High reproductive potential of the commercially exploited shark Squalus suckleyi in the major fishing grounds of the western North Pacific

Received: 3 October 2022 | Accepted: 9 May 2023
DOI: 10.1111/jfb.15430

REGULAR PAPER

JOURNAL OF FISH BIOLOGY fsbi

High reproductive potential of the commercially exploited shark *Squalus suckleyi* in the major fishing grounds of the western North Pacific

Toshikazu Yano[1] | Tsutomu Hattori[2†] | Yoji Narimatsu[3] | Jiro Nagao[3] | Sho Tanaka[4]

[1]National Fisheries University, Japan Fisheries Research and Education Agency, Yamaguchi, Japan

[2]Niigata Field Station, Fisheries Resources Institute, Japan Fisheries Research and Education Agency, Niigata, Japan

[3]Hachinohe Field Station, Fisheries Resources Institute, Japan Fisheries Research and Education Agency, Aomori, Japan

[4]Tokai University, Shizuoka, Japan

Correspondence
Toshikazu Yano, National Fisheries University, Japan Fisheries Research and Education Agency, 2-7-1 Nagata-honmachi, Shimonoseki, Yamaguchi 759-6595, Japan.
Email: tskzyn@fish-u.ac.jp

Funding information
Fisheries Agency of Japan

Abstract

The present study examined body length (precaudal length, PCL) and age at sexual maturity, as well as fecundity and maternal investment in the Pacific spiny dogfish *Squalus suckleyi*, a long-term commercially exploited shark in the western North Pacific, using samples caught in several fisheries and across seasons. The PCL and age at 50% sexual maturity of males were 60.6 cm and 9.4 years, respectively, and those of females were 73.1 cm and 17.8 years, respectively. The PCL and age at 50% maternity were 77.4 cm and 19.7 years, respectively. General or generalized linear models revealed that capture by different fishing method did not significantly correlate with sexual maturity and maternity rates or litter size. Other general linear models revealed an increase in offspring size with maternal size, but litter size was not affected by embryonic development. These findings indicate that the reproductive potential of Pacific spiny dogfish is relatively high throughout the whole North Pacific region because of a smaller size and earlier age at sexual maturation in both sexes. In addition, pregnant females displayed no resting phase and produced 0.45 more embryos per centimetre of PCL in their lifetime after the onset of maturity, which is higher than in the eastern North Pacific. We suggest that these qualities are not a consequence of stock decline associated with the long-term exploitation of the species, but that its high reproductive potential has likely contributed to the long-term stability of the landings in Japan.

Significance statement: While reproductive potential has been determined for many fish species, such information is scarce for Pacific spiny dogfish. We evaluated the reproductive characteristics of this species in the major fishing grounds of the western North Pacific. The productivity and rebound potential of sharks is extremely low compared with those of bony fishes. However, our results indicate that even if the reproductive potential has a small effect on the population dynamics, it should not be ignored for sustainable stock utilization.

KEYWORDS
data deficient shark, Japan, maternal effect, reproductive characteristics, sexual maturity, spiny dogfish

† Died February 19, 2023.

1 | INTRODUCTION

Sharks are apex predators in the food web and decreases in their biomass alter the balance of the ecosystem through a weakened top-down effect (Baum & Worm, 2009; Myers *et al*., 2007). The sustainable use of shark stocks requires careful monitoring. The Pacific spiny dogfish *Squalus suckleyi* is a commercially exploited shark endemic to the North Pacific (Ebert *et al*., 2010), where it is abundant in eastern and western regions (Yano, Ohshimo, *et al*., 2017) and is a key species in ecosystems (Harvey *et al*., 2012; Yonezaki *et al*., 2016). Until recently, this species was considered to be the same species as spiny dogfish *Squalus acanthias*, which is widely distributed throughout the temperate waters of the Atlantic and the South Pacific (Ebert *et al*., 2010). However, Pacific spiny dogfish shows slower growth, an older age at sexual maturation, and longer longevity compared with other elasmobranchs (McFarlane & Beamish, 1987; Saunders & McFarlane, 1993). The reproductive mode of pregnant females of Pacific spiny dogfish is classified as yolk sac viviparity (Conrath & Musick, 2012), and two to 25 embryos grow in a pair of uteri during a pregnancy of nearly 2 years (Ketchen, 1972). Such characteristics can result in lower intrinsic rates of increase (Smith *et al*., 1998) and lower resilience to fishing mortality (Hoenig & Gruber, 1990). Accordingly, Pacific spiny dogfish is vulnerable to excessive fishing pressure, as are numerous other shark species (Hoenig & Gruber, 1990; Holden, 1974). Pacific spiny dogfish is listed as Least Concern by the International Union for Conservation of Nature, although the status of stocks in the western North Pacific remains uncertain (Bigman *et al*., 2016).

Japan has historically exploited a great amount of Pacific spiny dogfish in the western North Pacific (Yano *et al*., 2022). Its landings in Japan reached 60,023 tons in 1949, around the time when it became the country's most-landed shark species (Yano *et al*., 2022). Thereafter, Pacific spiny dogfish landings began to drastically decrease, reaching <10,000 tons by 1965 (Taniuchi, 1990; Yano *et al*., 2022). Although the drastic drop suggests reduction of the stock (Taniuchi, 1990), recent research showed that the drop in landings was probably caused by the rapidly declining social demand for this species, rather than stock depletion (Yano *et al*., 2022). Nevertheless, since 1990, to satisfy local demand for this species as a food resource, the landings have remained relatively stable at 2800–4500 tons. These catch rates are lower than those prior to the 1950s (Yano *et al*., 2022). It was presumed that there has been long-term, low-level fishing pressure on Pacific spiny dogfish. The low demand for this species in recent decades may have induced frequent discards at sea, similar to other commercially unimportant sharks (Baba *et al*., 1987). Unfortunately, there is no information on the amounts of incidental catch and discards of this species in Japanese fisheries, like in many other countries (Worm *et al*., 2013), and hence the discard mortality of this species is also unknown. It is therefore important to verify the stock status of Pacific spiny dogfish in the western North Pacific.

Because of the lack of long-term continuous fishery or survey data in Japan that could be used to calculate stock index trends for Pacific spiny dogfish, determining the size at sexual maturity is one approach to discern the status of the stock. Earlier sexual maturation in squaloids, including Pacific spiny dogfish, has been observed when their population sizes decrease (Sosebee, 2005; Taylor & Gallucci, 2009). Fortunately, the approximate size at sexual maturity for Pacific spiny dogfish around Japan was determined during a period of high demand for the species (Yamamoto & Kibesaki, 1950) and therefore it can be compared with the maturity size at present. In addition, other reproductive parameters, such as age at sexual maturity, reproductive periodicity, and fecundity are required to estimate the productivity and rebound potential of sharks (Baremore & Passerotti, 2013). As maternal effects, the reproductive potential influences recruitment. While reproductive potential has been determined for many fish species (Kurita, 2010), information on the maternal investment to embryos is limited for Pacific spiny dogfish (Tribuzio & Kruse, 2012). While these data are needed for stock assessments and future fisheries management in Japan, such information is scarce for the western North Pacific and comprises only a few old studies (*e.g*., Tanabe *et al*., 1958; Yamamoto & Kibesaki, 1950), although some of these reproductive parameters will differ geographically (Ketchen, 1972; Tribuzio & Kruse, 2012; Yamamoto & Kibesaki, 1950).

The objective of the present study was to evaluate the reproductive characteristics of Pacific spiny dogfish collected from the Tsugaru Strait between Hokkaido and Aomori prefectures, and in adjacent waters off northern Japan where there are major fishing grounds and important habitat areas for this species in the western North Pacific (Tohoku National Fisheries Research Institute, Fisheries Agency of Japan, 1993; Yano, Ohshimo, *et al*., 2017). In this region, this shark has been captured using various fishing methods, including offshore bottom trawls, bottom longlines, gillnets, and set nets (Tanabe *et al*., 1958). While it is known that Pacific spiny dogfish caught in a particular fishery is biased toward mature individuals (Yano, Hattori, *et al*., 2017), the main fisheries for this species since the 1950s have been trawl, longline, and gillnet fisheries, although the latter has not been used in recent years (Yano *et al*., 2022). Thus, we examined whether the fishing methods have influenced the reproductive parameters of this species in our study area.

