Estimate of intrinsic rate of natural increase (*r*) of shortfin mako (*Isurus oxyrinchus*) based on life history parameters from Indian Ocean.

Yasuko Semba[1], Hiroki Yokoi, and Mikihiko Kai
National Research Institute of Far Seas Fisheries,
5-7-1, Orido, Shimizu-ward, Shizuoka City, Shizuoka Prefecture, 4248633, Japan.

Summary

Intrinsic rate of natural increase (*r*) of certain species is important parameter in the analysis of population dynamics, thus have large impact on the estimation of stock status and future projection of the stock. We applied a two-sex age-structured matrix population model developed by Yokoi *et al*. (2017) to the estimation of *r* for shortfin mako (*Isurus oxyrinchus*) based on the life history parameter obtained in the Indian Ocean as much as possible. As a result of 80 combinations of life history parameter (sex ratio, litter size, reproductive cycle, sex-specific maturity age, sex-specific estimated longevity, sex-specific growth curve, sex-specific length-weight relationship, and estimator of natural mortality), median *r* was estimated to be 0.113 with a range of minimum and maximum values of 0.060 and 0.132, respectively. This estimate can be used as a prior which uncertainty included in each parameter was taken into consideration or re-estimated value based on selected parameter would be another candidate for the input parameter in the stock assessment model.

Introduction

The shortfin mako, *Isurus oxyrinchus*, is widely distributed in the tropical and warm-temperate oceans worldwide. It is a common, extremely active, and highly migratory species, with occasional inshore movements (Compagno 2001). Shortfin mako is one of the common shark species caught in pelagic longline fisheries. In the Indian Ocean, shortfin mako sharks are often targeted by some semi-industrial, artisanal and recreational fisheries and are bycatch of industrial fisheries including pelagic longline tuna and swordfish fisheries and anecdotally by the purse seine fishery (IOTC 2019). Based on the susceptibility and low-productivity, it is suggested the vulnerability of this species is high in the longline fishery in the Indian Ocean (Murua *et al*. 2018).

Although there is no quantitative stock assessment currently available for shortfin mako in the Indian Ocean and therefore the stock status is unknown, stock assessment of this population is planned to be performed in 2021 Working Party on Ecosystems and Bycatch (WPEB) meeting. Intrinsic rate of natural increase (*r*) is a crucial parameter for determining the vulnerability of population decline (Frisk *et al*. 2005). In order to estimate this, various life history parameters including natural mortality, longevity, fecundity, mating system and maturation is necessary (Yokoi *et al*. 2017). In case of shortfin mako, reported biological parameters required for estimating *r* differ by sex (reviewed in Semba 2018) and display large variability and uncertainty among studies (reviewed in Cailliet 2015).

---

[1] senbamak@affrc.go.jp

Yokoi *et al*. (2017) developed a two-sex age-structured matrix population model and estimated the *r* using combinations of biological parameters. This approach takes into consideration the uncertainty of each parameter by treating each life history parameter equally like meta-analysis. In this document, we applied their approach to estimate the *r* of shortfin mako in the Indian Ocean, using the life history parameters obtained from Indian Ocean as much as possible.

Materials and methods

Life history parameter

In this analysis, we used sex ratio, litter size, reproductive cycle, sex-specific age at maturity, sex-specific longevity, and sex-specific growth parameters and sex-specific length-weight relationship (Table1). We selected parameters estimated for population in the Indian Ocean, except for the reproductive cycle which was estimated based on global study (3 years by Mollet *et al.* 2000) and longevity which was estimated based on Atlantic study (Natanson *et al*. (2006) and Barreto *et al*. (2016)). Regarding longevity, 23 and 29 for males and 32 and 38 for females were used. These estimates were selected outside the Indian Ocean because observed maximum age reported in the Indian Ocean was small, compared to other oceans and suggested to be underestimate of longevity. As sensitivity analysis, 2-year reproductive cycle (suggested by Semba *et al*. (2011) for North Pacific population) was included.

We used three growth parameters (sex-combined growth equation by Groeneveld *et al*. (2014) and sex-specific and sex-combined growth equations by Liu *et al*. (2018)). Regarding length-weight relationship, we used two equations corresponding to growth (sex-specific length-weight equation by Groeneveld *et al*. (2014) and sex-combined length-gutted weight equation by Liu *et al*. (2018)). When we convert processed weight (PW: kg) equation by Liu *et al*. (2018) to whole weight (WW: kg), we applied conversion factor of 1.6 (i.e., WW=1.6PW), assuming that product and corresponding conversion factor are same with those in Japan (Semba unpublished).

