DEMOGRAPHIC ANALYSES OF THE DATA LIMITED SILKY SHARK POPULATION IN THE INDIAN OCEAN USING A TWO-SEX STOCHASTIC MATRIX FRAMEWORK

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ABSTRACT

The silky shark, *Carcharhinus falciformis*, is a common by-catch species of tuna and swordfish longline fishing in the Indian Ocean. The high value of its fins makes it one of the most heavily fished shark species in the world. Concern over declining populations and the uncertainty surrounding its population dynamics has increased the urgency of developing appropriate methods to assess its stock status. This study developed a two-sex stage-based structured matrix model with Monte Carlo simulations to examine silky shark demography and population dynamics. The simulations indicate that, without mortality from fishing, the stock will increase slightly (sex combined mean annual population growth rates were 1.079 yr^{-1} and 1.030 yr^{-1} for 1-yr and 2-yr reproductive cycles, respectively). However, our analysis of various management scenarios shows that even with low levels of fishing mortality, the silky shark population may be on the edge of collapse. This study indicates that the protection of immature sharks is the most efficient conservation measure for this species, and that this will produce higher population growth rates than the protection of mature sharks only. As the data on stock status are inadequate, better estimates of current fishing levels are needed to obtain a more accurate estimate of the impact of fishing on the population. Against a background of increasing global shark catches and landings, it is important that silky shark populations are constantly monitored to ensure their sustainability in the Indian Ocean. We believe that the framework developed in this study can be used to evaluate the risk of decline among other widely distributed pelagic shark species.

I. INTRODUCTION

The silky shark, *Carcharhinus falciformis,* is one of the most abundant and cosmopolitan shark species in tropical and warm-temperate seas (Castro et al., 1999). Historically it has been the main shark by-catch of the longline and purse seine fisheries in the open ocean (Matsunaga and Nakano, 1999; Compagno et al., 2005; White and Cavanagh, 2007; Joung et al., 2008). Based on recent stock assessments by the Inter-American Tropical Tuna Commission (IATTC) and Western and Central Pacific Fisheries Commission (WCPFC), there is little doubt that silky shark populations have declined substantially in many regions (Aires-da-Silva et al., 2013; Rice and Harley, 2013). Like most large shark species, the life history characteristics of the silky shark, namely its late maturity, slow growth and limited offspring (Joung et al., 2008), make it particularly susceptible to over-exploitation (Hoenig and Gruber, 1990; Stevens et al., 2000). It has been listed in CITES Appendix II (CITES, 2016) and is currently listed as Vulnerable (VU) on the IUCN Red List (Rigby et al., 2017). The commercial retention of the silky shark is prohibited by several Regional Fisheries Management Organizations (RFMO's), such as ICCAT and WCPFC, but not in the Indian Ocean and IATTC waters. Its stock status (overfishing but not overfished) in the Indian Ocean is still highly uncertain, despite one recent stock assessment study (Ortiz et al., 2018). Moreover, as the assessment is in the preliminary stage and there is considerable uncertainty associated with the estimations, management advice remains unclear. Therefore, an alternative scientific basis for such advice is urgently needed.

A general problem in shark studies is that, because of their low commercial value, and a lack of systematic fishery records, the data required in conventional stock assessment models (e.g., virtual population analysis or surplus production models) are seldom available. Until such time as sufficient data become available for conventional stock assessment (Smart et al., 2017), demographic models can serve as population dynamic models and provide insights for management advice (Simpfen-

Table 1. Stages for the silky shark in the Indian Ocean.

Sex	Stage-class	Approximate ages (yr)	Expected stage duration (yr)
Male	Neonates	0-1	1
	Juveniles	1-10	9
	Subadults	10- a_{mat}	3-4
	Adults	a_{mat} - a_{max}	12-22
Female	Neonates	0-1	1
	Juveniles	1-10	9
	Subadults	10- a_{mat}	4-6
	[1]Pregnant adults	> a_{mat}	1
	Parturient adults	> a_{mat}	1[*]

[1]Only relevant for the 2-year reproductive cycle

[*]One year stage duration for 2-year reproductive cycle and range 11-21 for 1-year reproductive cycle
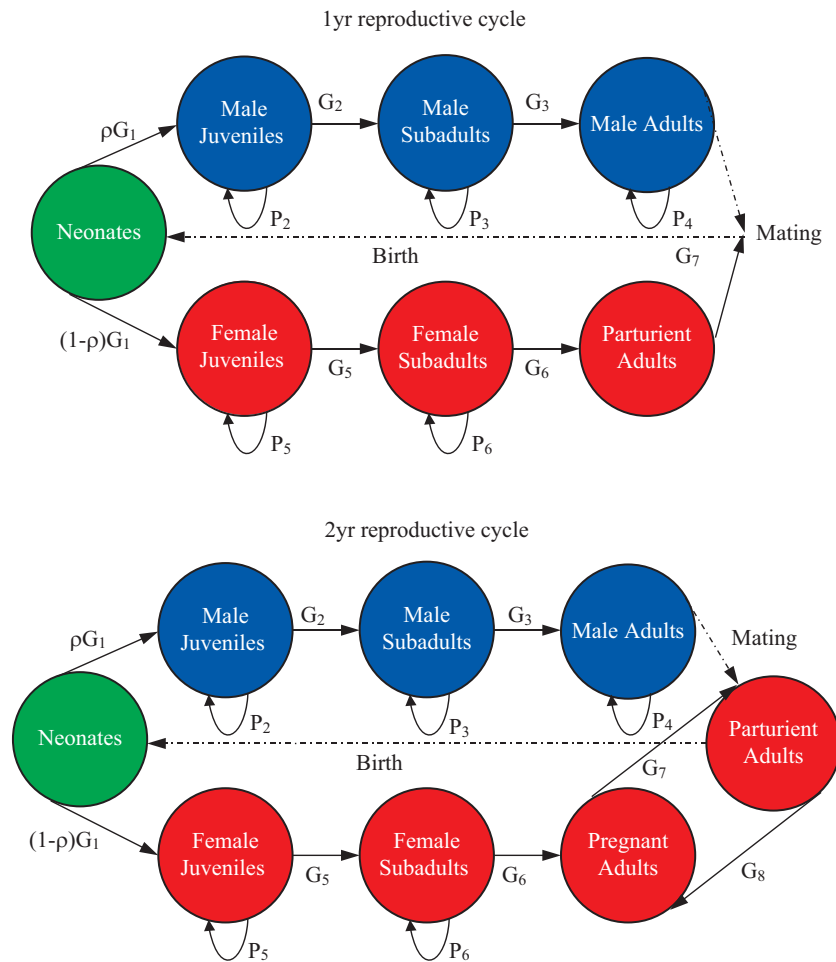
Fig. 1.   Stage-based matrix models for the 1-year and 2-year reproductive cycles. Arrows indicate individuals surviving and growing to the next stage or surviving and remaining in the same stage.