2 | MATERIALS AND METHODS

2.1 | Sampling and data collection

Sampling was performed monthly from November 2013 to October 2015, and a total of 1720 Pacific spiny dogfish (585 males, 1135 females) were obtained from the Tsugaru Strait and adjacent waters (Figure 1). Specimens were mainly caught by bottom longline fishery, but were also caught by offshore bottom trawl, gillnet, set net, and purse seine fisheries (Figure 2). An additional 242 individuals (120 males, 122 females) were obtained from offshore bottom-trawl surveys by the Fisheries Resources Institute of the Japan Fisheries Research and Education Agency, conducted in October 2013, April and June 2014, and June and October 2015; these surveys targeted multiple species, including Pacific spiny

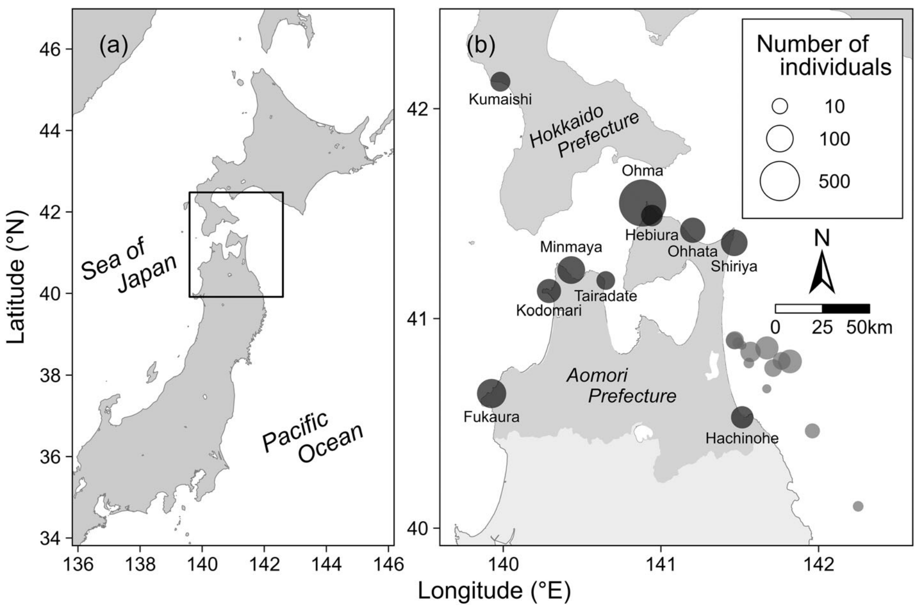

FIGURE 1 (a) Map of northern Japan indicating the Tsugaru Strait and its adjacent waters (black open square). (b) Enlarged map of the Tsugaru Strait showing numbers of Pacific spiny dogfish *Squalus suckleyi* specimens obtained from fisheries by landing port (dark grey circles) and numbers obtained in bottom-trawl surveys (light grey circles)

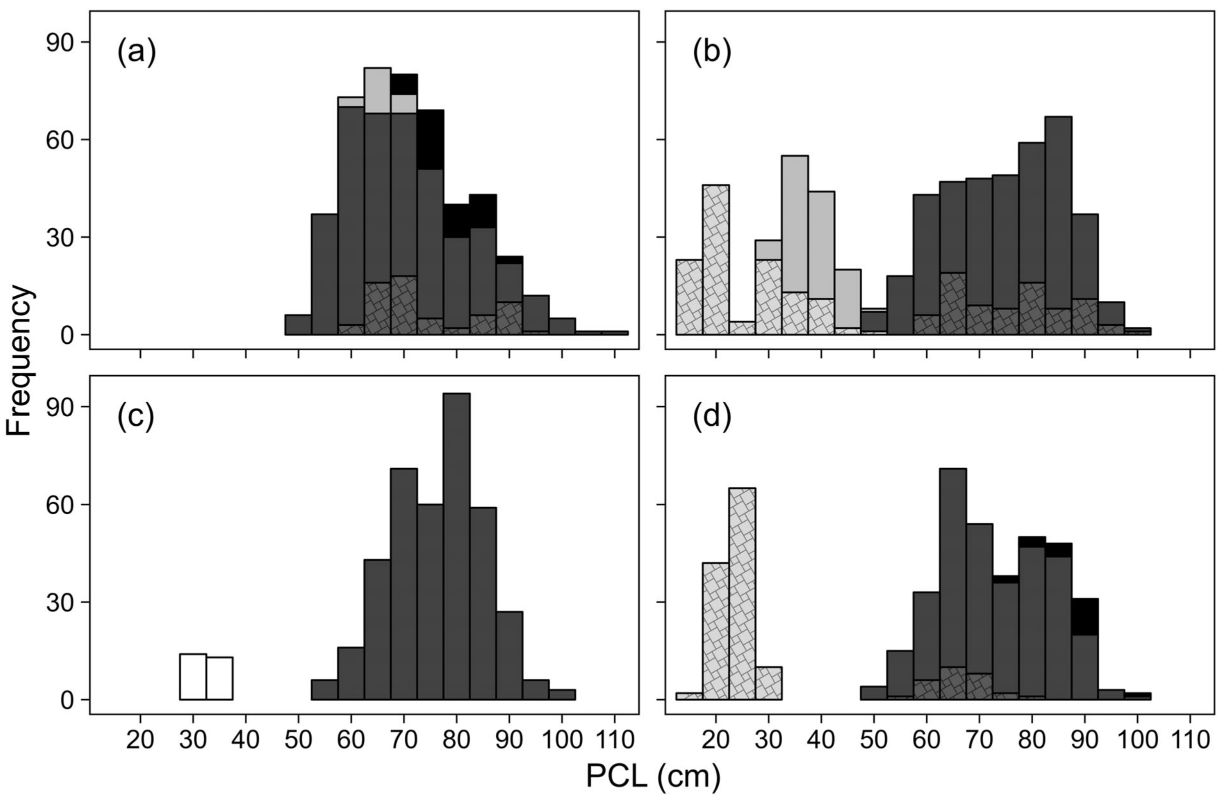

FIGURE 2 Frequency distribution of precaudal length (PCL) of Pacific spiny dogfish *Squalus suckleyi* in each seasonal quarter: (a) January–March, (b) April–June, (c) July–September and (d) October–December. Solid bar colours indicate specimens obtained from gillnet (black), bottom longline (dark grey), set net (light grey) and purse seine (white) fisheries; patterned bars indicate specimens obtained from fisheries (dark grey) or surveys (light grey) of offshore bottom trawls

dogfish, so fish with a wide range of body lengths were captured. The present study was conducted in accordance with the administrative provision of animal welfare of the Japan Fisheries Research and Education Agency. All specimens were collected in the exclusive economic zone of Japan, and all research cruises were approved by the Japanese Government.

First, the sex of each specimen was determined on the basis of the presence (males) or absence (females) of claspers. Each shark was then measured to determine total length (TL, from tip of the snout to dorsal tip of tail with upper lobe of caudal fin depressed to align with the horizontal axis of the body) and precaudal length (PCL, from tip of the snout to dorsal precaudal notch), which were recorded to the nearest 0.1 cm (Tribuzio *et al*., 2016). Body weight (BW) was recorded to the nearest 0.01 kg.

