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Estimation of population growth rate of the blue shark (Prionace glauca) using two-sex age-structure matrix model[1]

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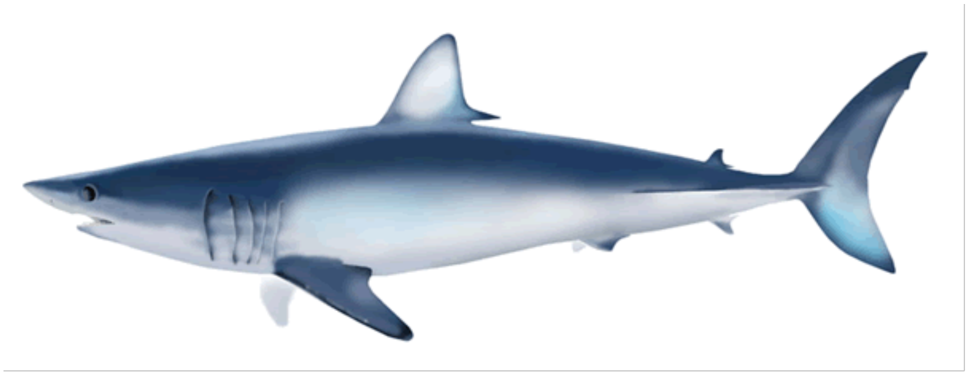

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Summary

Population growth rate, which depends on several biological parameters, is valuable information for the conservation and management of pelagic sharks, such as the blue shark. However, reported biological parameters for estimating the population growth rate of these sharks differ by sex and display large variability. To estimate the appropriate population growth rate and clarify the relationships between growth rate and relevant biological parameters, we developed a two-sex age-structured matrix population model and estimated the population growth rate using combinations of biological parameters. We addressed the sensitivity analysis of the population growth rate. The population growth rate of the blue shark was estimated to be 0.195–0.533 (median = 0.387). The maturity age of male sharks had the largest impact for blue sharks. The hypotheses for the survival process of sharks also had the large impact on the population growth rate estimation.

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Appendix 1: Detail of the two-sex age–structured matrix population model of the blue and shortfin mako shark.

The two-sex age–structured matrix population model of the blue shark and shortfin mako shark assumptions of the post-breeding census and life cycle graph shown in Figure S1. The population dynamics, which correspond to the life cycle graph can be described as

$$\mathbf{A}=\begin{pmatrix}
0 & F_{1,\mathrm{m}} & F_{2,\mathrm{m}} & \cdots & F_{a_{\max-1},\mathrm{m}} & 0 & 0 & F_{1,\mathrm{f}} & F_{2,\mathrm{f}} & \cdots & F_{a_{\max-1},\mathrm{f}} & 0\\
\rho S_0 & 0 & 0 & \cdots & 0 & 0 & 0 & 0 & 0 & \cdots & 0 & 0\\
0 & S_{1,\mathrm{m}} & 0 & \cdots & 0 & 0 & 0 & 0 & 0 & \cdots & 0 & 0\\
0 & 0 & S_{2,\mathrm{m}} & \cdots & 0 & 0 & 0 & 0 & 0 & \cdots & 0 & 0\\
\vdots & \vdots & \vdots & \ddots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots\\
0 & 0 & 0 & \cdots & S_{a_{\max-1},\mathrm{m}} & 0 & 0 & 0 & 0 & 0 & 0 & 0\\
(1-\rho)S_0 & 0 & 0 & \cdots & 0 & 0 & 0 & 0 & 0 & \cdots & 0 & 0\\
0 & 0 & 0 & \cdots & 0 & 0 & 0 & S_{1,\mathrm{f}} & 0 & \cdots & 0 & 0\\
0 & 0 & 0 & \cdots & 0 & 0 & 0 & 0 & S_{2,\mathrm{f}} & \cdots & 0 & 0\\
\vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \vdots & \ddots & \vdots & \vdots\\
0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & 0 & \cdots & S_{a_{\max-1},\mathrm{f}} & 0
\end{pmatrix}.$$