dorfer, 2005). Such models can be relatively simple, requiring only limited biological information, such as survival rate, age at maturity, litter size (no. of embryos), longevity and other reproductive parameters. For the silky shark, detailed biological information is available for the Atlantic Ocean (Branstetter, 1987; Bonfil et al., 1993) and the Pacific Ocean (Oshitani et al., 2003; Joung et al., 2008). However, there is little equivalent information for the Indian Ocean. To date, a single study in the eastern Indian Ocean provides the only detailed information on its age distribution, growth and reproductive biology (Hall

et al., 2012). Although this gives us a better picture of its biological parameters, the estimates of population growth rate may still be influenced by uncertainties about life-history parameters (such as natural mortality and reproductive cycle). In recent years, this uncertainty has been addressed by using Monte Carlo simulations, and this has now become a standard technique in assessing shark populations (Cortés, 2002; Tsai et al., 2014, 2015; Smart et al., 2017; Yokoi et al., 2017).

Since the target of this study, the silky shark, exhibits sexual segregation as well as segregation between juveniles and other stages (Clarke et al., 2011), a two-sex stage-based model with Monte Carlo simulations was developed to account for possible uncertainty in life history parameters. To evaluate the impact of fishing mortality on demographic parameter estimates, a range of scenarios was generated. As inferences about population growth rates and susceptibility to fishing pressure are important in drawing up management measures, it is hoped that the results obtained in this study will provide useful information for silky shark management and conservation in the Indian Ocean. It is further hoped that this approach can be applied to other shark species that have limited catch and effort data.

II. MATERIALS AND METHODS

1. Life History of the Silky Shark

The life history parameters of the silky shark were adopted from the best estimations by Hall et al. (2012). Although the authors suggested a 2-year reproductive cycle, a 1-year cycle could not be ruled out. Therefore, in this study, both possible reproductive traits were examined. Adult stage females were categorized as pregnant or parturient adults in the 2-year cycle models, and as parturient adults only in the 1-year cycle models. The life history of the female silky shark (Fig. 1) can be represented as follows: neonates (0-1 year), juveniles (1-10 years), sub-adults (10-16 years), pregnant adults (1 year; only in the 2-year reproductive cycle), parturient adults (1 year); and for males it can be represented as follows: neonates (0-1 year), juveniles (1-10 years), sub-adults (10-14 years) and adults (14 years and older) (Fig. 1 and Table 1).

2. Model Development

A stage-structured matrix population model (Caswell, 2001) was adopted to examine the demography of the silky shark in the Indian Ocean. The basic formulation for a typical demographic model is:

$$N_{t+1} = AN_t, \tag{1}$$

where N_t is the vector of numbers of sharks in each stage at time t and A is the life history projection matrix composed of survival and fecundity for adult stage (Caswell, 2001; Simpfendorfer, 2005). This model did not consider the density-dependent compensatory effects for the population, as the mechanisms for sharks are largely theoretical at present (Walker, 1998), and conse-

quently beyond the scope of this study. Since litter size for the silky shark does not increase with the body size of the breed (Hall et al., 2012), a knife-edge maturity was assumed in this model. The two-sex stage-structured model with a 1-yr reproductive cycle can be described as:

$$
\begin{bmatrix}
0 & 0 & 0 & f_{4,t}^{\text{mal}} & 0 & 0 & G_7^{\text{fem}} \times f_{7,t}^{\text{fem}} \\
\rho G_1 & P_2^{\text{mal}} & 0 & 0 & 0 & 0 & 0 \\
0 & G_2^{\text{mal}} & P_3^{\text{mal}} & 0 & 0 & 0 & 0 \\
0 & 0 & G_3^{\text{mal}} & P_4^{\text{mal}} & 0 & 0 & 0 \\
(1-\rho)G_1 & 0 & 0 & 0 & P_5^{\text{fem}} & 0 & 0 \\
0 & 0 & 0 & 0 & G_5^{\text{fem}} & P_6^{\text{fem}} & 0 \\
0 & 0 & 0 & 0 & 0 & G_6^{\text{fem}} & P_7^{\text{fem}}
\end{bmatrix}, \tag{2}
$$

and the model with 2-yr reproductive cycle is:

$$
\begin{bmatrix}
0 & 0 & 0 & f_{4,t}^{\text{mal}} & 0 & 0 & 0 & G_8^{\text{fem}} \times f_{8,t}^{\text{fem}} \\
\rho G_1 & P_2^{\text{mal}} & 0 & 0 & 0 & 0 & 0 & 0 \\
0 & G_2^{\text{mal}} & P_3^{\text{mal}} & 0 & 0 & 0 & 0 & 0 \\
0 & 0 & G_3^{\text{mal}} & P_4^{\text{mal}} & 0 & 0 & 0 & 0 \\
(1-\rho)G_1 & 0 & 0 & 0 & P_5^{\text{fem}} & 0 & 0 & 0 \\
0 & 0 & 0 & 0 & G_5^{\text{fem}} & P_6^{\text{fem}} & 0 & 0 \\
0 & 0 & 0 & 0 & 0 & G_6^{\text{fem}} & 0 & G_8^{\text{fem}} \\
0 & 0 & 0 & 0 & 0 & 0 & G_7^{\text{fem}} & 0
\end{bmatrix}, \tag{3}
$$

