Factors affecting gestation periods in elasmobranch fishes

Soma Tokunaga[1,2,*], Yuuki Y. Watanabe[2,3], Mai Kawano[4,5] and Yuuki Kawabata[6]

ABSTRACT

Gestation periods vary greatly across elasmobranch species. Differences in body size and body temperature (i.e. major determinants of metabolic rates) might explain such variation. Although temperature effects have been demonstrated for captive animals, body size effects remain undocumented. Moreover, whether metabolic rates of mothers or those of embryos affect gestation periods remains unclear. Because biological times generally scale with mass$^{1-\beta}$, where β is metabolic scaling exponent (0.8–0.9 in fishes), we hypothesized that elasmobranch gestation periods would scale with mass$^{0.1-0.2}$. We also hypothesized that regionally endothermic species with elevated metabolic rates should have shorter gestation periods than similar-sized ectothermic species if the metabolic rates of mothers are responsible. We compiled data on gestation periods for 36 elasmobranch species to show that gestation periods scale with $M^{0.11}$ and $m^{0.17}$, where M and m are adult female mass and birth mass, respectively. Litter size and body temperature also affected gestation periods. Our findings suggest that the body-mass dependence of metabolic rate explains some variations in elasmobranch gestation periods. Unexpectedly, regionally endothermic sharks did not have shorter gestation periods than their ectothermic counterparts, suggesting that the metabolic rates of embryos, which are likely ectothermic in all elasmobranch species, may be responsible.

This article has an associated First Person interview with the first author of the paper.

KEY WORDS: Endothermy, Metabolism, Phylogenetic analysis, Scaling, Viviparity

INTRODUCTION

Gestation periods, or the duration of pregnancies, are a crucial feature of animals' reproductive strategies and affect population dynamics. Viviparous (i.e. producing living young) species are found in all major vertebrate groups except for birds (Rothchild, 2003). Species-specific gestation periods and factors affecting them have long been studied primarily in mammals (Martin and MacLarnon, 1985;

[1]Faculty of Fisheries, Nagasaki University, Bunkyo, Nagasaki 852-8521, Japan. [2]Department of Polar Science, The Graduate University for Advanced Studies, SOKENDAI, Tachikawa, Tokyo 190-8518, Japan. [3]National Institute of Polar Research, Tachikawa, Tokyo 190-8518, Japan. [4]Faculty of Agriculture, Kyushu University, Nishi-ku, Fukuoka 819-0395, Japan. [5]Atmosphere and Ocean Research Institute, The University of Tokyo, Kashiwa, Chiba 277-8564, Japan. [6]Graduate School of Fisheries and Environmental Sciences, Nagasaki University, Bunkyo, Nagasaki 852-8521, Japan.

*Author for correspondence (tokunaga.soma@nipr.ac.jp)

S.T., 0000-0001-8298-3861; Y.Y.W., 0000-0001-9731-1769; Y.K., 0000-0001-8267-5199

Martin, 1996; Sacher and Staffeldt, 1974; Weisbecker and Goswami, 2010). Elasmobranch is another taxonomic group that has many viviparous species. Their gestation periods vary among species from a few months to years (Furumitsu et al., 2019; Hanchet, 1988). However, factors causing this variation are poorly understood. Each species is thought to have evolved specific gestation periods, so that fitness could be maximized under given ecological, physiological, and environmental constraints. Therefore, clarifying factors affecting elasmobranch gestation periods helps better understand the reproductive strategies, population dynamics, and evolutionary history of this group of animals.

Warm waters have been shown to facilitate embryonic growth and shorten gestation periods in elasmobranchs. Dogfish *Scyliorhinus canicula* exhibit twice higher embryonic growth rates when kept in waters that are 4°C warmer (Harris, 1952). Eagle rays *Aetobatus narinari* have a 180–188 day gestation period at 28.1–30.1°C water temperature, and this period increases to 328–399 days in cooler waters (23.5–24.5°C) (Swider et al., 2017). Moreover, many elasmobranch females seasonally migrate to warmer waters, presumably to facilitate embryo growth and shorten gestation periods (Bernal et al., 2012; Hight and Lowe, 2007; Jirik and Lowe, 2012). These temperature effects suggest that metabolic rate, the rate at which organisms produce energy, affects embryo growth rates and thus gestation periods. In addition to body temperature, metabolic rates are a function of body mass (Peters, 1983); however, the effects of body mass on elasmobranch gestation periods have never been investigated. Metabolic rate Y is proportional to mass$^{\beta}$, where β is a metabolic scaling exponent (Peters, 1983). In general, biological times (e.g. life span and population doubling time) are proportional to mass$^{1-\beta}$ (Lindstedt and Calder, 1981; Peters, 1983). Because β is approximately 0.8–0.9 in fishes (Clarke and Johnston, 1999; White et al., 2006), including sharks (0.84; Ste-Marie et al., 2020), we would predict that gestation periods of elasmobranchs scale with mass$^{0.1-0.2}$.

Given that metabolic rates affect gestation periods in elasmobranchs, a question arises: are metabolic rates of mothers or those of their embryos more important? If gestation period t is largely determined by the mother's biomass production rate or metabolic rate, t would be expressed as $t \propto M^{0.1-0.2}$, where M is mother's body mass. In a different scenario, consider that embryo growth rates are affected by the embryos' own metabolic rates, given that they receive sufficient nutrition and oxygen from their mother. In this case, the ontogenetic growth model would apply, where gestation period t is expressed by birth mass m as $t \propto m^{1-\beta}$ (Moses et al., 2008; West et al., 2001), that is, $t \propto m^{0.1-0.2}$ in elasmobranchs. Therefore, we would predict that elasmobranch gestation periods scale with $M^{0.1-0.2}$ or $m^{0.1-0.2}$, depending on whether the metabolic rates of mothers or embryos play a more important role.

Another important factor to consider is thermal physiology. Most elasmobranch species are ectotherms, with their body temperature being close to the ambient water temperature. Yet, regionally endothermic species (e.g. white sharks) maintain elevated body temperature by using the heat produced by continuous swimming activities (Bernal et al., 2012; Lowe and Goldman, 2001). They

have higher metabolic rates than similar-sized ectothermic species, even with the difference in body temperature taken into account (Carlson et al., 2004). On the other hand, their embryos are unlikely to have elevated metabolic rates, given that embryos cannot produce heat by continuous swimming activities. Therefore, if metabolic rates of mothers, rather than embryos, affect gestation periods, regionally endothermic species should have shorter gestation periods than ectothermic species for a given mass and body temperature. Furthermore, litter size (i.e. the number of offspring produced at one parturition) varies among species from a few to hundreds in elasmobranchs (Cortés, 2000; Joung et al., 1996; Nielsen et al., 2020). This variation may affect maternal investments per embryo and thus gestation periods.

In this study, we compiled data on elasmobranch gestation period from the literature and examined how the variations in gestation periods can be explained. Specifically, we examined (1) whether gestation period scales with $M^{0.1–0.2}$ or $m^{0.1–0.2}$ and (2) whether the regionally endothermic sharks have shorter gestation periods than ectothermic species for a given mass and body temperature.

