ISC/16/SHARKWG-1/01

Reproductive biology of the blue shark, *Prionace glauca*, in the western North Pacific Ocean†

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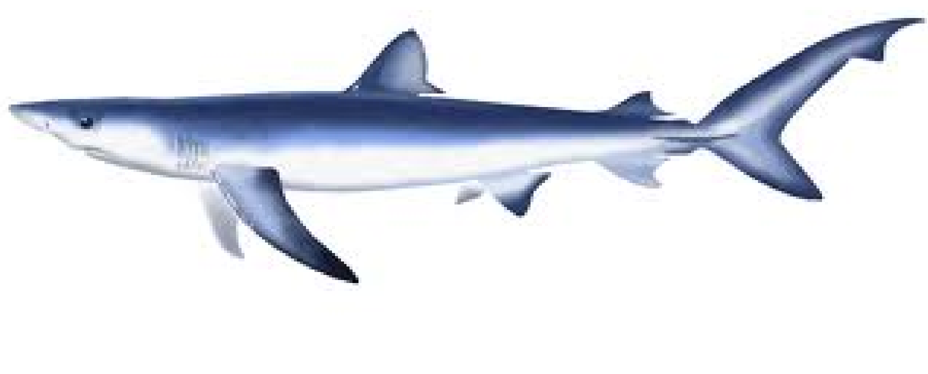

Working document submitted to the ISC Shark Working Group Workshop, 14-21 November 2016, Haeundae Grand Hotel, Busan, South Korea
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†A peer reviewed article of this work is in press in *Marine and Freshwater Research* as of March 2017 and should be cited instead of this Working Paper.

Abstract

The reproductive biology of the blue shark, *Prionace glauca*, in the western North Pacific Ocean was investigated to provide updated for future stock assessments of this population because of limited number of study after Nakano (1994) and lack of reliable estimate on reproductive cycle. Reproductive data were obtained from 484 males (precaudal length [PCL], 33.4–252.0 cm) and 432 females (PCL, 33.4–243.3 cm). Size at 50% maturity was estimated to be 160.9 cm for males and 156.6 cm PCL for females. Litter size based on the number of embryos and placentas varied from 15 to 112 (mean, 35.5) and was positively correlated with maternal PCL. Parturition, ovulation, and mating occurred sequentially from spring to summer, and parturition took place after an 11-month gestation. The ovarian follicles of pregnant females developed synchronously throughout the gestation period along with embryonic growth, indicating that females reproduce annually. Our results indicate that productivity of North Pacific blue shark is higher than previously thought based on larger fecundity and a shorter reproductive cycle than previously thought. These reproductive parameter estimates will be useful for stock assessments and fisheries management decisions regarding of this population.

Keywords: blue shark, fecundity, gestation, maturity, North Pacific, reproductive cycle.

Introduction

The blue shark, *Prionace glauca*, is the most abundant pelagic carcharhinid shark and has a circum-global distribution in tropical and temperate oceans (Nakano and Stevens 2008). This species is mainly captured by tuna longline and drift-net fisheries as a target or bycatch species (Nakano and Stevens 2008). Their fresh meat, liver-oil, cartilage, skin, and fins are used in many countries (Nakano and Seki 2003; Camhi *et al*. 2008); thus, they are considered as an important fisheries resource. Therefore, stock assessments of this species have been conducted by several regional fisheries management organizations (RFMOs) for sustainable exploitation of this species.¥

Knowledge of the current reproductive aspects of exploited species is essential for sustainable fisheries and conservation management. Reproductive parameters are used to estimate productivity and rebound potential of a fish stock in assessment models (Baremore and Passeroti 2013). To estimate those parameters, data and samples which cover whole stock should be analyzed, however few biological studies have covered all of habitats of this species in the North Pacific because of their wide distribution. Nakano (1994) reported a representative biological study on North Pacific blue shark, which was used as the basis for the stock assessment and modelling in the North Pacific. That study reported fundamental information on reproductive biology using samples collected from a broad area and all seasons between 1978 and 1987, but the length of the reproductive cycle was not estimated. Subsequently, Joung *et al*. (2011) reported the reproductive biology (e.g., size at maturity, litter size, and reproductive cycle) of this species in north and southeastern Taiwan. However, their samples were collected in a limited area.

Reproductive parameters in sharks are known to be variable depending on the density-dependence (Rose *et al*. 2001; Carlson and Baremore 2003). The stock abundance of the blue shark in the North Pacific has changed from 1980s in particular the stock biomass was lowest level between 1980s and early 1990s

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and then increased subsequently (ISC 2014; Ohshimo *et al*. 2016; Hiraoka *et al*. 2016). These results indicated the fact that samples by Nakano (1994) were collected at the period of lowest stock level, and the current reproductive parameters of North Pacific blue shark could be changed from those estimated by Nakano (1994). Therefore, the reproductive parameters of this population should be re-estimated using more recent samples. Moreover, it is necessary to estimate the reproductive periodicity of the blue shark for the future assessments because it is one of the most influential parameter to evaluate the productivity. In the present study, we updated the reproductive parameters and elucidated the reproductive cycle of blue shark collected from a relatively wide area in the western North Pacific Ocean.

Materials and methods

Sampling and data collection

Blue shark samples were collected between 2010 and 2016 by Japanese research (long-line, driftnet, and trawl) and commercial vessels (long-line and set net) operated in the western North Pacific Ocean (Fig. 1). Most of sharks (95%) were caught by long-line fisheries. Sex was determined by looking at the copulatory organ. Precaudal length (PCL), total length (TL), fork length (FL), and dorsal length (DL: length from the origin of the first dorsal fin to that of the second dorsal fin) in natural position were measured to the nearest centimeter by the scale for samples caught by research vessels, and body weight (BW) was measured to the nearest kilogram, if possible. The head and viscera had been removed from fish caught by commercial vessels; therefore, only DL was measured to the nearest centimeter. DL was converted to PCL with a conversion formula estimated using a linear regression model.