The parameters of matrix A are specified for males and females, denoted by subscripts mal and fem, respectively. Here, ρ is the sex ratio at birth (the ratio of male live births divided by total live births, set to 0.5 to achieve an equal sex ratio for embryos; Hall et al., 2012) and f_i is stage-specific per-capita fecundity. The impact of sex-ratio on mating success was modeled using the modified harmonic mean birth function of Caswell (2001):

$$f_{4,t}^{\text{mal}}(n) = \frac{kn_{\text{f},t}}{n_{\text{f},t} + n_{\text{m},t}}, \tag{4}$$

$$f_{\text{stage},t}^{\text{fem}}(n) = \frac{kn_{\text{m},t}}{n_{\text{f},t} + n_{\text{m},t}}, \tag{5}$$

where stage = 8 and 7 for 2-yr and 1-yr reproductive cycles respectively, k is the litter size, and $n_{m,t}$ and $n_{f,t}$ are the densities of reproductive males and females, respectively. In the absence of information about mating systems for silky sharks, Eqs. 4 and 5 assume monogamy and an equal litter size for both sexes, regardless of size or stage category.

For each sex, $G_{i,s}$ is the product of the probability of an individual in stage i surviving ($\sigma_{i,s}$) and the probability of its shifting to another stage ($\gamma_{i,s}$), i.e., $G_{i,s} = \sigma_{i,s} \times \gamma_{i,s}$, and $P_{i,s}$ is

the probability of an individual surviving and remaining in its current stage: $P_{i,s} = \sigma_{i,s} \times (1 - \gamma_{i,s})$ (Brewster-Geisz and Miller, 2000; Frisk et al., 2002). The $\sigma_{i,s}$ for a single stage is $\sigma_{i,s} = e^{-(M_{i,s}+F_{i,s})}$, where $F_{i,s}$ is the fishing mortality rate for stage i, which is set to the average over age of age-specific fishing mortality ($F_{a,s}$) and $M_{i,s}$ is the natural mortality at stage i set to the average over age of age-specific natural mortality. Values for the $\gamma_{i,s}$ are calculated by:

$$\gamma_{i,s} = \frac{(\sigma_{i,s}/\lambda_{init})^{T_{i,s}} - (\sigma_{i,s}/\lambda_{init})^{T_{i,s}-1}}{(\sigma_{i,s}/\lambda_{init})^{T_{i,s}} - 1}$$
$$= \frac{(\sigma_{i,s})^{T_{i,s}} - (\sigma_{i,s})^{T_{i,s}-1}}{(\sigma_{i,s})^{T_{i,s}} - 1},$$ (6)

where λ_{init} is an initial population growth rate (set to 1). $T_{i,s}$ is the stage duration of each sex and stage. An iterative approach is needed to estimate the matrix parameters using Eq. 6. Further details can be found in Caswell (2001). The population growth rate (λ) can be estimated by solving the equation: $|A - \lambda I| = 0$ where I is the identity matrix (Caswell, 2001).

3. Mortality Estimation

The natural mortality rates for shark species are often difficult to obtain and are the main source of uncertainty in stock assessment. To counter this problem, the probabilities of annual survivorship (S) were determined based on five indirect methods of estimating natural mortality (M), where $S = e^{-M}$. These approaches are derived from the relationships between natural mortality and various biological parameters, including growth coefficient, age at maturity (a_{mat}) and longevity (a_{max}) (Pauly, 1980; Hoenig, 1983; Jensen, 1996; Campana et al., 2001):

Pauly (1980): $\begin{aligned} \ln(M) = &-0.0066 - 0.279\ln(L_\infty) \\ &+ 0.6543\ln(K) + 0.463\ln(T); \end{aligned}$

Hoenig (1983): $\ln(M) = 0.941 - 0.873\ln(a_{max})$;

Jensen (1996): $M = 1.65/a_{mat}$;

Jensen (1996): $M = 1.6k$;

Campana et al. (2001): $M = -\ln 0.01/a_{max}$

in which L_∞ and k are growth parameters (Hall et al., 2012) and T is mean annual water temperature (set as 25°C in this study).

4. Uncertainty Used in Demographic Model

The life history parameters of the silky shark were obtained from previous studies (Table 1). However, limited data mean

that estimates of these parameters for many shark species can be difficult and are subject to high uncertainty (Caswell et al., 1998). It is necessary to take this into account in any demographic analysis (Cortés, 2002). Uncertainty in vital rates estimates was considered in the model to reflect possible variations in reported life history parameters by varying specific life history parameters (Cortés, 2002). The present study incorporated four key parameter uncertainties into the simulations, namely natural mortality, age-at-maturity, fecundity, and longevity. Life history parameters were sampled from assumed distributions (Table 2).