RESULTS

We compiled data on gestation periods for 36 elasmobranch species, spanning from 0.37–1159 kg in adult female mass, including four regionally endothermic species (Table1). Fig. 1 shows a phylogenetic tree used for our phylogenetically-informed analyses (see Materials and Methods). Gestation periods t ranged from 1.5 to 24 months (Table 1) and increased with adult female mass M as $t=6.8×M^{0.11}$ (Fig. 2A) and birth mass m as $t=10.5×m^{0.17}$ (Fig. 2B). The scaling exponents fell within the predicted range (0.1–0.2) both for M (0.11; 95% confidence interval 0.01–0.21) and m (0.17; 95% confidence interval 0.07–0.28).

When M, m, and whether the species has regional endothermy were inputted as predictor variables, the best model included m rather than M. The effect of regional endothermy was not included in the best model. When litter size L was added as a predictor variable, the best model included M and L as $t=10.6×M^{0.16}×L^{−0.32}$ (Table 2). The partial regression coefficient for L was negative (−0.32), meaning that gestation periods decrease as litter size increases. Birth mass increased with adult female mass as $m=0.064×M^{0.68}$ ($R^2=0.60$) (Fig. 3A). Residuals of this relationship [i.e. $\log_{10}$ (observed m)– $\log_{10}$ (predicted m)] were negatively associated with $\log_{10}$ (L) as: Residual=$−0.86×\log_{10}$ (L)+0.69 (R^2=0.60) (Fig. 3B).

We compiled data on body temperature T (i.e. preferred water temperature for ectothermic species and reported body temperature for regionally endothermic species) for 34 out of 36 species (Table 1). Gestation periods were best explained by M, L, and T as $t=26.9×M^{0.16}×L^{−0.33}×10^{−0.017T}$ (Table 2). The partial regression coefficient for T was negative (−0.017; 95% confidence interval −0.004 – −0.029), indicating that gestation period decreases as body temperature increases.

DISCUSSION

Consistent with our hypothesis, elasmobranch gestation periods scaled with mass$^{0.1–0.2}$, suggesting that body mass (adult female mass and birth mass) affects gestation periods through its effects on metabolic rates. Large variations around the regression lines are partly explained by the variations in litter size and body temperature, as shown in our analyses. Furthermore, viviparous elasmobranchs exhibit various reproductive modes (e.g. ovoviviparous, placental viviparous), which may also influence gestation periods. Depending on the mode, embryos receive nutrition from their mother in different forms, such as yolk-sacs, placental transfer, uterine

secretions, ova, or siblings (Hamlett et al., 2005; Parsons et al., 2008). However, reproductive modes are still uncertain for many species, and some rely on a combination of multiple nutrient sources (Cotton et al., 2015; Sato et al., 2016). These complexities precluded us from modeling the effect of different reproductive modes in this study. Nevertheless, we found a robust result that elasmobranch gestation periods scaled with mass$^{0.1–0.2}$.

Gestation periods decreased as body temperature increased among different elasmobranch species. This result is consistent with previous studies that examined the effect of water temperature on gestation period with captive individuals (Harris, 1952; Swider et al., 2017). The 95% confidence interval for the regression coefficient (i.e. −0.004 – −0.029) indicates that a 10°C decrease in body temperature is associated with 1.1–1.9-times longer gestation periods within the temperature range covered by our dataset (9.9–28.3°C; Table 1). This value is lower than the temperature dependence of metabolic rate in elasmobranch with an interspecific Q_{10} of 2.23 (95% confidence interval 1.74–2.85; Ste-Marie et al., 2020), possibly due to errors in our body temperature estimates (discussed below).

Unexpectedly, regionally endothermic sharks did not have shorter gestation periods than their ectothermic counterparts. Regionally endothermic sharks have higher metabolic rates than ectothermic sharks for a given mass and body temperature (Carlson et al., 2004), allowing them to cruise at faster speeds and migrate longer distances (Watanabe et al., 2015). By contrast, their embryos are likely ectothermic without elevated metabolic rates because embryos cannot produce metabolic heat by continuous swimming activities. Thus, our results suggest that metabolic rates of embryos may have stronger effects on gestation periods than those of mothers. Yet, we need to be cautious, because direct measurements of embryo body temperature or metabolic rates are currently lacking. The possibility that even embryos have elevated metabolic rates (via maternal investment or innately) cannot be ruled out.

The best model included adult female mass, rather than birth mass when litter size was added as a predictor variable (Table 2). The negative regression coefficient indicates that gestation periods decrease as litter size increases. This finding can be explained by our observation that larger litter size is associated with smaller birth mass relative to adult mass (Fig. 3). An ontogenetic growth model (Moses et al., 2008; West et al., 2001) predicts that smaller relative birth mass leads to shorter gestation periods unless $M \gg m$ (for details, see Moses et al., 2008). Our results provide support for this prediction. The ontogenetic growth model assumes that embryo growth rates are not limited by maternal investment. Therefore, our analyses of litter size further suggest that the metabolic rates of embryos, rather than those of their mothers, may affect elasmobranch gestation periods.

We acknowledge several limitations of this study. First, we were unable to directly compare gestation periods with metabolic rate due to the sparseness of metabolic rate data in elasmobranch. Second, although we considered that metabolic rate affects growth rate, causality may be the reverse, or body mass and body temperature may influence growth rate independently of metabolic rate (Glazier, 2015). Third, the metabolic scaling exponent β may vary between 0.67 and 1 depending on ecological lifestyle and activity level of organisms (Glazier, 2010). Fourth, our estimate of body temperature for each species (see Materials and Methods) may be inaccurate. For example, because sexual segregation is common in elasmobranch (Wearmouth and Sims, 2008), preferred water temperature for pregnant females may be different from that reported for the species in general. Therefore, further research is needed to better understand

