

Data-limited approach to the management and conservation of the pelagic thresher shark in the Northwest Pacific

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Abstract

The pelagic thresher shark is among the most heavily exploited shark species in the commercial fisheries of the tropical Indo-Pacific oceans. Despite this severe exploitation, little is known about pelagic thresher population dynamics, particularly the species' life history traits, and overall stock status. The pelagic thresher exhibits slow growth and extremely low fecundity, indicating the need for reassessment of the population status of this globally threatened shark. Because information on catch and effort of this bycatch species is scarce, several data-limited methods—quantitative demographic methods, per-recruit analysis, and risk assessment—were employed in this study to provide an accurate measurement of the status of pelagic thresher shark stocks. For each sex, the composite risk assessments indicated that the probability of the current fishing mortality increasing beyond any level of yield-per-recruit (YPR) was approximately zero given the biological reference points (BRPs). Moreover, the current spawning potential ratio (SPR) was found to be significantly below the target reference point of SPR60%, but slightly above the limit reference point of SPR40%. However, because SPR-based BRPs are much less sensitive to input parameter uncertainties than YPR-based BRPs, results derived from the SPR model are more suitable for species management. Management strategy simulations based on demographic two-sex models indicated that without mortality from fishing, female pelagic threshers have a higher population growth rate than males. However, the stock status of female pelagic thresher shark is poorer than that of males under current conditions. The findings suggest that sex-specific management decisions must be made to achieve the sustainable utilization of this species. Overall, both the sex-specific per-recruit and demographic models determined that recruitment overfishing has occurred in the female pelagic thresher population of the Northwest Pacific Ocean, indicating that close monitoring of female sharks is urgent and necessary to ensure that stocks remain sustainable.

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KEYWORDS

biological reference points, data-limited approaches, demographic analysis, pelagic thresher sharks, risk assessment

1 | INTRODUCTION

The conservation and management of sharks, which are major ocean predators, are essential to the protection of marine biodiversity and maintenance of the ecosystem's structure and function (Liu et al., 2021; Ritchie et al., 2012). However, sharks are vulnerable to overexploitation by fisheries (as target and bycatch) because of particular biological characteristics such as their slow growth, late maturity, long life span, and low numbers of offspring (Adams et al., 2018; Booth et al., 2019; Dulvy et al., 2014; Liu et al., 2015). Compared with other pelagic sharks, thresher sharks (of the family Alopiidae) are likely the shark species most vulnerable to fishing, partially owing to their limited reproductive potential (2–6 pups/litter; Dulvy et al., 2008). All thresher shark species were included in Appendix II of the Convention on International Trade in Endangered Species of Wild Fauna and Flora (CITES, 2016) and listed as globally vulnerable on the International Union for Conservation of Nature (IUCN) Red List (Amorim et al., 2009) as a result of their marked decline in abundance (overall decline in nominal catch per unit effort and mean weight) in the ocean (Reardon et al., 2009). In the reassessed 2019 IUCN Red List of Threatened Species, only the pelagic thresher shark (*Alopias pelagicus*) was elevated to an endangered level (Rigby et al., 2019). Furthermore, a study revealed that oceanic sharks and rays, including all thresher species, have declined in number by at least 70% over the last 50 years (Pacoureau et al., 2021).

The pelagic thresher shark is among the most heavily exploited shark species in commercial fisheries of the tropical Indo-Pacific oceans (Compagno, 2001). Despite severe exploitation, little is known about pelagic thresher population dynamics, particularly their life history traits and overall stock status. Limited information on the population status of pelagic threshers is available, but some studies have suggested their decline and the need for close monitoring in the Northwest Pacific Ocean (Liu et al., 2006; Tsai et al., 2010). Currently, this species has been prohibited to be retained on board for commercial use by two regional fishery management organizations (RFMOs), namely the International Commission for the Conservation of Atlantic Tunas (ICCAT, Compliance Committee, 2010) and Indian Ocean Tuna Commission (IOTC, 2010). However, no conservation or management measures specific to pelagic thresher are in place for the Pacific Ocean. To date, a full stock assessment of the

pelagic thresher has never been conducted by any RFMO because of the lack of reliable catch, effort, and abundance index information. Pelagic thresher sharks exhibit slow growth and extremely low fecundity, indicating the need for reassessment of the population status of this globally threatened shark.

The effects of fishing activities on nontarget species are often complex and difficult to assess as a result of the limited available data. Most RFMO stock assessments rely heavily on indices of exploitable abundance (usually the standardization of catch per unit effort) derived from accurate catch statistics (e.g., ICCAT and IOTC). However, the general lack of fishery-independent and fishery-dependent abundance indices for bycatch species such as pelagic thresher sharks hinders the development of a meaningful stock assessment. Therefore, an alternative method to measuring pelagic thresher stock status is urgently required to aid the development of suitable fishery management strategies.

As a result of the information gaps for many bycatch species, data-limited approaches such as demographic techniques and risk assessments have been widely applied to data-poor species to provide recommendations on the relative levels of risk associated with various fishery strategies (Aires-da-Silva & Gallucci, 2007; Brewster-Geisz & Miller, 2000; Cortés, 2002; Mollet & Cailliet, 2002; Simpfendorfer, 1999a, 1999b). Demographic (age-based or stage-based) methods have been employed to estimate population metrics, such as the population growth rate, and the generation time based on basic life history information including rates of growth, mortality, and fecundity. In addition, demographic techniques enable the calculation of elasticities (proportional sensitivities) of the population growth rate to changes in vital rates, which can assist in distinguishing vulnerable life stages (Heppell et al., 2000). Other data-limited methods, such as the biological reference points (BRPs) obtained from per-recruit models, can identify sustainability limits for fishing pressure with respect to the designated target levels (Tsai et al., 2011, 2020). In this study, we employed several data-limited methods—quantitative demographic methods, per-recruit analysis (age/length based), and risk assessment—to provide the most accurate measurement of the status of pelagic thresher shark stocks.

Because sexual segregation has been observed for this species (Romero-Cacedo et al., 2014), a two-sex matrix-based population model was developed to investigate pelagic thresher demographic dynamics. All analyses

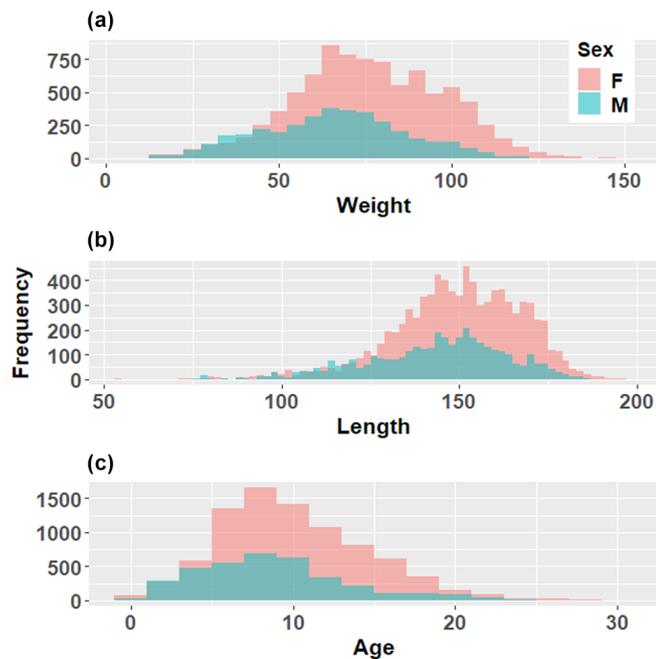


FIGURE 1 Deterministic estimated sex-specific weight frequency, length frequency, and age frequency for the combined 5-year data (2015–2019) on pelagic thresher sharks in the Northwest Pacific Ocean: (a) weight-frequency distributions; (b) length-frequency distributions; and (c) age-frequency distributions

were conducted for both male and female sharks except for spawning potential ratio assessment (female only) in this study. In addition to traditional deterministic approaches, a stochastic framework that accounted for possible uncertainty in the biological parameters was introduced and implemented using the Monte Carlo simulation approach, and different scenarios were designed to assess the effects of these uncertainties on BRPs and population growth rate estimates. The specific objectives of this study were to estimate the current and sustainable fishing mortality and BRPs for the pelagic thresher shark and to evaluate strategies for managing stocks of this species in the Northwest Pacific Ocean. The results obtained provide valuable information on fishery strategies and conservation to enable better management of the pelagic thresher population in the Northwest Pacific region. The approach used herein is also applicable to other fish species for which sufficient time-series data on abundance are lacking.