Probability distributions were created for each parameter based on previous biological studies (Hall et al., 2012). For each scenario, the mean and standard deviation (sd) obtained for five M across methods for each sex and stage were used to define a lognormal distribution. A lognormal error structure for M ensures that the resulting survival estimates range between 0 and 1. Ages-at-maturity of 13-14yr for males and 14-16yr for females were used as the bounds of a discrete uniform probability mass function. Stochasticity in fecundity was assumed to be lognormal with a mean of 7.2 and standard deviation of 2.4. The maximum observed age for the silky shark (O_{max}) is 25, while a theoretical estimate of longevity suggests 35 (Joung et al., 2008; Ortiz et al., 2018). The empirical and theoretical values were used as the bounds of a discrete uniform distribution for longevity. Monte Carlo simulations were then employed to assess the possible uncertainties and to produce confidence intervals for output values such as population growth rate.

5. Modelling Performance Management Measures

Since detailed historical catch and effort data for the Indian Ocean silky shark are not available, it is difficult to estimate current fishing levels. Therefore, a range of fishing exploitation scenarios were assessed by setting different fishing mortality levels. As the population segregates between juveniles and adults (Oshitani et al., 2003), it should be relatively easy to implement size limits for the silky shark. In total, 14 harvest strategies were conducted to examine the status trajectories and explore the implications of alternative harvest strategies. These strategies were assessed for each of the one- and two-year reproductive cycle models, as follows:

(1) Natural conditions (Scenario 1): fishing mortality for all ages is set to 0 (Cases 1 and 8).
(2) 80% of the current fishing mortality (Scenario 2): fishing mortality is equal to 80% of natural mortality level by stage (MacCall, 2009) (Cases 2 and 9).
(3) 60% of the current fishing mortality (Scenario 3): fishing mortality is equal to 60% of natural mortality level by stage (Cases 3 and 10).
(4) 40% of the current fishing mortality (Scenario 4): fishing mortality is equal to 40% of natural mortality level by stage (Cases 4 and 11).
(5) 20% of the current fishing mortality (Scenario 5): fishing mortality is equal to 20% of natural mortality level by stage

Table 2. Uncertainty values used in the stochastic simulations.

Source of uncertainty	Male	Female	Assumed distribution
Natural mortality	ln (mean, sd)*	ln (mean, sd)*	Lognormal
Age at maturity	13-14 yr	14-16 yr	Uniform
Fecundity	ln $(7.2, 2.4^2)$	ln $(7.2, 2.4^2)$	Lognormal
Longevity	25-35 yr	25-35 yr	Uniform

*The mean and standard deviation (sd) obtained for M across five methods for each sex and stage were used to define a lognormal distribution.

Table 3. Natural mortality estimates for the Indian Ocean silky shark using five different methods.

Method	Relies on Parameters	Male M (yr^{-1})	Female M (yr^{-1})
Jensen (1996)	k	0.106	0.103
Jensen (1996)	a_{mat}	0.118-0.127	0.103-0.118
Pauly (1980)	L_∞,T, k*	0.152	0.152
Hoenig (1983)	a_{max}	0.115-0.154	0.115-0.154
Campana et al. (2001)	a_{max}	0.132-0.184	0.132-0.184

*L_∞ and k are growth parameters (Hall et al., 2012) and T is temperature (set as 25 in this study) in °C.

Table 4. Demographic estimates for different scenarios based on a 1-yr reproductive cycle.

		1 year reproductive cycle					
Case	Model	λ	Lower CL	Upper CL	r	Lower CL	Upper CL
Scenario 1	Two-sex	1.079	1.018	1.146	0.075	0.018	0.136
Case 1 (F = 0)	Single-sex	1.073	1.005	1.144	0.070	0.005	0.134
Scenario 2	Two-sex	0.934	0.873	0.995	-0.068	-0.136	-0.005
Case 2 (F = 0.8M)	Single-sex	0.926	0.847	0.999	-0.077	-0.166	-0.001
Scenario 3	Two-sex	0.967	0.907	1.027	-0.034	-0.097	0.027
Case 3 (F = 0.6M)	Single-sex	0.960	0.883	1.029	-0.042	-0.125	0.029
Scenario 4	Two-sex	1.003	0.943	1.065	0.003	-0.058	0.063
Case 4 (F = 0.4M)	Single-sex	0.996	0.923	1.068	-0.005	-0.080	0.065
Scenario 5	Two-sex	1.039	0.979	1.102	0.038	-0.021	0.098
Case 5 (F = 0.2M)	Single-sex	1.033	0.962	1.101	0.032	-0.038	0.096
Scenario 6	Two-sex	1.033	0.972	1.097	0.032	-0.028	0.092
Case 6 ($F_{immature}$ = 0)	Single-sex	1.026	0.955	1.095	0.025	-0.046	0.091
Scenario 7	Two-sex	0.982	0.926	1.038	-0.019	-0.077	0.038
Case 7 (F_{mature} = 0)	Single-sex	0.977	0.909	1.042	-0.024	-0.095	0.041

(Cases 5 and 12).

(6) Protection of immature sharks (Scenario 6): the same as scenario 2, except that fishing mortality for neonates (age 0-1) and juveniles (immature sharks, below the threshold age of knife-edge maturity) is set to 0. (Cases 6 and 13).

(7) Protection of mature sharks (Scenario 7): the same as scenario 2, except that fishing mortality for adults (above the threshold age of knife-edge maturity) is set to 0. (Cases 7 and 14).

For each scenario, 10,000 replicates of population growth rate were estimated by incorporating parameter uncertainty in Monte Carlo simulation. The median and the inter-quartile range were then used to quantify the central tendency and variation for the distributions. All demographic and simulation analyses were conducted using CSIRO program—PopTools (Hood, 2004).