Natural Mortality

Regarding natural mortality (*M*), equations by Peterson and Wroblewski (1984) and Hoenig (1983) were applied as common estimators, following Yokoi *et al*. (2017).

According to Peterson and Wroblewski (1984),

$$M_w = 1.92 * W^{-0.25}\ (g)\ (Dry\ weight; Original)$$

$$M_w = 1.28 * W^{-0.25}\ (g)\ (Wet\ weight; Kenchigton\ 2014)$$

, where M_w is natural mortality at certain weight (W: g). In this study, we used the equation for wet weight. As shown in the equation, combining growth curve and length-weight relationship (see Table1), *M* at age was obtained in this estimator.

According to Hoenig (1983),

$$\ln(M) \cong \ln(Z) = 0.941 - 0.873 * \ln(longevity) \qquad (Cetaceans)$$

, where *Z* is total mortality, and this is widely applied to sharks although original equation was developed for cetaceans. In this estimator, estimates of longevity is necessary and we used estimates in the Atlantic Ocean following Yokoi *et al*. (2017) as described above. In contrast to Peterson and Wroblewski (1984), constant *M* across all ages is obtained.

Intrinsic rate of natural increase

Based on parameters above, the number of combinations of parameter is 72 for the calculation by Peterson and Wroblewski (1984); 2 (female longevity) × 2(male longevity) × 2(reproductive cycle) × 3 (growth curve for male) × 3 (growth curve for female). That of Hoenig (1983) is 8; 2 (female longevity) × 2(male longevity) × 2(reproductive cycle). The total number of combinations of parameter is 80. Details of two-sex age-structured matrix population model are described in Yokoi et al. (2017). There calculations were carried out using Mathematica (Wolfram Research, Inc. 2019).

We reviewed the difference of each parameter regarding growth parameter, age-weight relationship, and estimator of *M* and then report the *r* by the assumption of reproductive cycle and estimator of *M*.

Results

In advance of estimation of growth rate, difference of growth parameter, age-weight relationship and *M* among studies or type of estimator was reviewed. Regarding sex-combined growth curve (Figure 1), little difference was observed between Groeneveld *et al*. (2014) and Liu *et al*. (2018), especially for sharks smaller than 200 cm fork length. Sexual difference was observed with females grow larger than males in Liu *et al*. (2018). On the other hand, relationship between age and whole weight was variable depending on growth parameter used (Figure 2) with weight at certain age from Liu *et al*. (2018) heavier than that from Groenveld *et al*. (2014). Although the direct comparison of *M* between two estimator is difficult, estimated *M*s by Peterson and Wroblewski (1984) tended to be lower than that by Hoenig (1983) (Figure 3).

Estimated median value (with highest and lowest value) of *r* for shortfin mako in the Indian Ocean was shown by reproductive cycle (i.e., 2 or 3) and estimator of *M* (i.e., Peterson and Wroblewski (1984) or Hoenig (1983)) in Table2. Median of averaged *r* was 0.113 (minimum-maximum:0.060-0.132). Under 2-year reproductive cycle assumption, medians are 0.130 for Peterson and Wroblewski (1984) and 0.089 for Hoenig (1983), while 0.111 for Peterson and Wroblewski (1984) and 0.070 for Hoenig (1983) under 3-year reproductive cycle. As expected, *r* with assumption of 2-year cycle was higher than that of 3-year cycle in both estimator of *M*. Between estimator of *M*, median value by Peterson and Wroblewski (1984) was higher than that by Hoenig (1983). Derived *r* by each combination of parameter is shown in Appendix.