Size at maturity and maternity

Left inner clasper length was measured to the nearest centimeter with calipers, the degree of calcification of the clasper was recorded (un-calcified, partly calcified, or fully calcified). Weight of both testes combined was measured to the nearest 0.1 g. In addition, the presence of semen in the seminal vesicle was noted. We determined the degrees of male maturation based on Stehmann (2002), McAuley *et al*. (2007) and Chin *et al.* (2013) as the three stages (Table 1). The maturation stage of each individual was converted into binary data (immature = 0, mature = 1) at 5-cm intervals for the statistical analysis. A logistic regression model was fit to the binomial maturity data to determine male size at 50% maturity. This model is described as follows:

$$Y = 1 \ / \ [1 + exp\{-(\alpha + \beta X)\}]$$

, where Y is the proportion of mature individuals in each interval, X is PCL, and α and β are coefficients. A generalized linear model (GLM) with a binomial error structure and logit-link function was used to estimate the α- and β- coefficients using R statistical software (R 3.2.1; R Development Core Team).

The uterus widths at the widest point and the largest follicle diameter were measured to the nearest millimeter, and ovarian weight was measured to the nearest 0.1 g. The presence or absence and number of embryos, fertilized eggs, placenta, and an umbilical cord in the uterus were recorded. Sexual maturation in females was classified into five stages (Table 1). Female size at 50% maturity were estimated using the same equation as for males. Size at 50% maternity was also estimated using the data of recent or current pregnancy (mature–pregnant or mature–postpartum) or non-pregnancy (immature or mature–adult) were converted to

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binary data (recent or current pregnancy = 1, non-pregnancy = 0). The logistic function was fit to these data in the same way as for estimating the size at maturity.

Fecundity and gestation period

Litter size was estimated by counting the number of embryos. When the number of embryos was extremely low (<10) and the placenta was not retained in the uterus, or embryos were only in one side of the uterus, the female was judged to have had a preterm delivery and was not included in the analysis. The number of placentas without embryos was counted and added to the number of embryos with a placenta to prevent the underestimate of litter size due to early delivery or abortion. The relationship between litter size and PCL of pregnant females was estimated using a linear regression model.

Sex, and PCL (nearest 0.1 cm) for all embryos was recorded. Neonates were identified by an open, fresh umbilical scar. Mean size of near-term embryos per litter and the size of neonates were used to estimate size at birth and the parturition period. In addition, the gestation period was estimated as the approximate length in months between the mean ovulation date and the mean parturition date.

Reproductive seasonality and periodicity

The mating period was judged from the monthly trend in gonadosomatic index (GSI) of mature males and females. The GSI was calculated as GSI = (gonad weight (g) / BW (g)) × 10^2. Mean GSI was calculated for all months. The ovulation period was estimated from the monthly changes in follicle diameters of mature females. To fill the missing month, the values reported by Nakano (1994) and Joung *et al*. (2011) were used for these analyses.

The reproductive cycle of females is comprised of three phases: 1) vitellogenesis, 2) gestation, and 3) resting (Castro 2009). We verified whether the development of ovarian follicle and embryonic growth occurred synchronously or asynchronously and estimated the duration of the reproductive cycle based on the gestation period and resting phase.

Results

Sample collection and conversion factors

A total of 1,402 individuals were collected. Samples for reproductive parameters were obtained from 916 (484 males and 432 females) between 2011 and 2016 (Tables 2). PCL of males was 33.4–252.0 cm, and that of females was 33.4–243.3 cm. The relationships among the four lengths (PCL, TL, FL, and DL) and between PCL and BW are described in Table 3. No differences in PCL-TL or PCL-FL were observed between the sexes (ANCOVA, PCL-TL; $P = 0.10$, PCL-FL; $P = 0.41$); however, significant differences were observed in the PCL-DL and PCL-BW between males and females (ANCOVA, PCL-DL; $P = 0.002$, PCL-BW; $P = 0.022$).

Size at maturity and maternity

The smallest mature male was 140 cm PCL, and the largest immature male was 180 cm PCL. The size at

50% maturity in males were 160.9 (CI: 158.5–163.0 cm) cm PCL (Fig. 2a), and the estimated parameters and standard errors (in parentheses) for the model were –25.46 (2.84) for α, and 0.16 (0.02) for β.

A total of 139 pregnant females were caught, with a size range of 143.7–243.3 cm PCL. Postpartum females were 159.5–219.7 cm PCL (n = 22). The smallest mature female was 141 cm PCL, and the largest immature female was 180 cm PCL. The estimated size at 50% maturity in females were 156.6 (CI: 154.4–158.6 cm) cm PCL (Fig. 2b), and the estimated parameters and standard errors for the model were –24.52 (2.78) for α, and 0.16 (0.02) for β. Also, the size at 50% maternity was 167.4 (CI: 164.1–171.0 cm) cm PCL (Fig. 2c), and the parameters and standard error were –13.07 (1.52) for α, and 0.08 (0.01) for β. Size at 50% maternity was 10.8 cm larger than estimated size at maturity.