2 | MATERIALS AND METHODS

2.1 | Data sources

The pelagic thresher catch data (numbers and individual whole weights) used in the present study were obtained

TABLE 1 Life history parameters used in this study for the pelagic thresher shark

Parameter	Male	Female
Sex ratio (Φ_W) ^a	$1 - \Phi_W$	Φ_W
Weight < 30 kg	0.5	0.5
$30 \leq \text{weight} \leq 130$ kg	α	β
α	0.090	0.482
β	0.482	0
Weight > 130 kg	0	1
Length–weight relationship ^b		
a	2.66×10^{-4}	2.56×10^{-4}
b	2.493	2.511
VBGE ^b		
L_∞	182.196	197.153
K	0.118	0.085
t_0	-5.482	-7.669
Longevity ^b		
a_{\max}	22 years	30 years
Maturity ^c		
a_{mat}	7 years	8 years

^aBased on Liu et al. (1999).

^bIn this study, the sex ratios (the proportion of females) of sharks smaller than 30 kg and greater than 130 kg were set as 0.5 and 1.0, respectively, on the basis of our observations. For fish between 30 and 130 kg, the sex ratio by weight (Φ_W) was obtained using the following equation: $\Phi_W = \alpha \times W^\beta$, where α and β are estimated parameters. ($R^2 = 0.965$; $n = 1975$, 5-kg classes, $p < .0001$).

^cMaturity–length data were converted into maturity–age data by using growth curves from Liu et al. (1999).

through the daily auction records of the Nanfangao fish market for fishing vessels operating in eastern Taiwan (see Figure 1 in Tsai et al., 2010) between January 2015 and December 2019. However, because of the lack of information regarding individual sex and length in these records, a subsample of 1975 fish (1341 females and 634 males) were randomly collected from the landings to obtain the weight-specific sex ratio relation. Specimen sex was identified, and the precaudal length (PCL) was measured. Thus, the sex of each landed shark could be calculated using the weight-specific sex ratio (more details can be found in Tsai et al., 2011). Because the sex ratio (the percentage of females) increased with shark size in the samples (Figure 1), the sex ratios of sharks weighing less than 30 kg and more than 130 kg were set at 0.5 and 1.0, respectively. For sharks between 30 and 130 kg, the sex ratio of weight (Φ_W) was derived from the whole weight (W) through the equation $\Phi_W = \alpha \times W^\beta$, where α and β are estimated parameters. The whole weights were then converted into a PCL by using the sex-specific weight–PCL

relationship $W = x_s PCL^{y_s}$ (Liu et al., 1999), where x_s and y_s are parameters for sex s . Catch-at-age composition was then calculated from the converted PCL by using the von Bertalanffy growth equations (VBGEs) provided by Liu et al. (1999). All values are presented in Table 1.

2.2 | Deterministic estimates

2.2.1 | Mortality estimation

Direct estimates of natural mortality (M) for pelagic thresher sharks were not available. Hence, several empirical equations that were either recently developed or specifically formulated for shark species were adopted in this study. The sex-specific natural mortality (M_s) was then quantified using the following set of indirect techniques [Equation (1): Then et al., 2015; Equation (2): Then et al., 2015; Equation (3): Then et al., 2015; Equation (4): Hamel, 2015; Equation (5): Hamel, 2015; Equation (6): Frisk et al., 2001; Equation (7): Frisk et al., 2001; Equation (8): Hisano et al., 2011; Equation (9): Campana et al., 2001; Equation (10): Jensen, 1996; Equation (11): Jensen, 1996]:

$$M_s = 4.899 a_{\max,s}^{-0.916} \quad (1)$$

$$\ln(M_s) = 1.717 - 1.01 \times \ln(a_{\max,s}) \quad (2)$$

$$M_s = 4.118 k_s^{0.73} L_{\infty,s}^{-0.33} \quad (3)$$

$$M_s = 4.374 / a_{\max,s} \quad (4)$$

$$M_s = 1.753 k_s \quad (5)$$

$$\ln(M_s) = 0.42 \times \ln(k_s) - 0.83 \quad (6)$$

$$M_s = \frac{1}{0.4 \times a_{\max,s} + 1.8} \quad (7)$$

$$M_s = \frac{1.6}{a_{\max,s} - t_{0,s}} \quad (8)$$

$$M_s = -\ln 0.01 / a_{\max,s} \quad (9)$$

$$M_s = 1.6 k_s \quad (10)$$

$$M_s = 1.65 / a_{\max,s} \quad (11)$$

where a is age; $a_{\max,s}$ is longevity, set at 22 and 30 years (Liu et al., 2006; Mollet & Cailliet, 2002; Tsai

et al., 2010) for males and females, respectively; $a_{\text{mat},s}$ is the age-at-maturity, set at 7 and 8 years (Liu et al., 1999) for males and females, respectively; $L_{\infty,s}$, k_s , and $t_{0,s}$ are the growth parameters of the VBGE. To simplify the model, the sex-specific natural mortality (M_s), based on the median value from the 11 methods above, was assumed to be constant for subsequent deterministic analyses.

In conventional age-based catch curve methodology (Ricker, 1975), total mortality (Z_s) for each sex can be obtained from the estimated slope of the linear regression:

$$\ln(C_{t,s}) = \alpha_s - Z_s t_s, \quad (12)$$

where $C_{t,s}$ is the value for sex-specific catch, α_s is a constant, and t_s is commonly defined based on age at full recruitment, which is the age with the highest frequency in the age distribution. Sex-specific fishing mortality (F_s) was then calculated as the difference between Z_s and M_s . The estimated F_s was considered to be the current fishing mortality.

2.2.2 | Biological reference points

BRPs are generally subdivided into limit reference points (minimum safe levels not to be exceeded) and target reference points (to attain the ultimate management goal; FAO, 1995). Two common approaches, the yield-per-recruit (YPR) model and spawning-per-recruit curves (SSB/R), were employed in this study to estimate suitable BRPs for pelagic thresher sharks. YPR and SSB/R analyses were conducted using the following methodology.

The YPR can be calculated as (Thompson & Bell, 1934)

$$Y_{/R} = \sum_{a=a_{c,s}}^{a_{\max,s}} \left(\bar{W}_{a,s} \frac{F_s}{F_s + M_s} \left(1 - e^{-(F_s + M_s)} \right) e^{-\sum_{i=a_{c,s}}^{a-1} (F_s + M_s)} \right), \quad (13)$$

where $a_{c,s}$ is the age at first capture in sex s (set as age 1 for each sex), $\bar{W}_{a,s}$ is the mean body weight in kilograms for fish of age a and sex s , and $a_{\max,s}$ is the longevity, set at 22 years for males and 30 years for females (Mollet & Cailliet, 2002; Tsai et al., 2010).

In practice, the $F_{0.1}$ and F_{\max} derived from YPR analysis have been frequently used in fisheries as target and limit reference points in the context of precautionary management (Tsai et al., 2011). The management target BRP ($F_{0.1}$) and limit BRP (F_{\max}) were estimated using the following calculation:

$$\frac{\partial(Y/R)}{\partial F} \Big|_{F=F_{0.1}} = 0.1 \times \frac{\partial(Y/R)}{\partial F} \Big|_{F=0} \quad (14)$$

$$\frac{\partial(Y/R)}{\partial F} \Big|_{F=F_{\max}} = 0 \quad (15)$$

The spawning potential ratio (SPR) is defined as the proportion of the unfished reproductive potential left at a selected level of fishing pressure (Goodyear, 1993). The SPR analysis only conducted for female population:

$$SPR = \frac{SSB/R}{SSB/R|_{F=0}} \times 100\%. \quad (16)$$

In addition to the conventional age-based approach, the length-based SPR (LBSPR, Hordyk, Loneragan, & Prince, 2015; Hordyk, Ono, et al., 2015) model has been developed and currently widely used for many data-poor or data-limited fisheries to assess proxies of stock status (e.g., Pons et al., 2019; Prince et al., 2015, 2020). In this study, the estimation of the SPR was also conducted using the LBSPR (Hordyk, 2021) package version 0.1.6 in R (R Core Team, 2021).