Table 1. Gestation period and other information for elasmobranchs

Order	Species	Gestation period (month)	Adult mass (kg)	Birth mass (kg)	Mean litter size	Regional endo-thermy	Body temp. (°C)	Reference
Squatiniformes	African angel shark *Squatina africana*	12	4.7	0.21	6	No	18.2	Shelmerdine and Cliff (2006)
	Pacific angel shark *Squatina californica*	10	7.4[b]	0.14[b]	6	No	21	Natanson and Cailliet (1986)
	Atlantic angel shark *Squatina dumeril*	12	5.1	0.16	7.4	No	–	Baremore (2010)
Squaliformes	Spiny dogfish *Squalus acanthias*	24	1.3	0.047	5.2	No	9.9	Avsar (2001); Hanchet (1988)
Orectolobiformes	Nurse shark *Ginglymostoma cirratum*	5–6	65	0.17	34	No	25.5	Castro (2000)
Lamniformes	Pelagic thresher *Alopias pelagicus*	9	50	7.3	2	No	26.7	Romero-Caicedo et al. (2014); Varghese et al. (2015)
	Sand tiger shark *Carcharias taurus*	9–12	58	8.2	2	No	24.6	Gilmore et al. (1983); Goldman et al. (2006); Lucifora et al. (2002)
	Salmon shark *Lamna ditropis*	8–9	107	8.2	3.9	Yes	25	Conrath et al. (2014); Goldman and Musick (2006)
	Porbeagle shark *Lamna nasus*	8–9	63	3.1	3.9	Yes	18.3	Francis (2000); Kohler et al. (1996)
	White shark *Carcharodon carcharias*	20	1159	14	6	Yes	26.3	Christiansen et al. (2014); Francis (1996)
	Shortfin mako shark *Isurus oxyrinchus*	15–18	210	2.4	12.5	Yes	22	Kohler et al. (1996); Mollet et al. (2000)
Carcharhiniformes	Whiskery shark *Furgaleus macki*	7–9	6.5	0.10	19	No	16	Simpfendorfer et al. (2000); Simpfendorfer and Unsworth (1998)
	Japanese topeshark *Hemitriakis japanica*	10	6.4	0.17	14	No	20.2	Chen and Mizue (1973); Kamura et al. (2000)
	Starspotted dogfish *Mustelus manazo*	11–12	1.4	0.035	6	No	23.2	Yamaguchi et al. (1997); Yamaguchi et al. (1998)
	Smoothhound shark *Mustelus mustelus*	10–11	8.3	0.27	11.8	No	15.3	Saïdi et al. (2008)
	Brown smoothhound shark *Mustelus henlei*	10	0.95[b]	0.081[b]	10	No	15.4	Pérez-Jiménez and Sosa-Nishizaki (2008)
	Tiger shark *Galeocerdo cuvier*	15–16	247	1.7	32.6	No	26.4	Kohler et al. (1996); Whitney and Crow (2007)
	Winghead shark *Eusphyra blochii*	10–11	6.8	0.25	11.8	No	28.3	Stevens and Lyle (1989)
	Great hammerhead shark *Sphyrna mokarran*	11	41	0.92	15.4	No	27.2	Stevens and Lyle (1989)
	Bonnethead shark *Sphyrna tiburo*	5	2.9	0.26	17.5	No	25	Parsons (1993); Pulver and Whatley (2016)
	Atlantic sharpnose shark *Rhizoprionodon terraenovae*	11	2.4	0.12	3.9	No	27	Loefer and Sedberry (2003)
	Finetooth shark *Carcharhinus isodon*	12	13	0.75	4	No	27	Castro (1993)
	Sandbar shark *Carcharhinus plumbeus*	12	24	0.73	6.5	No	27	Joung et al. (2004); Mcauley et al. (2007)
	Bull shark *Carcharhinus leucus*	12–14	140	2.2	9.5	No	27.5	Branstetter and Stiles (1987); Pirog et al. (2019)
	Spinner shark *Carcharhinus brevipinna*	10–12	72	1.7	8.5	No	27.4	Joung et al. (2005)
	Dusky shark *Carcharhinus obscurus*	20	117	5.3	7.1	No	12.6	Compagno (1984); Kohler et al. (1996); Romine et al. (2009)
	Blue shark *Prionace glauca*	9–11	28	0.3	33	No	14.8	Carrera-Fernández et al. (2010)
	Blacktip reef shark *Carcharhinus melanopterus*	10–11	8.4	0.58	3.8	No	27.4	Stevens (1984)
	Blacktip shark *Carcharhinus limbatus*	12–13	50	1.4	6	No	27.4	Dudley and Cliff (1993)
Rhinopristiformes	Ringstreaked guitarfish *Rhinobatos hynnicephalus*	3[a]	0.37	0.022	4.4	No	–	Kume et al. (2009)
	Whitesnout guitarfish *Rhinobatos leucorhynchus*	5–6	0.66	0.037	4	No	28.3	Romero-Caicedo and Carrera-Fernández (2015)
Myliobatiformes	Cownose ray *Rhinoptera bonasus*	11–12	4.9	0.67	1	No	26.7	Neer and Thompson (2005); Smith and Merriner (1986)
	Pacific cownose ray *Rhinoptera steindachneri*	11–12	6	1.3	1	No	24.2	Bizzarro et al. (2007)
	Red stingray *Hemitrygon akajei*	1.5[a]	4.7	0.044	12.3	No	28.1	Furumitsu et al. (2019)
	Atlantic stingray *Dasyatis sabina*	3.5–4	0.52	0.046	2.3	No	25.5	Johnson and Snelson (1996); Schwartz and Dahlberg (1978)
	Southern stingray *Dasyatis americana*	7–8	15	0.76	2.5	No	27.3	Henningsen and Leaf (2010); Ramirez Mosqueda et al. (2012)

[a]Diapause period was subtracted from the entire gestation period.
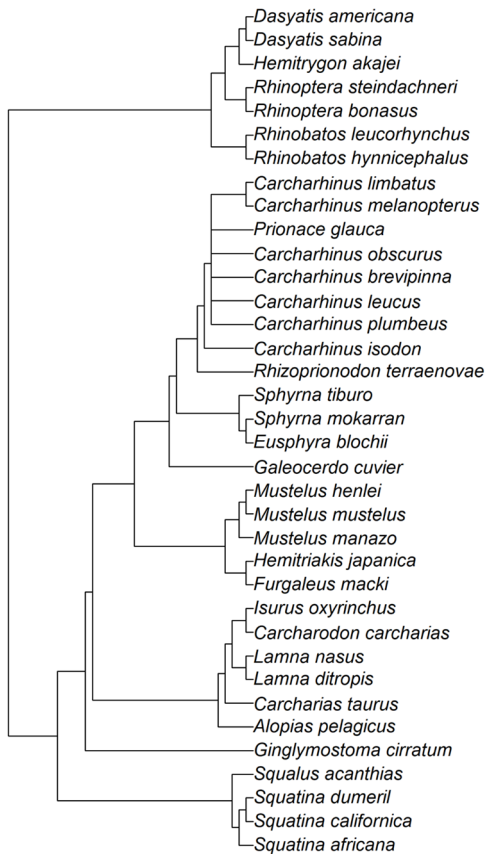[b]Calculated by using Bayesian length-weight relationships (Froese et al., 2014).

Fig. 1. Phylogenetic tree used for PGLS analysis.

Fig. 2. Gestation period *t* plotted against (A) adult female mass *M* and (B) birth mass *m*. Solid lines represent the PGLS regression lines [(A) $t=6.8×M^{0.11}$; (B) $t=10.5×m^{0.17}$]. Dashed lines represent the 95% confidence interval of the regression lines. Plots were colored by order to visualize phylogenetic relationships.

Table 2. Fitting of phylogenetically-informed multiple regression models

Predictor variables	N	Model	R^2	AIC	ΔAIC
M, m, E	**36**	**t~m**	**0.25**	**−17.3**	**0**
		t~m+E	0.26	−15.4	1.93
		t~M	0.13	−12.2	5.10
M, m, E, L	**36**	**t~M+L**	**0.36**	**−19.4**	**0**
		t~M+L+E	0.38	−17.9	1.42
		t~m+L	0.31	−17.5	1.87
M, m, E, L, T	**34**	**t~M+L+T**	**0.43**	**−21.4**	**0**
		t~M+L+T+E	0.44	−19.5	1.90
		t~m+L+T	0.36	−17.9	3.50

The best models were represented in bold. *N*, number of species; t, gestation period (month); M, adult female mass (kg); m, birth mass (kg); E, whether the fish has regional endothermy or not; L, mean litter size; T, body temperature (°C). All continuous variables except for body temperature (i.e. gestation period, adult female mass, birth mass, and litter size) were log_{10}-transformed.

the association between metabolic rates and elasmobranch gestation periods. In mammals, allometric relationships between gestation period and body mass are consistent with the metabolism framework (i.e. *t* scales with mass$^{1−β}$) in some studies (Blueweiss et al., 1978; Sacher and Staffeldt, 1974), but not others (Clauss et al., 2014; Western and Ssemakula, 1982).