Where $S_{a,s}$ is given by $S_{a,s}=e^{-M_{a,s}}$ and $M_{a,s}$ is the natural mortality at age by each sex. S_0 is the calculated mean of natural mortality at age 0 for both sexes $S_0=0.5(e^{-M_{0,\mathrm{m}}}+e^{-M_{0,\mathrm{f}}})$. We assumed two types of natural mortality mechanisms. First, we estimated age–constant natural mortality using longevity equation $\ln(M_{a,s})=0.941-0.873\ln(a_{\max})$[1]. These coefficients have been assumed for whales and are typically used for large size pelagic sharks[2–7]. Alternatively, age–different natural mortality was estimated using mean body weight at age by sex $W_{a,s}$ with values $M_{a,s}=1.28W_{a,s}^{-0.25}$[8]. $W_{a,s}$ is given by the weight–length relationship $W_{a,s}=10^{-3}aL_{a,s}^{b}$, where a and b are coefficients to convert length to weight. $L_{a,s}$ is the total length (for blue shark) or precaudal length (for shortfin mako shark) that was given by the growth curve from the Von Bertalanffy or Gompertz equations. The growth curves of both sharks were reported by fork length (FL), total length (TL), and precaudal length (PL). The total length and fork length data of the blue shark were converted to precaudal length, because the weight–length relationship assumed precaudal length[9]. To convert total length to precaudal length, we used the transformation equation $PL=0.762TL-2.505$[10]. Fork length was changed by $PL=0.975FL-0.395$[11]. According to shortfin mako shark, we converted fork length and precaudal length to total length because the weight–length relationship was written in total length[3]. Hence, precaudal lengths were converted by $PL=0.84TL-2.13$[12]. Fork lengths were converted by $PL=0.894FL+2.192$ (male) and $PL=0.905FL+1.345$ (female)[13]. $F_{a,s}$ is a nonlinear equation with $F_{a,s}=f_{\mathrm{s}}\gamma_{a,s}S_{a,s}\delta$. f_{s} was derived from the equation of the relative number of births by individual[5,6,14]:

$$f_{\mathrm{s}}=\begin{cases}\frac{kR_f}{R_f+R_m} & \mathrm{s}=\mathrm{m}\\ \frac{kR_m}{R_f+R_m} & \mathrm{s}=\mathrm{f}\end{cases},$$

where R_{s} is the relative abundance of adult males or females, k is the litter size R_{s} is composed of the maturity rate by age and sex ($\gamma_{a,s}$), relative population number ($n_{a,s}$) and reproduction cycle δ as $R_s=\sum_{a=1}^{a_{\max}}\gamma_{a,s}n_{a,s}\delta$. We assumed that male sharks reproduce every year ($\delta=1$). The reproduction cycle of the female shark was assumed to be one year ($\delta=1$), two years ($\delta=0.5$), or three years ($\delta=0.33$).

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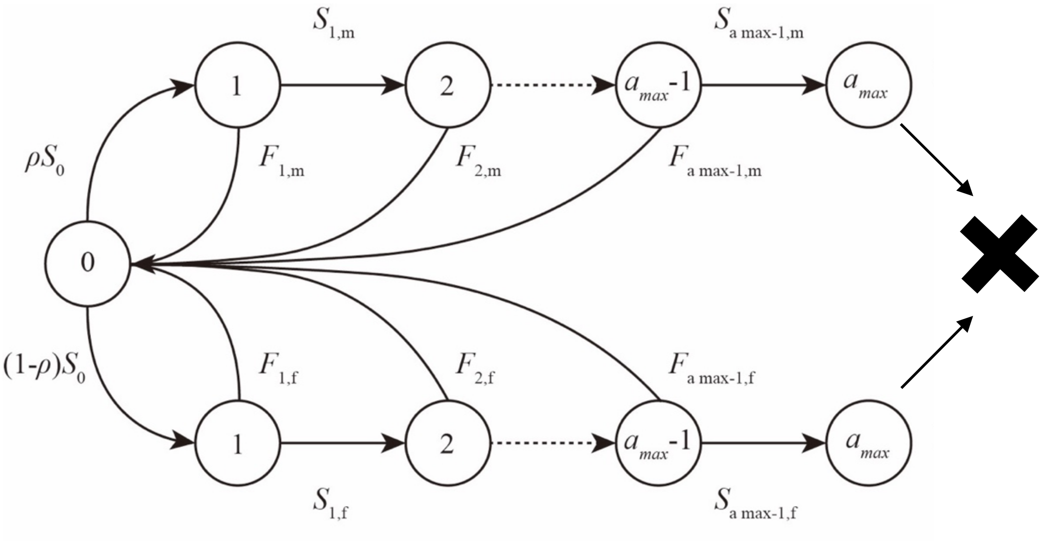

Figure S1. The life cycle of blue shark.