Although the frilled shark *Chlamydoselachus anguineus* maintains its embryos only in the right uterus, both the right and left uteri are functional in many other sharks (Tanaka *et al*., 1990). Previous studies measured only one side of reproductive organs for Pacific spiny dogfish (Tribuzio *et al*., 2009; Tribuzio & Kruse, 2012) because the reproductive organs of the left and right are similar in size, therefore reproductive organs from the left side of the body were measured in the present study for consistency. For males, the clasper inner length (CIL, from the anterior margin of the cloaca to the posterior tip of the left clasper) was measured to the nearest 0.01 mm, and the clasper condition (uncalcified or calcified) was recorded. The presence or absence of semen was confirmed by applying pressure to a seminal vesicle. For females, the left oviducal gland width (OGW) was measured to the nearest 0.01 mm. Based on observations of the uterus, each female was classified as nonpregnant or as an individual carrying candle-stage embryos (translucent gelatinous fertilized egg cases contained within the uteri, a stage that lasts ~4 months) or developing embryos (each embryo is free in the uterine lumen, but has a large pendent external yolk sac that is completely absorbed by the time of birth). For pregnant females carrying candle-stage embryos, as an estimation of litter size, the number of fertilized eggs or embryos within the candles was recorded if the candle was not broken. The internal organs were then extracted and frozen until later measurements. Defrosted gonad weight (GW) was recorded to the nearest 0.01 g. Oocyte diameter (OD) in each ovary was measured to the nearest 0.01 mm; the OD was recorded as the mean value of up to three oocytes from the largest follicle groups because it is difficult to select the largest one from a group of similarly sized follicles within a limited measurement time. The number of embryos within a pair of uteri and their PCL were recorded along with information on the presence or absence of an external yolk sac.

2.2 | Sexual maturity assessment

To characterize gonadal development, the gonadosomatic index (GSI) was calculated for males and females based on GW divided by BW and multiplied by 100. Individuals were secondarily classified as immature or mature based on clasper condition and the presence of semen in males, and pregnancy status and development of the oviducal gland and ovarian oocytes in females (Yano *et al*., 2020).

Szöcs and Schäfer (2015) strongly recommended that proportions from counts should be analysed using a generalized linear model (GLM) because proportion data are rarely normally distributed and the use of proportions loses sample size information. In the present study, the proportions of mature males and mature females at a given PCL were estimated using a GLM with binomial distribution:

$$Y \cong \mathrm{Bin}(1,\pi) \tag{1}$$

$$\mathrm{var}(Y) = \pi \times (1-\pi) \tag{2}$$

and

$$\mathrm{logit}(\pi) \cong \alpha + \mathrm{PCL} + \mathrm{FM} + \mathrm{PCL} \times \mathrm{FM} \tag{3}$$

where *Y* is the response variable for the binary response of immature or mature and π represents the probability of maturation, Bin and logit represent the binominal error and logit link, respectively, α is a constant (also called the intercept), PCL is precaudal length (a continuous variable), FM is the effect of fishing method (a categorical variable), and PCL × FM is the interaction term among explanatory variables. The best model was selected from those including all possible combinations of explanatory variables on the basis of the Akaike information criterion (AIC) value. All analyses were conducted in R version 4.1.2 (R Core Team, 2021) using the package 'MuMIn' (Bartoń, 2020). The model with the lowest AIC value was considered the best. The PCL at 50% and 95% sexual maturity was estimated from the GLM for each sex. The same procedure was conducted for calculating PCL at 50% and 95% maternity, with the response variables being a binary choice of pregnant or nonpregnant females, and the explanatory variables the same as those in the sexual maturity model. While the reported reproductive periodicity is the same between the western and eastern North Pacific, the timing of parturition and subsequent mating are different (Jones & Geen, 1977; Ketchen, 1972; Tanabe *et al*., 1958; Tribuzio *et al*., 2009; Tribuzio & Kruse, 2012). Around Japan, parturition occurs from February to April and mating occurs soon after, finishing by June at the latest (Ketchen, 1972; Yamamoto & Kibesaki, 1950). To eliminate the influence of mature females with an empty uterus during the period from the birth of juveniles to subsequent mating and ovulation events, all females collected from February to June were excluded from the analysis of length at maternity. We did not carry out age determinations, thus the 50% and 95% ages at sexual maturity and maternity were derived from parameters of the von Bertalanffy growth equation as provided by Orlov *et al*. (2011), using consistent lengths estimated in the present study. A bootstrapping procedure was used to the calculate 95% confidence interval (CI) of each estimated value based on re-sampling 1000 times. The PCL and age at sexual maturity were considered significantly different if the bootstrap confidence intervals and previously reported values did not overlap.

2.3 | Examination of fecundity and embryonic development

Individual fecundity of fish, including Pacific spiny dogfish, is generally reported as a linear function of maternal length (Tribuzio & Kruse, 2012). A general linear model was used to determine the relationship between maternal PCL and litter size for pregnant females carrying candle-stage embryos or developing embryos, respectively, and these were continuous variables. The explanatory variables in the model were the same as those that would be used in a GLM. The slope and intercept between two regressions were tested by analysis of covariance (ANCOVA) implemented in the R package 'car' (Fox *et al*., 2021).

To assess whether the size of pregnant females or number of embryos carried affected embryonic development, the embryo PCL at a given PCL and litter size of the pregnant female carrying them was examined using a general linear model. A total of 1019 embryos were used for this analysis; notably, two groups of embryos at different growth stages can be observed in a pregnant female owing to the long gestation period of approximately 2 years (*i.e*., first- and second-year embryos can be observed in the same month). To eliminate bias for embryo PCL, only embryos with a completely absorbed yolk sac (*i.e*., those in the last half of the gestation period or the second year in the uteri) were included in this analysis. The PCL of embryos is a continuous variable and was used as the response variable. The explanatory variables, that is, the body length and litter size of pregnant females, were also continuous. Time was specified in 3-month intervals, whereby January–March, April–June, July–September and October–December constituted the first, second, third and fourth quarters, respectively. The effect of quarters was included in the model as a categorical variable because the embryo PCL varies with growth depending on when the female shark was caught. We assessed the influence of the second to fourth quarters relative to the first quarter.

We also examined embryonic development within the same pregnant female based on the coefficient of variation (CV) for the embryos retained in each pregnancy, generated from the mean and standard deviation (SD) for embryos from each pregnant female. To confirm good or poor development among embryos within a pregnancy, embryo PCL was normalized so that 1 was the median value for embryos in the same pregnancy. Then, box and whisker plots of normalized embryo PCL were created at 1-cm length intervals based on the median PCL for embryos in the same pregnancy. In this study, outliers outside the whiskers extending to the minimum and maximum values within 1.5 times the length of the box (where the bottom and top of the box represent the 25th and 75th percentiles, respectively) were considered as good or poorly growing embryos.

A general linear model was also used to convert TL to PCL, enabling comparison of our data with those reported in previous studies. The TL was used as the response variable to determine relationships between PCL and TL. Each variable was continuous, and a model was created for each sex, with the slope and intercept between two regressions tested by ANCOVA. A bootstrapping procedure was also used to calculate the 95% CIs in the general linear model analysis.

3 | RESULTS

3.1 | Body-length frequency in different fisheries

The range of minimum to maximum PCL was 17.5–79.5 cm for males and 17.7–111.5 cm for females (Figure 2). Pacific spiny dogfish with

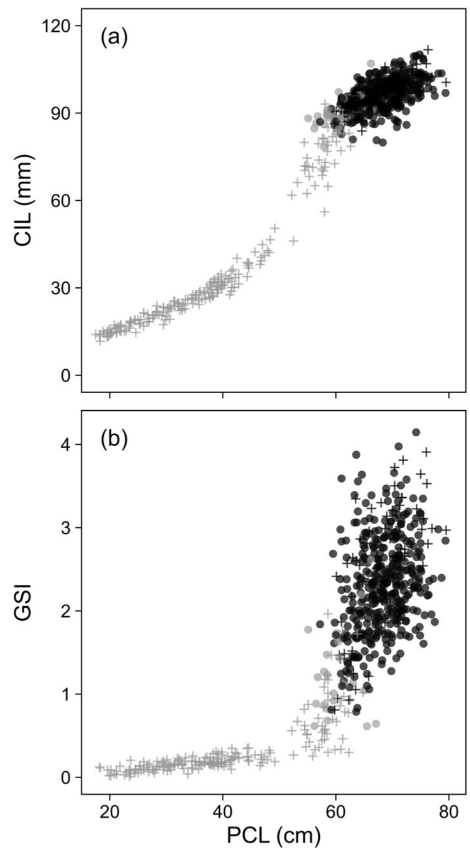

FIGURE 3 Relationship between precaudal length (PCL) and (a) clasper inner length (CIL) or (b) gonadosomatic index (GSI) of male Pacific spiny dogfish *Squalus suckleyi*. Light- and dark-grey colours indicate males with uncalcified and calcified claspers, respectively; crosses and solid circles indicate absence and presence of sperm, respectively

PCL of <30 cm (mainly 20–25 cm PCL) were observed in all quarters outside the first quarter; such small sharks were more frequently caught in the trawl survey conducted offshore of Aomori Prefecture from Hachinohe City to Misawa City, an area south of the Tsugaru Strait mouth on the Pacific Ocean side (Figures 1 and 2). These small sharks were judged to have been caught shortly after birth because an obvious umbilical cord scar was present.