In conclusion, our comparative analyses show that elasmobranch gestation periods scaled with mass$^{0.1–0.2}$, suggesting that the body-mass dependence of metabolic rate can explain some variations in gestation periods. Litter size and body temperature also affect gestation periods. Unexpectedly, regionally endothermic sharks did not have shorter gestation periods than their ectothermic counterparts. Metabolic rates of embryos, which are likely ectothermic in all elasmobranch species, may have stronger effects on gestation periods than those of their mothers. The empirical relationships shown in this study provide a new perspective for understanding the life history of elasmobranchs.

MATERIALS AND METHODS
Data compilation
We compiled data on gestation periods (in months) for as many elasmobranch species as possible from the literature. Gestation periods have been estimated for captive and wild individuals. However, captive individuals likely have different nutritional conditions and body temperature from wild individuals, presumably leading to different embryo growth rates and gestation periods. Because we aimed to understand elasmobranch natural life histories, we only compiled data on wild individuals. The following three methods have been used to estimate elasmobranch gestation periods in the wild: (1) plotting the sampled embryo size against the time of year for a species and estimating the duration required for embryo to grow to
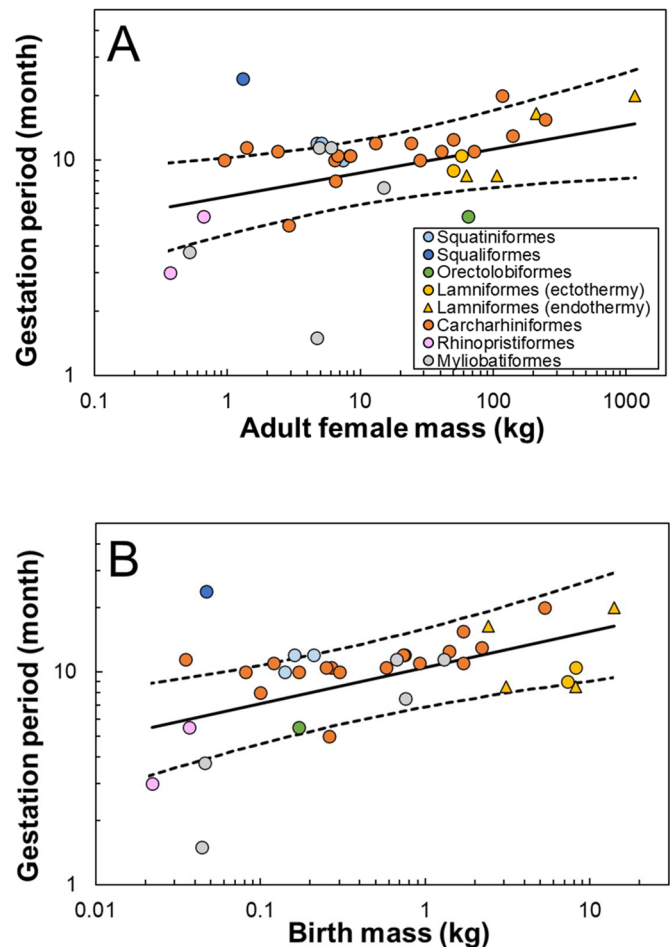
birth size; (2) estimating mating season and pupping season and calculating the difference between the two; (3) extrapolating length-age relationships to the point where body length is zero. We considered the first method most accurate and accepted the literature that used this method. In the second method, embryo growth rates are uncertain, and whether gestation periods are less than a year or more than a year remains a question. In the third
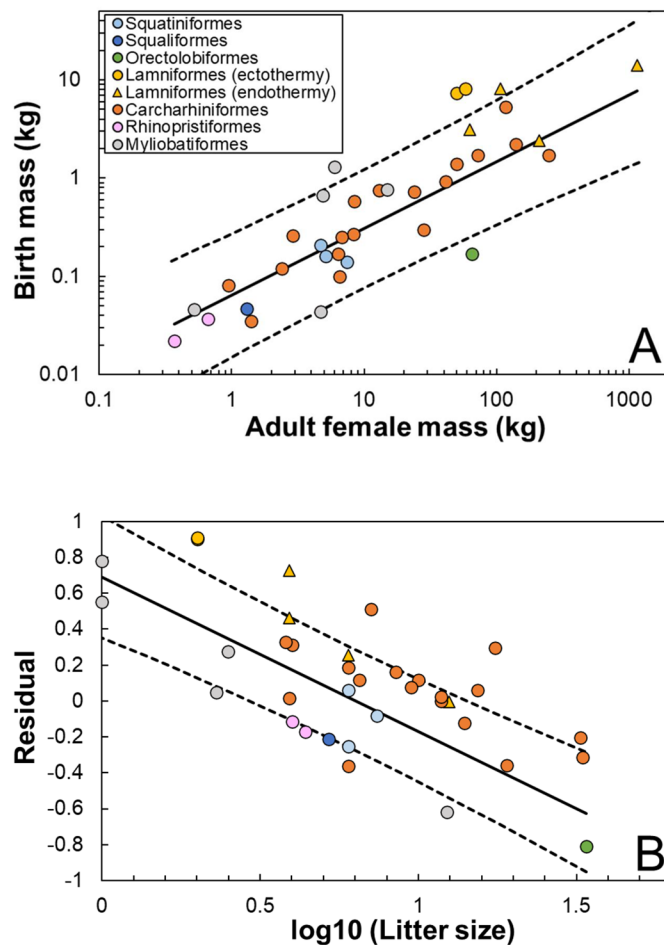
Fig. 3. Relationship between relative birth mass and mean litter size L.
(A) Relationship between adult female mass M and birth mass m. Solid line represents PGLS regression line: $m=0.064 \times M^{0.68}$ ($R^2=0.60$). (B) Relationship between residuals calculated from the regression line in A [i.e. $\log_{10}$ (observed m)–$\log_{10}$ (predicted m)] and $\log_{10}$ (L). Solid line represents PGLS regression line: Residual$=-0.86 \times \log_{10}$ (L)$+0.69$ ($R^2=0.60$). Dashed lines represent the 95% confidence interval of the regression lines.

method, embryo growth rates are uncertain. When multiple studies were found for a species, we accepted the study with the largest sample size. Regional variations within species (Lombardi-Carlson et al., 2003; Yamaguchi et al., 2000) were not considered in this study. In our dataset, ringstreaked guitarfish *Rhinobatos hynnicephalus* and red stingray *Hemitrygon akajei* appear to exhibit embryonic diapause. During this diapause period, uterine eggs without macroscopic embryos are observed, and embryonic growth begins after this period (Furumitsu et al., 2019; Kume et al., 2009). Hence, for these species, we estimated gestation periods as the length between the beginning and completion (i.e. parturition) of embryonic growth by subtracting the diapause period from the entire gestation period.