III. RESULTS

1. Natural Mortality Estimates

The range of natural mortality (M), produced by the five indirect methods, was 0.103-0.184 yr^{-1} for females, and 0.106-0.184 yr^{-1} for males. The lowest estimates of M (0.103 yr^{-1} for females and 0.106 yr^{-1} for males) were obtained using the technique of Jensen (1996), which relies on the von Bertalanffy growth parameters. The highest estimates of M (0.184 yr^{-1} for both males and females) were obtained using the method of

Table 5. Demographic estimates for different scenarios based on a 2-yr reproductive cycle.

				2 year reproductive cycle			
Case	Model	λ	Lower CL	Upper CL	r	Lower CL	Upper CL
Scenario 1	Two-sex	1.030	0.979	1.084	0.030	-0.021	0.080
Case 8 (F = 0)	Single-sex	1.020	0.956	1.078	0.019	-0.045	0.075
Scenario 2	Two-sex	0.905	0.848	0.958	-0.100	-0.164	-0.043
Case 9 (F = 0.8M)	Single-sex	0.891	0.809	0.960	-0.117	-0.212	-0.041
Scenario 3	Two-sex	0.934	0.879	0.988	-0.068	-0.129	-0.012
Case 10 (F = 0.6M)	Single-sex	0.921	0.844	0.987	-0.083	-0.169	-0.013
Scenario 4	Two-sex	0.965	0.911	1.019	-0.036	-0.093	0.019
Case 11 (F = 0.4M)	Single-sex	0.953	0.880	1.016	-0.049	-0.128	0.016
Scenario 5	Two-sex	0.997	0.944	1.051	-0.003	-0.057	0.050
Case 12 (F = 0.2M)	Single-sex	0.986	0.917	1.046	-0.015	-0.086	0.045
Scenario 6	Two-sex	0.991	0.937	1.047	-0.010	-0.065	0.046
Case 13 ($F_{immature}$ = 0)	Single-sex	0.975	0.907	1.039	-0.026	-0.098	0.038
Scenario 7	Two-sex	0.951	0.899	1.000	-0.051	-0.106	0.0001
Case 14 (F_{mature} = 0)	Single-sex	0.944	0.876	1.004	-0.058	-0.133	0.004
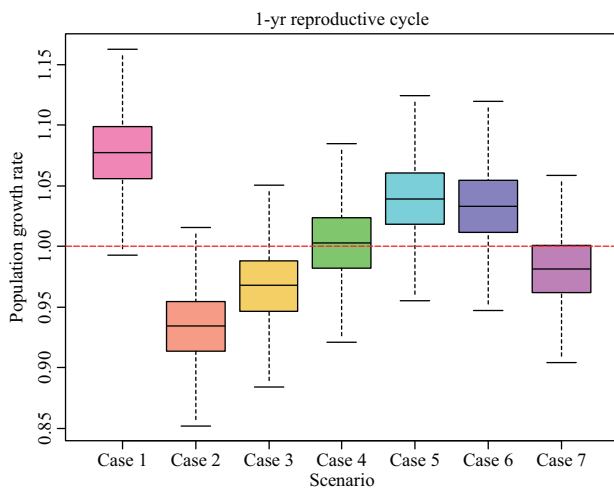
Fig. 2. Box plot for different cases of a 1yr reproductive cycle. The red dotted line shows a stable population growth rate.
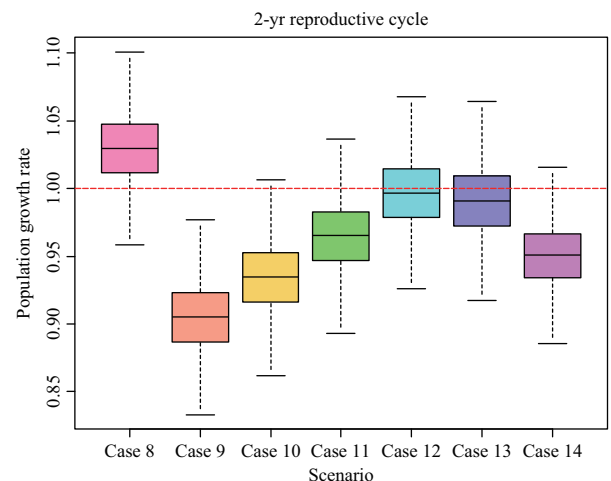
Fig. 3. Box plot for different cases of a 2yr reproductive cycle. The red dotted line shows a stable population growth rate.

Campana et al. (2001), based on same age at longevity (Table 3).

2. Demographic Single-Sex and Two-Sex Models

Uncertainty estimates and the mean projected population growth rates obtained from the 14 harvest scenarios are shown in Tables 4-5. The estimates (λ) were higher for a 1-year reproductive cycle than for a 2-year reproductive cycle. Estimates of λ without fishing mortality for the total population (two-sex model) were 1.079 yr^{-1} and 1.030 yr^{-1} for 1-yr and 2-yr reproductive cycles, respectively. For the single-sex (female only) model, the respective values for λ were 1.073 and 1.020 yr^{-1}. However, when fishing mortality was introduced (Scenarios 2-5), all 2-year reproductive cycle models produced values of λ less than 1 (e.g., 0.905 yr^{-1} in two-sex model (single-sex = 0.891 yr^{-1}), 0.934 yr^{-1} (single-sex = 0.921 yr^{-1}), 0.965 yr^{-1}

(single-sex = 0.953 yr^{-1}) and 0.997 yr^{-1} (single-sex = 0.986 yr^{-1}) for cases 9-12, respectively) (Tables 4-5). The results showed that the single-sex model underestimated the population growth rate compared to the two-sex models.

3. Management Measures

Figs. 2 and 3 show the box plots for λ for scenarios 1-7. The wide variation in λ reflects parameter uncertainty. In general, management measures based on the one-year reproductive cycle model grossly overestimate the population growth rate. Scenarios of 20% and 40% of the current fishing pressure (Scenarios 4-5) resulted in a higher population growth rate for one-year reproductive cycle models, but not for 2-year reproductive cycle models (Cases 11-12) (Figs. 2 and 3). The one-year reproductive cycle model predicted an increasing population when imma-

Table 6. Comparison of silky shark population growth rates (without fishing mortality) from different studies.