The two regressions between PCL and TL for both sexes showed significant differences in slopes (ANCOVA, $F = 68.69$, $P < 0.001$) and intercepts (ANCOVA, $F = 40.55$, $P < 0.001$), thus we determined conversion equations as follows for males:

$$PCL = 0.81 \times TL - 1.02$$

and females:

$$PCL = 0.83 \times TL - 1.72$$

where the coefficient of determination (r^2) was 0.999 for both males and females.

3.2 | Size and age at sexual maturity

The inner length of the claspers rapidly increased for males in size class 50–60 cm PCL (Figure 3a). The proportion of individuals with calcified claspers changed drastically from 11.5% in the 50–60 cm PCL group to 89.9% in the 60–70 cm PCL group. The minimum PCL of males with calcified claspers was 57.2 cm, and the maximum PCL of males with uncalcified claspers was 67.1 cm. These males had semen in their seminal vesicles. Approximately half (44.8%) of males with uncalcified claspers and >60 cm PCL had semen in their vesicles, indicating that the male sharks can produce semen before their claspers are fully calcified. The GSI values increased with clasper development (Figure 3b). Thus, males were regarded as mature if their claspers were calcified and other males were treated as immature. When the explanatory variable related to fishing method was dropped from the best GLM (Table 1), male PCL at 50% and 95% sexual maturity as estimated by the best model was 60.6 cm (95% CI 60.0–61.2 cm) and 65.0 cm (95% CI 64.0–65.9 cm), respectively. The 50% and 95% ages at sexual maturity based on those sexual maturity lengths were computed to be 9.4 years (95% CI 9.2–9.6 years) and 10.8 years (95% CI 10.5–11.2 years), respectively.

The GSI showed high variability among females sized >70 cm PCL (Figure 4a). Gonadal development was observed at an OD of >20 mm and OGW of >15 mm (Figure 4b,c). The smallest pregnant female was 67.4 cm PCL with 8.29 mm OD and 8.51 mm OGW, and was caught in August 2015. Accordingly, nonpregnant females were regarded as mature if their ovarian OD was >20 mm or their OGW was >15 mm. All other females were regarded as immature.

TABLE 1 Results of the best-fit generalized linear models to predict sexual maturity and maternity of Pacific spiny dogfish *Squalus suckleyi*

Coefficient	Parameter	Standard error	*P* value
Male maturity model			
Intercept	−40.84	4.80	<0.001
PCL	0.67	0.08	<0.001
Female maturity model			
Intercept	−28.02	2.03	<0.001
PCL	0.38	0.03	<0.001
Maternity model			
Intercept	−21.91	1.97	<0.001
PCL	0.28	0.02	<0.001

Note: PCL, precaudal length.

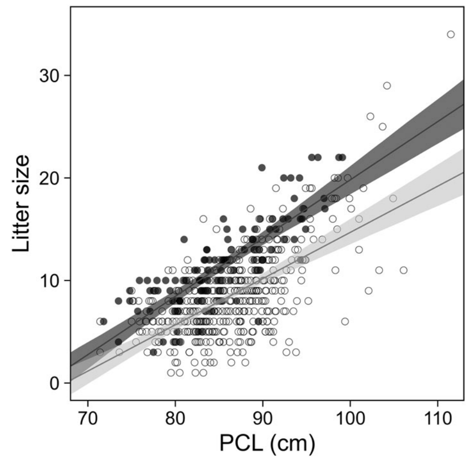

FIGURE 5 Relationship between precaudal length (PCL) and number of embryos in individual pregnant females of Pacific spiny dogfish *Squalus suckleyi*. Dark solid circles and open circles represent females carrying candle-stage embryos or developing embryos, respectively. Dark-grey and light-grey solid lines indicate linear regression lines fitted to data of females carrying candle-stage embryos or developing embryos, respectively; shaded regions around solid lines depict 95% confidence intervals

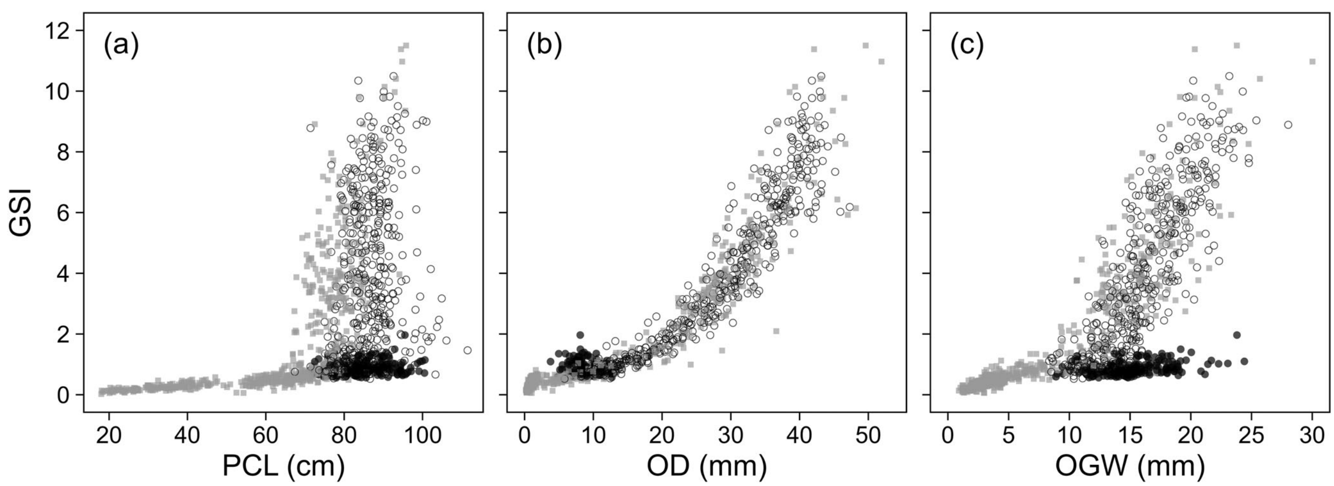

FIGURE 4 Relationship between gonadosomatic index (GSI) to (a) precaudal length (PCL), (b) oocyte diameter (OD) and (c) oviducal gland width (OGW) in female Pacific spiny dogfish *Squalus suckleyi*. Light-grey solid squares indicate nonpregnant females; dark-grey solid and open circles represent females carrying candle-stage embryos or developing embryos, respectively

The explanatory variable related to fishing method was also dropped from the best model of female maturity (Table 1). As a result, female PCL at 50% and 95% sexual maturity was estimated as 73.1 cm (95% CI 72.4–73.7 cm) and 80.7 cm (95% CI 79.7–81.7 cm), respectively. Based on those lengths at sexual maturity, the ages at 50% and 95% sexual maturity were computed to be 17.8 years (95% CI 17.5–18.0 years) and 21.3 years (95% CI 20.8–21.8 years), respectively. These determinations of PCL and age at sexual maturity for females were significantly larger than those for males as the bootstrap confidence intervals for males and females did not overlap.

