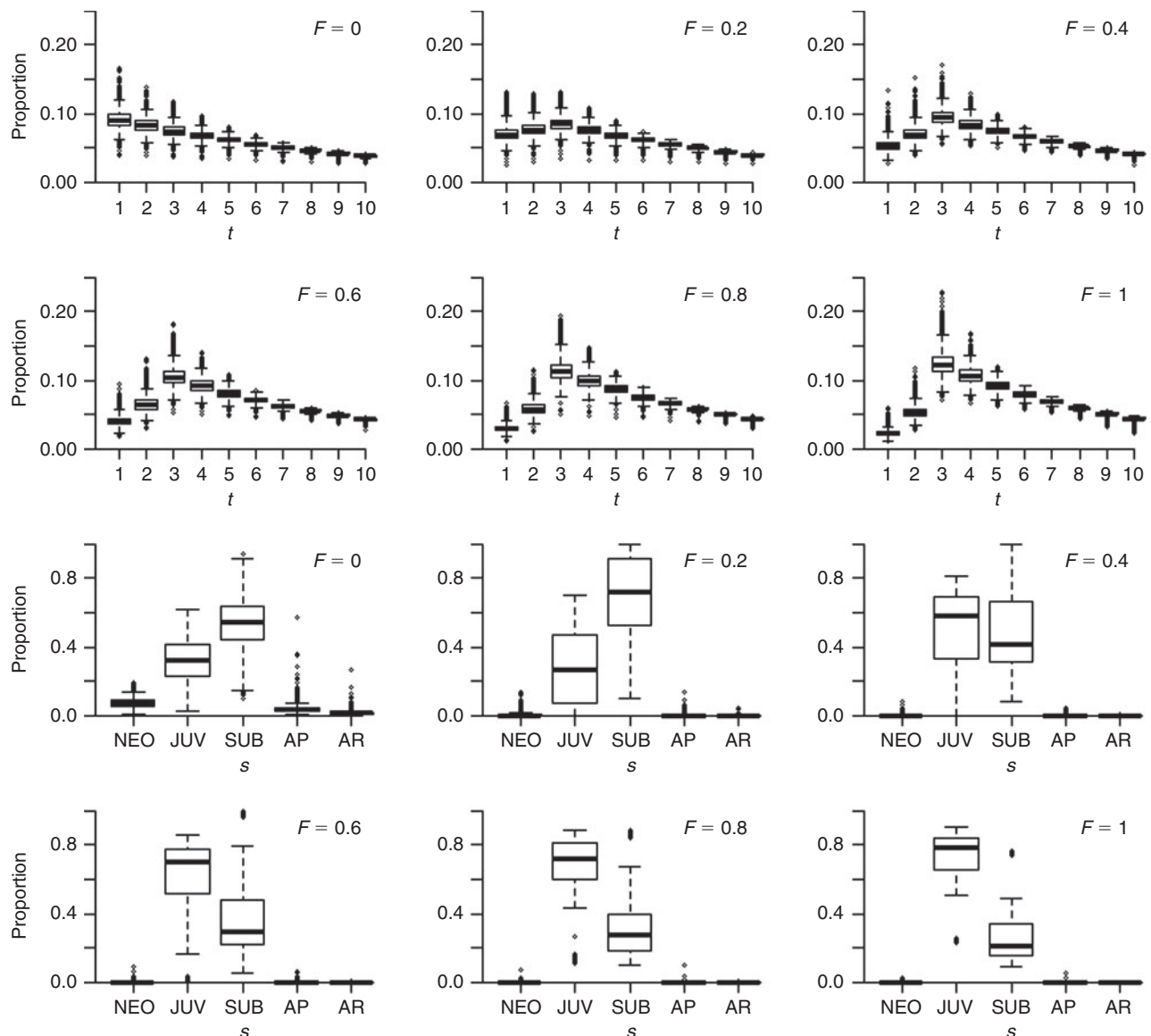


Fig. 2. Stable age and stage distributions at varying levels of instantaneous fishing mortality (F), truncated at 10 years for clarity. The top two rows are age distributions at $F = 0, 0.2, 0.4, 0.6, 0.8$ and 1.0 . The bottom two rows are the stage distributions at the same levels of F .

shark populations, such as *S. suckleyi*, well above B_{MSY} levels owing to time lags associated with their delayed maturity and high longevity (Musick *et al.* 2000). Therefore, for this study we chose to evaluate three threshold values, B_{MSY} , $B_{40\%}$ and $B_{50\%}$ (based on B_{2006}).