The use of LBSPR requires only length composition data and input estimates of key life history parameters. These parameters are the asymptotic length (L_{∞}), lengths at 50% (L_{50}) and 95% maturity (L_{95}), and the ratio of natural mortality to von Betalanffy growth coefficient (M/k). The life history information such as L_{∞} and k was obtained from Liu et al. (1999) and M was set as median value from above 11 empirical methods. Population-specific values for L_{50} and L_{95} were estimated based on the raw data from Liu et al. (1999) for the pelagic thresher. Herein, length of maturity (m_L) was represented by a logistic regression fitted to the observed maturity data. The form of the logistic equation is:

$$m_L = \frac{1}{1 + \exp \left[-\ln 19 \times \frac{L - L_{50}}{L_{95} - L_{50}} \right]}, \quad (17)$$

where L_{50} and L_{95} are the length at 50% and 95% sexual maturity.

To avoid low sample size in some years, the 5 years (2015–2019) of length data were aggregated into a single dataset for the LBSPR model to produce estimates of SPR, gear selectivity (SL_{50} and SL_{95} ; lengths at 50% and 95% selectivity), and the ratio of fishing mortality to natural mortality (F/M).

Several studies have explored the levels of SPR to be used as management reference points for fish species; a SPR = 40% (SPR40%) is commonly used as the target reference point and 20% as the lowest safe limit (Clark, 2002; Hordyk, Loneragan, & Prince, 2015; Punt, 2000). However, it has been

proposed that shark species require much higher SPR level. Clarke and Hoyle (2014) recommended that an SPR > 40% should meet management needs, but noted that for long-lived and low-productivity shark stocks, the appropriate SPR level could be 60% or even 70%. In this study, in addition to the YPR-based BRPs, SPR60% was adopted as the precautionary management target and SPR40% as the limit reference point (Tsai et al., 2019, 2020), defining unsustainable levels of fishing. The estimations of BRPs without considering the parameter uncertainty are set as the base case.

2.3 | Demographic analyses

2.3.1 | Stage classifications of pelagic thresher sharks

The biological parameters for the pelagic thresher shark were adopted from the estimations of Liu et al. (1999). Consequently, the life history of the female pelagic thresher can be represented as follows: neonates (0–1 year), juveniles (1–5 years), subadults (5–8 years), and adults (8–30 years). The life history of males can be represented as follows: neonates (0–1 year), juveniles (1–4 years), subadults (4–7 years), and adults (7 years and older; Table 2).

2.3.2 | Model development

Similar to other thresher sharks, pelagic threshers exhibit sexual segregation (Romero-Caicedo et al., 2014) and year-round parturition (Liu et al., 2006; Mollet & Cailliet, 2002; Tsai et al., 2010). Both of these factors could be accounted for in the demographic matrix model. Because direct estimates of age-specific vital rates were unavailable for pelagic threshers, demographic analyses were undertaken with a stage-structured matrix model (Caswell, 2001) by using the CSIRO PopTools program (Hood, 2010). Following Caswell (2001), a birth-flow matrix model with continuous reproduction was then developed to estimate pelagic threshers' demographic parameters. For sharks with continual reproduction, the projection matrix (A) corresponding to the life cycle can be expressed as follows:

$$\begin{bmatrix} 0 & 0 & f_3^{\text{mal}} & f_4^{\text{mal}} & 0 & f_6^{\text{fem}} & f_7^{\text{fem}} \\ (1-\rho)G_1 & P_2^{\text{mal}} & 0 & 0 & 0 & 0 & 0 \\ 0 & G_2^{\text{mal}} & P_3^{\text{mal}} & 0 & 0 & 0 & 0 \\ 0 & 0 & G_3^{\text{mal}} & P_4^{\text{mal}} & 0 & 0 & 0 \\ \rho G_1 & 0 & 0 & 0 & P_5^{\text{fem}} & 0 & 0 \\ 0 & 0 & 0 & 0 & G_5^{\text{fem}} & P_6^{\text{fem}} & 0 \\ 0 & 0 & 0 & 0 & 0 & G_6^{\text{fem}} & P_7^{\text{fem}} \end{bmatrix},$$

Sex	Stage-class	Approximate ages (year)	Expected stage duration (year)
Male	Neonates	0–1	1
	Juveniles	1–4	3
	Subadults	4– a_{mat}	3–4
	Adults	$a_{\text{mat}}-a_{\text{max}}$	13–20
Female	Neonates	0–1	1
	Juveniles	1–5	4
	Subadults	5– a_{mat}	3–4
	Adults	$a_{\text{mat}}-a_{\text{max}}$	20–29

TABLE 2 Stages for the pelagic thresher shark in the Northwest Pacific

Note: a_{mat} : 7–8 years for males and 8–9 years for females. a_{max} : 20–26 years for males and 28–36 years for females.

where $^{\text{mal}}$ and $^{\text{fem}}$ denote males and females, respectively. The sex ratio at birth is represented by ρ (defined as the ratio of female to total births, set as 0.5 to achieve an equal offspring sex ratio; Liu et al., 1999). The $f_{i,s}$ is the stage-specific per-capita fecundity, which can be estimated using the modified harmonic mean method of Caswell (2001):

$$f_{i,s} = l(0.5) \left(\frac{(1 + P_{i,s})m_{i,s} + G_{i,s}m_{i+1,s}}{2} \right), \quad (18)$$

where $l(0.5)$ is the probability of newborn pups surviving to an age of 0.5, and m_i is the number of pups per individual in stage i (set as 1 based on an equal offspring sex ratio).

For each sex, the product of the probability of an individual surviving ($\sigma_{i,s}$) and moving to another stage ($G_{i,s}$) or remaining in its current stage ($P_{i,s}$), that is, $G_{i,s} = \sigma_{i,s} \times \gamma_{i,s}$; $P_{i,s} = \sigma_{i,s} \times (1 - \gamma_{i,s})$; $\sigma_{i,s} = \exp^{-Z_{i,s}}$, was calculated as described in Tsai et al. (2010, 2014). The probability of shifting to another stage ($\gamma_{i,s}$) was estimated by using the equation $\gamma_{i,s} = \frac{(\sigma_{i,s})^{T_{i,s}} - (\sigma_{i,s})^{T_{i,s}-1}}{(\sigma_{i,s})^{T_{i,s}} - 1}$ (Brewster-Geisz & Miller, 2000), where $T_{i,s}$ is the stage duration of a single stage. When the population matrix was constructed, the population growth rate (λ) was estimated by extracting its dominant eigenvalue. Estimates of λ provided a solid foundation for calculating other demographic parameters, including the intrinsic rate of population increase (e.g., $r = \ln \lambda$), mean generation length (μ_1), and stage elasticity (proportional sensitivities, E_i ; Heppell et al., 1999; de Kroon et al., 2000; Tsai et al., 2020). These demographic parameters were estimated using the methods and definitions in Tsai et al. (2010, 2014). Furthermore, this analysis did not include the harvest (or exploitation) elements into the matrix model due to the estimated total catch of pelagic thresher shark in the Northwest Pacific were not available.

2.4 | Estimates with uncertainty

2.4.1 | Uncertainty in life history parameters

Monte Carlo simulations were used to incorporate different sources of uncertainty (i.e., growth parameters, catch, and life history parameters). To account for length-at-age variation, catch-at-age was estimated on the basis of the growth parameters from the VBGEs under assumed normal distributions with means μ and standard errors se (Table A1, Liu et al., 1999). A total of 10,000 repeated samplings were conducted to generate the *growth* parameters ($L_{\infty,s}$, k_s , and $t_{0,s}$). In all cases, catch curves were computed based on the input of biased *growth* parameters for the derivation of total mortality. Similarly, *values of natural mortality could be obtained* based on the subsequent biological parameters from distributions (Tables 2 and A1).

To account for the uncertainty in the input parameters, three possible sources of random errors were included in both the BRP and demographic analyses. All values for different sources of uncertainty are described in Table 3. Values of the mean (μ) and standard deviation (SD) for sex-specific growth parameters and mortality rates are presented in Table A1. These uncertainties were estimated as follows:

- Ages at maturity of 7–8 years for males and 8–9 years for females were used as the lower and upper bounds to define the uniform probability mass function (Table 3).
- Based on the VBGE of Liu et al. (1999), male pelagic threshers may have longevity (O_{max}) exceeding 20 years and females 28 years. Theoretical estimates of longevity were 26 and 36 years for males and females, respectively, based on $t_{\text{max}} = O_{\text{max}} \times 1.3$ (Cortés, 2002). However, for simplicity, longevity were fixed at 22 and 30 years for males and females,

TABLE 3 Uncertainty values used in the stochastic simulations in this study

Source of uncertainty	Male	Female	Assumed distribution
Natural mortality	ln(mean,SD) ^a	ln(mean,SD) ^a	Lognormal
Longevity	Triangle (20, 22, 26) years	Triangle (28, 30, 36) years	Triangular distribution
Age at maturity	7–8 years	8–9 years	Uniform

^aThe mean and standard deviation (*SD*) obtained for *M* across all 11 methods for each sex and stage were used to define a lognormal distribution.

respectively, in deterministic cases; these are the most likely values for pelagic thresher sharks. Thus, the triangular probability distribution was introduced to incorporate a lower limit, upper limit, and mode for generating longevity (Table 3).