The explanatory variable fishing method was dropped from the best GLM of maternity, as with the model of sexual maturity (Table 1). The PCLs of pregnant females at 50% and 95% maternity estimated by the resultant model were 77.4 cm (95% CI 76.5–78.3 cm) and 87.8 cm (95% CI 85.8–89.6 cm), respectively. The ages at 50% and 95% maternity based on those lengths were 19.7 years (95% CI 19.3–20.1 years) and 25.3 years (95% CI 24.1–26.5 years), respectively.

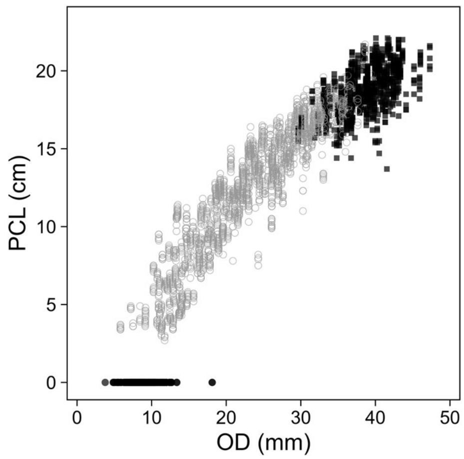

FIGURE 6 Relationship between oocyte diameter (OD) and precaudal length (PCL) of embryos in Pacific spiny dogfish *Squalus suckleyi*. Dark-grey circles represent females carrying candle-stage embryos. Light-grey open circles and dark-grey solid squares indicate embryos with or without external yolk sac, respectively

3.3 | Fecundity and embryonic development

The number of embryos ranged from three to 22 in females carrying candle-stage embryos and from one to 34 in females carrying developing embryos (Figure 5). Litter size increased with maternal length. In the present study, the pregnant female with the most embryos had a PCL of 111.5 cm and was the largest individual collected; the smallest litter size was observed in four pregnant females, with a PCL range of 79.5–83.2 cm.

Embryonic growth and the mother's ovarian oocyte development occurred synchronously (Figure 6), indicating that once females experience pregnancy they may be pregnant continuously. In the two regressions between maternal length and litter size for pregnant

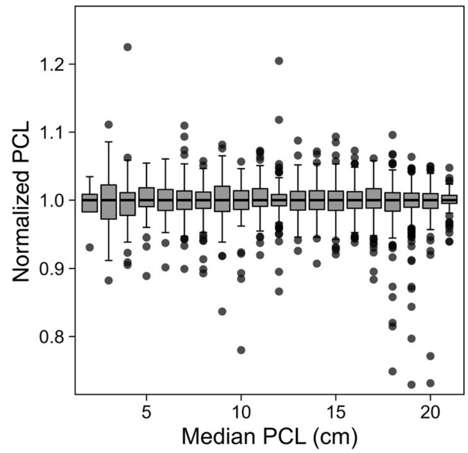

FIGURE 8 Box and whisker plots for embryonic development of Pacific spiny dogfish *Squalus suckleyi* embryos within pregnant females. Precaudal length (PCL) of embryos was normalized so that 1 is the median value for embryos in the same pregnancy. Each plot was created with 1-cm length intervals based on median PCL for embryos in the same pregnancy. The horizontal black bar in the box indicates the median value and the bottom and top of the box indicate the 25th and 75th percentiles, respectively. Whiskers extend to minimum and maximum values within 1.5 times the length of the box; dark-grey solid circles represent outliers

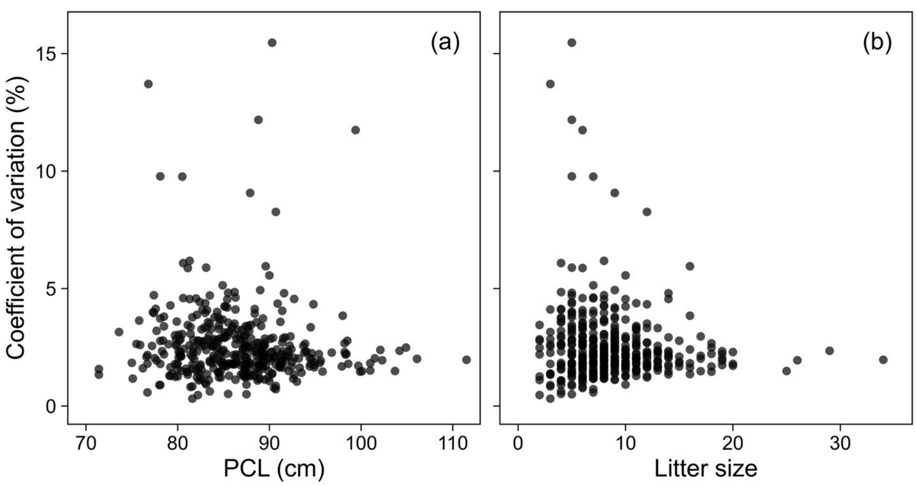

FIGURE 7 Relationship between coefficients of variation for precaudal length (PCL) of retained embryos of Pacific spiny dogfish *Squalus suckleyi* in a given pregnancy to (a) maternal PCL and (b) litter size

females carrying candle-stage embryos and those carrying developing embryos, the explanatory variable fishing method was dropped from the best model (as with the other models). Significant differences between the two groups were then observed in the slopes (ANCOVA, $F = 4.57$, $P < 0.05$) and intercepts (ANCOVA, $F = 105.92$, $P < 0.001$), and the litter size of pregnant females carrying candle-stage embryos was larger than that of pregnant females carrying developing embryos (Figure 5). These results indicate that regardless of the body length of the female, a certain number of embryos will flow from the cloaca of females carrying developing embryos, with pup abortion more prevalent in larger females. The linear regression for litter size in pregnant females carrying candle-stage embryos was:

$$\text{litter size} = 0.57 \times \text{PCL} - 37.00$$

and for pregnant females carrying developing embryos was:

$$\text{litter size} = 0.45 \times \text{PCL} - 30.39$$

where the r^2 is 0.64 for females carrying candle-stage embryos and 0.41 for females carrying developing embryos.

TABLE 2 Results of the general linear model analysis for embryonic development in Pacific spiny dogfish *Squalus suckleyi*

Coefficient	Parameter	Standard error	*P* value
Intercept	12.89	0.82	<0.001
Maternal precaudal length	0.08	0.01	<0.001
Litter size	−0.01	0.01	0.53
Second quarter	−2.49	0.32	<0.001
Third quarter	−1.78	0.14	<0.001
Fourth quarter	−0.90	0.11	<0.001

Relatively high CV values of >8% were observed for the PCL of embryos in individual pregnant females (Figure 7). While these high values exhibited no clear relationship with maternal length (Figure 7a), they tended to be higher with decreasing litter size (Figure 7b); however, there were few such pregnant females. Regardless of the stage of embryonic growth, individuals with good growth and individuals with poor growth were observed, although there was a clear trend toward poorer growth (Figure 8). The proportion of good or poorly growing embryos out of all embryos was 5.1% and the growth of such embryos was 1.23 at best and 0.73 at worst to achieve a median of 1. Although the embryo body length and the PCL or litter size of the pregnant female carrying them displayed an unclear relationship ($r^2 = 0.26$), embryonic growth was significantly better in larger pregnant females whereas litter size had no effect on embryonic growth (Table 2).