The assumption of uniform F across all susceptible classes is not realistic, but data is lacking to create selectivity curves. For the risk analysis, we created hypothetical harvest scenarios where F was allowed to vary independently for ages and stages (all animals within an age or stage class had equal probability of capture). Harvest scenarios for the age model consisted of two fishing mortalities, one for juveniles and one for adults (e.g. $F_J = 0$, $F_A = 0.04$), whereas the scenarios for the stage model had three fishing mortalities, one each for juveniles, subadults and adults-pregnant/resting (e.g. $F_J = 0$, $F_S = 0.1$,

$F_A = 0.04$). Projections were made over a 20 year period, with 1000 replications for each harvest scenario. A risk statistic was calculated as the proportion of the simulated populations that fell below the threshold criteria after 20 years.

Results

Scenario 1

Age-based model estimates for the unfished GOA population are $r = 0.034 \text{ year}^{-1}$ (0.012–0.06 year^{-1} , 95% confidence intervals) and $\lambda = 1.035 \text{ year}^{-1}$ (1.012–1.064 year^{-1}). The stage-based model estimates are $r = 0.020 \text{ year}^{-1}$ (–0.031–0.082 year^{-1}) and $\lambda = 1.020 \text{ year}^{-1}$ (0.969–1.086 year^{-1}). The net reproductive rate, R_0 , is 4.794 female pups (1.967–8.445 female pups) for the age model and 2.438 female pups