Discussion

Estimates of *r* was largely different, depending on the estimator of *M*. Method proposed by Peterson and Wroblewski (1984) was based on empirical value of dried weight of various marine species (sharks are not included), but age-specific *M* is obtained. Method proposed by Hoenig (1983) has been regarded as the most reasonable approach theoretically (Then *et al*. 2015), but obtained *M* is constant among ages and affected by the estimates of longevity. In this calculation, observed maximum age was clearly lower than those in the other ocean, which may cause underestimation of longevity and not used in the estimation of *r*. As the number of parameter limited to Indian Ocean is not so large, WG can discuss the reasonable parameter of Indian shortfin mako and then *r* can be re-estimated. For example, estimator of *M* has each pros and cons, thus they are equally weighted (both estimators retained). Regarding male longevity, 29 is used, because male longevity of 23 is underestimate (Yokoi *et al*. 2017) and the estimate is not available. Female longevity can be fixed to be 38, because 32 is observed maximum age with possibility of underestimation. Regarding growth curve, sex-specific growth by Liu *et al*. (2018) is used, because sexual difference in growth is commonly reported in other oceans. In this case, median of *r* is 0.114 for Peterson and Wroblewski (1984) and 0.080 for Hoenig (1983).

Conclusion

Intrinsic rate of natural increase (*r*) of shortfin mako was estimated based on the best available parameter of this species in the Indian Ocean. Obtained median value of averaged among assumptions was 0.113 with a range of minimum and maximum values of 0.060 and 0.132. Although this value may be slightly changed depending on the parameters selected as a result of discussion by WG, we propose to use the estimate by this approach as the prior of Bayesian surplus production model if the model is used for the stock assessment of this population.

References

Barreto, R. R., Farias, W. K. T. de, Andrade, H., Santana, F. M. and Lessa, R. (2016) Age, Growth and Spatial Distribution of the Life Stages of the Shortfin Mako, *Isurus oxyrinchus* (Rafinesque, 1810) Caught in the Western and Central Atlantic. PLoS One 11, e0153062.

Cailliet, G. M. (2015) Perspectives on elasmobranch life-history studies: a focus on age validation and relevance to fishery management. J. Fish. Biol. 87:1271-1292.

Compagno L. J. V. (2001) FAO Species Catalogue for Fishery Purposes No.1. Sharks of the world: An Annotated and Illustrated Catalogue of Shark species Known to Date, Vol. 2: Bullhead, Mackerel and Carpet sharks (Heterodontiformes, Lamniformes and Orectolobiformes). FAO, Rome, 269pp.

Frisk, M. G. Miller, T. J. and Dulvy, N. K. (2005) Life histories and vulnerability to exploitation of elasmobranchs: Inferences from elasticity, perturbation and phylogenetic analyses. J. Northwest Atl. Fish. Sci. 35:27-45.

Groeneveld, J. C., Cliff, G., Dudley, S. F. J., Foulis, A. J., Santos, J. and Wintner, S. P. (2014) Population structure and biology of shortfin mako, *Isurus oxyrinchus*, in the south-west Indian Ocean. Mar. Freshw. Res. 65, 1045.

Hoenig, J. (1983) Empirical use of longevity data to estimate mortality rates. Fish. Bull. 82, 898–903.

IOTC (2019) Shortfin mako shark. Supporting information. http://www.iotc.org/sites/default/files/documents/science/species_summaries/english/Shortfin%20mako%20shark%20Supporting%20Information.pdf

Liu, K-M., Sibagariang, R. D., Joung, S-J. and Wang, S-B. (2018) Age and Growth of the Shortfin Mako shark in the Southern Indian Ocean. Marine and Coastal Fisheries: Dynamics, Management, and Ecosystem Science. 10, 577-589.

Mollet, H. F., Cliff, G., Pratt, H. L. and Stevens, J. D. (2000) Reproductive biology of the female shortfin mako, *Isurus oxyrinchus* Rafinesque, 1810, with comments on the embryonic development of lamnoids. Fish. Bull. 98, 299–318.

Murua, H., J. Santiago, R. Coelho, I. Zudaire, C. Neves, D. Rosa., Y. Semba, Z. Geng., P. Bach, H. Arrizabalaga, J.C. Baez, M. L. Ramos, J.F Zhu, and J. Ruiz. (2018) Updated Ecological Risk Assessment (ERA) for shark species caught in fisheries managed by the Indian Ocean Tuna Commission (IOTC). IOTC-2018-SC21-14. 28pp.

Natanson, L. J., Kohler, N. E., Ardizzone, D., Cailliet, G. M., Wintner, S. P. and Mollet, H. F. (2006) Validated age and growth estimates for the shortfin mako, *Isurus oxyrinchus*, in the North Atlantic Ocean. Environ. Biol. Fishes 77, 367–383.

Peterson, I. and Wroblewski, J. S. (1984) Mortality rate of fishes in the pelagic ecosystem. Can. J. Fish. Aquat. Sci. 41, 1117–1120.