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Appendix 2: List of available biological parameters

Table A1. Summary of the biological parameters of the blue shark (*Prionace glauca*). Bold letters are used to estimate population growth rates.

Definition	Value / Equation	Covered area	Reference
Sex ratio	**0.5**	North Pacific	9
	0.5	North Pacific	16
	0.5	South Pacific	15
Litter size	1–62 (n=669, mean=**25.6**)	North Pacific	9
	25–43 (n=5068, mean=**37.1**)	Global	19
	9–64 (n=37, mode=33)	North Pacific	18
	2–52 (mean=25.2)	North Pacific	17
	13–68 (n=46, mean=**35**)	South Pacific	15
Maturity age	[a] Male: **4**–**5**, [a] Female: **5**–**6**	North Pacific	9
	[b] Male: 4–5, [b] Female: 5	North Pacific	20
	[a] Male: **7**, [a] Female: **6**	South Africa	21
Reproduction cycle (years)	**2**	North Pacific	17
	1	North Pacific	*
Longevity (age)	[c,d] Male: **16**, **16.5**, [c,d] Female: **15**, **26.1**	North Atlantic	20
	[c] Male: 16, [c] Female: 12	North Pacific	22
	[e] Male: 27, [f] Female: 21.1	South Pacific	23
	[f] Male: **26.866**, **28.642**, [g] Female: **24.068**, **20.150**	North Pacific	24
	[c,e,g] All:15, 21.4, 26.6	South Atlantic	28
Growth curve (cm)	[h] $L_a = 423.0[1-e^{-0.11(a+1.035)}]$	North Atlantic	29
	[h] $L_a = 401.55[1-e^{-0.13(a+0.62)}]$	Mediterranean	30
	[h] $L_{a,\mathrm{m}} = \mathbf{295.3}[1-e^{\mathbf{-0.175}(a+\mathbf{1.113}})]$, [h] $L_{a,\mathrm{f}} = \mathbf{241.9}[1-e^{\mathbf{-0.251}(a+\mathbf{0.795})}]$	North Pacific	25

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	$^{h}L_{a,\mathrm{m}} = \mathbf{369.0}[1-e^{\mathbf{-0.10(}a\mathbf{+1.38)}}]$, $^{h}L_{a,\mathrm{f}} = \mathbf{304.0}[1-e^{\mathbf{-0.16(}a\mathbf{+1.01)}}]$	North Pacific	26
	$^{i}L_{a,\mathrm{m}} = \mathbf{289.7}[1-e^{\mathbf{-0.129(}a\mathbf{+0.756)}}]$, $^{i}L_{a,\mathrm{f}} = \mathbf{243.3}[1-e^{\mathbf{-0.144(}a\mathbf{+0.849)}}]$	North Pacific	9
	$^{j}L_{a,\mathrm{m}} = \mathbf{282.3}[1-e^{\mathbf{-0.18(}a\mathbf{+1.35)}}]$, $^{j}L_{a,\mathrm{f}} = \mathbf{310.8}[1-e^{\mathbf{-0.13(}a\mathbf{+1.77)}}]$	North Atlantic	11
	$^{h}L_{a} =352.1[1-e^{-0.157(a+1.01)}]$	South Atlantic	27
	$^{h}L_{a,\mathrm{m}} = \mathbf{299.85}[1-e^{\mathbf{-0.10(}a\mathbf{+2.44)}}]$, $^{h}L_{a,\mathrm{f}} = \mathbf{237.5}[1-e^{\mathbf{-0.15(}a\mathbf{+2.15)}}]$	North Pacific	22
	$^{h}L_{a} = 311.6[1-e^{-0.12(a+1.66)}]$	South Africa	21
	$^{h}L_{a} = 352.1[1-e^{-0.13(a+1.31)}]$	South Atlantic	28
	$^{h}L_{a,\mathrm{m}} = \mathbf{376.6}[1-e^{\mathbf{-0.128(}a\mathbf{+1.482)}}]$, $^{h}L_{a,\mathrm{f}} = \mathbf{330.4}[1-e^{\mathbf{-0.164(}a\mathbf{+1.294)}}]$	South Pacific	23
Weight–length relationship (kg)	$^{k}W_{a,m} = 0.392\times10^{-6}\,L_{a,\mathrm{m}}^{\;3.41}$, $^{k}W_{a,\mathrm{f}} =0.131\times10^{-5}\,L_{a,\mathrm{f}}^{\;3.2}$	North Atlantic	29
	$^{k}W_{a} =2.57\times10^{-5}\,L_{a}^{\;3.05}$	North Pacific	31
	$^{l}W_{a,\mathrm{f}} =\mathbf{5.388\times10^{-6}}\,L_{a,\mathrm{m}}^{\;\mathbf{3.102}}$, $^{l}W_{a,\mathrm{m}} = \mathbf{3.293\times10^{-6}}\,L_{a,\mathrm{f}}^{\;\mathbf{3.225}}$	North Pacific	9