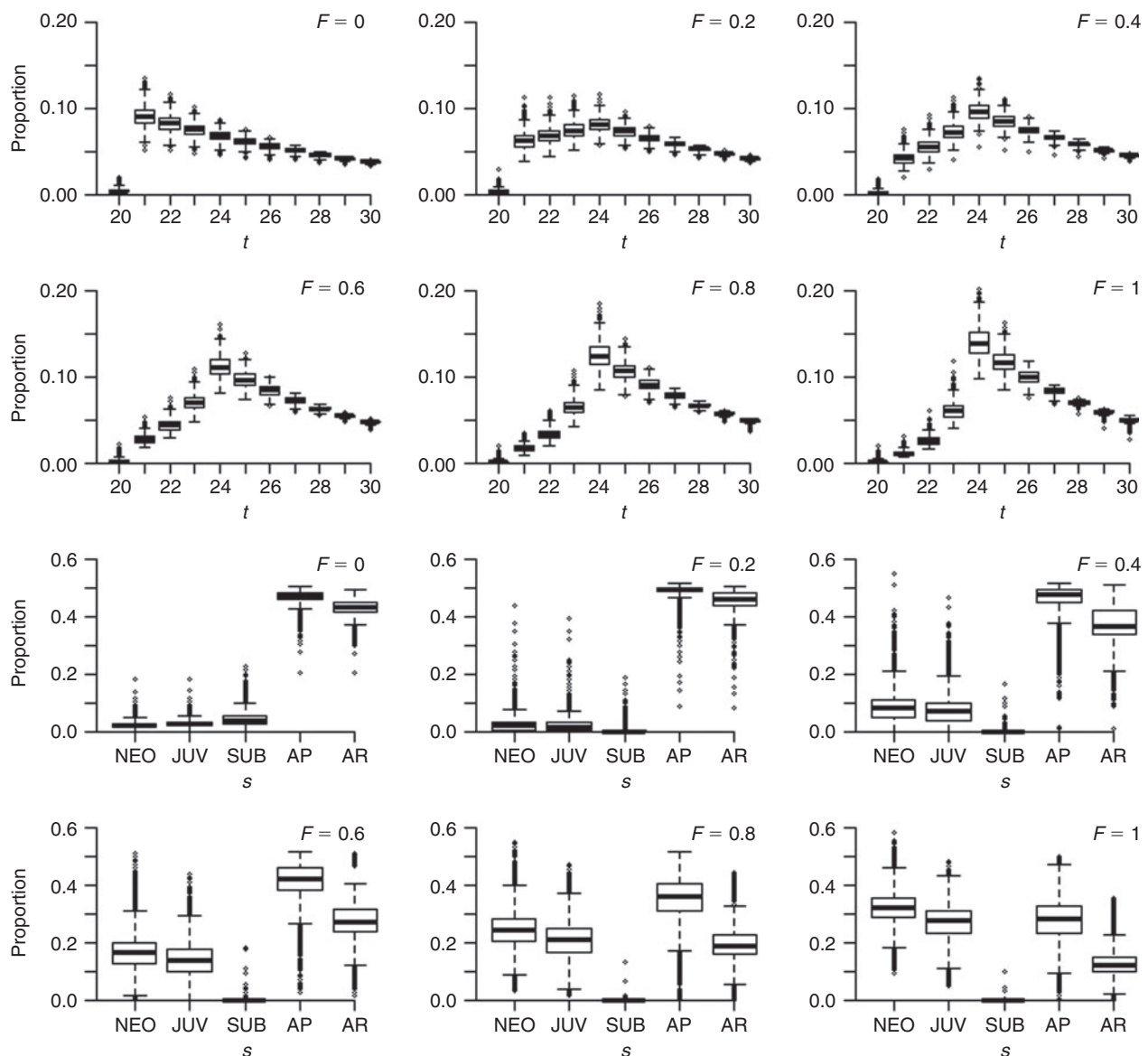


Fig. 3. Reproductive value distributions for the age- and stage-based models at varying levels of instantaneous fishing mortality (F), truncated at 10 years for clarity. The top two rows are age distributions at $F = 0, 0.2, 0.4, 0.6, 0.8$ and 1.0 . The bottom two rows are the stage distributions at the same levels of F .

(0.233–8.192 female pups) for the stage model. The mean generation time is 46.3 years (33.6–59.5 years) and 34.9 years (23.9–48.9 years). The doubling time is 20.4 years (11.1–56.7 years) and 35.4 years (13.1–43.8 years) and the mean age of parents is 49.0 years (38.0–60.9 years) and 38.0 years (30.2–47.0 years), for the age and stage models respectively.

Estimation of the SAD/SSD and RV for the two models had some similarities and some differences. For the age model, the majority of the virgin population is <20 years old with young-of-the-year (or neonates) being dominant at 9.2% (Fig. 2a), whereas the stage model estimates the majority of the population to be subadults at 51.9% followed by juveniles at 33% (Fig. 3b). The neonates in the stage model (which are the

same as young-of-the-year in the age model) account for 8.5% of the population. Reproductive value is maximised at 47 years for the age model (0.019, Fig. 4a) and in the AP stage for the stage model (0.463, Fig. 4b). Although the RV for all age classes is a bell-shaped curve, showing small changes between age classes, the stage model RV is low for the N, J and S stages and nearly all of the RV is contained in the AP and AR stages.

Elasticity analysis showed that changes in the survival of S stage or <20-year-old *S. suckleyi* have the greatest impact on r . In the age model, annual survival at ages <24 years all had a 2.2% elasticity and the elasticity decreased to near zero by age 54 (Fig. 5a). The maximum contribution of fecundity to changes in r was <1% for an 18-year-old *S. suckleyi* (Fig. 5b). In the

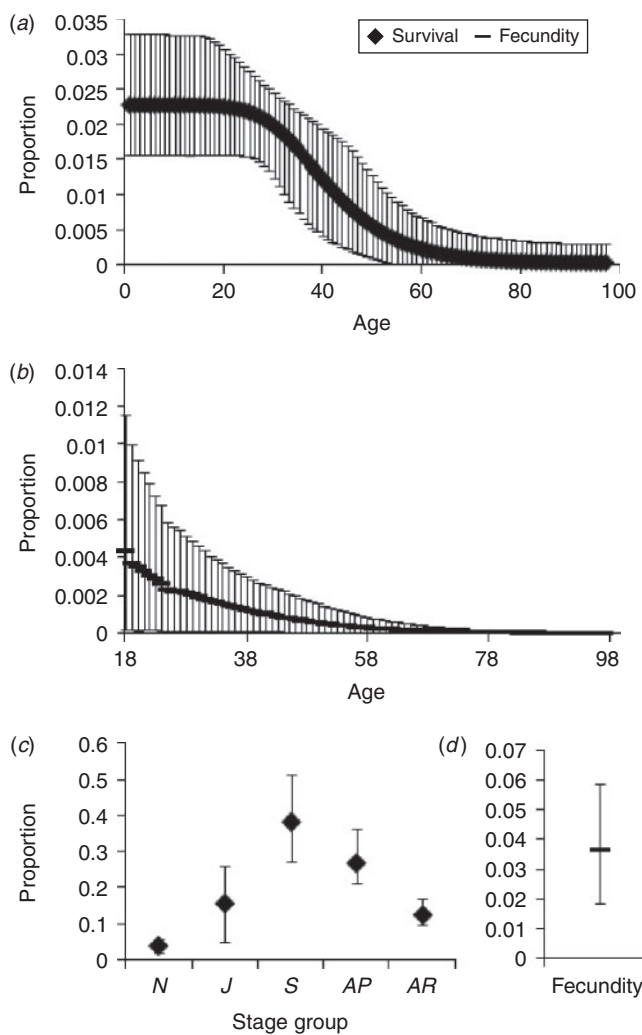


Fig. 4. Elasticities of (a) survival and (b) fecundity parameters for the age model; and elasticities of (c) survival and (d) fecundity parameters for the stage model. Error bars are 95% confidence intervals.