Semba, Y., Aoki, I., and Yokawa, K. (2011) Size at maturity and reproductive traits of shortfin mako, *Isurus oxyrinchus*, in the western and central North Pacific. Mar Freshw Res 62:20-29.

Semba Y. (2018) Chapter5. Significance of sex-specific ecological and life history traits on the sustainable exploitation of sharks. Pp. 77-104. In Fish Population Dynamics, Monitoring, and Management: Sustainable Fisheries in the Eternal Ocean. (Eds. by Aoki, I., Yamakawa, T., and Takasuka, A.)

Then, A.Y., Hoenig, J.M., Hall, N.G. and Hewitt, D.A. (2015) Evaluating the predictive performance of empirical estimators of natural mortality rate using information on over 200 fish species. ICES J. Mar. Sci. 72, 82–92.

Wolfram Research, Inc., Mathematica, Version 12.0, Champaign, IL (2019).

Yokoi, H., Ijima, H., Ohshimo, S. and Yokawa, K. (2017). Impact of biology knowledge on the conservation and management of large pelagic sharks. Sci. Rep. 7(1), p.10619.

Table1. Parameters used in the estimation of r in this analysis. IO, NP and AO in area denote Indian Ocean, North Pacific, and Atlantic Ocean, respectively.

Definition	Value	Area	Reference
Sex ratio	0.5	IO	Groeneveld *et al.* (2014)
Litter size	11.7	IO	Groeneveld *et al.* (2014)
Reproduction cycle	2 or 3	Global, NP	Mollet *et al.* (2000) Semba *et al.* (2011)
Maturity age (Female)	15	IO	Groeneveld *et al.* (2014)
Maturity age (Male)	7	IO	Groeneveld *et al.*

			(2014)
Maximum observed age (not used)	F: 18.5, M: 19.5	IO	Groeneveld *et al.* (2014)
Longevity	F: 32, 38, M: 23, 29	AO	Natanson *et al.* (2006) Barreto *et al.* (2016)
Growth curve	$FL_t\ (cm) = 285.4 - (285.4 - 90.4) * e^{-0.113t}\ (combined)$ $CFL_t\ (cm) = 323.8 * \left(1 - e^{-0.075(t+4.360)}\right)\ (female)$ $CFL_t\ (cm) = 251.6 * \left(1 - e^{-0.151(t+2.488)}\right)\ (male)$ $CFL_t\ (cm) = 267.6 * \left(1 - e^{-0.123(t+2.987)}\right)\ (combined)$	IO	Groeneveld *et al.* (2014) Liu *et al.* (2018)
Length- weight relationship	$WW\ (kg) = (8.0 * 10^{-6}) * FL^{3.0412}\ (cm)\ (female)$ $WW\ (kg) = (1.0 * 10^{-5}) * FL^{2.9596}\ (cm)\ (male)$ $PW\ (kg) = (1.0 * 10^{-4}) * CFL^{2.517}\ (cm)\ (combined)$	IO	Groeneveld *et al.* (2014) Liu *et al.* (2018)

Table2. Minimum, median and maximum value obtained in the calculation of each assumption.

	Minimum	Median	Maximum
All (Reproductive cycle 2 and 3 year)	0.060	0.113	0.132
Reproductive cycle 2year			
Peterson and Wroblewski (1984)	0.127	0.130	0.132
Hoenig (1983)	0.079	0.089	0.099
Reproductive cycle 3year			
Peterson and Wroblewski (1984)	0.108	0.111	0.114
Hoenig (1983)	0.060	0.070	0.080

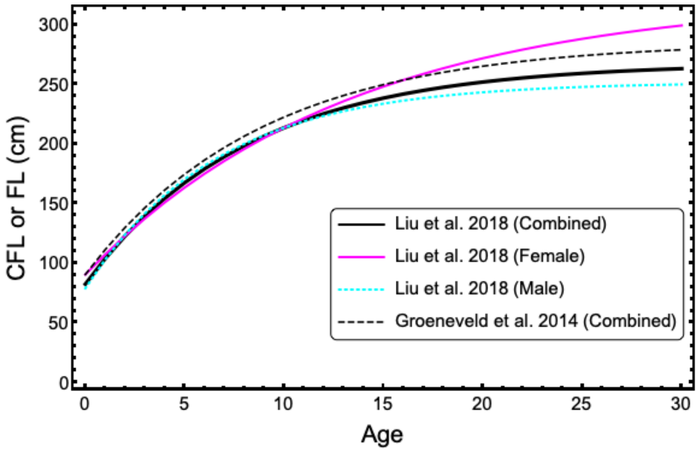

Figure 1. Growth curve estimated for shortfin mako in the Indian Ocean based on Groeneveld *et al.* (2014) and Liu *et al.* (2018)