- For each scenario, the mean (μ) and *SD* obtained from the 11 *M* across methods were used to define a lognormal distribution for each sex and stage (Table 3). The μ and *SD* of *Z* calculated from the generation of a catch curve were also assumed to follow a lognormal distribution (Table A1). A lognormal error structure was adopted for the mortality rate to ensure that survival estimates were positive and between 0 and 1.

2.4.2 | Estimates of population decline risk

Monte Carlo simulations were performed to assess the risk of the population growth rate falling below 1 and the current fishing mortality (F_{cur}) exceeding the management reference points. Three main sources of uncertainty—age at maturity, longevity, and mortality rate—were incorporated into the model simulations. Life history parameters for each sex were sampled from their assumed distributions (Table 3). In terms of demographic analyses, six harvest strategies were employed to examine the status and explore the effect of alternative management strategies. These potential harvest strategies were as follows:

- Natural condition (Scenario 1): fishing mortality for all stages is set to 0.
- Status quo (Scenario 2): fishing mortality equals its current level by stage.
- Protection of immature male sharks (Scenario 3): same as Scenario 1 except that fishing mortality for male neonates, juveniles, and subadults is set to 0.
- Protection of mature male sharks (Scenario 4): same as Scenario 1 except that fishing mortality for the male adult stage is set to 0.
- Protection of immature female sharks (Scenario 5): same as Scenario 1 except that fishing mortality for female neonates, juveniles, and subadults is set to 0.

- Protection of mature female sharks (Scenario 6): same as Scenario 1 except that fishing mortality for the female adult stage is set to 0.

The variations in the estimated demographic parameters and BRPs were calculated by identifying the upper (97.5th) and lower (2.5th) percentiles for each probabilistic model. All demographic simulations and BRPs calculations were conducted using PopTools (Hood, 2010) and the R statistical programming language (R Core Team, 2021).

3 | RESULTS

3.1 | Deterministic estimates

3.1.1 | Sex-specific catch compositions and maturity curve

The sex ratio of weight (Φ_W) over the range 30–130 kg was calculated using the following equation: $\Phi_W = 0.090 \times W^{0.482}$ ($R^2 = 0.965$; $n = 1975$, 5 kg classes, $p < .0001$; Table 1). A total of 12,391 pelagic thresher sharks landed at Nanfangao fish market between 2015 and 2019, were calculated to comprise 8739 females and 3652 males. The majority of the fish fell within the range 60–80 kg (Figure 1a), corresponding to a PCL of 160–180 cm (Figure 1b) and age of 6–9 years for both sexes (Figure 1c). The logistic curve that described the proportion of mature females (m_L) at each age was estimated to be $m_L = \frac{1}{1 + \exp\left[-\ln 19 \times \frac{L - 145.419}{157.424 - 145.419}\right]}$ ($n = 262$) by using the data from Liu et al. (1999).

3.1.2 | Mortality estimates

The sex-specific natural mortality (M_s) of the fish was estimated using the 11 indirect methods presented in Table 4. Because the values of M_s obtained using most of the 11 methods were markedly different (Table 4), the natural mortality based on the median values of M_s was employed and assumed to be known and constant in

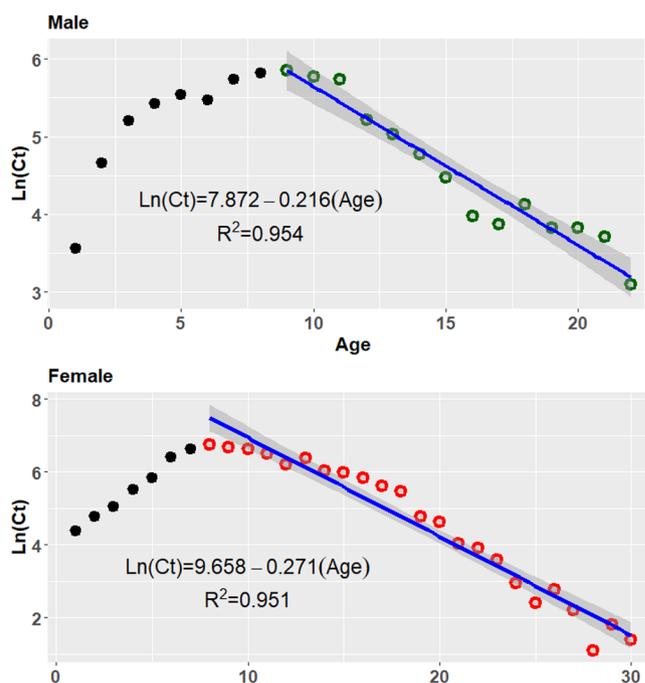
TABLE 4 Deterministic estimates of mortality rate for the pelagic thresher shark in the Northwest Pacific Ocean when using 11 indirect methods

Mortality	Method	Relies on parameters	Male	Female
Natural mortality	Then et al. (2015) nls	a_{max}	0.289	0.217
	Then et al. (2015) lm	a_{max}	0.245	0.179
	Then et al. (2015) $VBGE$	k, L_{∞}	0.155	0.119
	Hamel (2015) a_{max}	a_{max}	0.199	0.146
	Hamel (2015) k	k	0.206	0.149
	Frisk et al. (2001) k	k	0.177	0.155
	Frisk et al. (2001) a_{mat}	a_{mat}	0.217	0.200
	Hisano et al. (2011) a_{mat}	a_{mat}, t_0	0.128	0.102
	Campana et al. (2001) a_{max}	a_{max}	0.209	0.154
	Jensen (1996) k	k	0.188	0.136
	Jensen (1996) a_{mat}	a_{mat}	0.236	0.206
	Median	–	0.206	0.154
Total mortality	Ricker (1975)	Catch curve	0.216	0.271
Fishing mortality	$Z - M$	–	0.010	0.118

deterministic simulations to reduce the complexity of models. The estimated sex-specific values were higher for males than for females in all cases. For these methods, M_s ranged from 0.128 to 0.289 year⁻¹ for males and 0.102 to 0.217 year⁻¹ for females. The lowest estimates of M_s for both sexes were obtained using the empirical equation of Hisano et al. (2011), which relies on age at maturity and t_0 . The highest estimates of M_s for both sexes were derived using the Then et al. (2015) method, which is based on Longevity. The median value of M_s , with the median being that over the 11 methods, was 0.206 and 0.154 year⁻¹ for males and females, respectively (Table 4). The total mortality (Z_s) derived from the age-based catch curve was 0.216 and 0.271 year⁻¹ for males and females, respectively (Figure 2). The current fishing mortality (F_s) was obtained by subtracting M_s from Z_s and was 0.010 and 0.118 year⁻¹ for male and female pelagic threshers, respectively (Table 4).

3.1.3 | Input parameters for LBSRP

A total of 8739 female samples of pelagic thresher sharks were collected from 2015 to 2019 and the length-frequency distribution and maturity curve of pelagic thresher are shown in Figure A1. Length at 50% and 95% maturity were estimated to be 145.419 and 157.424 cm, respectively. The life history ratio (M/k) was calculated as 1.812 based on the median value of natural mortality (0.154 year⁻¹) obtain from 11 indirect methods. The life history parameters prepared for the LBSRP assessment are shown in Table A2.