stage model, because there were fewer groupings the impact of one group was larger. Survival of the subadult class contributed 38.5% to changes in r and pregnant adult survival contributed 26.8% (Fig. 5c). Similarly, fecundity in the stage model only contributed 3.7% (Fig. 5d).

Scenario 2

Both models were dramatically impacted with the inclusion of fishing mortality (Fig. S3, available as an Accessory Publication to this paper). The r value dropped to negative values (i.e. $0 < \lambda < 1$) at $F > 0.04$ for the age model and 0.03 for the stage model. Both R_0 and t_{x2} decreased to negative values with $F > 0.03$ and 0.04 respectively. Likewise, μ_1 also decreased. The T only decreased slightly and for the stage model it increased at $F > 0.1$. The SAD/SSD shifted to younger ages, but the overall pattern of age distributions did not change (Fig. 3a, b). The RVs

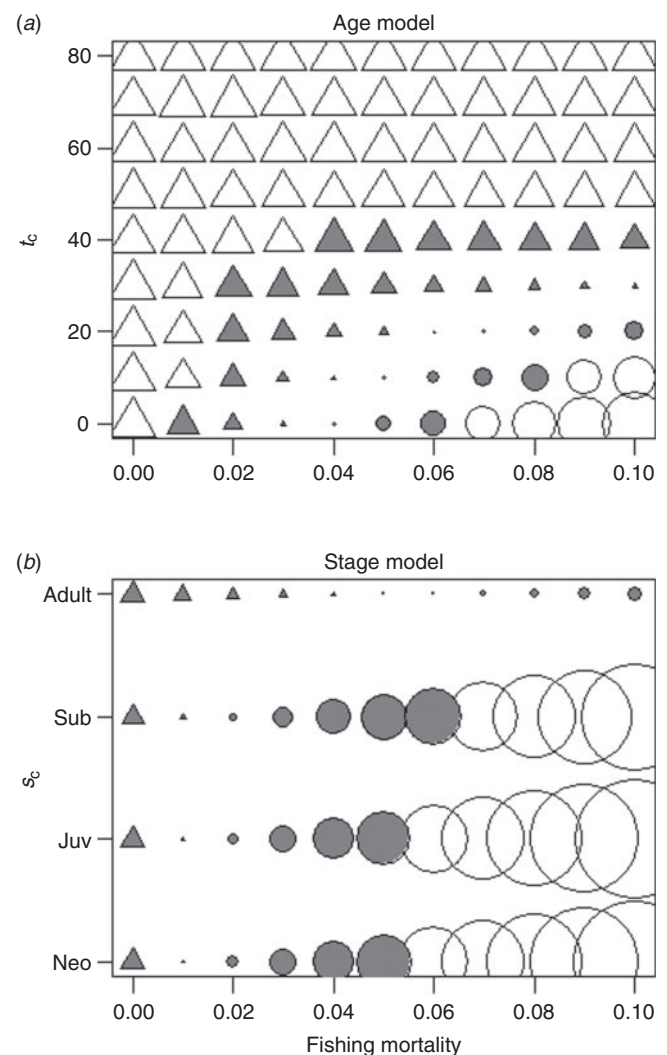


Fig. 5. Rebound potential (r) with changes in fishing mortality (F) and (a) age at first capture or (b) stage at first capture (t_c or s_c respectively). Triangles represent positive values of r (sustainable fishing) and circles represent negative values (unsustainable fishing). Grey shaded symbols show values of r that are not significantly different from zero. The size of the symbol is the relative value of r scaled to the largest value. Symbol sizes are comparable across panels with smaller symbols being near zero and larger symbols having a larger absolute value.

for the two models behaved differently. In the age model, there was very little change in RV at age with changes in F (Fig. 4a). In contrast, in the stage model as F increased and the RV of AP and AR decreased the RV of N and J increased (Fig. 4b).