For each species in our dataset, female body mass at maturity (kg) was estimated based on information on body length at maturity and length-weight relationships found either in the literature or FishBase (http://www. fishbase.org. Version 02/2021). When body length at maturity was reported as a range, we used the middle value. Birth mass (kg) was also compiled based on the previously documented birth size, the largest embryo size, or the smallest neonate size combined with length-weight relationships. Regionally endothermic species was identified following Dickson and Graham (2004). The mean litter size was compiled from the same literature as that which reported gestation periods. When litter size was reported as a range, we used the middle value. As an approximation of body temperature, the mean preferred water temperature was compiled for each ectothermic

species using FishBase. For regionally endothermic species, the mean body temperature measured for free-swimming fish using bio-telemetry or for freshly caught specimen was compiled (Carey et al., 1981; Goldman, 1997; Goldman et al., 2004; Sepulveda et al., 2004).

Statistical analyses

We examined the allometric relationships between gestation period and body mass (i.e. adult female mass and birth mass) by using the Phylogenetic Generalized Least Squares (PGLS) method, which controls for phylogenetic non-independence of each species' traits (Lavin et al., 2008). We created a phylogenetic tree using the software Mesquite with the phylogenetic relationships based on Chondrichthyan Tree of Life website (https://sharksrays.org/; accessed 20 December 2020) and an arbitrary branch length (Grafen, 1989). Then, we computed the PGLS regressions with their 95% confidence intervals using the software R with 'caper', 'evomap', and 'geiger' package (Smaers and Rohlf, 2016). We used Pagel's λ to maximize the model's likelihood (Freckleton et al., 2002).

Multiple regression analyses were performed with gestation periods as the response variable. Predictors included continuous variables (i.e. adult female mass, birth mass, litter size, and body temperature) and a categorical variable (i.e. regional endothermy or ectothermy). Adult female mass was strongly correlated to birth mass, posing a risk of collinearity; therefore, we only used these variables in different models. All continuous variables except for body temperature (i.e. gestation period, adult mass, birth mass, and litter size) were $\log_{10}$-transformed to improve the linearity of relationships among the variables. Plots were checked visually to ensure that model assumptions (i.e. homogeneity of variance, normality of error) were reasonably met. The best models were selected based on Akaike Information Criteria (AIC). In our hypothesis-driven analyses, interactions among predictor variables were not considered.

Author contributions
Conceptualization: S.T.; Methodology: S.T.; Formal analysis: S.T.; Data curation: S.T., M.K.; Writing - original draft: S.T.; Writing - review & editing: Y.Y.W., Y.K.; Supervision: Y.K.

Data availability
Data used in this study are available in Table 1.

References
Avsar, D. (2001). Age, growth, reproduction and feeding of the spurdog (*Squalus acanthias* Linnaeus, 1758) in the south-eastern Black Sea. *Estuar. Coast. Shelf Sci.* **52**, 269-278. doi:10.1006/ecss.2000.0749

Baremore, I. E. (2010). Reproductive aspects of the Atlantic angel shark *Squatina dumeril. J. Fish Biol.* **76**, 1682-1695. doi:10.1111/j.1095-8649.2010.02608.x

Bernal, D., Carlson, J. K., Goldman, K. J. and Lowe, C. G. (2012). Energetics, metabolism, and endothermy in sharks and rays. In *Biology of Sharks and Their Relatives* (ed. J. C. Carrier, J. A. Musick and M. R. Heithaus), pp. 211-237. Boca Raton, FL: CRC Press.

Bizzarro, J. J., Smith, W. D., Márquez-Farías, J. F. and Hueter, R. E. (2007). Artisanal fisheries and reproductive biology of the golden cownose ray, *Rhinoptera steindachneri* Evermann and Jenkins, 1891, in the northern Mexican Pacific. *Fish. Res.* **84**, 137-146. doi:10.1016/j.fishres.2006.10.016

Blueweiss, L., Fox, H., Kudzma, V., Nakashima, D., Peters, R. and Sams, S. (1978). Relationships between body size and some life history parameters. *Oecologia* **37**, 257-272. doi:10.1007/BF00344996

Branstetter, S. and Stiles, R. (1987). Age and growth estimates of the bull shark, *Carcharhinus leucas*, from the northern Gulf of Mexico. *Environ. Biol. Fishes* **20**, 169-181. doi:10.1007/BF00004952

Carey, F. G., Teal, J. M. and Kanwisher, J. W. (1981). The visceral temperatures of mackerel sharks (Lamnidae). *Physiol. Zool.* **54**, 334-344. doi:10.1086/physzool. 54.3.30159948

Carlson, J. K., Goldman, K. J. and Lowe, C. G. (2004). Metabolism, energetic demand, and endothermy. In *Biology of Sharks and Their Relatives* (ed. J. C. Carrier, J. A. Musick and M. R. Heithaus), pp. 203-224. Boca Raton, FL: CRC Press.

Carrera-Fernández, M., Galván-Magaña, F. and Ceballos-Vázquez, B. P. (2010). Reproductive biology of the blue shark *Prionace glauca* (Chondrichthyes: Carcharhinidae) off Baja California Sur, México. *aqua* **16**, 101-110.

Castro, J. I. (1993). The biology of the finetooth shark, *Carcharhinus isodon*. *Environ. Biol. Fishes* **36**, 219-232. doi:10.1007/BF00001717

Castro, J. I. (2000). The biology of the nurse shark, *Ginglymostoma cirratum*, off the Florida east coast and the Bahama Islands. *Environ. Biol. Fishes* **58**, 1-22. doi:10. 1023/A:1007698017645

Chen, C.-T. and Mizue, K. (1973). Studies on sharks—VI Reproduction of *Galeorhinus japonicus*. *Bull. Fac. Fish. Nagasaki Univ.* **36**, 37-51.

Christiansen, H. M., Lin, V., Tanaka, S., Velikanov, A., Mollet, H. F., Wintner, S. P., Fordham, S. V., Fisk, A. T. and Hussey, N. E. (2014). The last frontier: catch records of white sharks (*Carcharodon carcharias*) in the northwest Pacific Ocean. *PLoS ONE* **9**, e94407. doi:10.1371/journal.pone.0094407

Clarke, A. and Johnston, N. M. (1999). Scaling of metabolic rate with body mass and temperature in teleost fish. *J. Anim. Ecol.* **68**, 893-905. doi:10.1046/j.1365-2656.1999.00337.x

Clauss, M., Dittmann, M. T., Müller, D. W. H., Zerbe, P. and Codron, D. (2014). Low scaling of a life history variable: analysing eutherian gestation periods with and without phylogeny-informed statistics. *Mamm. Biol.* **79**, 9-16. doi:10.1016/j. mambio.2013.01.002

Compagno, L. J. (1984). FAO species catalogue. Vol. 4. Sharks of the world. An annotated and illustrated catalogue of shark species known to date. Part 2. Carcharhiniformes. *FAO Fisheries Synopsis No. 125*, **4**, 251-655.