**FIGURE 2** Estimation of sex-specific total mortality, obtained using age-converted catch curve analysis for the combined 5-year data (2015–2019), for pelagic thresher sharks in the Northwest Pacific Ocean

3.1.4 | Biological reference points

The results of the BRP analysis are summarized in Table 5. However, the estimates of F_{max} and Y/R_{max} were not available for either male or female pelagic thresher sharks in the deterministic models because the Y/R

TABLE 5 Estimates of current fishing mortality (F_{cur}) and BRPs derived from the YPR and LBSPR models for the pelagic thresher shark in the Northwest Pacific Ocean during the period January 2015 to December 2019

Yield per recruit model						
Parameter	F_{cur} (year ⁻¹)	F_{max} (year ⁻¹)	$F_{0.1}$ (year ⁻¹)	Y/R_{cur} (kg)	Y/R_{max} (kg)	$Y/R_{0.1}$ (kg)
Male	0.010	–	0.231	2.097	–	18.468
Female	0.118	–	0.169	20.170	–	22.794
Length based spawning per recruit model						
Parameter	SL50 (cm)	SL95 (cm)	F/M	LBSPR (%)		
Female	164.09 (160.9–167.28)	199.63 (195.83–203.43)	3.53 (2.84–4.22)	43 (37–49)		

curves tended to be asymptotic. $F_{0.1}$ was 0.231 and 0.169 year⁻¹ for males and females, respectively. The estimates of Y/R_{cur} were 2.097 and 20.170 kg for males and females, respectively, and for $Y/R_{0.1}$ were 18.468 and 22.794 kg, respectively. The LBSPR analysis determined that the current SPR (SPR_{cur}) was 43% (Figure 3), and the relative fishing mortality (F/M) was 3.53. The specific estimated parameters SL_{50} , SL_{95} , F/M ratio, and SPR are presented in Table 5. In conclusion, the results of deterministic YPR analysis showed that the current fishing mortality was lower than the BRP of $F_{0.1}$ for both males and females. Moreover, the current SPR was found to be significantly below the target reference point of SPR60%, but slightly above the limit reference point of SPR40%, indicating high concern for the sustainability of current female fishing pressure (Table 5).

3.1.5 | Demographic analyses

The estimated elements of life history matrix A for all deterministic cases are shown in Table A3. The deterministic model without fishing mortality projected increasing population growth ($\lambda = 1.068$ year⁻¹) for the total population based on the most optimistic input parameters. The sex-specific values for λ were 1.050 and 1.082 year⁻¹ for males and females, respectively. Under the current fishing mortality, a two-sex model would result in an approximately stationary population (e.g., $\lambda = 0.999$ year⁻¹ for the total population and 1.033 and 0.955 year⁻¹ for males and females, respectively). However, the analyses also indicated that female populations would almost certainly shrink ($\lambda = 0.955$ year⁻¹) under current fishing conditions. Furthermore, without fishing mortality, the generation time of the pelagic thresher was estimated as 9.565 years. Expressed as a percentage, the elasticity of the stages of immaturity (neonates + juveniles + sub-adults) was 27.37% for males and 38.96% for females, whereas that of the mature stage (adults) was 11.96% and 21.71%, respectively. The elasticity analysis demonstrated

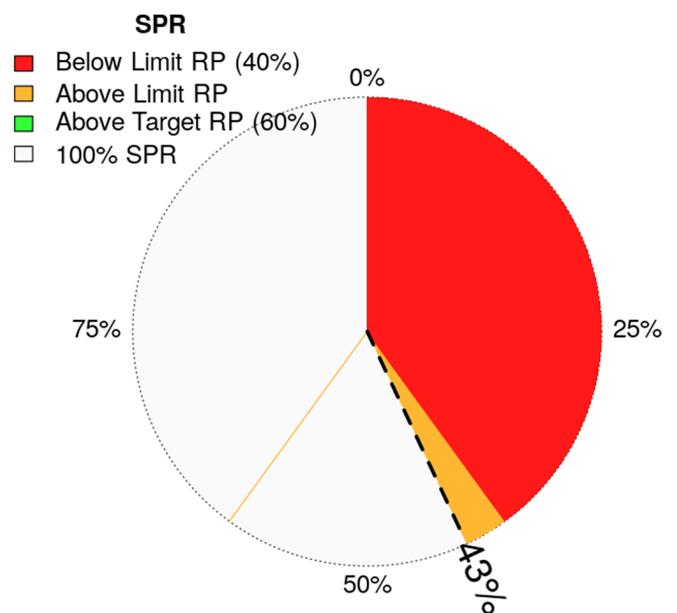


FIGURE 3 Proportions of the current spawning potential ratio (SPR) by the categories of the SPR-based reference points for the pelagic thresher in the Northwest Pacific Ocean

that λ was more sensitive to changes in demographic parameters related to female stages. Additionally, the stages of immaturity for both sexes had the greatest influence on λ .

3.2 | Estimates with uncertainty

3.2.1 | Stochastic BRPs and risk analyses

Box plots of simulation BRPs derived from the YPR and SPR models are presented in Figures 4 and 5. The considerable uncertainty regarding the life history parameters in BRP values had to be taken into account when the BRPs were estimated. The YPR-based BRPs were more sensitive, particularly for F_{max} (wider uncertainty intervals) to changes in parameter input than the SPR-based

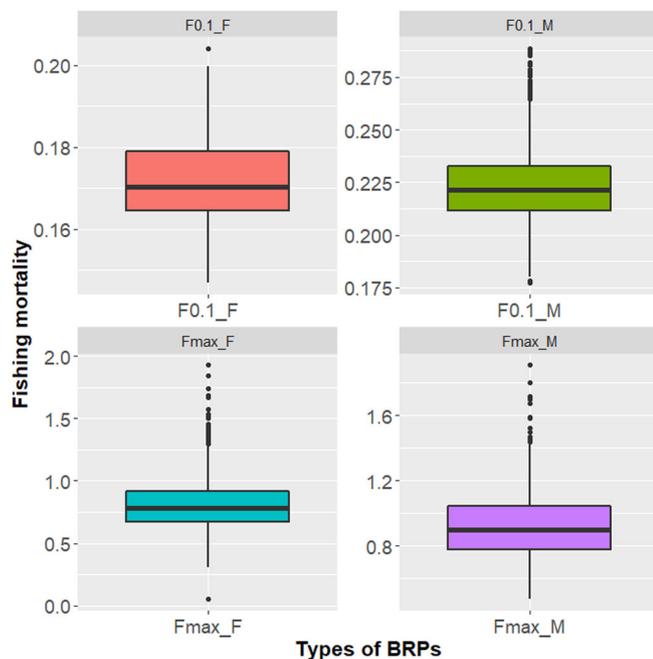


FIGURE 4 Box plots for the estimates of YPR-based BRPs of the pelagic thresher in the Northwest Pacific Ocean when assuming the uncertainty with a high variation for population growth rate (λ)

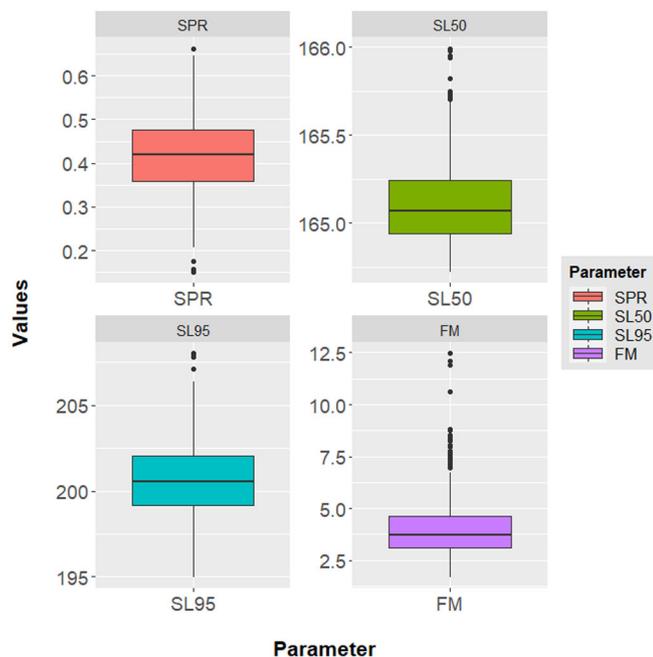


FIGURE 5 Box plots for the estimates of selectivity parameters and SPR-based BRPs of the pelagic thresher in the Northwest Pacific Ocean

BRPs. In addition, across stochastic LBSPR assessments conducted, the estimated average SPR was 0.417 (95% confidence interval [CI]: 0.248–0.566) and the average relative fishing mortality (F/M) was 3.999 (95% CI: 2.330–7.184).

However, the estimates of F/M should be ignored in this analysis as the definition used for this calculation failed to account for the effects in fish size selectivity.