Fecundity and gestation period

Litter size (127 pregnant females) estimated based only on the number of embryos ranged from 1 to 112 (mean and standard deviation [SD], 33.1 ± 15.9), whereas litter size based on the sum number of embryos and placentas (124 pregnant females, three females removed for preterm delivery) ranged from 15 to 112 (mean, 35.5 ± 14.8). The latter litter size was positively correlated with maternal PCL (Fig. 3). Relationship between litter size and maternal PCL was statistically significant ($P < 0.01$). The linear regression was as follows:

$$\text{Litter size} = 0.46\ \text{PCL} - 45.54\ (n = 124,\ r^2 = 0.412)$$

A total of 4,165 embryos were observed; 1,908 were males and 1,967 were females. The sex of 290 individuals was unknown. The ratio of male to female embryos was not statistically different from 1:1 (chi-square test, $P = 0.34$). Embryos ranged in size from 1.2 to 41.2 cm PCL, and mean embryo size per litter varied widely within month. The largest embryos were observed from females caught in April, whereas the smallest were observed in October (Fig. 4). A total of 559 near-term embryos (16 litters) were observed from January to April, and their size range was 30.2–41.2 cm PCL (mean, 34.3 ± 2.11). Six neonates (PCL, 33.4 to 39.6; mean, 36.2 ± 2.41 cm) were observed in late June and July. Therefore, size at birth was estimated to be 34–36 cm PCL, and parturition was estimated to occur between April and July. Because high female GSI and mean follicle diameter were observed in summer (see following paragraphs and discussion), ovulation was estimated to occur in summer. Based on these results, the mean parturition occurs in May and the mean ovulation period is during July, indicating 11-month gestation period.

Reproductive seasonality and periodicity

Monthly changes in GSI showed an opposite trend between the sexes (Fig. 5). Mean GSI of mature males tended to increase from summer to winter and then decrease in spring. GSI was lowest (0.22) in July and highest (0.65) in December (Fig. 5a). Although mature female data were lacking for July, August, and November, mean GSI was highest (0.20) in June and lowest (0.04) in January and showed an increasing trend from winter to summer (Fig. 5b). The mean largest follicle diameter in females increased from winter to summer and was highest in June (Fig. 5c).

The ovarian follicles of pregnant females developed synchronously with embryonic growth throughout the gestation period, and pregnant females carried developing follicles and embryos at the same time (Fig.

6). As a result, the development of ovarian follicle and embryonic growth occurred synchronously.

Discussion

Size at maturity and maternity

Male size at 50% maturity estimated in the present study (PCL, 160.9 cm) was slightly larger than that reported in other studies for blue sharks in the North Pacific (e.g., Carrera-Fernández *et al*. 2010; Joung *et al*. 2011, Table 4). The most important factor associated with this difference is use of different maturation criteria. Natanson and Gervelis (2013) suggested that clasper calcification is the most accurate way to determine male maturation. They also reported that the presence of sperm alone was not a good indicator of maturity since juveniles were actively producing and storing sperm prior to clasper calcification. Therefore, we used calcification of the clasper as the main indicator for maturation. Carrera-Fernández *et al*. (2010) and Joung *et al*. (2011) used the presence of semen or spermatozeugmata as an indicator of maturation, and thus their estimate was suggested to be smaller than our estimates. Sizes at 50% maturity reported in the Atlantic (Joly *et al*. 2013; Montealegre-Quijano *et al*. 2014) and Mediterranean (Megalofonou *et al*. 2009) are similar to our results (Table 4), which were mainly determined using clasper calcification as a maturation indicator. Consequently, the size estimate of mature males in our study could be the most reasonable value for blue sharks in the North Pacific Ocean.

Estimated size at 50% maturity and maternity for females were 156.6 and 167.4 cm PCL, respectively. These value are similar to those by other studies in the northern and southern hemispheres (Table 4). The present study suggests little regional differences in size at maturity in female blue sharks. In addition, the size of these fish has not changed in the North Pacific since the 1980s because our results are similar to those reported by Nakano (1994).

Fecundity

In the present study, the number of embryos ranged from one to 112 (mean, 33.1, SD: 15.9) which is wider than that reported by Nakano (1994) (range, 1–62, mean ± SD, 25.6 ± 8.90; Table 6). The difference in mean litter size was caused by the larger females sampled in the present study than that by Nakano (1994) because litter size increases with maternal size. In addition, we added the number of placentas without embryo to the number of embryos in the uteri to prevent underestimating litter size. Adjusted litter size ranged from 15 to 112 with a mean of 35.5 per litter. Minimum litter size of blue sharks using this modified method of the present study was relatively higher than that reported previously (Table 4). Some authors have reported that females in the terminal phase of pregnancy were aborting when brought on board (e.g., Strasburg 1958; Nakano 1994; Carrera-Fernández *et al*. 2010, Montealegre-Quijano *et al*. 2014), suggesting that the recorded litter size might be less than the actual litter size. Analyzing the number of placental remains in the uterus or excluding sharks with near-term embryos may be necessary to reliably estimate fecundity. This is the first study showing a reliable blue shark litter size adjusted by the number of placentas.

Gestation period and parturition

Our estimate of gestation period based on the mean ovulation date and the mean parturition date (11 months) were similar to those reported previously (9–12 months) based on monthly changes in embryo size (e.g., Suda 1953; Pratt 1979; Nakano 1994; Carrera-Fernández *et al*. 2010).

Estimated birth size was 34–36 cm PCL and did not remarkably differ from that reported previously (Table 6). The parturition period was estimated April–July, being the months when the largest embryos and smallest neonates were present. This result is similar to Pratt (1979) (April–July) and Nakano (1994) (peak in May–June) but different from that reported by Suda (1953) (December–April). In our study, embryo size varied widely among month, and near-term embryos were already present in January samples, although most of them occurred in spring. Nakano (1994) reported same results. Suda (1953) also reported embryos of 30–35 cm PCL in December. Therefore, blue sharks seem to have a relatively broad mating and fertilization period, which caused wide variations in embryonic development and prolonged parturition period. However, our observations indicate that peak parturition occurred in spring and summer because most of the near-term embryos were observed in spring and neonates appeared in early summer.