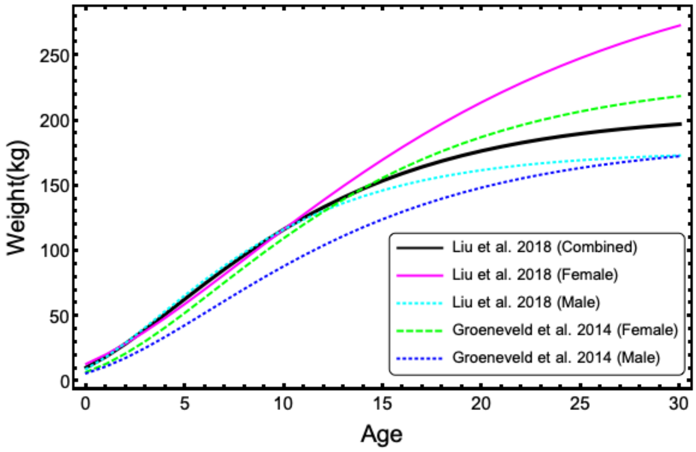

Figure 2. Relationship between age of shortfin mako and whole weight (kg) by growth equation. For the weight derived by Liu *et al*. (2018), original gutted weight was multiplied by 1.6 under the assumption of same type of product and conversion factor with that of Japan.

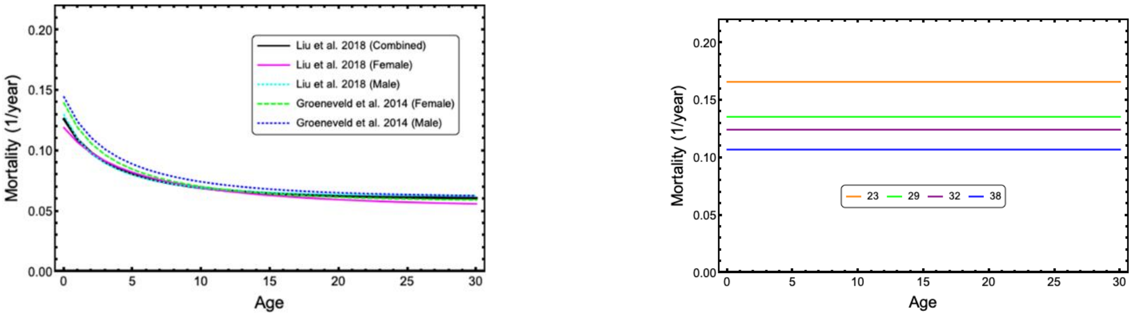

Figure 3. Estimates of *M* at ages for shortfin mako in the Indian Ocean. Age-specific *M* is obtained for Peterson and Wroblewski (1984:left) and constant *M* among ages is obtained for Hoenig (1983: right).

Appendix. Summary table of calculated *r* under each combination of parameter.