Furthermore, in this study, Monte Carlo simulations indicated that F_{\max} cannot be well defined in most scenarios for pelagic thresher sharks, suggesting that F_{\max} is not a suitable BRP candidate for the management of this species. The composite risk assessment revealed that the probability of the current fishing mortality (F_{cur}) being higher than $F_{0.1}$ was approximately 0 for males and 0.06 for females. F_{cur} was estimated to be lower than F_{\max} in all simulations. However, most of the SPR values based on length-frequency data were estimated to be below 60% which is believed to be appropriate level for low-productivity shark species (Clarke & Hoyle, 2014; Tsai et al., 2019). In addition, the probability of the current SPR% being lower than SPR40% and SPR60% was 0.42 and 1.00, respectively, indicating that the overexploitation risk is higher for female pelagic thresher sharks in the Northwest Pacific Ocean.

3.2.2 | Stochastic demographic analyses and risk analyses

A large variation in estimates of λ was observed for pelagic threshers under the different management measure scenarios tested in the demographic model (Table 6, Figure 6). In the absence of fishing mortality (Scenario 1), the simulation results clearly indicated that stocks would increase ($\lambda = 1.077$, 95% confidence interval [CI] = 1.037–1.110 year⁻¹). Nevertheless, under the status-quo scenario (Scenario 2), a λ of approximately 1 ($\lambda = 0.995$, 95% CI = 0.971–1.013 year⁻¹) was determined (Table 6), suggesting that the pelagic thresher stock in the Northwest Pacific is around the level of optimum utilization. Furthermore, the generation time obtained under the natural condition simulation (Scenario 1) averaged 9.596 years (95% CI = 8.716–10.769 years). The elasticity patterns indicated that the stages of immaturity for both sexes are the dominant contributor to population growth (mean aggregated elasticity of 69.92%, Figure 7). Comparatively, the adult stages (mean aggregated elasticity of 30.08%) contribute considerably less to λ (Figure 7).

The simulations generally predict a growing population when male stages are protected (immature or mature stages, Scenarios 3 and 4, respectively). However, the female stock would almost certainly decrease (mean $\lambda = 0.965$ and 0.957 year⁻¹, Scenarios 3 and 4, respectively) under those management measures (Table 6 and Figure 6). Clear population growth ($\lambda = 1.036$ year⁻¹ for the total population, 1.025 and 1.045 year⁻¹ for males and females, respectively) is associated with protection

TABLE 6 Estimated demographic parameters with lower and upper variation boundaries of each scenario from the stochastic models

Scenario	Sex	λ	Lower	Upper	r	Lower	Upper
1	Total	1.077	1.037	1.110	0.074	0.036	0.105
	Male	1.063	1.006	1.111	0.061	0.006	0.105
	Female	1.085	1.034	1.128	0.082	0.034	0.120
2	Total	0.995	0.971	1.013	-0.005	-0.030	0.013
	Male	1.025	0.987	1.049	0.025	-0.013	0.048
	Female	0.957	0.936	0.978	-0.044	-0.066	-0.022
3	Total	1.016	0.979	1.048	0.016	-0.021	0.047
	Male	1.054	0.996	1.100	0.052	-0.004	0.096
	Female	0.965	0.940	0.988	-0.036	-0.062	-0.012
4	Total	1.000	0.973	1.021	0.000	-0.028	0.021
	Male	1.031	0.990	1.059	0.031	-0.010	0.058
	Female	0.957	0.935	0.978	-0.044	-0.067	-0.022
5	Total	1.036	1.006	1.062	0.035	0.006	0.060
	Male	1.025	0.986	1.049	0.025	-0.014	0.048
	Female	1.045	0.996	1.084	0.044	-0.004	0.080
6	Total	1.009	0.986	1.029	0.009	-0.014	0.028
	Male	1.025	0.987	1.049	0.025	-0.013	0.047
	Female	0.994	0.963	1.023	-0.006	-0.038	0.023

strategies that focused on the stages of female immaturity (Scenario 5, Figure 6). A high risk (0.639, Table 7) remains that the female population growth rate will be less than the threshold level of $\lambda = 1$ even if female adults are protected (Scenario 6). Consequently, the possible sexual dimorphism of this species must be carefully considered when developing management strategies to determine whether more accurate estimates of decline risk can be obtained by using a two-sex matrix model rather than a conventional single-sex model.

4 | DISCUSSION

4.1 | Data-limited approach for pelagic thresher stock assessment

Model applications such as MULTIFAN-CL and Stock Synthesis version 3 are commonly used for fish stock assessment by many RFMOs (e.g., ICCAT and IOTC). However, these applications require substantial data and analytical support, which is particularly challenging for shark species with insufficient catch and effort data. This study aimed to investigate whether similar assessment results could be achieved using data-limited methods as opposed to more complex conventional stock assessment methods. Therefore, our methods are not designed to account for fishery complexities such as gear selectivity. Instead, a conventional age-based catch curve (Ricker, 1975) was employed to

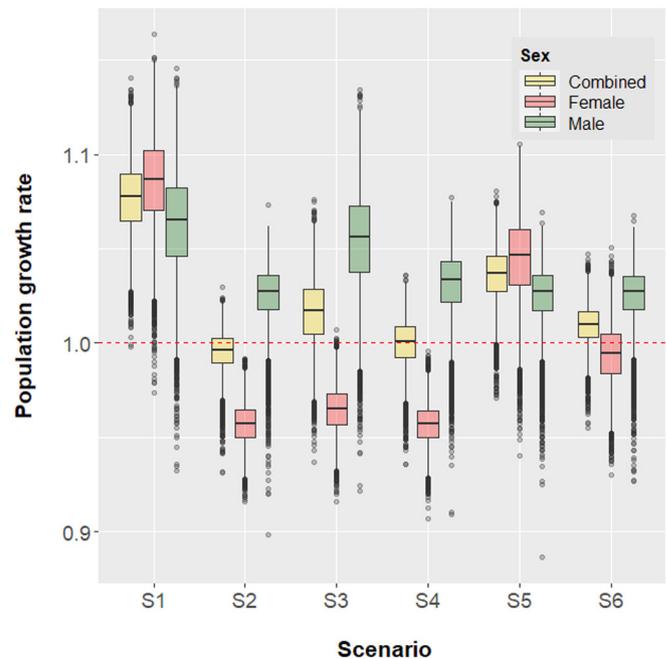


FIGURE 6 Box plots for the population growth rate of the pelagic thresher in various scenarios. The red dotted line indicates the stable population growth rate

estimate mortality. In this study, data-limited methods, demographic methods, per-recruit analysis, and risk assessment were applied for the risk and status assessment of the pelagic thresher shark in the Northwest Pacific.

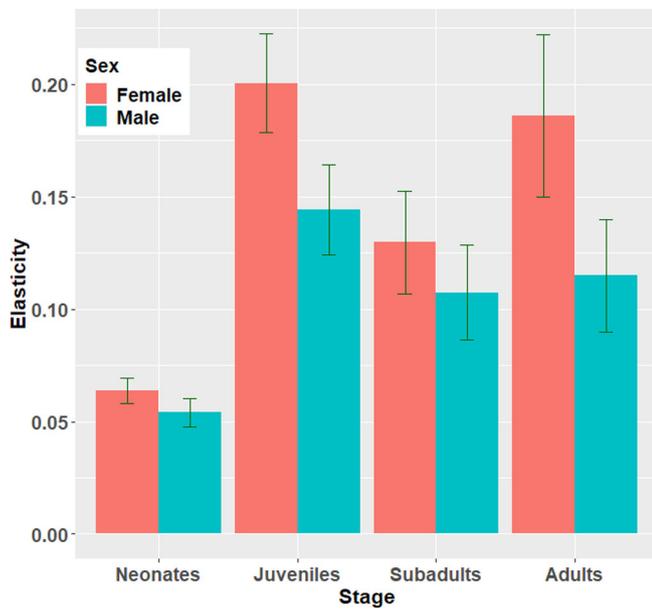


FIGURE 7 Elasticity of each stage with error bars (standard deviation) for female and male pelagic thresher sharks

TABLE 7 Risk analysis for each scenario from the stochastic models

Scenario	Sex	Risk
1	Total	0
	Male	0
	Female	0
2	Total	0.6477
	Male	0.0654
	Female	0.9999
3	Total	0.1769
	Male	0.0302
	Female	0.9993
4	Total	0.4733
	Male	0.0509
	Female	1
5	Total	0.0126
	Male	0.0710
	Female	0.0342
6	Total	0.1770
	Male	0.0666
	Female	0.6390

The YPR analysis indicated that F_{max} cannot be well defined within a plausible range of fishing mortality in most scenarios because the species tends to produce asymptotic YPR relationships with fishing mortality. The simulations also indicated that F_{max} is more biased and

less precise than $F_{0.1}$ as a result of high uncertainty, suggesting that it is not an appropriate BRP candidate for the management of pelagic threshers. For each sex, the composite risk assessments revealed that the probability of the current fishing mortality is higher than any YPR-based BRP was approximately zero. Moreover, BRPs based on the spawning-per-recruit model have often been proposed for data-limited species such as sharks (Clarke & Hoyle, 2014; Hordyk et al., 2016; Tsai et al., 2019, 2020). However, the SPR analysis indicated that the current SPR % was significantly lower than the target level (SPR60%) with a high risk of below the limit level (SPR40%; Figure 5 and Table 5), which implies that pelagic threshers may be currently subject to a risk of recruitment overfishing. Because SPR-based BRPs were less sensitive to parameter uncertainty than YPR-based BRPs, the results derived from the SPR model would be recommended for the management consideration of this species.