Mating, ovulation, and fertilization period

Monthly changes in male GSI tended to be higher in winter and lower in summer, and were similar trend to the results reported by Nakano (1994). The mating period of male blue sharks based on GSI was June–August with a peak in July. Monthly changes in female GSI showed an opposite trend to those of males, with high values from spring to summer and low values from autumn to winter. The mating season for blue sharks in the northern hemisphere has been reported to be summer (Suda 1953; Stevens 1974; Pratt 1979; Nakano 1994; Joung *et al*. 2011). Our results were similar to other studies; thus, the mating period for the North Pacific blue shark is in summer.

Monthly changes in the largest follicle diameter were larger from spring to summer. Large yolky follicles indicate forthcoming ovulation; thus ovulation occur during summer. The ovulatory period has been reported to be summer (Nakano 1994) or July and August (Joung *et al*. 2011; Fig. 5c) in the North Pacific Ocean. Based on these findings, parturition, mating, and ovulation by blue sharks in the North Pacific occurs sequentially from spring to summer.

Female reproductive cycle

Our results suggest that female blue sharks have an annual reproductive cycle based on the synchronous ovarian follicle development and embryonic growth, and the 11-months gestation period with no resting phase. These results indicate that the ovarian follicles were ready to be ovulated during late gestation and that ovulation and pregnancy occur after parturition. Several authors have reported that female blue sharks store semen in their oviductal glands (Pratt 1979; Joung *et al*. 2011), enabling females to breed consecutively.

Joung *et al*. (2011) reported that the reproductive cycle of female blue shark in the Northwest Pacific is biannual because not all pregnant females had large oocytes in their ovaries. However, the number and monthly sample size of embryos observed in their study were insufficient, and most embryos were at an early developmental stage. Therefore, these sampling biases might affect their gestation and reproductive cycle estimates. Our result covers the samples from early to near-term embryos, thus it seems reasonable to conclude that the reproductive cycle of female blue shark in the western North Pacific is annual.

The reproductive parameters in our study differed little from those reported by Nakano (1994), except fecundity, but the present study extends the reproductive parameter estimates reported by Nakano (1994). Our results indicate that productivity of the blue shark in the North Pacific Ocean is higher than previously thought, as fecundity was higher and the reproductive cycle was shorter than those reported previously. As a future study, more female samples must be collected during summer. Additionally, a biochemical analysis on the temporal changes in steroid hormones would help verify our estimates of the reproductive cycle, necessary for the evaluation of resting phase.

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Table 1. Maturation stages of male and female blue sharks based on Stehmann (2002), McAuley *et al*. (2007) and Chin *et al*. (2013)

Sex	Organ	Description	Maturity status	Stage
Male	Clasper, testis, and semen in the seminal vesicle.	Clasper un-calcified, semen not present, and testis is thin.	Immature	Juvenile
		Clasper partially calcified, semen may be present, and testis is thickened.	Immature	Adolescent
		Clasper fully calcified, semen may be present, and testis is enlarged.	Mature	Adult
Female	Uterus, ovary, and ovarian follicle	Uterus thin and whit, and ovary very small.	Immature	Juvenile
		Uterus thin and white but partly enlarged posteriorly, and ovary developing but no mature follicles.	Immature	Adolescent
		Uterus enlarged but empty, and ovary enlarged with developed follicles.	Mature	Adult
		Uterus enlarged with embryos or fertilized eggs present.	Mature	Pregnant
		Uterus greatly enlarged, flaccid, and distended. Placenta or umbilical cord may be present in uterus.	Mature	Postpartum

Table 2. Monthly numbers of the observed blue sharks by maturity status

Sex	Maturity status	Stage	Month													Total
			Jan	Feb	Mar	Apr	May	Jun	Jul	Aug	Sep	Oct	Nov	Dec	Unknown	
Male	Immature	Juvenile	1	5		30	25	22	17			6	48	30		184
	Immature	Adolescent		1		14	42	36	7	1	5	40	6	2		154
	Mature	Adult	3	1	5	6	18	39	7	1	14	36	12	4		146
Female	Immature	Juvenile				10	17	19	20			2	8	14	2	92
	Immature	Adolescent	2	5	4	14	12	15			12	20	17	12		113
	Mature	Adult		1	4	15	17	25			4					66
	Mature	Pregnant	18	16	16	12	8	1			3	42		22	1	139
	Mature	Postpartum	1		1	10	4	6								22
Total			25	29	30	111	143	163	51	2	38	146	91	84	3	916

Table 3. Length–length and length–weight relationships for blue shark collected in the western North Pacific Ocean.

PCL, TL, FL, BW denote precaudal length, total length, fork length, and body weight

Conversion	Equations	Sex	n	r^2	P
TL to PCL	PCL = 0.78 TL – 3.75	Combined	396	0.994	0.10
FL to PCL	PCL = 0.92 FL – 0.22	Combined	338	0.998	0.41
DL to PCL	PCL = 2.51 DL + 12.33	Male	587	0.961	0.021
DL to PCL	PCL = 2.62 DL + 7.48	Female	275	0.983	
PCL to BW	$BW = 1.21 \times 10^{-5} \times PCL^{2.94}$	Male	756	0.954	0.022
PCL to BW	$BW = 5.86 \times 10^{-6} \times PCL^{3.09}$	Female	283	0.985	

Table 4. Size at maturity, birth, and litter size of blue sharks from previous studies.