4 | DISCUSSION

4.1 | Data collection and influence of fishing method on reproductive parameters

Understanding the reproduction of elasmobranchs is an integral part of successful management because stock or population assessments require accurate data on maturity and reproductive potential (Walker, 1998). It is therefore necessary to collect a set of samples with a wide range of body lengths to obtain relevant biological parameters. In addition, the sample set should include fish caught by various fishing methods and throughout the year to ensure the assessment accuracy. This is because data limited to certain seasons or fishing methods may weaken the representativeness of the biological

TABLE 3 Comparison of the results for precaudal length (PCL) and age at maturity or maternity for Pacific spiny dogfish *Squalus suckleyi* in the present study versus previous studies

	PCL (cm)		Age (years)		Maternity		
Region	Males	Females	Males	Females	PCL (cm)	Age (years)	Source
Tsugaru Strait	**60.6** (60.0–61.2)	**73.1** (72.4–73.7)	**9.4** (9.2–9.6)	**17.8** (17.5–18.0)	**77.4** (76.5–78.3)	**19.7** (19.3–20.1)	Present study
Sea of Japan	56.0–60.0	72.7–76.8					Yamamoto and Kibesaki (1950)
Strait of Georgia		75.6					Ketchen (1972)
Strait of Georgia		**75.9** (75.5–76.3)		**35.5** (35.0–35.9)			Saunders and McFarlane (1993)
Puget Sound		**76.0** for the 1940s **71.2** for the 2000s		**43.3** for the 1940s **31.5** for the 2000s			Taylor and Gallucci (2009)
Puget Sound	**53.2** (52.8–53.8)	**72.6** (71.9–72.7)					Tribuzio *et al.* (2009)
Gulf of Alaska	**59.6** (58.5–60.4)	**78.7** (77.6–79.6)	**20.9** (19.9–22.0)	**36.1** (34.0–38.9)	**80.5** (80.0–81.1)		Tribuzio and Kruse (2012)

Note: Bold font indicates values at 50% maturity or maternity; values in parentheses are the 95% CIs.

characteristics of the study species, ultimately leading to assessment failures. The previously reported maximum body length of Pacific spiny dogfish in the western North Pacific, as converted from TL measurements and binned in 10-cm length intervals, was 80.4–88.5 cm PCL and 105.8–113.0 cm PCL for males and females, respectively (Yamamoto & Kibesaki, 1950). The largest male (79.5 cm PCL) in our study was close to the maximum length previously reported; the largest female was within the range of the maximum PCL interval previously reported. Overall, our specimens that were collected year-round covered a wide size range of immature to mature individuals (Figure 2).

The criteria used to determine maturation were almost the same between our study in the western North Pacific and previous studies conducted in the eastern North Pacific (*i.e.*, Ketchen, 1972; Saunders & McFarlane, 1993; Taylor & Gallucci, 2009; Tribuzio *et al.*, 2009; Tribuzio & Kruse, 2012), but our methods of assessing both sexes differed slightly from those used in an earlier study in Japan (*i.e.*, Yamamoto & Kibesaki, 1950). In the latter study, male maturation was determined based on drastically elongated claspers without information on whether they were uncalcified or calcified; the criteria for female maturation were based on uterus condition and OD in the ovaries, and the OGW was not considered (Yamamoto & Kibesaki, 1950).

Analyses of multiple fishery data using sexual maturity, maternity, and fecundity models showed that capture by different fishing method did not significantly correlate with sexual maturity and maternity rates or litter size depending on body length among the captured sharks (Table 1). This result indicated that the reproductive parameters could be analysed without considering the effect of the fishing methods used in our study area. Furthermore, because sharks' body size is generally larger than that of bony fishes, data can be efficiently collected using the most convenient fishing methods.

4.2 | Size and age at sexual maturity and maternity

Taylor and Gallucci (2009) stated that the size at sexual maturity of Pacific spiny dogfish in Puget Sound (eastern North Pacific) was possibly density-dependent, based on a decline in abundance caused by the lingering effects of an intense liver fishery in the 1940s. The Pacific spiny dogfish in the present study encountered a similar situation between the 1940s and the 2000s. Nevertheless, our recent estimated length at 50% sexual maturity does not significantly differ from that in 1948–1949 for each sex (Table 3), hence, based on the length at sexual maturity, we found no evidence to suggest that populations of this shark in the western North Pacific have declined compared with those during a period of high demand for this species.

A previous study found that the body lengths of Pacific spiny dogfish at sexual maturity differ geographically, even between closely located habitat areas. This was thought to be caused by very low long-term mixing of the sharks inhabiting each area (Tribuzio & Kruse, 2012). Populations of this species do not carry out large-scale movements or migrations between the western and eastern North Pacific (Yano, Ohshimo, *et al.*, 2017). The significant difference in maturity size between our study area and each region supported the previous findings (Table 3). Around Japan, Pacific spiny dogfish seasonally migrate in the Sea of Japan and areas of the North Pacific near Japan, moving northward in spring/summer and southward in autumn/winter (Tanabe *et al.*, 1958). Thus, geographical differences in size at maturity do not seem to occur, and the results from the present study are considered to be representative of the population.

While the maturity size was similar for each sex among some areas, differences of more than 10 years and around 18 years in age at 50% sexual maturity were observed for males and females, respectively (Table 3). Although the large difference in sexual maturity age between Pacific spiny dogfish in the western and eastern North Pacific is surprising, the regional age differences revealed in the present study are considered probable because reproductive parameters such as size and age at sexual maturity or the number of embryos are variable in Pacific spiny dogfish (Taylor & Gallucci, 2009). Ageing of Pacific spiny dogfish was historically conducted using the spine located anterior to the dorsal fin, but the spine is subject to wear and breakage (Tribuzio *et al.*, 2017), therefore several approaches were proposed to estimate the number of band pairs lost because of spine erosion. However, these approaches and a new method involving stained thin sections of vertebral centra were also problematic (Taylor *et al.*, 2013; Tribuzio *et al.*, 2017). Age information can be a vital parameter in stock or population assessments, thus, although bolstered by our results, any conclusions should bear in mind the difficulty and potential errors of age determination for Pacific spiny dogfish.

The difference in values between 50% maturity and corresponding 50% maternity was 4.3 cm for length and 1.9 years for age (Table 3). The length values represent the approximate amount of growth that females undergo from the time at first maturity to being in a maternal condition, which fits well with the timing of the biennial reproductive cycle. Thus, our results may support the validity of the parameters of the von Bertalanffy growth equation, as provided by Orlov *et al.* (2011), although various problems remain in age estimation for Pacific spiny dogfish. For future stock or population assessments, it is important to acknowledge the time-lag between maturity and when actual reproduction occurs because a major bias will be generated if the number of births is overestimated (Walker, 2005). Based on the length at 50% maternity in the western North Pacific, half of the females with ~77 cm PCL were reproductively well advanced. Minmaya is a main landing port for Pacific spiny dogfish catches in Japan, and mostly female sharks are caught at the fishing grounds in the Tsugaru Strait (Figure 1); most annual catches at Minmaya comprised sharks of 65–85 cm PCL and the mean PCL of the landings was ~77 cm (Yano, Hattori, *et al.*, 2017). Thus, roughly half of the individuals will have given birth at least once before capture, and larger individuals will contribute more to sustainability of the stock because litter size increases with maternal length (Figure 5).

4.3 | Fecundity and embryonic development

The fecundity of Pacific spiny dogfish is considered to be higher in the western North Pacific than in other regions. A small percentage of mature females in the resting period was observed in the Gulf of Alaska (Tribuzio & Kruse, 2012). In contrast, our data indicate that, in the western North Pacific, embryonic growth and ovarian oocyte development occurred synchronously across all pregnant females (Figure 6), thus a resting period was not observed. In addition, pregnant females carrying developing embryos produced 0.45 more embryos per centimetre of PCL after the onset of maturity (Figure 5), which is higher than estimates of 0.24–0.30 embryos per centimetre in the eastern North Pacific (Ketchen, 1972; Taylor & Gallucci, 2009; Tribuzio *et al*., 2009; Tribuzio & Kruse, 2012), as calculated using the TL to PCL conversion equation used in the present study.

In the future, the high fecundity obtained in the present study should be verified and compared with more appropriate data from each region because some embryos will have aborted by the time developing embryos in pregnant females can be counted (Tribuzio & Kruse, 2012). We observed this in the present study, based on the ANCOVA for the general linear model of fecundity on maternal PCL, and we found that pup abortion was more frequent in larger pregnant females (Figure 5). While there is no concern about embryo outflow from the uterus during counting embryos in pregnant females carrying candle-stage embryos, freezing the samples will cause the candles to deteriorate and become fragile. In such cases, counting is not appropriate. Fertilized eggs or embryos within the candle should be counted in fresh fish. Nonetheless, these counts are thought to be the most appropriate method for determining litter size in Pacific spiny dogfish.