[a] 50% maturity age. [b] Full maturity age. [c] Maximum observed age from vertebral band counts. [d] Age at L_∞ from the von Bertalanffy growth equation. [e] Theoretical longevity[48]. [f] Theoretical longevity[49] using von the Bertalanffy growth equation[9,23]. [g] Theoretical longevity[50]. [h] Total length at age. [i] Precaudal length at age. [j] Fork length at age. [k] Weight and total length relationship. [l] Weight and precaudal length relationship. *Fujinami et al. (under review)

Appendix 3: Simple example for calculating population growth rate

```
# Parameters--------------------------------------------------------------------------------------------------------------------------

# Longevity of male shark

long_m = 17

# Longevity of female shark

long_f = 21

# Survival rate of age 0 shark (Male and Female)
```

```
s_0 = 0.391581151

# Survival rate of male shark

s_m = c(0.834331185, 0.867872344, 0.88615173, 0.897594563, 0.905359817, 0.91091273, 0.915030454,
0.918165398, 0.920599639, 0.922518564, 0.9240492, 0.925281553, 0.92628118, 0.927096924, 0.927765872,
0.928316636, 0)

# Survival rate of female shark

s_f = c(0.861727024, 0.885356998, 0.899798628, 0.909515666, 0.916468953, 0.921661023, 0.925660109,
0.928813362, 0.931345349, 0.933408041, 0.935108101, 0.936522679, 0.937709009, 0.938710462, 0.939560518,
0.940285431, 0.940906073, 0.941439239, 0.941898585, 0.942295316, 0)

# Maturity at age of male shark

mat_m = c(0, 0, 0, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1)

# Maturity at age of female shark

mat_f = c(0, 0, 0, 0, 0, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1, 1)

# Reproduction cycle of male shark

delta_m = 1

# Reproduction cycle of female shark (2 years)

delta_f = 0.5

#Litter size

k = 33




# Two sex age-structured Matrix model-----------------------------------------------------------------------------------------------

N = list()

# Set the initial population vector

N[[1]] = runif(long_f + long_m + 1) # Add age 0 shark


# 3000 times iteration
```

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```
for (i in 1:3000) {

  # Calculate scaled population vector
  N[[i]] = N[[i]] / sum(N[[i]])

  # Calculate adult shark
  R_m = sum(mat_m * N[[i]][2:(long_m + 1)] *delta_m)
  R_f = sum(mat_f * N[[i]][(long_m + 2) : (long_f + long_m + 1)] * delta_f)

  # Calculate fecundity
  F_m = k * R_f / (R_f + R_m)
  F_f = k * R_m / (R_f + R_m)

  # Make the two sex age-structured matrix model
  A = matrix(0, nrow = long_f + long_m + 1, ncol = long_f + long_m + 1)

  A[1,] = c(0, F_m * mat_m * s_m * delta_m, F_f * mat_f * s_f * delta_f)
  A[2, 1] = s_0
  A[(long_m + 2), 1] = s_0

  S = c(s_m[-long_m], 0, s_f[-long_f])
  length_S = length(S)

  for (j in 1:length_S) {
    A[j+2, j+1] = S[j]
```

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```
  }


  # Calculate next step population vector

  N[[i+1]] = A %*% N[[i]]


}


# Calculate population growth rate---------------------------------------------------------------------------------------------------


r = log(eigen(A)$values[1])
```

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