Conrath, C. L., Tribuzio, C. A. and Goldman, K. J. (2014). Notes on the reproductive biology of female salmon sharks in the eastern North Pacific Ocean. *Trans. Am. Fish. Soc.* **143**, 363-368. doi:10.1080/00028487.2013.862179

Cortés, E. (2000). Life history patterns and correlations in sharks. *Rev. Fish. Sci.* **8**, 299-344. doi:10.1080/10408340308951115

Cotton, C. F., Grubbs, R. D., Dyb, J. E., Fossen, I. and Musick, J. A. (2015). Reproduction and embryonic development in two species of squaliform sharks, *Centrophorus granulosus* and *Etmopterus princeps*: evidence of matrotrophy? *Deep Sea Res. II Topi. Stud. Oceanogr.* **115**, 41-54. doi:10.1016/j.dsr2.2014.10. 009

Dickson, K. A. and Graham, J. B. (2004). Evolution and consequences of endothermy in fishes. *Physiol. Biochem. Zool.* **77**, 998-1018. doi:10.1086/423743

Dudley, S. F. J. and Cliff, G. (1993). Sharks caught in the protective gill nets off Natal, South Africa. 7. The blacktip shark *Carcharhinus limbatus* (Valenciennes). *S. Afr. J. Mar. Sci.* **13**, 237-254. doi:10.2989/025776193784287356

Francis, M. P. (1996). Observations on a pregnant white shark with a review of reproductive biology. In *Great White Sharks: The Biology of Carcharodon carcharias* (ed. A. P. Klimley and D. G. Ainley), Vol. 157, p. 172. San Diego, CA: Academic Press.

Francis, M. (2000). Reproduction, embryonic development, and growth of the porbeagle shark, *Lamna nasus*, in the southwest Pacific Ocean. *Fish. Bull.* **98**, 41-63.

Freckleton, R. P., Harvey, P. H. and Pagel, M. (2002). Phylogenetic analysis and comparative data: a test and review of evidence. *Am. Nat.* **160**, 712-726. doi:10. 1086/343873

Froese, R., Thorson, J. T. and Reyes, R.Jr. (2014). A Bayesian approach for estimating length-weight relationships in fishes. *J. Appl. Ichthyol.* **30**, 78-85. doi:10.1111/jai.12299

Furumitsu, K., Wyffels, J. T. and Yamaguchi, A. (2019). Reproduction and embryonic development of the red stingray *Hemitrygon akajei* from Ariake Bay, Japan. *Ichthyol. Res.* **66**, 419-436. doi:10.1007/s10228-019-00687-9

Gilmore, R. G., Dodrill, J. and Linley, P. A. (1983). Reproduction and embryonic development of the sand tiger shark, *Odontaspis taurus* (Rafinesque). *Fish. Bull.* **81**, 201-225.

Glazier, D. S. (2010). A unifying explanation for diverse metabolic scaling in animals and plants. *Biol. Rev.* **85**, 111-138. doi:10.1111/j.1469-185X.2009.00095.x

Glazier, D. S. (2015). Is metabolic rate a universal 'pacemaker'for biological processes? *Biol. Rev.* **90**, 377-407. doi:10.1111/brv.12115

Goldman, K. J. (1997). Regulation of body temperature in the white shark, *Carcharodon carcharias*. *J. Comp. Physiol. B* **167**, 423-429. doi:10.1007/ s003600050092

Goldman, K. J. and Musick, J. A. (2006). Growth and maturity of salmon sharks (*Lamna ditropis*) in the eastern and western North Pacific, and comments on back-calculation methods. *Fish. Bull.* **104**, 278.

Goldman, K. J., Anderson, S. D., Latour, R. J. and Musick, J. A. (2004). Homeothermy in adult salmon sharks, *Lamna ditropis*. *Environ. Biol. Fishes* **71**, 403-411. doi:10.1007/s10641-004-6588-9

Goldman, K. J., Branstetter, S. and Musick, J. A. (2006). A re-examination of the age and growth of sand tiger sharks, *Carcharias taurus*, in the western

North Atlantic: the importance of ageing protocols and use of multiple back-calculation techniques. *Environ. Biol. Fishes* **77**, 241-252. Doi:10.1007/978-1-4020-5570-6_4

Grafen, A. (1989). The phylogenetic regression. *Philos. Trans. R. Soc. Lond. B Biol. Sci.* **326**, 119-157. Doi:10.1098/rstb.1989.0106

Hamlett, W. C., Kormanik, G., Storrie, M., Stevens, B. and Walker, T. I. (2005). Chondrichthyan parity, lecithotrophy and matrotrophy. In *Reproductive Biology and Phylogeny Of Chondrichthyes* (ed. W. C. Hamlett), pp. 395-434. Enfield: Science Publishers.

Hanchet, S. (1988). Reproductive biology of *Squalus acanthias* from the east coast, South Island, New Zealand. *N. Z. J. Mar. Freshw. Res.* **22**, 537-549. doi:10.1080/ 00288330.1988.9516324

Harris, J. E. (1952). A note on the breeding season, sex ratio and embryonic development of the dogfish *Scyliorhinus canicula* (L.). *J. Mar. Biol. Assoc. UK.* **31**, 269-276. doi:10.1017/s002531540005298x

Henningsen, A. D. and Leaf, R. T. (2010). Observations on the captive biology of the southern stingray. *Trans. Am. Fish. Soc.* **139**, 783-791. doi:10.1577/t09-124.1

Hight, B. V. and Lowe, C. G. (2007). Elevated body temperatures of adult female leopard sharks, *Triakis semifasciata*, while aggregating in shallow nearshore embayments: evidence for behavioral thermoregulation? *J. Exp. Mar. Biol. Ecol.* **352**, 114-128. doi:10.1016/j.jembe.2007.07.021

Jirik, K. E. and Lowe, C. G. (2012). An elasmobranch maternity ward: female round stingrays *Urobatis halleri* use warm, restored estuarine habitat during gestation. *J. Fish Biol.* **80**, 1227-1245. doi:10.1111/j.1095-8649.2011.03208.x

Johnson, M. R. and Snelson, F. F.Jr. (1996). Reproductive life history of the Atlantic stingray, *Dasyatis sabina* (Pisces, Dasyatidae), in the freshwater St. Johns River, Florida. *Bull. Mar. Sci.* **59**, 74-88.

Joung, S.-J., Chen, C.-T., Clark, E., Uchida, S. and Huang, W. Y. P. (1996). The whale shark, *Rhincodon typus*, is a livebearer: 300 embryos found in one 'megamamma'supreme. *Environ. Biol. Fishes* **46**, 219-223. doi:10.1007/ BF00004997

Joung, S.-J., Liao, Y.-Y. and Chen, C.-T. (2004). Age and growth of sandbar shark, *Carcharhinus plumbeus*, in northeastern Taiwan waters. *Fish. Res.* **70**, 83-96. doi:10.1016/j.fishres.2004.06.018

Joung, S.-J., Liao, Y.-Y., Liu, K.-M., Chen, C.-T. and Leu, L.-C. (2005). Age, growth, and reproduction of the spinner shark, *Carcharhinus brevipinna*, in the northeastern waters of Taiwan. *Zool. Stud.* **44**, 102-110.