The pregnant female produces larger embryos as she grows and this characteristic was not affected by litter size (Table 2). The results show that embryo development is enhanced in larger pregnant females, which likely reflects the fact that growing maternal bodies require more energy. Additionally, a smaller number of good or poorly growing embryos were observed in small litter sizes, regardless of the maternal body length (Figures 7 and 8). There was an extremely low number of such embryos present in the same pregnancy, suggesting that the mother's nutritional intake may have a limited effect on specific embryos within the same pregnant female. In Pacific spiny dogfish, it takes approximately 2 years for ovarian oocytes to mature and become ready to form the next embryos (Figure 6; Ketchen, 1972). The embryos are mostly nourished by yolk sac reserves (Jones & Geen, 1977), as revealed in other *Squalus* species (Braccini *et al*., 2007). It remains to be clarified how nutrients accumulate for the ovarian oocytes and how this affects egg quality. Pacific spiny dogfish seem to require small or few, albeit nutritious, prey items because they need to maintain a large space in the abdominal cavity for more embryos. The feeding habits of this species differ between the eastern and western North Pacific (Yano, Ohshimo, *et al*., 2017), which may also help to explain the relatively early age of sexual maturity in both sexes in the present study.

The natural mortality rate generally decreases with growth, yet the fishing mortality rate increases for commercially exploited fishes. In addition, most fisheries target large individuals and excessive exploitation is biased toward large individuals. Thus, fishery captures diminish the productivity of populations because the reproductive potential becomes higher with larger and older individuals, as shown in bony fishes (Katsukawa & Watanabe, 2010). Pacific spiny dogfish females tend to be larger than males, and this size difference causes differential exploitation of the sexes, coupled with market demand (Dell'Apa *et al*., 2015). The fecundity of sharks is extremely low compared with that of bony fishes, thus the maternal investment is considered to have a small effect on the population dynamics. Even though fisheries target larger individuals because of their higher commercial value (Yano, Hattori, *et al*., 2017) and fishing pressure may be applied continuously for a long time (Yano *et al*., 2022), sustainable stock utilization should not ignore the maternal effect.

5 | CONCLUSIONS

The reproductive characteristics of Pacific spiny dogfish, as elucidated here, may explain why the landing amounts in Japan have remained stable over a long period (Yano *et al*., 2022). The reproductive potential of Pacific spiny dogfish appears to be higher in the western North Pacific than in other regions. The sexual maturity size of males hardly differs among areas, but the age to reach that size is younger in the western North Pacific than in other areas (Table 3). Females exhibit a smaller size and earlier age at sexual maturation, with no apparent resting phase. In addition, the pregnant female produces more embryos than in the eastern North Pacific as she grows, and such embryo development largely does not decrease in relation to increasing maternal body length or litter size. We sought to elucidate the reproductive characteristics of Pacific spiny dogfish in the western North Pacific by collecting a wide range of specimens, from small to large body lengths, captured by several fishing methods and across seasons. However, the data were not suitable for some analyses, such as calculating the average number of embryos, which can be pointless unless there is reasonable assurance that the average length of pregnant females in the samples is close to the average for the pregnant population overall. Future research to obtain quantitative estimates of this reproductive parameter will contribute to more-effective stock assessments and appropriate management for sustainable stock utilization.

AUTHOR CONTRIBUTIONS

T.Y. conceived the research idea, and conducted field and laboratory work together with T.H. Y.N. and J.N., and processed and analysed the data. T.H. and Y.N. obtained funding. S.T. contributed to the research idea and data analysis. T.Y. wrote the manuscript with input from all co-authors.

ACKNOWLEDGEMENTS

We thank Mr Tsuneshiro Tamukai of Tamukai Syoten Ltd, who kindly cooperated with collecting sharks. We acknowledge Ms Minami Sato of the Japan Fisheries Research and Education Agency for help with measuring the Pacific spiny dogfish. We are grateful to Dr Cynthia Kulongowski and Dr Jennifer Smith from Edanz Inc. for professional

English editing. We also appreciate the helpful comments from two referees. The present study was conducted as a part of the research and assessment program for internationally managed fisheries resources, Fisheries Agency of Japan.

FUNDING INFORMATION

This study was funded by the Fisheries Agency of Japan, but the views expressed here do not necessarily reflect those of the funding agency.

ORCID

Toshikazu Yano https://orcid.org/0000-0002-5866-7444

REFERENCES

Baba, O., Taniuchi, T., & Nose, Y. (1987). Depth distribution and food habits of three species of small squaloid sharks off Choshi. *Nippon Suisan Gakkaishi*, *53*, 417–424 (in Japanese with English abstract).

Baremore, I. E., & Passerotti, M. S. (2013). Reproduction of the blacktip shark in the Gulf of Mexico. *Marine and Coastal Fisheries*, *5*, 127–138.

Bartoń, K. (2020). Package "MuMIn": multi-model inference. Available at https://CRAN.R-project.org/package=MuMIn (last accessed 14 September 2022).

Baum, J. K., & Worm, B. (2009). Cascading top-down effects of changing oceanic predator abundances. *Journal of Animal Ecology*, *78*, 699–714.

Bigman, J. S., Ebert, D. A., & Goldman, K. J. (2016). *Squalus suckleyi*. The IUCN Red List of Threatened Species 2016: e.T195488A2382480. Available at https://doi.org/10.2305/IUCN.UK.2016-1.RLTS.T195488A2382480.en (last accessed 14 September 2022).

Braccini, J. M., Hamlett, W. C., Gillanders, B. M., & Walker, T. I. (2007). Embryo development and maternal–embryo nutritional relationships of piked spurdog (*Squalusmegalops*). *Marine Biology*, *150*, 727–737.

Conrath, C. L., & Musick, J. A. (2012). Reproductive biology of elasmobranchs. In J. C. Carrier, J. A. Musick, & M. R. Heithaus (Eds.), *Biology of sharks and their relatives* (2nd ed., pp. 291–311). Boca Raton: CRC Press.

Dell'Apa, A., Bangley, C. W., & Rulifson, R. A. (2015). Who let the dogfish out? A review of management and socio-economic aspects of spiny dogfish fisheries. *Reviews in Fish Biology and Fisheries*, *25*, 273–295.

Ebert, D. A., White, W. T., Goldman, K. J., Compagno, L. J. V., Daly-Engel, T. S., & Ward, R. D. (2010). Resurrection and redescription of *Squalus suckleyi* (Girard, 1854) from the North Pacific, with comments on the *Squalus acanthias* subgroup (Squaliformes: Squalidae). *Zootaxa*, *2612*, 22–40.

Fox, J., Weisberg, S., Price, B., Adler, D., Bates, D., Baud-Bovy, G., … R-Core. (2021). Package "car": companion to applied regression. Available at https://CRAN.R-project.org/package=car (last accessed 14 September 2022).

Harvey, C. J., Williams, G. D., & Levin, P. S. (2012). Food web structure and trophic control in Central Puget Sound. *Estuaries and Coasts*, *35*, 821–838.

Hoenig, J. M., & Gruber, S. H. (1990). Life-history patterns in the elasmobranchs: Implications for fisheries management. In H. L. Pratt, Jr., S. H. Gruber, & T. Taniuchi (Eds.), *NOAA technical report NMFS* (pp. 1–16). Silver Spring, MD: US Department of Commerce, National Oceanic and Atmospheric Administration.

Holden, M. J. (1974). Problems in the rational exploitation of elasmobranch populations and some suggested solutions. In F. R. Harden-Jones (Ed.), *Sea fisheries research* (pp. 117–137). London: Paul Elek.

Jones, B. C., & Geen, G. H. (1977). Reproduction and embryonic development of spiny dogfish (*Squalus acanthias*) in the strait of Georgia, British Columbia. *Journal of the Fisheries Research Board of Canada*, *34*, 1286–1292.