Scenario 3

We observed that delaying age of entry into the fishery increases the values of F that are sustainable. In the age model, fishing at all levels is sustainable if the $t_c > 50$ years and sustainable for $t_c = 40$ years at $F < 0.03$ (Fig. 5a). Delaying the stage of entry into the fishery does not result in sustainable values of F where r is significantly greater than zero (Fig. 5b).

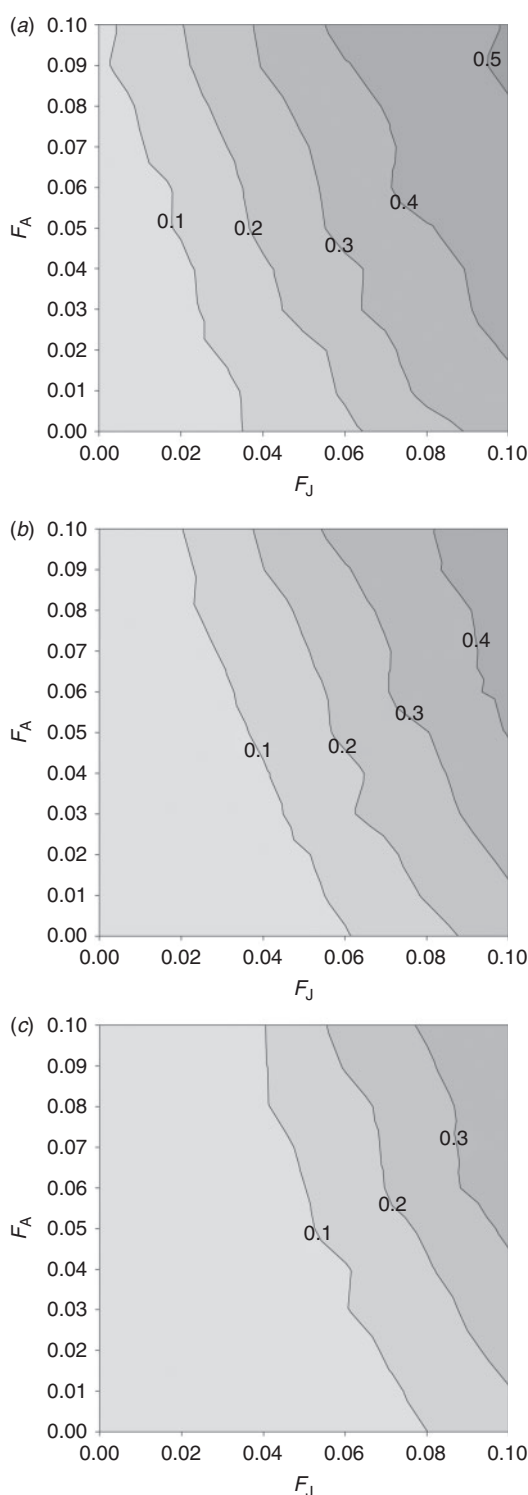


Fig. 6. Proportional risk for populations with different rates of harvest for juveniles and adults in the age model. The proportional risk is the proportion of the simulated populations that declined below a threshold value (B_{MSY} , B_{50} or B_{40}) after 20 years of constant harvest. Each panel is a different threshold value: (a) B_{MSY} , (b) B_{50} and (c) B_{40} . The fishing mortality (F) value for adults (F_A) is shown along the y-axis and the F value for juveniles (F_J) is along the x-axis. The contours are the risk statistics with darker shading indicating greater risk.

Risk assessment

The analysis of impacts of various harvest strategies indicates that targeting the juveniles in the age model and the subadults in the stage model has the greatest impact on the proportional risk of a population reaching the threshold criteria. In both models, the populations had a higher risk of decline to B_{MSY} than B_{50} and B_{40} under any given harvest scenario. If F_J was held at zero in the age model, only a small increase was seen in the risk as F_A increased, but if F_A was held at zero there was an increase in risk as F_J increased (Fig. 6). Similarly, for the stage model, the greatest increase in risk was seen as F_S increased, with only slight increases as F_J and F_A increased (Fig. 7).

Discussion

Demographic and risk analysis

Our results suggest that the GOA *S. suckleyi* population can tolerate only a very low harvest rate ($F < 0.04$). This population has a very low growth rate, which only decreases with increased fishing pressure and the rebound potential of the population is among the lowest of all shark species (Smith *et al.* 1998). Further, the present study demonstrated the use of multiple demographic model approaches for a long-lived, slow-growing species, approaches which can be applied to other shark and teleost species.