Study	Methods	Age-at-maturity	longevity	Reproductive cycle	λ
Cortés, (2002)[1]	Stochastic age-based model	7-9	14-18	1	1.108 (1.075-1.139)
Beerkircher et al. (2003)[2]	Stochastic age-based model	11-13	22	1	1.049 (1.027-1.074)
Chen and Yuan (2006)[3]	Deterministic age-based model	8	27	1	1.145
Cortés (2008)[4]	Stochastic age-based model	7-9	22-29	1	1.076 (1.057-1.091)
Ortiz et al. (2018)[5]	Stochastic age-based model	15	35	1	1.066
				2	1.026
This study[5]	Two-sex stochastic stage-based model	14-16	25-35	1	1.079 (1.018-1.146)
				2	1.030 (0.979-1.084)

[1]Data from Northwestern Gulf of Mexico
[2]Data from Global sea
[3]Data from Southeast USA
[4]Data from Southern Gulf of Mexico
[5]Data from Indian Ocean

ture stages are protected (Case 6). However, the remaining analyses indicated that the stock would almost certainly decrease under those management measures (Cases 7, 13 and 14). There remains a high probability (> 0.5) that the population growth rate will be less than the threshold level of $\lambda = 1$, even if adults are protected (Figs. 2 and 3, Cases 7 and 14). Accordingly, conservation managers should carefully consider the possible sexual dimorphism of this species in order to determine whether more accurate estimates of decline risk may be obtained from a two-sex matrix model than from conventional single-sex models.

IV. DISCUSSION

1. Demographic Models

Demographic matrix population models, such as age-structured (Leslie Matrix) and stage-structured models, are commonly used in the assessment of shark populations. These approaches provide similar results if the same life history parameters are used (Mollet and Cailliet, 2002). In some situations, the life history of a shark species can be represented by several discrete stages (e.g., for the sandbar shark-neonate, juvenile, sub-adult, pregnant adults and resting adults) (Cortés, 1998; Mollet and Cailliet, 2002). In this case, the stage-based model can be useful where there is only limited age information, or where the life history exhibits complex reproductive physiologies (e.g., resting stages, extended gestation periods) (Tsai et al., 2014, 2015). It seems appropriate to apply a stage-based model to the silky shark, given that the population segregates between sexes, as well as between juveniles and adults (Clarke et al., 2011). Most demographic models are single sex, and assume both sexes have identical vital rates, or that the dynamics of the population are determined by females only (Caswell, 2001; Tsai et al., 2010). However, there are many species that display sexual dimorphism in vital rates,

such as sailfish and shortfin mako shark, and these consequently require a two-sex model (Caswell, 2001; Tsai et al., 2014, 2015). Although there is no significant difference in growth between sexes for the silky shark (Hall et al., 2012), other life history parameters, such as age-at maturity and mortality, may differ between sexes (Tables 2 and 3). In addition, the silky shark exhibits sexual segregation, as well as segregation among the juvenile stages (Clarke et al., 2011). These attributes suggest that a two-sex, rather than a single sex assessment, should be used to evaluate the stock status. Since life history parameters differ by sex, a two-sex stage-structured matrix population model was appropriate in this study.

2. Life History Information and Uncertainty

A comparison of the results obtained by the current study with those from previous demographic analyses (Cortés, 2002, 2008; Beerkircher et al., 2003; Chen and Yuan, 2006) highlights the considerable life history variation in different oceans. Our estimates of population growth rate are generally lower than those reported in other oceans (Table 6). This discrepancy may be the result of a relatively late maturity (the most likely value = 15 yr) and much greater longevity (25-35 yr) in the Indian Ocean (Table 6). It has long been recognized that age at maturity and longevity are correlated negatively with population growth rate in sharks (Cortés, 2002; Mollet and Cailliet, 2002; Tsai et al., 2010). Another possible explanation is that different studies have adopted different models (e.g., single sex vs. two sex). It has been noted that although dependable demographic estimates do exist for other oceans (Cortés, 2002, 2008; Beerkircher et al., 2003), due to differences in geography, the life history parameters (e.g., natural mortality, rate of population increase) of the Indian Ocean silky shark cannot be assumed to be the same as those in other oceans.

Several uncertainties could not be considered in this study. One possible source of bias in our demographic model is that the information on the biological and life history traits of the Indian Ocean silky shark are poorly understood compared with those in other oceans. Very limited literature is available and therefore our analysis had to rely on a single study by Hall et al. (2012). To improve demographic analysis and enable a more comprehensive stock assessment, additional studies of the biology of silky sharks are necessary. More accurate growth curves are particularly necessary, as this uncertainty significantly affects population growth rates (Tsai et al., 2014). Another possible shortcoming of this study is the use of indirect estimates of natural mortality based on life history parameters. For most fish stocks, direct estimates of natural mortality (e.g., from tagging data) are rarely available. In such data-poor situations, it is especially important to take into account the possible uncertainty of life history parameters. With no direct methods available for the silky shark, this study adopted five indirect methods. However, the true variation in natural mortality may in fact be much higher than this study has assumed. Since the estimation of M is essential in stock assessment, a more robust estimator of natural mortality is needed, and this will require greater efforts in the future, such as tagging research.