Kamura, S., Hashimoto, H. and Gushima, K. (2000). The second record, tendency of occurrence and food habit of Eiraku shark *Hemitriakis japanica* (Mueller et Henle) in the Seto Inland Sea. *J. Fac. Appl. Biol. Sci. Hiroshima Univ.* **39**, 1-7.

Kohler, N. E., Casey, J. G. and Turner, P. A. (1996). Length-length and length-weight relationships for 13 shark species from the Western North Atlantic. *NOAA Technical Memorandum NMFS-NE-110*. Retrieved from https://repository.library. noaa.gov/view/noaa/2990.

Kume, G., Furumitsu, K., Tanaka, S. and Yamaguchi, A. (2009). Reproductive biology of the guitarfish *Rhinobatos hynnicephalus* (Batoidea: Rhinobatidae) in Ariake Bay, Japan. *Environ. Biol. Fishes* **85**, 289-298. doi:10.1007/s10641-009-9487-2

Lavin, S. R., Karasov, W. H., Ives, A. R., Middleton, K. M. and Garland, T.Jr. (2008). Morphometrics of the avian small intestine compared with that of nonflying mammals: a phylogenetic approach. *Physiol. Biochem. Zool.* **81**, 526-550. doi:10. 1086/590395

Lindstedt, S. L. and Calder, W. A. (1981). Body size, physiological time, and longevity of homeothermic animals. *Q Rev. Biol.* **56**, 1-16. doi:10.1086/412080

Loefer, J. K. and Sedberry, G. R. (2003). Life history of the Atlantic sharpnose shark (*Rhizoprionodon terraenovae*) (Richardson, 1836) off the southeastern United States. *Fish. Bull.* **101**, 75-88.

Lombardi-Carlson, L. A., Cortés, E., Parsons, G. R. and Manire, C. A. (2003). Latitudinal variation in life-history traits of bonnethead sharks, *Sphyrna tiburo*, (Carcharhiniformes: Sphyrnidae) from the eastern Gulf of Mexico. *Mar. Freshw. Res.* **54**, 875-883. doi:10.1071/MF03023

Lowe, C. G. and Goldman, K. J. (2001). Thermal and bioenergetics of elasmobranchs: bridging the gap. *Environ. Biol. Fishes* **60**, 251-266. doi:10. 1023/A:1007650502269

Lucifora, L. O., Menni, R. C. and Escalante, A. H. (2002). Reproductive ecology and abundance of the sand tiger shark, *Carcharias taurus*, from the southwestern Atlantic. *ICES J. Mar. Sci.* **59**, 553-561. doi:10.1006/jmsc.2002.1183

Martin, R. D. (1996). Scaling of the mammalian brain: the maternal energy hypothesis. *Physiology* **11**, 149-156. doi:10.1152/physiologyonline. 1996.11.4.149

Martin, R. and MacLarnon, A. (1985). Gestation period, neonatal size and maternal investment in placental mammals. *Nature* **313**, 220-223. doi:10.1038/313220a0

Mcauley, R. B., Simpfendorfer, C., Hyndes, G. A. and Lenanton, R. (2007). Distribution and reproductive biology of the sandbar shark, *Carcharhinus plumbeus* (Nardo), in Western Australian waters. *Mar. Freshw. Res.* **58**, 116-126. doi:10.1071/MF05234

Mollet, H., Cliff, G., Pratt, H., Jr. and Stevens, J. (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.

Moses, M. E., Hou, C., Woodruff, W. H., West, G. B., Nekola, J. C., Zuo, W. and Brown, J. H. (2008). Revisiting a model of ontogenetic growth: estimating model parameters from theory and data. *Am. Nat.* **171**, 632-645. doi:10.1086/587073

Natanson, L. J. and Cailliet, G. M. (1986). Reproduction and development of the Pacific angel shark, *Squatina californica*, off Santa Barbara, California. *Copeia* **1986**, 987-994. doi:10.2307/1445296

Neer, J. A. and Thompson, B. A. (2005). Life history of the cownose ray, *Rhinoptera bonasus*, in the northern Gulf of Mexico, with comments on geographic variability in life history traits. *Environ. Biol. Fishes* **73**, 321-331. doi:10.1007/s10641-005-2136-5

Nielsen, J., Hedeholm, R. B., Lynghammar, A., McClusky, L. M., Berland, B., Steffensen, J. F. and Christiansen, J. S. (2020). Assessing the reproductive biology of the Greenland shark (*Somniosus microcephalus*). *PLoS One* **15**, e0238986. doi:10.1371/journal.pone.0238986

Parsons, G. R. (1993). Geographic variation in reproduction between two populations of the bonnethead shark, *Sphyrna tiburo*. *Environ. Biol. Fishes* **38**, 25-35. doi:10.1007/978-94-017-3450-9_3

Parsons, G. R., Hoffmayer, E. R., Hendon, J. M. and Bet-Sayad, W. V. (2008). A review of shark reproductive ecology: life history and evolutionary implications. In *Fish Reproduction* (ed. M. A. Rocha, A. Arukwe and B. G. Kapoor), pp. 435-469. Enfield: Science Publishers.

Pérez-Jiménez, J. C. and Sosa-Nishizaki, O. (2008). Reproductive biology of the brown smoothhound shark *Mustelus henlei*, in the northern Gulf of California, México. *J. Fish Biol.* **73**, 782-792. doi:10.1111/j.1095-8649.2008.01939.x

Peters, R. H. (1983). *The Ecological Implications of Body Size*. Cambridge: Cambridge university press.

Pirog, A., Magalon, H., Poirout, T. and Jaquemet, S. (2019). Reproductive biology, multiple paternity and polyandry of the bull shark *Carcharhinus leucas*. *J. Fish Biol.* **95**, 1195-1206. doi:10.1111/jfb.14118

Pulver, J. R. and Whatley, A. (2016). Length-weight relationships, location, and depth distributions for select Gulf of Mexico reef fish species. *NOAA Technical Memorandum NMFS-SEFSC-693*. Retrieved from https://repository.library.noaa.gov/view/noaa/12412.

Ramirez Mosqueda, E., Perez Jimenez, J. C. and Mendoza Carranza, M. (2012). Reproductive parameters of the southern stingray *Dasyatis Americana* in southern gulf of Mexico. *Lat. Am. J. Aquat. Res.* **40**, 335-344. doi:10.3856/vol40-issue2-fulltext-8.

Romero-Caicedo, A. F. and Carrera-Fernández, M. (2015). Reproduction of the whitesnout guitarfish *Rhinobatos leucorhynchus* in the Ecuadorian Pacific Ocean. *J. Fish Biol.* **87**, 1434-1448. doi:10.1111/jfb.12794

Romero-Caicedo, A., Galvan-Magaña, F. and Martínez-Ortiz, J. (2014). Reproduction of the pelagic thresher shark *Alopias pelagicus* in the equatorial Pacific. *J. Mar. Biol. Assoc. UK.* **94**, 1501-1507. doi:10.1017/S0025315414000927

Romine, J. G., Musick, J. A. and Burgess, G. H. (2009). Demographic analyses of the dusky shark, *Carcharhinus obscurus*, in the Northwest Atlantic incorporating hooking mortality estimates and revised reproductive parameters. *Environ. Biol. Fishes* **84**, 277-289. doi:10.1007/s10641-008-9435-6.