In terms of the demographic model, although no significant difference was noted in terms of growth and maturity between sexes (Liu et al., 1999; Tsai et al., 2010), other life history parameters, such as longevity and mortality, may differ between sexes (Tables 1–3). In addition, this species exhibits sexual segregation (Clarke et al., 2011), the phenomenon for which has been identified in many shark species (e.g., the shortfin mako shark, *Isurus oxyrinchus*, and silky shark, *Carcharhinus fal-ciformis*). These attributes suggest that a two-sex assessment model must be used to evaluate stock status (Tsai et al., 2014, 2015, 2019). Because life history parameters such as longevity and mortality differ by sex, a two-sex stage-based population model was appropriate in this study.

The two-sex demographic analysis determined that the pelagic thresher is one of the least productive shark species. In the absence of fishing mortality, the mean estimates of the population growth rate ($\lambda = 1.077 \text{ year}^{-1}$ for the total population, 1.063 and 1.085 year^{-1} for males and females, respectively) are slightly higher (female only) than those derived from previous deterministic or stochastic demographic analyses (Mollet & Cailliet, 2002; Tsai et al., 2010) but are markedly different from those reported by Cortés (2002) (Table 8). This discrepancy may be attributable to the different female longevity proposed in this study (30 years in the deterministic model and 28–36 in the stochastic simulation). Additionally, age and longevity underestimations have been documented in multiple shark species (Francis et al., 2007; Frazier et al., 2014; Kalish & Johnston, 2001). Given the currently available information (Liu et al., 1999) and empirical equations (Cortés, 2002), the use of 28- to 36-year female longevity in this study was reasonable. Therefore, the results obtained in this study are expected to provide

TABLE 8 Comparison of population increase rates for the pelagic thresher shark from various studies

Study	Model	Sex	α_{mat}	Life span	λ
Mollet and Cailliet (2002)	Deterministic age-based model	Female	8	30	1.056 ^a
Mollet and Cailliet (2002)	Deterministic stage-based model	Female	8	30	1.056 ^a
Mollet and Cailliet (2002)	Deterministic stage-based model (birth-flow)	Female	8	30	1.066 ^a
Cortés (2002)	Stochastic age-based model	Female	7–10	16–21	1.020 ^b (1.001–1.041) ^e
Tsai et al. (2010)	Stochastic stage-based model (birth-flow)	Female	6–10	30	1.058 ^c (1.014–1.102) ^e
This study	Stochastic stage-based model (birth-flow)	Pool	–	–	1.077 ^d (1.037–1.110) ^e
		Male	7–8	20–26	
		Female	8–9	28–36	

^aNatural mortality (M) was estimated by Campana et al. (2001).

^bNatural mortality (M) was randomly selected from six empirical equations, those of (1) Hoenig (1983); (2) Pauly (1980); (3) Chen and Watanabe (1989); (4) Peterson and Wroblewski (1984); and (5) and (6) Jensen (1996).

^cNatural mortality (M) was randomly selected from the following six methods: (1) Hoenig (1983); (2) Campana et al. (2001); (3) Chen and Watanabe (1989); (4) Peterson and Wroblewski (1984); and (5) and (6) Jensen (1996).

^dNatural mortality (M) was randomly selected from the following 11 methods: (1–3) Then et al. (2015); (4–5) Hamel (2015); (6–7) Frisk et al. (2001); (8) Hisano et al. (2011); (9) Campana et al. (2001); and (10) and (11) Jensen (1996).

^eValues in parentheses are lower and upper 95% CIs calculated as the 2.5th and 97.5th percentiles.

more accurate information regarding the population dynamics of this species.

On the other hand, the intrinsic rebound potential of productivity (r_Z) has been used to assess the relative vulnerability or productivity of shark species (Au et al., 2008, 2016; Simpfendorfer, 2005; Smith et al., 1998). Currently, the $r_{Z=1.5M}$ is now considered to be the more appropriate level of maximum sustainable yield (MSY) for sharks (Au et al., 2016) compared to teleosts (usually set as $r_{Z=2M}$). Additional calculations were therefore conducted to estimate the intrinsic rebound potential of productivity for pelagic thresher sharks. The intrinsic rebound ($r_{Z=1.5M}$) of pelagic thresher derived from the deterministic demographic model was 0.043 year^{-1} (0.025 year^{-1} for male and 0.057 year^{-1} for female), confirming the low resiliency of the species. Furthermore, the estimated female total mortality ($Z = 0.271 \text{ year}^{-1}$) was higher than ($Z_{MSY} = 1.5 M = 0.231 \text{ year}^{-1}$), also implying that female stock is overexploited. This conclusion is consistent with the results of per-recruit analyses.

4.2 | Consideration of uncertainties

Natural mortality (M) is critical to understanding the status of fish populations but is also among the most difficult quantities to estimate (Cortés, 2002; Simpfendorfer, 2005; Then et al., 2015). Estimates of natural mortality are the main driver of results in the demographic analyses of sharks, and any study publishing them must therefore estimate them effectively. Because estimating M directly (e.g., from tagging studies) is either difficult or

impossible for most shark species, the estimation of natural mortality for pelagic thresher sharks still relies on empirical methods. Since the derivation of estimates depends on life-history parameters, possible uncertainty in correlated input parameters must be considered. Life history data such as growth parameters contain inherent uncertainty that must be factored into natural mortality estimates. To address this, the distributions of life history parameters (L_{inf} , k , etc.) were calculated from Liu et al. (1999) and then used within Monte Carlo simulations to determine M for various methods. Subsequently, one set of M values could be used in each simulation to determine the resultant rate of increase. This analysis captured much of the uncertainty in the species life history and natural mortality within the population model. Therefore, this study provides a more robust analysis than previous demographic analyses of this species.

Unfortunately, the effects of several uncertainties could not be completely eliminated. For instance, the biological and life history traits of the pelagic thresher shark in the Northwest Pacific are poorly understood. Limited research is available, and our analysis relied on a single study, which was conducted by Liu et al. (1999). To improve stock assessments, more robust growth curves are necessary because uncertainty affects the results of demographic and per-recruit modes (Tsai et al., 2011, 2014). Another possible research limitation was the exclusion of density-independent factors in this study. However, empirical evidence for density-dependent responses to population reduction are unavailable for most sharks (Cortés, 2004, 2007) or difficult to measure (Brewster-Geisz & Miller, 2000). Although it has been

proposed that the density-dependence effect may result in compensatory increases in fecundity and growth rate for marine fishes (Carlson & Baremore, 2003; Romine et al., 2009), these responses are likely to be smaller in shark species because of their life history characteristics (Brewster-Geisz & Miller, 2000; Tsai et al., 2014, 2019). In regards to the life history traits of pelagic thresher sharks (slow growth, low fecundity, and late maturity), density-dependent effects are unlikely to affect this species (Tsai et al., 2010).

Another possible limitation of this approach is that our demographic analyses were based on the assumption of equilibrium dynamics that is the population growth rates and resultant elasticities were assumed to be at equilibrium (Caswell, 2001). However, any change to life history parameters will have nonlinear consequences for the estimates of population growth rate. To counter this problem, analysis of nonequilibrium using transient matrix models (Ezard et al., 2010; Gerber & Kendall, 2016; Tremblay et al., 2015) has recently been applied to characterize population dynamics over time. We would recommend that transient matrix models be developed in the future for pelagic thresher sharks to better understand of perturbation effects on their life history parameters and realistic population growth.