Original total length (TL) and fork length (FL) data were converted to precaudal length (PCL) using the estimated conversion factors. * Size at 50 % maturity or maternity

Region	Size at maturity (cm)		Size at maternity (cm)	Size at birth (cm)	Litter size (mean value)	Reference
	Male	Female				
North Pacific			150	30–35	(30)	Suda (1953)
North Pacific	150–155	159			1–59 (25.7)	Nakano *et al.* (1985)
North Pacific	130–160	140–160		30–35	1–62 (27.6)	Nakano (1994)
NE Pacific	*139.8	*149.1			7–64	Carrera-Fernández *et al.* (2010)
NW Pacific	*140.2	*147.0		27.5	2–52 (25.2)	Joung *et al.* (2011)
NW Pacific	***160.9**	***156.6**	***167.4**	**34–36**	**15–112 (35.5)**	**The present study**
Central Pacific			158.4–188.9	22.7–33.6	4–38	Strasburg (1958)
SW Pacific	174.6–179.2	156.2–174.6	152.5–231.6			Francis and Duffy (2005)
SE Pacific			154.4–226.1		13–68 (35)	Zhu et al. (2011)
North Atlantic			162.4–186.5		28–54 (41)	Bigelow and Schroeder (1948)
North Atlantic	180.3					Aasen (1966)
NW Atlantic	168.1	170.0		23.5–30.5		Pratt (1979)
SW Atlantic	*153.3	*147.8				Joly *et al.* (2013)
SW Atlantic	*165.6	*157.3	*178.2		9–74 (33.5)	Montealegre-Quijano *et al.* (2014)
SE Atlantic			165.4		4–75 (37)	Castro and Mejuto (1995)
Indian Ocean		>136.7		27.5–35.3	10–135 (56)	Gubanov and Grigor'yev (1975)
Mediterranean	*154.5	*163.7				Megalofonou *et al.* (2009)

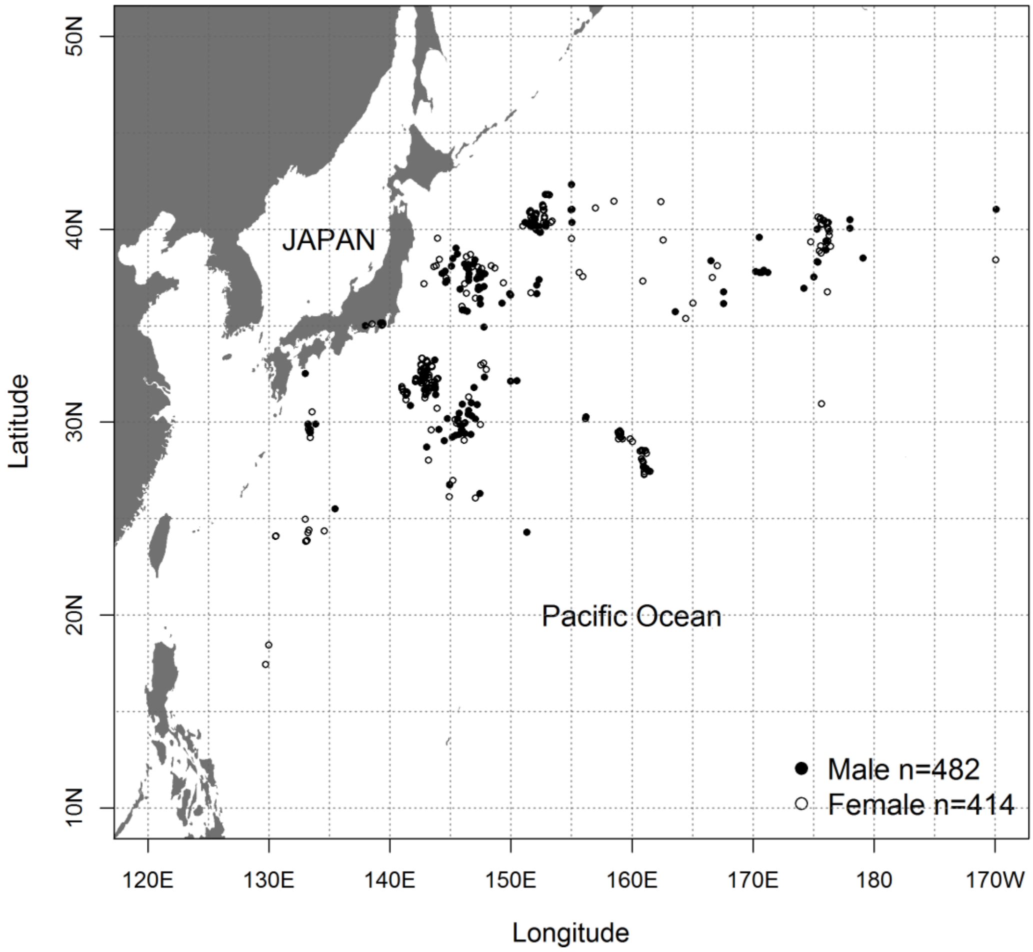

Fig. 1. Blue shark (*Prionace glauca*) sampling locations in the western North Pacific. Black and white circles indicate males and females, respectively.

* Working document submitted to the ISC Shark Working Group Workshop, 14-21 November 2016, Busan, Korea. **Document not to be cited without author's permission.**