Rothchild, I. (2003). The yolkless egg and the evolution of eutherian viviparity. *Biol. Reprod.* **68**, 337-357. doi:10.1095/biolreprod.102.004531

Sacher, G. A. and Staffeldt, E. F. (1974). Relation of gestation time to brain weight for placental mammals: implications for the theory of vertebrate growth. *Am. Nat.* **108**, 593-615. doi:10.1086/282938

Saïdi, B., Bradaï, M. N. and Bouaïn, A. (2008). Reproductive biology of the smooth-hound shark *Mustelus mustelus* (L.) in the Gulf of Gabès (south-central Mediterranean Sea). *J. Fish Biol.* **72**, 1343-1354. doi:10.1111/j.1095-8649.2008.01801.x

Sato, K., Nakamura, M., Tomita, T., Toda, M., Miyamoto, K. and Nozu, R. (2016). How great white sharks nourish their embryos to a large size: evidence of lipid histotrophy in lamnoid shark reproduction. *Biol. Open* **5**, 1211-1215. doi:10.1242/bio.017939

Schwartz, F. J. and Dahlberg, M. D. (1978). Biology and Ecology of the Atlantic Stingray, *Dasyatis sabina* (Pisces: Dasyatidae) in North Carolina and Georgia. *Gulf Mex. Sci.* **2**, 1. doi:10.18785/negs.0201.01

Sepulveda, C., Kohin, S., Chan, C., Vetter, R. and Graham, J. (2004). Movement patterns, depth preferences, and stomach temperatures of free-swimming juvenile mako sharks, *Isurus oxyrinchus*, in the Southern California Bight. *Mar. Biol.* **145**, 191-199. doi:10.1007/s00227-004-1356-0

Shelmerdine, R. L. and Cliff, G. (2006). Sharks caught in the protective gill nets off KwaZulu-Natal, South Africa. 12. The African angel shark *Squatina africana* (Regan). *Afr. J. Mar. Sci.* **28**, 581-588. doi:10.2989/18142320609504208

Simpfendorfer, C. A. and Unsworth, P. (1998). Reproductive biology of the whiskery shark, *Furgaleus macki*, off south-western Australia. *Mar. Freshw. Res.* **49**, 687-793. doi:10.1071/MF97052

Simpfendorfer, C. A., Chidlow, J., McAuley, R. and Unsworth, P. (2000). Age and growth of the whiskery shark, *Furgaleus macki*, from southwestern Australia. *Environ. Biol. Fishes* **58**, 335-343. doi:10.1023/A:1007624828001

Smaers, J. and Rohlf, F. (2016). Testing species' deviation from allometric predictions using the phylogenetic regression. *Evolution* **70**, 1145-1149. doi:10.1111/evo.12910

Smith, J. W. and Merriner, J. (1986). Observations on the reproductive biology of the cownose ray, *Rhinoptera bonasus*, in Chesapeake Bay. *Fish. Bull.* **84**, 871.

Ste-Marie, E., Watanabe, Y. Y., Semmens, J. M., Marcoux, M. and Hussey, N. E. (2020). A first look at the metabolic rate of Greenland sharks (*Somniosus microcephalus*) in the Canadian Arctic. *Sci. Rep.* **10**, 19297. doi:10.1038/s41598-020-76371-0

Stevens, J. (1984). Life-history and ecology of sharks at Aldabra Atoll, Indian Ocean. *Proc. R. Soc. Lond. B Biol. Sci.* **222**, 79-106. doi:10.1098/rspb.1984.0050

Stevens, J. and Lyle, J. (1989). Biology of three hammerhead sharks (*Eusphyra blochii*, *Sphyrna mokarran* and *S. lewini*) from northern Australia. *Mar. Freshw. Res.* **40**, 129-146. doi:10.1071/MF9890129

Swider, D. A., Corwin, A. L., Kamerman, T. Y., Zimmerman, S. L., Violetta, G. C., Davis, J. and Janse, M. (2017). Reproduction of spotted eagle rays, Aetobatus narinari, in aquaria. In *Elasmobranch husbandry Manual II: Recent Advances in the Care of Sharks, Rays and Their Relatives* (ed. M. Smith, D. Warmolts, D. Thoney, R. Hueter, M. Murray and J. Ezcurra), pp. 433-442. Columbus, OH: The Ohio State University Printing Servicies.

Varghese, S. P., Vijayakumaran, K., Tiburtius, A. and Mhatre, V. D. (2015). Diversity, abundance and size structure of pelagic sharks caught in tuna longline survey in the Indian seas. *Indian J. Geo-Mar. Sci.* **44**, 26-36.

Watanabe, Y. Y., Goldman, K. J., Caselle, J. E., Chapman, D. D. and Papastamatiou, Y. P. (2015). Comparative analyses of animal-tracking data reveal ecological significance of endothermy in fishes. *Proc. Natl Acad. Sci. USA* **112**, 6104-6109. doi:10.1073/pnas.1500316112

Wearmouth, V. J. and Sims, D. W. (2008). Chapter 2 sexual segregation in marine fish, reptiles, birds and mammals: behaviour patterns, mechanisms and conservation implications. *Adv. Mar. Biol.* **54**, 107-170. doi:10.1016/S0065-2881(08)00002-3

Weisbecker, V. and Goswami, A. (2010). Brain size, life history, and metabolism at the marsupial/placental dichotomy. *Proc. Natl Acad. Sci. USA* **107**, 16216-16221. doi:10.1073/pnas.0906486107

West, G. B., Brown, J. H. and Enquist, B. J. (2001). A general model for ontogenetic growth. *Nature* **413**, 628-631. doi:10.1038/35098076

Western, D. and Ssemakula, J. (1982). Life history patterns in birds and mammals and their evolutionary interpretation. *Oecologia* **54**, 281-290. doi:10.1007/BF00379994

White, C. R., Phillips, N. F. and Seymour, R. S. (2006). The scaling and temperature dependence of vertebrate metabolism. *Biol. Lett.* **2**, 125-127. doi:10.1098/rsbl.2005.0378

Whitney, N. M. and Crow, G. L. (2007). Reproductive biology of the tiger shark (*Galeocerdo cuvier*) in Hawaii. *Mar. Biol.* **151**, 63-70. doi:10.1007/s00227-006-0476-0

Yamaguchi, A., Taniuchi, T. and Shimizu, M. (1997). Reproductive biology of the starspotted dogfish *Mustelus manazo* from Tokyo Bay, Japan. *Fish. Sci.* **63**, 918-922. doi:10.2331/fishsci.63.918

Yamaguchi, A., Taniuchi, T. and Shimizu, M. (1998). Geographic variation in growth of the starspotted dogfish *Mustelus manazo* from five localities in Japan and Taiwan. *Fish. Sci.* **64**, 732-739. doi:10.2331/fishsci.64.732

Yamaguchi, A., Taniuchi, T. and Shimizu, M. (2000). Geographic variations in reproductive parameters of the starspotted dogfish, *Mustelus manazo*, from five localities in Japan and in Taiwan. *Environ. Biol. Fishes* **57**, 221-233. doi:10.1023/A:1007558324902