Intrinsic rate of natural increase (r)	Maturity age (male)	Longevity (male)	Maturity age (female)	Longevity (female)	Litter size	Reproductive cycle	Mortality method	Growth curve (male)	Growth curve (female)
0.127	7	23	15	32	11.7	2	Peterson and Wroblewski (1984)	Groeneveld	Groeneveld
0.130	7	23	15	32	11.7	2	Peterson and Wroblewski (1984)	Groeneveld	Liu (female)
0.129	7	23	15	32	11.7	2	Peterson and Wroblewski (1984)	Groeneveld	Liu (combined)
0.128	7	23	15	32	11.7	2	Peterson and Wroblewski (1984)	Liu (male)	Groeneveld
0.131	7	23	15	32	11.7	2	Peterson and Wroblewski (1984)	Liu (male)	Liu (female)
0.130	7	23	15	32	11.7	2	Peterson and Wroblewski (1984)	Liu (male)	Liu (combined)
0.128	7	23	15	32	11.7	2	Peterson and Wroblewski (1984)	Liu (combined)	Groeneveld
0.131	7	23	15	32	11.7	2	Peterson and Wroblewski (1984)	Liu (combined)	Liu (female)
0.130	7	23	15	32	11.7	2	Peterson and Wroblewski (1984)	Liu (combined)	Liu (combined)
0.108	7	23	15	32	11.7	3	Peterson and Wroblewski (1984)	Groeneveld	Groeneveld
0.111	7	23	15	32	11.7	3	Peterson and Wroblewski (1984)	Groeneveld	Liu (female)
0.110	7	23	15	32	11.7	3	Peterson and Wroblewski (1984)	Groeneveld	Liu (combined)
0.109	7	23	15	32	11.7	3	Peterson and Wroblewski (1984)	Liu (male)	Groeneveld
0.112	7	23	15	32	11.7	3	Peterson and Wroblewski (1984)	Liu (male)	Liu (female)
0.111	7	23	15	32	11.7	3	Peterson and Wroblewski (1984)	Liu (male)	Liu (combined)
0.109	7	23	15	32	11.7	3	Peterson and Wroblewski (1984)	Liu (combined)	Groeneveld
0.112	7	23	15	32	11.7	3	Peterson and Wroblewski (1984)	Liu (combined)	Liu (female)
0.111	7	23	15	32	11.7	3	Peterson and Wroblewski (1984)	Liu (combined)	Liu (combined)
0.128	7	23	15	38	11.7	2	Peterson and Wroblewski (1984)	Groeneveld	Groeneveld
0.131	7	23	15	38	11.7	2	Peterson and Wroblewski (1984)	Groeneveld	Liu (female)
0.130	7	23	15	38	11.7	2	Peterson and Wroblewski (1984)	Groeneveld	Liu (combined)
0.129	7	23	15	38	11.7	2	Peterson and Wroblewski (1984)	Liu (male)	Groeneveld
0.132	7	23	15	38	11.7	2	Peterson and Wroblewski (1984)	Liu (male)	Liu (female)
0.131	7	23	15	38	11.7	2	Peterson and Wroblewski (1984)	Liu (male)	Liu (combined)
0.129	7	23	15	38	11.7	2	Peterson and Wroblewski (1984)	Liu (combined)	Groeneveld
0.132	7	23	15	38	11.7	2	Peterson and Wroblewski (1984)	Liu (combined)	Liu (female)
0.131	7	23	15	38	11.7	2	Peterson and Wroblewski (1984)	Liu (combined)	Liu (combined)
0.109	7	23	15	38	11.7	3	Peterson and Wroblewski (1984)	Groeneveld	Groeneveld
0.112	7	23	15	38	11.7	3	Peterson and Wroblewski (1984)	Groeneveld	Liu (female)
0.112	7	23	15	38	11.7	3	Peterson and Wroblewski (1984)	Groeneveld	Liu (combined)
0.110	7	23	15	38	11.7	3	Peterson and Wroblewski (1984)	Liu (male)	Groeneveld
0.113	7	23	15	38	11.7	3	Peterson and Wroblewski (1984)	Liu (male)	Liu (female)
0.112	7	23	15	38	11.7	3	Peterson and Wroblewski (1984)	Liu (male)	Liu (combined)
0.110	7	23	15	38	11.7	3	Peterson and Wroblewski (1984)	Liu (combined)	Groeneveld
0.113	7	23	15	38	11.7	3	Peterson and Wroblewski (1984)	Liu (combined)	Liu (female)
0.112	7	23	15	38	11.7	3	Peterson and Wroblewski (1984)	Liu (combined)	Liu (combined)
0.127	7	29	15	32	11.7	2	Peterson and Wroblewski (1984)	Groeneveld	Groeneveld
0.130	7	29	15	32	11.7	2	Peterson and Wroblewski (1984)	Groeneveld	Liu (female)
0.129	7	29	15	32	11.7	2	Peterson and Wroblewski (1984)	Groeneveld	Liu (combined)
0.128	7	29	15	32	11.7	2	Peterson and Wroblewski (1984)	Liu (male)	Groeneveld

Appendix (continued)