Our application of these models does not take into account the possibility of density-dependent compensation and assume that all model inputs are static throughout time, both of which could cause the model to underestimate the population's ability to cope with fishing pressure. The nature of demographic models is a snapshot of the population, so the only way to address the issue of static input information would be to have a time series of data on vital rates and to run the demographic models independently for each time step.

The effects of density dependence may be difficult or impossible to completely elucidate (Walker 1998); however, several studies have tried. First, it is important to consider the point in time when vital rate data (fecundity, growth and survival) were collected; that is, whether they were collected early on from a virgin population or later after harvest has been ongoing, because density dependent effects may vary with F (Smith *et al.* 1998). Second, density-dependent responses may be less dramatic in elasmobranchs than in teleosts because of slow growth, low fecundity and late maturity characteristics (Cortés 1998). The instantaneous population growth rate is related to the population size, such that the intrinsic rebound potential ($r_{intrinsic}$) is the maximum growth rate (which occurs only in the absence of fishing at low population sizes) and the conditional rebound potential ($r_{conditional}$) is the growth rate at given population conditions in the absence of fishing (Gedamke *et al.* 2007). It may be more appropriate for our study to consider r to be $r_{conditional}$, as opposed to $r_{intrinsic}$, because we are looking at a snapshot of a population that has not undergone intense fishing pressure and the effects of density dependence are unknown.

Sensitivity analysis suggested that r is most sensitive to juvenile survival. Indeed, small changes in M can result in large changes in r , such that a slight increase in juvenile survival may increase r substantially (Simpfendorfer 2005). The sensitivity of