3. Management Implementation for the Silky Shark

Apart from the unique challenges of assessing a by-catch species, the Indian Ocean silky shark is particularly difficult to examine owing to a lack of landings data, the absence of population size estimates, and limited information on its life history. No quantitative stock assessment or fishery indicator of status is currently available. However, this species is commonly taken by a range of fisheries in the Indian Ocean, and there is some indication that the population has declined (overfishing but not overfished) over recent decades (Ortiz et al., 2018). Although the studies referred to above provide a general attempt at stock status assessment (Table 6), they are very much preliminary, in particular because they ignore sexual dimorphism. This phenomenon has different and significant implications for fishery selectivity and hence fishing mortality. In other words, if measures are based on a single sex model alone, the population may not be optimally managed.

This study constructed a population assessment method specifically to account for sexual dimorphism. As expected, the population growth rate differed between the sexes under fished and unfished conditions (Tables 4 and 5). Our findings indicate that sex-specific management decisions should be enacted to ensure the sustainable utilization of the silky shark. This is because interaction of the sexes has been shown to have important implications in management and conservation (Tsai et al., 2014, 2015). In addition, we examined various fishery management strategies (e.g., setting the fishing mortality rate equal to 80% of natural mortality rate). This assumption is currently taken as a reference point for sustainable fishing and induces the maximum possible compensatory productivity response in the population (MacCall, 2009). However, our demographic models suggest that even under moderate levels of fishing mortality (Tables 4 and 5), the silky shark population may be on the edge of collapse. Further, the size limit scenarios laid out in this study (Cases 6-7 and 13-14, Tables 4 and 5) show that protection of immature sharks will produce a higher population growth rate than protection of adults. This is in line with many shark demographic studies which have found that population growth is most sensitive to juvenile survival (Mollet and Cailliet, 2002; Tsai et al., 2010; Smart et al., 2017), The implication is that protection of immature silky sharks may be the most efficient conservation measure for this species.

Previous demographic modeling for the Pacific and the Atlantic Oceans (Cortés, 2002, 2008; Beerkircher et al., 2003) classify silky sharks as having a moderate capacity to recover from over-exploitation. However, this study shows that in the Indian Ocean, even under natural conditions of no fishing, the population will grow at a rate of just ~8% and ~3% per year, for 1-yr and 2-yr reproductive cycles respectively. Furthermore, the estimated λ for the silky shark are extremely low compared to the Indian blue shark (1.284-1.391 yr^{-1} and 1.209-1.221 yr^{-1} for 1-yr and 2-yr reproductive cycles respectively, Geng and Zhu, 2017) and any added anthropogenic source of mortality (Tables 4 and 5) will likely result in its decline. These findings imply that management measures should be implemented to reduce the fishing pressure on the Indian Ocean silky shark. Given the lack of adequate data to evaluate stock status, better knowledge of current fishing levels (e.g., fishing mortality obtained from Bayesian virtual population analysis if data become available) is needed to obtain a more robust estimate of the impact of commercial fishing on the silky shark population. Given the increase in global shark catches and landings, the silky shark population in the Indian Ocean needs constant monitoring to ensure its sustainability. Ultimately, our understanding of the species' population structure, movement, and productivity will require improved data for the entire Indian Ocean. Meanwhile, the approach taken in this study can be used as an assessment tool for other widely distributed pelagic shark species with insufficient catch and effort data.

REFERENCES

Aires-da-Silva, A., C. Lennert-Cody and M. Maunder (2013). Stock status of the silky shark in the eastern Pacific Ocean. 4th Meeting of the IATTC Scientific Advisory Meeting.

Beerkircher, L. R., M. S. Shivji and E. Cortés (2003). A Monte Carlo demographic analysis of the silky shark (*Carcharhinus falciformis*): implications of gear selectivity. Fishery Bulletin 101, 168-174.

Bonfil, R., R. Mena and D. de Anda. (1993). Biological parameters of commercially exploited silky sharks, *Carcharhinus falcifomis*, from the Campeche Bank, Mexico. NOAA Technology Reper NMFS 115, 73-86.

Branstetter, S. (1987). Age, growth and reproductive biology of the silky shark,

Carcharhinus falciformis, and the scalloped hammerhead, *Sphyrna lewini*, from the northwestern Gulf of Mexico. Environmental Biology of Fishes 19, 161-173.

Brewster-Geisz, K. K. and T. J. Miller (2000). "Management of the sandbar shark, *Carcharhinus plumbeus*: implications of a stage-based model." Fishery Bulletin 98, 236-249.

Campana, S., L. Marks, W. Joyce and S. Harley (2001). Analytical assessment of the porbeagle shark (*Lamna nasus*) population in the northwest Atlantic, with estimates of long-term sustainable yield. Stock Assessment Secretariat 2001/067, Ottawa, Ontario.

Castro, J. I., C. M. Woodley and R. L. Brudek (1999). A preliminary evaluation of the status of shark species. Food and Agriculture Organization.

Caswell, H., S. Brault, A. J. Read and T. D. Smith (1998). Harbor porpoise and fisheries: an uncertainty analysis of incidental mortality. Ecological Applications 8, 1226-1238.

Caswell, H. (2001). "Matrix Population Models. Construction, Analysis, and Interpretation." 2nd edn. (Sinauer Associates, Inc. Publishers: Sutherland, MA.)

Chen, P. and W. Yuan (2006). Demographic analysis based on the growth parameter of sharks. Fisheries Research 78, 374-379.

CITES Animals Committee (2016). Conservation and Management of Sharks and Stingrays: Other Animals Committee Tasks Related to Conservation and Management of Sharks. seventeenth meeting of the Conference of the Parties Bangkok (South Africa) from 24 September to 5 October 2016.

Clarke, C., J. S. E. Lea and R. F. G. Ormond (2011). "Reef-use and residency patterns of a baited population of silky sharks, *Carcharhinus falciformis*, in the Red Sea." Marine and Freshwater Research 62, 668-675.

Compangno, L., M. Dando and S. Fowler (2005). Field Guide to the Sharks of the World. London: Harper Collins Publishers.