Intrinsic rate of natural increase (r)	Maturity age (male)	Longevity (male)	Maturity age (female)	Longevity (female)	Litter size	Reproductive cycle	Mortality method	Growth curve (male)	Growth curve (female)
0.131	7	29	15	32	11.7	2	Peterson and Wroblewski (1984)	Liu (male)	Liu (female)
0.130	7	29	15	32	11.7	2	Peterson and Wroblewski (1984)	Liu (male)	Liu (combined)
0.128	7	29	15	32	11.7	2	Peterson and Wroblewski (1984)	Liu (combined)	Groeneveld
0.131	7	29	15	32	11.7	2	Peterson and Wroblewski (1984)	Liu (combined)	Liu (female)
0.130	7	29	15	32	11.7	2	Peterson and Wroblewski (1984)	Liu (combined)	Liu (combined)
0.108	7	29	15	32	11.7	3	Peterson and Wroblewski (1984)	Groeneveld	Groeneveld
0.111	7	29	15	32	11.7	3	Peterson and Wroblewski (1984)	Groeneveld	Liu (female)
0.110	7	29	15	32	11.7	3	Peterson and Wroblewski (1984)	Groeneveld	Liu (combined)
0.109	7	29	15	32	11.7	3	Peterson and Wroblewski (1984)	Liu (male)	Groeneveld
0.112	7	29	15	32	11.7	3	Peterson and Wroblewski (1984)	Liu (male)	Liu (female)
0.111	7	29	15	32	11.7	3	Peterson and Wroblewski (1984)	Liu (male)	Liu (combined)
0.109	7	29	15	32	11.7	3	Peterson and Wroblewski (1984)	Liu (combined)	Groeneveld
0.112	7	29	15	32	11.7	3	Peterson and Wroblewski (1984)	Liu (combined)	Liu (female)
0.111	7	29	15	32	11.7	3	Peterson and Wroblewski (1984)	Liu (combined)	Liu (combined)
0.128	7	29	15	38	11.7	2	Peterson and Wroblewski (1984)	Groeneveld	Groeneveld
0.131	7	29	15	38	11.7	2	Peterson and Wroblewski (1984)	Groeneveld	Liu (female)
0.130	7	29	15	38	11.7	2	Peterson and Wroblewski (1984)	Groeneveld	Liu (combined)
0.129	7	29	15	38	11.7	2	Peterson and Wroblewski (1984)	Liu (male)	Groeneveld
0.132	7	29	15	38	11.7	2	Peterson and Wroblewski (1984)	Liu (male)	Liu (female)
0.131	7	29	15	38	11.7	2	Peterson and Wroblewski (1984)	Liu (male)	Liu (combined)
0.129	7	29	15	38	11.7	2	Peterson and Wroblewski (1984)	Liu (combined)	Groeneveld
0.132	7	29	15	38	11.7	2	Peterson and Wroblewski (1984)	Liu (combined)	Liu (female)
0.131	7	29	15	38	11.7	2	Peterson and Wroblewski (1984)	Liu (combined)	Liu (combined)
0.110	7	29	15	38	11.7	3	Peterson and Wroblewski (1984)	Groeneveld	Groeneveld
0.113	7	29	15	38	11.7	3	Peterson and Wroblewski (1984)	Groeneveld	Liu (female)
0.112	7	29	15	38	11.7	3	Peterson and Wroblewski (1984)	Groeneveld	Liu (combined)
0.111	7	29	15	38	11.7	3	Peterson and Wroblewski (1984)	Liu (male)	Groeneveld
0.114	7	29	15	38	11.7	3	Peterson and Wroblewski (1984)	Liu (male)	Liu (female)
0.113	7	29	15	38	11.7	3	Peterson and Wroblewski (1984)	Liu (male)	Liu (combined)
0.111	7	29	15	38	11.7	3	Peterson and Wroblewski (1984)	Liu (combined)	Groeneveld
0.114	7	29	15	38	11.7	3	Peterson and Wroblewski (1984)	Liu (combined)	Liu (female)
0.113	7	29	15	38	11.7	3	Peterson and Wroblewski (1984)	Liu (combined)	Liu (combined)
0.079	7	23	15	32	11.7	2	Hoenig (1983)		
0.060	7	23	15	32	11.7	3	Hoenig (1983)		
0.095	7	23	15	38	11.7	2	Hoenig (1983)		
0.077	7	23	15	38	11.7	3	Hoenig (1983)		
0.082	7	29	15	32	11.7	2	Hoenig (1983)		
0.063	7	29	15	32	11.7	3	Hoenig (1983)		
0.099	7	29	15	38	11.7	2	Hoenig (1983)		
0.080	7	29	15	38	11.7	3	Hoenig (1983)		