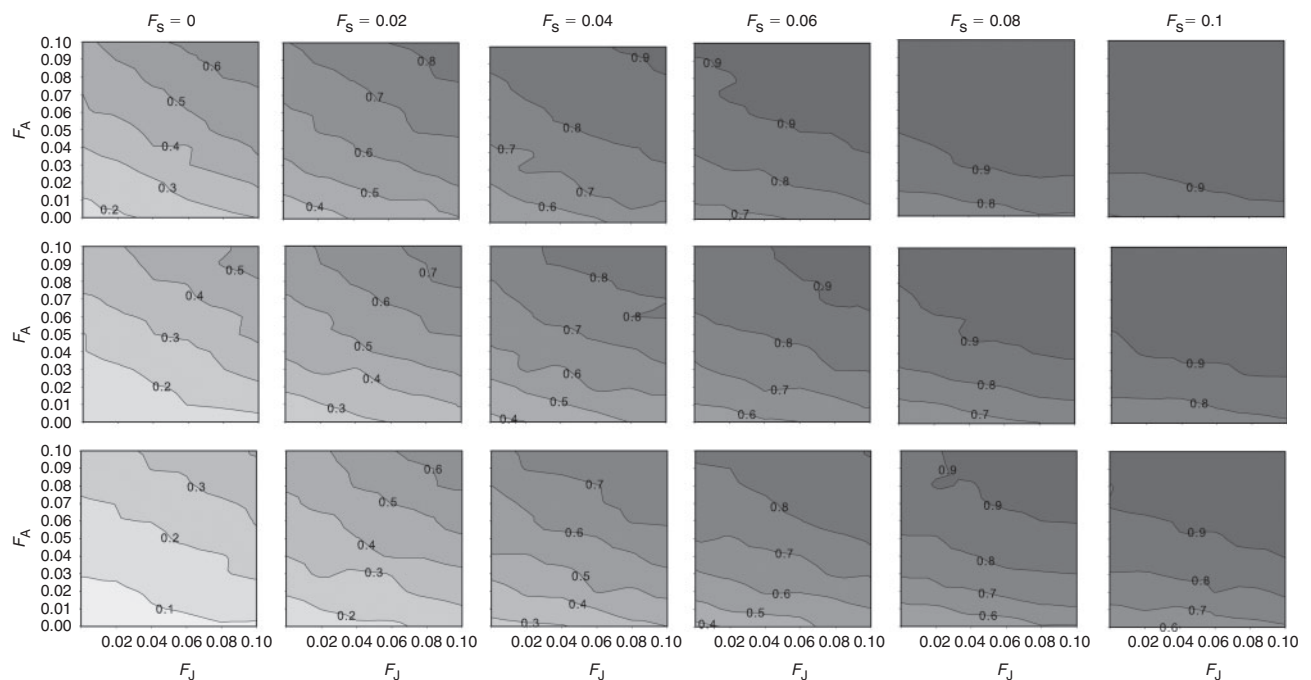


Fig. 7. Proportional risk for populations with different rates of harvest for juveniles and adults in the stage model. The proportional risk is the proportion of the simulated populations that declined below a threshold value (B_{MSY} , B_{50} or B_{40}) after 20 years of constant harvest. Each row is a different threshold value: (top) B_{MSY} , (middle) B_{50} and (bottom) B_{40} . Each column is a different level of fishing mortality (F) for subadults (left to right: $F = 0, 0.02, 0.04, 0.06, 0.08$ and 0.1). The F value for adults (F_A) is shown along the y-axis and the F value for juveniles (F_J) is along the x-axis. The contours are the risk statistics with darker shading indicating greater risk.

models to changes in M is especially important because of the uncertainty surrounding the indirect estimates of M (Pascual and Irbine 1993). Sensitivities are not consistent across all shark species; large pelagic species tend to be more sensitive to juvenile and adult survival, whereas small coastal species tend to be more sensitive to changes in fertility (Simpfendorfer 2005). This is mostly because small coastal species tend to have higher fecundity, mature earlier and have shorter generation times, whereas pelagic species are older at maturity, have lower fecundity and long generation times. Lower productivity species tend to be more sensitive to changes in juvenile survivals (Heppell *et al.* 2000). *S. suckleyi*, although a small coastal species, is similar to the large pelagic species in their life history traits and should be managed more similarly to pelagic species. An analysis such as ours identifies specific life history groups that may require more conservative management than other groups (de Kroon *et al.* 2000), for example, size limits to increase survival of specific age- or stage classes.

S. suckleyi are amongst the longest lived, slowest growing and least productive of all shark species (Smith *et al.* 1998; Cortés 2002). Sharks in general have low productivities (most $r < 0.1$) in comparison to teleost species; however, some small or more productive species can have an r value as high as 0.28 and sustain harvest (Stevens 1999; Frisk *et al.* 2002; Aires-da-Silva and Gallucci 2007). For example, the North Atlantic blue shark (*Prionace glauca*) population is highly productive (for a shark) with $r = 0.21$ and has tolerated harvest for many years (Aires-da-Silva and Gallucci 2007). Also in the North Atlantic, a demographic analysis of the little (*Leucoraja erinacea*), winter

(*Leucoraja ocellata*) and barndoor skates (*Dipturus laevis*) showed that the smaller more productive species have higher r values and were more tolerant to fishing pressure than the larger less productive barndoor skate (Frisk *et al.* 2002).

Harvest strategies that would allow for sustainable fishing of low productivity species are possible. For instance, because r is most sensitive to late juvenile and adult survival, harvest of neonate or small juvenile Australian sharpnose sharks (*Rhizoprionodon taylori*) may be sustainable at fairly high levels ($F = 0.67$), if the large juvenile and adult stages are protected (Simpfendorfer 1999). This strategy may work in fisheries that routinely target or incidentally catch neonates and small juveniles, but in the case of the *S. suckleyi*, the neonates and small juveniles are not encountered in commercial fisheries and F occurs on large juveniles and adults. The commercial fishery in British Columbia has targeted the largest females historically due to market demands and increased price per pound for larger fish and it is unlikely that a management strategy including size restrictions would occur.

In the GOA, *S. suckleyi* are not targeted but do occur (sometimes frequently) as by-catch in many fisheries and it is mostly large juveniles and adults that are caught. Discard mortality has not been investigated in these fisheries, but has been observed (C. A. Tribuzio, personal observation) to be as high as 100% in some cases. The demographic models presented here assume that the GOA population is essentially in a virgin state because abundance is estimated to be 90% of the theoretical carrying capacity (Rice 2007). Although F (as a result of by-catch) is small for GOA *S. suckleyi*, estimated to be only 1%

of the total GOA population (Courtney *et al.* 2006), the simulations presented here suggest that directed fishing of *S. suckleyi* would not be sustainable. Fishing mortality would be almost exclusively on large juveniles and adults and as shown here, this would result in a significant reduction in r .

Our analyses have assumed that *S. suckleyi* in the GOA are a closed population. Thus, the rebound potential estimated here does not include potential migration into and out of the GOA. The GOA population of *S. suckleyi* may be more tolerant to fishing pressure than our analyses indicated if *S. suckleyi* from neighbouring areas (e.g. British Columbia) contribute to recruitment or the adult spawning population in the GOA. Tagging studies have been conducted on British Columbia and Washington (reviewed by Taylor 2008) *S. suckleyi* populations and studies are on-going for GOA populations. The two previous tagging studies reported release and recovery locations over total time at liberty and do not provide insight into annual movement patterns. The ongoing tagging study in the GOA is designed to look at fine-scale movement within a year and may be used to estimate migration rates, which could then be incorporated into these models (following a model structure similar to work by Heifetz and Quinn 1998).