Cortés, E. (1998). Demographic analysis as an aid in shark stock assessment and management. Fisheries research 39, 199-208.

Cortés, E. (2002). Incorporating uncertainty into demographic modeling: application to shark populations and their conservation. Conservation Biology 16, 1048-1062.

Cortés, E. (2008). Comparative life history and demography of pelagic sharks. Sharks of the Open ocean: biology, fisheries and conservation 13, 309-322.

Frisk, M. G., T. J. Miller and M. J. Fogarty (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 Journal of Marine Science 59, 576-586.

Geng, Z. and J. F. Zhu (2017). Estimating population growth rate for Indian Ocean blue shark using demographic method. IOTC-WPEB13-2017-021.

Hall, N. G., C. Bartron, W. T. White, W. T. Dharmadi and I. C. Potter (2012). Biology of the silky shark *Carcharhinus falciformis* in the eastern Indian Ocean, including an approach to estimating age when timing of parturition is not well defined. Journal of Fish Biology 80, 1320-1341.

Hoenig, J. M. (1983). Empirical use of longevity data to estimate mortality rates. Fishery Bulletin 82, 898-903.

Hoenig, J. M. and S. H. Gruber (1990). "Life-history patterns in the elasmobranchs: implications for fisheries management." NOAA Technical Report NMFS 90.1-16.

Hood, G. (2004). "PopTools. Pest animal control co-operative research center."

Jensen, A. L. (1996). Beverton and Holt life history invariants result from optimal trade-off of reproduction and survival. Canadian Journal of Fisheries and Aquatic Sciences 53, 820-822.

Joung, S. J., C. T. Chen, H. H. Lee and K. M. Liu (2008). Age, growth, and reproduction of silky sharks, *Carcharhinus falciformis,* in northeastern

Taiwan waters. Fisheries Research 90, 78-85.

MacCall, A. D. (2009). Depletion-corrected average catch: a simple formula for estimating sustainable yields in data-poor situations. ICES Journal of Marine Science 66, 2267-2271.

Matsunaga, H. and H. Nakano (1999). Species composition and CPUE of pelagic sharks caught by Japanese longline research and training vessels in the Pacific Ocean. Fisheries Science 65, 16-22.

Mollet, H. F. and G. M. Cailliet (2002). "Comparative population demography of elasmobranchs using life history tables, Leslie matrices and stage-based matrix models." Marine and Freshwater Research 53, 503-515.

Ortiz, J. U., T. Brunel., R. Coelho, G. Merino, D. Rosa, C. Santos, H. Murua, P. Bach, S. Saber and D. Macias (2018). A preliminary stock assessment for the silky shark in the Indian Ocean using a data-limited approach. IOTC-WPEB14-2018-033.

Oshitani, S., H. Nakano and S. Tanaka (2003). Age and growth of the silky shark *Carcharhinus falciformis* from the Pacific Ocean. Fisheries Science 69, 456-464.

Pauly, D. (1980). On the interrelationships between natural mortality, growth parameters, and mean environmental temperature in 175 fish stocks. ICES Journal of Marine Science 39, 175-192.

Rice, J. and S. Harley (2013). Updated stock assessment of silky sharks in the western and central Pacific Ocean. Scientific Committee Ninth Regular Session, 6-14.

Rigby, C. L., C. S. Sherman, A. Chin and C. Simpfendorfer (2017). *Carcharhinus falciformis*. The IUCN Red List of Threatened Species 2017: e.T39370A117721799.

Simpfendorfer, C. A. (2005). Demographic models: life tables, matrix models and rebound potential. In Management Techniques for Elasmobranch Fisheries, pp. 143-144. Ed. by J. A. Musick, and R. Bonfil. FAO Fisheries Technical Paper 479, Rome, Italy.

Smart, J. J., A. Chin, A. J. Tobin, W. T. White, B. Kumasi and C. A. Simpfendorfer (2017). Stochastic demographic analyses of the silvertip shark *(Carcharhinus albimarginatus)* and the common blacktip shark *(Carcharhinus limbatus)* from the Indo-Pacific. Fisheries Research 191, 95-107.

Stevens, J. D., R. Bonfil, N. K. Dulvy and P. A. Walker (2000). The effects of fishing on sharks, rays, and chimaeras (*chondrichthyans*), and the implications for marine ecosystems. ICES Journal of Marine Science 57, 476-494.

Tsai, W. P., K. M. Liu and S. J. Joung (2010). Demographic analysis of the pelagic thresher shark, *Alopias pelagicus*, in the north-western Pacific using a stochastic stage-based model. Marine and Freshwater Research 61, 1056-1066.

Tsai, W. P., S. L. Sun, A. E. Punt and K. M. Liu (2014). Demographic analysis of the shortfin mako shark, *Isurus oxyrinchus*, in the Northwest Pacific using a two-sex stage-based matrix model. ICES Journal of Marine Science 71, 1604-1618.

Tsai, W. P., K. M. Liu, A. E. Punt and C. L. Sun. (2015). Assessing the potential biases of ignoring sexual dimorphism and mating mechanism in using a single-sex demographic model: the shortfin mako shark as a case study. ICES Journal of Marine Science, 72(3): 793-803.

Walker, T I. (1998). "Can shark resources be harvested sustainably? A question revisited with a review of shark fisheries." Marine and Freshwater research 49, 553-572.

White, W. T. and R. D. Cavanagh (2007). "Whale shark landings in Indonesian artisanal shark and ray fisheries." Fisheries Research 84, 128-131.

Yokoi, H., H. Ijima, S. Ohshimo and K. Yokawa (2017). Impact of biology knowledge on the conservation and management of large pelagic sharks. Scientific Reports 7, 10619.