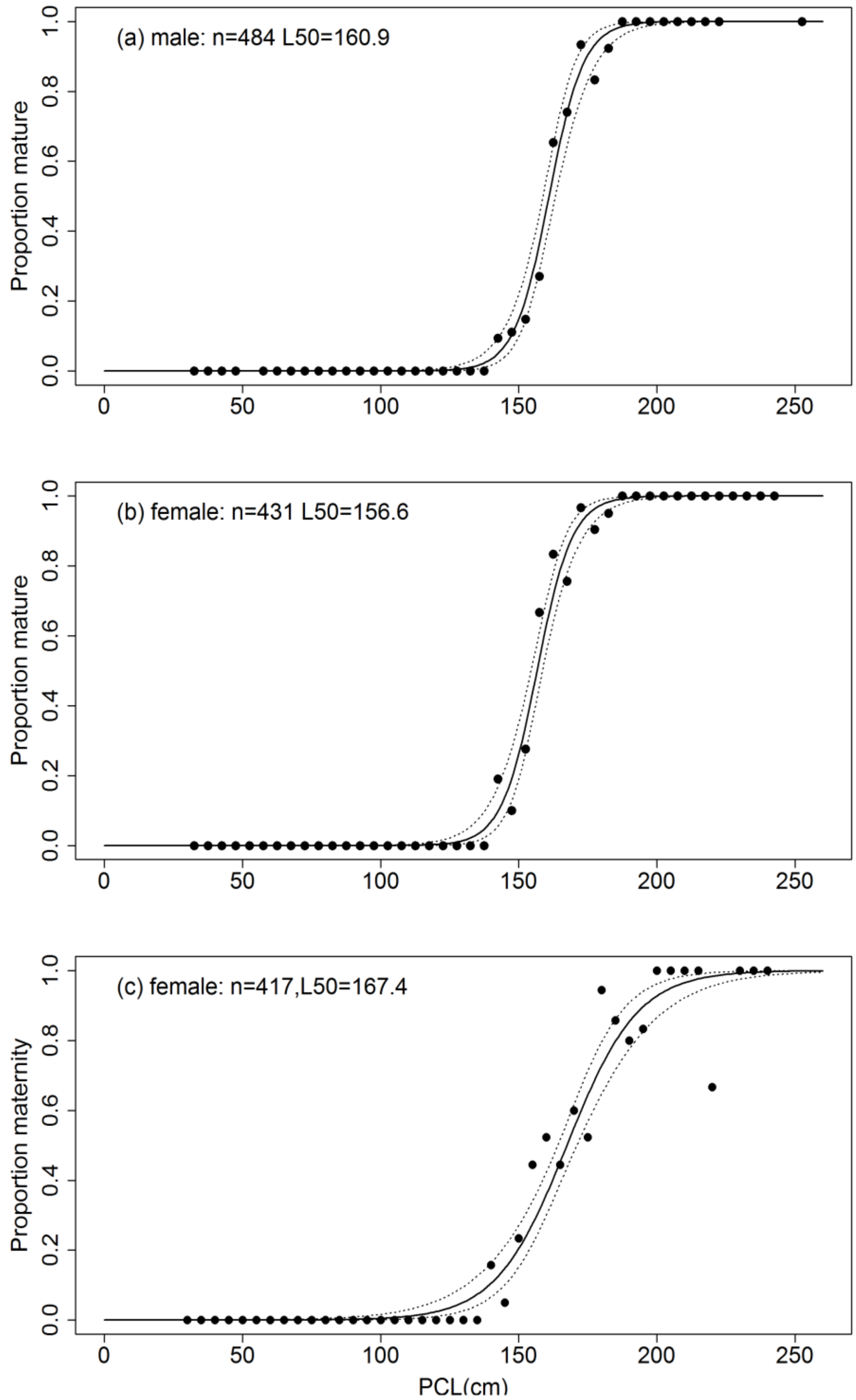

Fig. 2. Maturity and maternity ogives for blue shark. (a) Maturity ogives for males and (b) females and (c) maternity ogive for females. Size class interval is 5-cm of precaudal length. Dotted lines indicate 95% confidence intervals.