Although this study is specific to *S. suckleyi* in the GOA, the results and methods are broadly applicable. This study is a good case study of not only in applying demographic models, but in how to interpret the various results, especially with regards to low productivity species. Demographic models are commonly used for shark species but are also easily adapted to other teleost or terrestrial species.

Age class vs stage class models

We examined both a fully age-structured model and a stage-structured model to determine if the less cumbersome stage-based model would produce comparable results for the GOA *S. suckleyi*. In some cases, the two methods produced comparable results, whereas in others the results were quite different. For example, the SAD/SSD distributions performed similarly for both models, in both cases as fishing mortality increased the peak of abundance shifted towards younger ages or stages, but the overall distribution did not change markedly. This similarity extended to the RV distributions as well. As F increased, the RV of the older immature *S. suckleyi* decreased and for the youngest *S. suckleyi* it increased. The overall pattern was consistent between both models, but was exaggerated in the stage model, as was expected because of the condensed groupings.

The estimated parameters did not follow the same consistent pattern between models. The rebound potential (r) for both models was low in the absence of fishing and became negative quickly as F increased ($>4\%$); however, r from the age model decreased linearly whereas the estimated r from the stage model reached an asymptote at about -0.3 . The important factor here is not that they decrease at different rates, but instead that both models had similar estimates of sustainable F , where $r = 0$. The two age-dependent parameters (μ_1 and T) were quite different between the two models. Unlike the age model, where each age class has a specific age attached to it, the stage model is essentially age-independent, in that time is only included in the stage durations, which could lead to the differences in

μ_1 and T . The R_0 did perform similarly between the two models; with the only difference being that the age model had greater R_0 for a virgin population.

A similar study found that the two modelling approaches resulted in similar demographic outcomes (Mollet and Cailliet 2002). However, this was true only if the stage groupings were appropriately specified in the stage model (Mollet and Cailliet 2002). For example, Mollet and Cailliet (2002) found that a three-stage model (with stage durations of 1, 1 and 8 years) produced comparable results to the age model for the pelagic stingray (*Dasyatis violacea*), but not a two-stage model (with durations of 2 and 8 years). In the case of the sandbar shark, a five-stage model was most appropriate because it was longer lived and had a more complex life history (Brewster-Geisz and Miller 2000). We adopted a similar five-stage model here as they seemed most biologically meaningful and logical for *S. suckleyi*. Although previous studies have cited no evidence that *S. suckleyi* have a resting period between pregnancies in British Columbia and Puget Sound (Tribuzio *et al.* 2009); we included a resting stage in our model because evidence in the GOA suggests that a resting period of a year or more may occur in this northern population (Tribuzio and Kruse in press). Regardless, misspecification of the reproductive cycle may have a small effect on the model outcome as the model is most sensitive to juvenile and adult survival, not reproductive cycle (Secor 2008).

Besides the number of stages, there are other considerations with the stage models. For models with few stages, T may be better represented by μ_1 , because correcting for the slow down of juveniles through the stages defeats the purpose of using the stage model (Heppell *et al.* 2000; Mollet and Cailliet 2002). Models with only a few stages may be more appropriate for fast-growing species that reach maturity quickly. Owing to their grouped nature, stage models also have larger dampening ratios and may reach stable populations sooner than age models.

Conclusion

Squalus suckleyi is a long-lived, slow-growing species with low fecundity and low productivity and if all of the age or stage classes were open to exploitation, it would be highly susceptible to overfishing. Future development of harvest strategies for *S. suckleyi* should consider the stock structure and migration rates between the GOA and neighbouring management areas. A better understanding of migration and stock structure could alter our results and should be incorporated if management decisions are to be based on this type of modelling exercise. Regardless of whether an age class or a stage class model is used, the conclusions regarding the impacts of fishing are essentially the same; a *S. suckleyi* stock can only sustain a very low overall harvest rate. In the case of the GOA *S. suckleyi*, the stage model produces similar results to the age class model, in regards to estimating the rebound potential and sustainable fishing mortality of the population, while being much simpler to implement. Thus, the stage-based model is an appropriate substitute.

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