4.3 | General conclusions and recommendations

This study is the first to perform simulations to test the uncertainty in growth parameters by using sex-specific per-recruit and demographic models for pelagic thresher sharks in the Northwest Pacific. Conclusions are drawn from the per-recruit and demographic models revealed that the stock status of the pelagic thresher shark differs between the sexes under fished and unfished conditions (Tables 5–7). Consistent with other reports (Liu et al., 2006; Tsai et al., 2010), the results obtained from this study indicate that the female pelagic thresher shark is overexploited under current conditions. However, the total population is likely to be in a stable condition (λ is approximately 1 with a 50% decline risk, Scenario 2, Tables 6 and 7) because of the relatively low fishing pressure for male sharks.

Simulation-based management strategies demonstrated that without mortality from fishing, female pelagic threshers have a higher population growth rate than males (Scenario 1, Table 6). However, the stock of female pelagic thresher sharks is deficient compared with that of males under the current conditions (Scenario 2, Table 6). These findings suggest that sex-specific management decisions must be implemented to ensure the sustainable utilization of this species. Furthermore, the elasticity analyses and size limit scenarios outlined in this

study (Scenarios 3–6, Table 6) indicate that protection of immature sharks would result in a higher population growth rate than the protection of adults. The findings are congruent with previous shark demographic studies reporting that the population growth rate is most sensitive at the stage of immaturity, particularly during the juvenile stage in females (Smart et al., 2017; Tsai et al., 2010). Therefore, we recommend that management actions focus on the protection of females during the stages of immaturity.

In conclusion, the data-limited models developed in this study indicated that the pelagic thresher shark stock in the Northwest Pacific is at risk of further decline. To more fully understand the stock status of sharks, additional studies on the biology of pelagic thresher sharks are necessary, particularly for obtaining accurate natural mortality and growth parameters to prevent uncertainty in stock assessment results. Overall, both the sex-specific per-recruit and demographic models demonstrated that recruitment overfishing has occurred in the female pelagic thresher population in the Northwest Pacific Ocean, indicating that close monitoring of female sharks is urgent and necessary to ensure that stocks remain sustainable.

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CONFLICT OF INTEREST

The authors declare no conflict of interest.

AUTHOR CONTRIBUTIONS

Wen-Pei Tsai: Conceptualized and designed the study and analytical methods, conducted the analysis and interpretation and led on writing the manuscript. **Chia-Han Huang:** Data mining, literature reviews, and some preliminary data analysis.

ETHICS STATEMENT

The authors are not aware of any ethical issues regarding this study.

DATA AVAILABILITY STATEMENT

All data are presented in the article or the supplemental materials.

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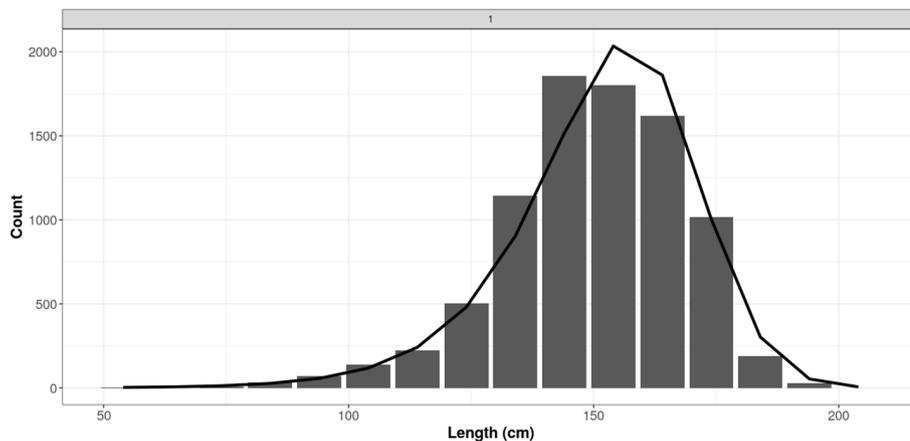
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(a) The size distribution (bar) and curve fitting (solid line)



(b) The specified size of the maturity curve (red line) and yearly estimated selectivity curve (blue line).

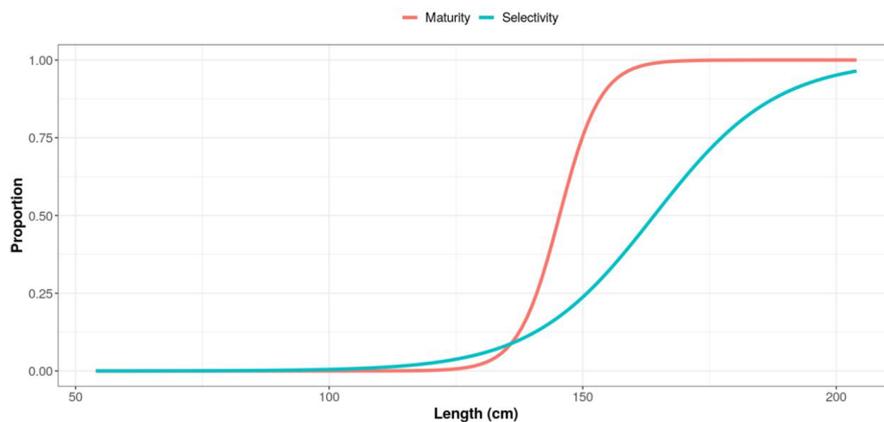


FIGURE A1 The results obtained from length-based spawning potential ratio model for the female pelagic thresher shark in the Northwest Pacific. (a) The size distribution (bar) and curve fitting (solid line) and (b) The specified size of the maturity curve (red line) and yearly estimated selectivity curve (blue line)

TABLE A1 Estimated mean (μ) and standard deviation (SD) of the growth parameters and mortality rates for the pelagic thresher shark in the Northwest Pacific

Parameter	Male	Female
VBGE		
L_{∞}	(182.196, 8.939) ^a	(197.153, 12.767) ^a
K	(0.118, 0.025) ^a	(0.085, 0.020) ^a
t_0	(-5.482, 1.174) ^a	(-7.669, 1.603) ^a
Mortality		
M	(0.205, 0.044) ^b	(0.160, 0.037) ^b
Z	(0.213, 0.009) ^c	(0.269, 0.010) ^c

Note: Mean (μ) and standard deviation (SD) are reported in parentheses.
^aThe μ and SD were re-estimated using data from Liu et al. (1999). In this case, SD had to be transformed into SE (SD divided by the square root of the sample size; $n = 115$ and 156 for males and females, respectively).
^bThe μ and SD obtained for M across the 11 methods for each sex and stage were used to define a lognormal distribution.
^cThe μ and SD obtained for Z from the catch curve were used to define a lognormal distribution.

TABLE A2 Life history parameters used as an input to assess LBSPR for the pelagic thresher shark in the Northwest Pacific

Parameter	Value
L_{∞}	197.153
K	0.085
L_{50}	145.419
L_{95}	157.424
M	0.154
M/k	1.812

TABLE A3 Estimated elements of the matrix a for all deterministic cases

The projection matrix (A) for the pelagic thresher shark in the un-fished condition.

$$\begin{bmatrix} 0 & 0 & 0.818 & 0.814 & 0 & 0.838 & 0.838 \\ 0.407 & 0.668 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.145 & 0.449 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.365 & 0.805 & 0 & 0 & 0 \\ 0.407 & 0 & 0 & 0 & 0.734 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.123 & 0.462 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.396 & 0.858 \end{bmatrix}$$

The projection matrix (A) for the pelagic thresher shark under current condition.

$$\begin{bmatrix} 0 & 0 & 0.799 & 0.796 & 0 & 0.780 & 0.780 \\ 0.392 & 0.664 & 0 & 0 & 0 & 0 & 0 \\ 0 & 0.141 & 0.446 & 0 & 0 & 0 & 0 \\ 0 & 0 & 0.359 & 0.798 & 0 & 0 & 0 \\ 0.392 & 0 & 0 & 0 & 0.680 & 0 & 0 \\ 0 & 0 & 0 & 0 & 0.082 & 0.433 & 0 \\ 0 & 0 & 0 & 0 & 0 & 0.330 & 0.762 \end{bmatrix}$$