Katsukawa, Y., & Watanabe, Y. (2010). Fisheries-induced life history evolution. *Bulletin of the Japanese Society of Fisheries Oceanography*, *74*, 84–89 (in Japanese with English abstract).

Ketchen, K. S. (1972). Size at maturity, fecundity, and embryonic growth of the spiny dogfish (*Squalus acanthias*) in British Columbia waters. *Journal of the Fisheries Research Board of Canada*, *29*, 1717–1723.

Kurita, Y. (2010). Influence of spatio-temporal changes in stock reproductive potential on the recruitment levels of fish. *Bulletin of the Japanese Society of Fisheries Oceanography*, *74*, 4–18 (in Japanese with English abstract).

McFarlane, G. A., & Beamish, R. J. (1987). Validation of the dorsal spine method of age determination for spiny dogfish. In R. C. Summerfelt & G. E. Hall (Eds.), *Age and growth of fish* (pp. 287–300). Ames, IA: Iowa State University Press.

Myers, R. A., Baum, J. K., Shepherd, T. D., Powers, S. P., & Peterson, C. H. (2007). Cascading effects of the loss of apex predatory sharks from a coastal ocean. *Science*, *315*, 1846–1850.

Orlov, A. M., Kulish, E. F., Mukhametov, I. N., & Shubin, O. A. (2011). Age and growth of spiny dogfish *Squalus acanthias* (Squalidae, Chondrichthyes) in Pacific waters off the Kuril Islands. *Journal of Ichthyology*, *51*, 42–55.

R Core Team. (2021). R: A language and environment for statistical computing. Vienna: R Foundation for Statistical Computing Available at https://www.R-project.org/ (last accessed 14 September 2022).

Saunders, M. W., & McFarlane, G. A. (1993). Age and length at maturity of the female spiny dogfish, *Squalus acanthias*, in the strait of Georgia, British Columbia, Canada. *Environmental Biology of Fishes*, *38*, 49–57.

Smith, S. E., Au, D. W., & Show, C. (1998). Intrinsic rebound potentials of 26 species of Pacific sharks. *Marine and Freshwater Research*, *49*, 663–678.

Sosebee, K. A. (2005). Are density-dependent effects on elasmobranch maturity possible? *Journal of Northwest Atlantic Fishery Science*, *35*, 115–124.

Szöcs, E., & Schäfer, R. B. (2015). Ecotoxicology is not normal: A comparison of statistical approaches for analysis of count and proportion data in ecotoxicology. *Environmental Science and Pollution Research*, *22*, 13990–13999.

Tanabe, M., Fukuhara, A., Kanno, Y., Ukawa, M., Yusa, T., Kojima, I., & Nagamine, Y. (1958). *North Pacific spiny dogfish. Tsushima Danryu Kaihatsu Chosa Hokokusho*. Tokyo: Fisheries Agency of Japan (in Japanese).

Tanaka, S., Shiobara, Y., Hioki, S., Abe, H., Nishi, G., Yano, K., & Suzuki, K. (1990). The reproductive biology of the frilled shark, *Chlamydoselachus anguineus*, from Suruga bay, Japan. *Japanese Journal of Ichthyology*, *37*, 273–291.

Taniuchi, T. (1990). The role of elasmobranch research in Japanese fisheries. In H. L. Pratt, Jr., S. H. Gruber, & T. Taniuchi (Eds.), *NOAA technical report NMFS* (pp. 415–426). Silver Spring, MD: U.S. Department of Commerce, National Oceanographic and Atmospheric Administration.

Taylor, I. G., & Gallucci, V. F. (2009). Unconfounding the effects of climate and density dependence using 60 years of data on spiny dogfish (*Squalus acanthias*). *Canadian Journal of Fisheries and Aquatic Sciences*, *66*, 351–366.

Taylor, I. G., Gertseva, V., & Matson, S. E. (2013). Spine-based ageing methods in the spiny dogfish shark, *Squalus suckleyi*: How they measure up. *Fisheries Research*, *147*, 83–92.

Tohoku National Fisheries Research Institute, Fisheries Agency of Japan. (1993). *Report of biological research for elasmobranch species in the western Pacific*. Miyagi: Tohoku National Fisheries Research Institute, Fisheries Agency of Japan (in Japanese).

Tribuzio, C. A., Gallucci, V. F., & Bargmann, G. G. (2009). Reproductive biology and management implications for spiny dogfish in Puget Sound, Washington. In V. F. Gallucci, G. A. McFarlane, & G. G. Bargmann (Eds.), *Biology and management of dogfish sharks* (pp. 181–194). Bethesda, MD: American Fisheries Society.

Tribuzio, C. A., & Kruse, G. H. (2012). Life history characteristics of a lightly exploited stock of *Squalus suckleyi*. *Journal of Fish Biology*, *80*, 1159–1180.

Tribuzio, C. A., Matta, M. E., Gburski, C., Atkins, N., & Bubley, W. (2016). Methods for the preparation of Pacific spiny dogfish, *Squalus suckleyi*, fin spines and vertebrae and an overview of age determination. *Marine Fisheries Review*, *78*, 1–13.

Tribuzio, C. A., Matta, M. E., Gburski, C., Blood, C., Bubley, W., & Kruse, G. H. (2017). Are Pacific spiny dogfish lying about their age? A comparison of ageing structures for *Squalus suckleyi*. *Marine and Freshwater Research*, *69*, 37–47.

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

Walker, T. I. (2005). Reproduction in fisheries science. In W. C. Hamlett (Ed.), *Reproductive biology and phylogeny of chondrichthyes: Sharks, batoids and chimaeras* (pp. 81–127). Enfield, NH: Science Publishers Inc.

Worm, B., Davis, B., Kettemer, L., Ward-Paige, C. A., Chapman, D., Heithaus, M. R., … Gruber, S. H. (2013). Global catches, exploitation rates, and rebuilding options for sharks. *Marine Policy*, *40*, 194–204.

Yamamoto, T., & Kibesaki, O. (1950). Studies on the spiny dog fish *Squalus suckleyi*. (I) on the development and maturity of the genital glands with growth. *Nippon Suisan Gakkaishi*, *15*, 531–538 (in Japanese with English abstract).

Yano, T., Hattori, T., Shibata, Y., & Tanaka, S. (2022). Over 120 years of landing trends in Japan, for the commercially exploited shark species, *Squalus Suckleyi*. *Fisheries Research*, *249*, 106257.

Yano, T., Hattori, T., Tamukai, T., & Ohshimo, S. (2017). Body-length frequency and spatial segregation of the North Pacific spiny dogfish *Squalus suckleyi* in Tsugaru Strait, northern Japan. *Fisheries Science*, *83*, 917–928.

Yano, T., Ohshimo, S., Kanaiwa, M., Hattori, T., Fukuwaka, M., Nagasawa, T., & Tanaka, S. (2017). Spatial distribution analysis of the North Pacific spiny dogfish, *Squalus suckleyi*, in the North Pacific using generalized additive models. *Fisheries Oceanography*, *26*, 668–679.

Yano, T., Ohshimo, S., Sakai, T., & Yoda, M. (2020). Filling gaps in the biology and habitat use of two spurdog sharks (*Squalus japonicus* and *Squalus brevirostris*) in the East China Sea. *Marine and Freshwater Research*, *71*, 1719–1731.

Yonezaki, S., Kiyota, M., Narimatsu, Y., Hattori, T., & Ito, M. (2016). Quantification of the demersal marine ecosystem structure in the northern district of the Tohoku Sea area, northeastern Japan based on Ecopath approach. *Bulletin of the Japanese Society of Fisheries Oceanography*, *80*, 1–19 (in Japanese with English abstract).

How to cite this article: Yano, T., Hattori, T., Narimatsu, Y., Nagao, J., & Tanaka, S. (2023). High reproductive potential of the commercially exploited shark *Squalus suckleyi* in the major fishing grounds of the western North Pacific. *Journal of Fish Biology*, *103*(2), 260–271. https://doi.org/10.1111/jfb.15430