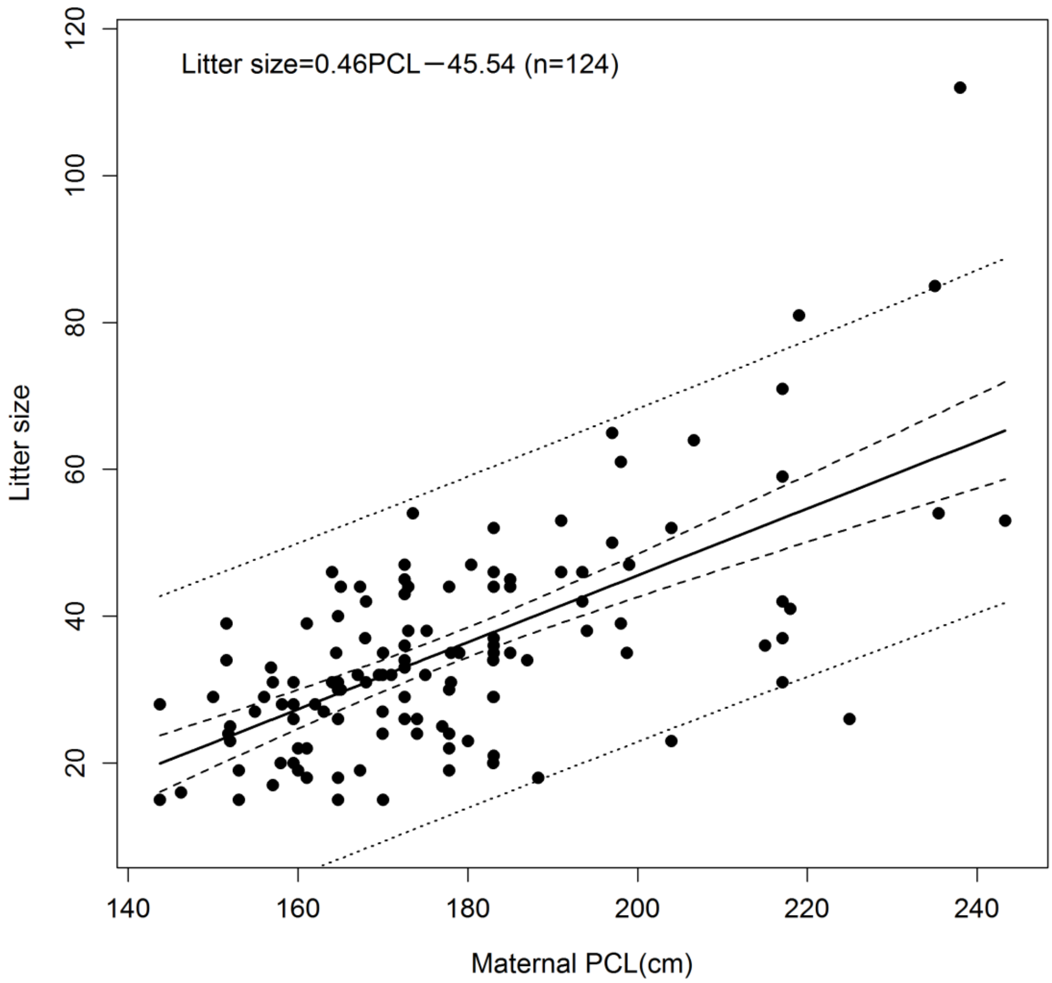

Fig. 3. Relationships between precaudal length (PCL, cm) of 124 pregnant females and litter size based on the number of embryos and placenta in uteri. Solid line indicates the fitted linear regression, broken lines indicate 95% confidence intervals, and dotted lines indicate 95 % prediction intervals, respectively.

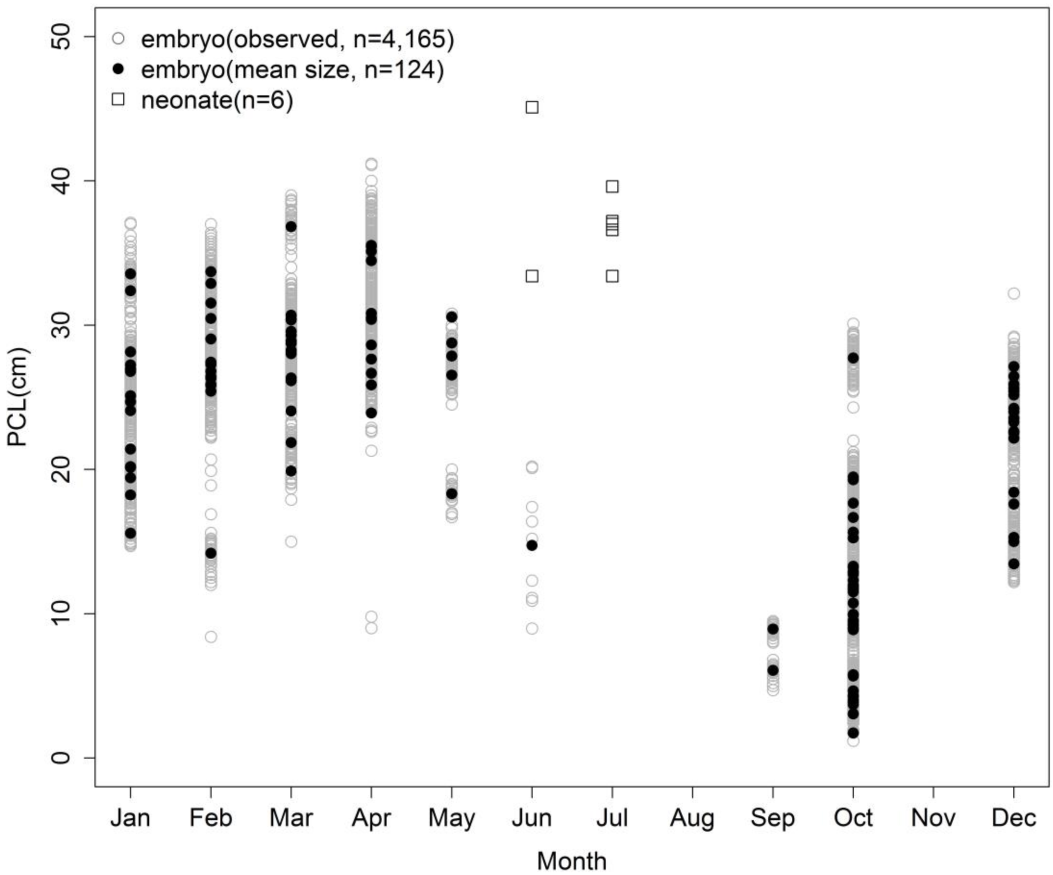

Fig. 4. Monthly changes in precaudal length (PCL, cm) of embryos and neonates. Gray circles indicate the size of each embryo. Black circles indicate mean PCL of embryos per litter. Squares indicate PCL of neonates.

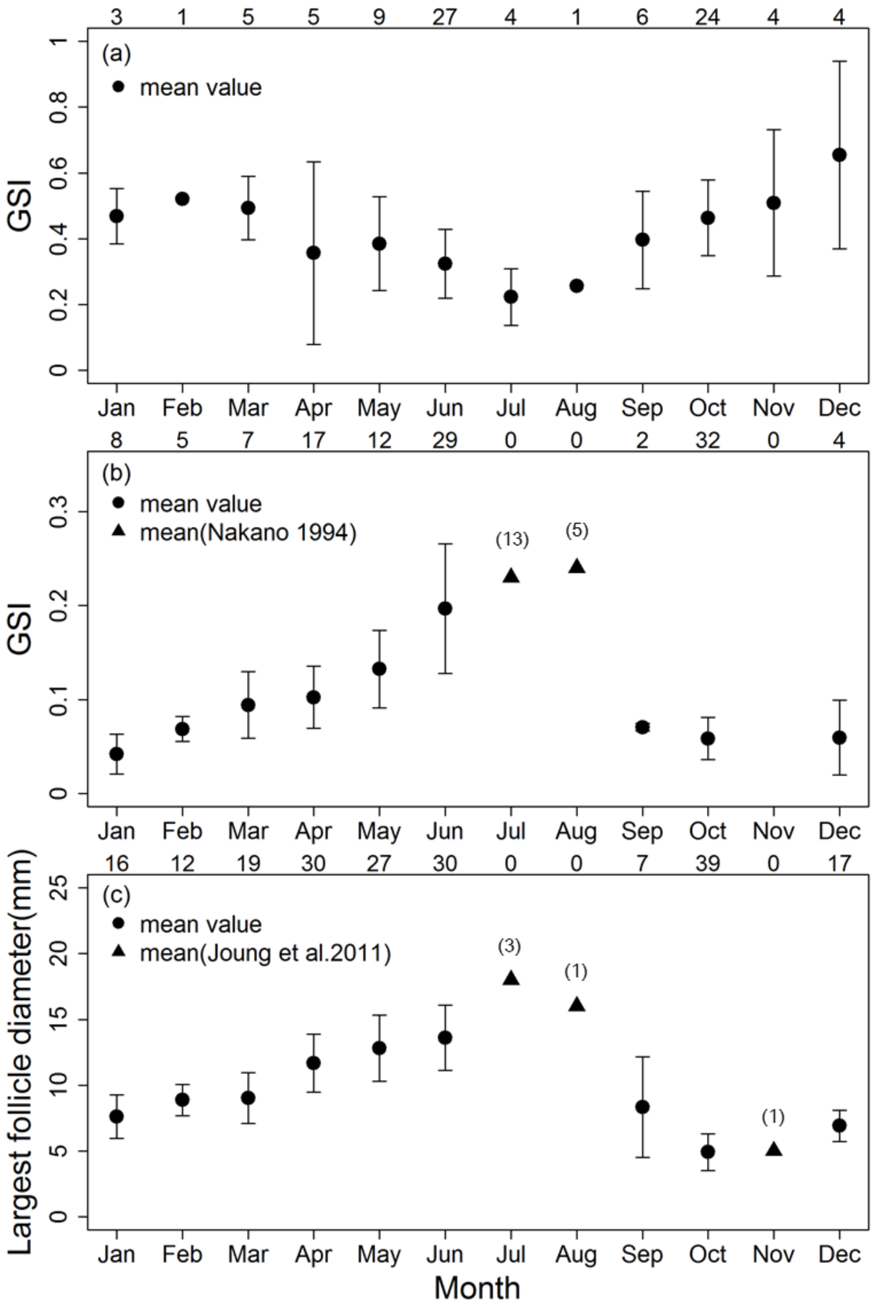

Fig. 5. Monthly change in gonadosomatic index (GSI) for mature (a) males and (b) females and (c) the largest follicle diameter (mm) in mature females. Values from Nakano (1994) and Joung *et al*. (2011) are used for months without data. Error bars are standard deviations. Numbers in the margin represent monthly sample size and those in parenthesis represent sample sizes of previous studies.

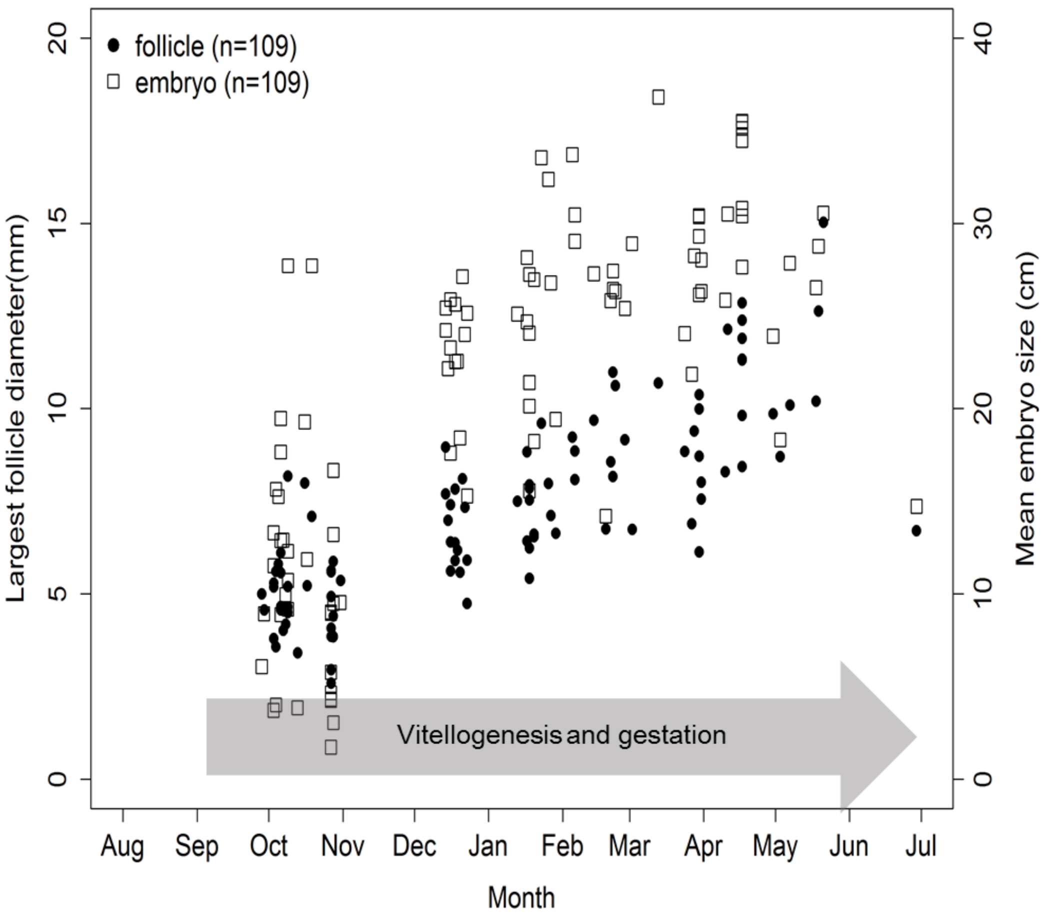

Fig. 6. Temporal changes in largest follicle diameter (mm; main Y-axis) and mean embryo size (second Y-axis) in pregnant female blue sharks (n = 109). Circles represent follicles, and squares represent embryos.