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Maternal risk-management elucidates the evolution of reproductive adaptations in sharks by means of natural selection

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Maternal investment theory is the study of how breeding females allocate resources between offspring size and brood size to achieve reproductive success. In classical trade-off models, r/K-selection and bet-hedging selection, the primary predictors of maternal investments in offspring are population density and resource stability. In crowded, stable environments, K-selected females invest in large offspring at an equivalent cost in brood size. In uncrowded, unstable environments, r-selected females invest in large broods at an equivalent cost in offspring size. In unpredictable resource environments, bet-hedging females invest moderately in brood size and offspring size. The maternal risk-management model represents a profound departure from classical trade-off models. Maternal investments in offspring size, brood size, and brood number are shaped independently by autonomous risk factors: the duration of gaps in resources during seasonal cycles, rates of predation, and unpredictable catastrophic events. To date, no single model has risen to a position of preeminence. Here in sharks, we show that maternal investments within and across species do not agree with the predictions of trade-off models and instead agree with the predictions of the maternal risk-management model. Within and across shark species, offspring size and brood size were independent maternal investment strategies. The risk of starvation favored investments in larger offspring. The risk of predation favored investments in larger broods. If empirical studies continue to confirm its predictions, maternal-risk management may yet emerge as a unifying model of diverse reproductive adaptations by means of natural selection.

Life history's, zero-sum trade-off models begin with the premise that populations compete for finite resources[1–4]. An energy investment in growth incurs an equivalent cost in reproduction[5–9]. An energy investment in offspring size incurs an equivalent cost in offspring number per reproductive event[10–14]. Classic trade-off models, including the fast-slow continuum, explore the impact of finite resources on the rates of population growth and the size of populations at equilibrium[15–30]. The maternal risk management model[31,32] represents a profound departure from these classical life history trade-off models.

First, the maternal risk management model assumes that the evolution of each maternal investment trait—adult female size, relative offspring size at independence, offspring number per reproductive event, and the number of reproductive events per female lifetime—are independent reproductive adaptations in response to different ecological and environmental risk categories (Fig. 1).

Maternal risk management is an empirical model with four testable predictions. (1) The evolution of offspring size at independence from the female is shaped by the duration of spatiotemporal gaps in resource abundance that vary by diurnal, lunar, and seasonal cycles[33–37]. Depending on each species' developmental life cycle, offspring

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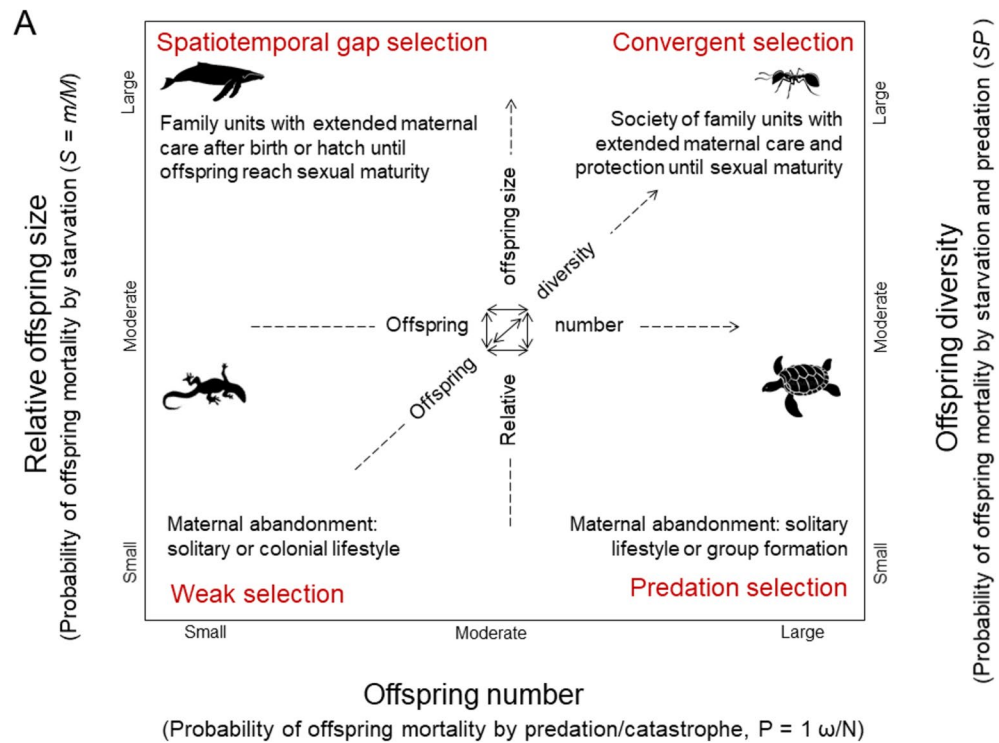
Fig. 1. The maternal risk management model. The "y" axis represents the relative size of offspring at dispersal (*m/M*). The "x" axis represents the number of offspring per spawn, clutch or birth (*N*). The diagonal "z" axis represents offspring diversity within a reproductive event. Silhouettes display representative species in each of the four broad categories of this model[31].

may experience radically different trophic levels that translate into shorter or longer gaps in resource abundance. For example, large sea turtle females are able to abandon their eggs after clutching because hatchlings are capable of independently foraging at a trophic level with short gaps between abundant prey[38]. In contrast, the large humpback whale female nurses her calf until it is large enough to migrate and harvest resources at the same trophic level as its mother[39].

(2) The rates of predation, including parasites, bacteria, and viruses that prey at different levels of biological organization, shape offspring number per reproductive event[40–42]. (3) The type and intensity of unpredictable, localized mass mortality events such as those caused by Las Niñas, Los Niños, anoxia, drought, floods, famine, and wildfires, shape the number of reproductive events over the lifetime of a female[32,43,44]. (4) The convergence of extended temporal or seasonal gaps in resources and high rates of predation select for offspring diversity in phenotype and fertility[45–47].

In another significant departure from classic trade-off models, the maternal risk management model defines reproductive fitness as a replacement constant across species ($\omega = 2$). Replacement fitness applies to breeding females, not to males or immature offspring. Replacement fitness is the survival of one daughter to replace the female and *at least* one outbreeding son to replace her mate(s)[48,49]. Maternal investments and other life history traits evolve as some females exceed replacement fitness, and others fail to meet replacement fitness. It is important to note that replacement fitness does not negate the utility of absolute fitness when modeling a population's genotypic abundance, or the utility of relative fitness when modeling the relative frequency of a population's genotypes.

Here, we tested two of the predictions of the maternal risk management model with published data on adult female size, offspring size and offspring number[14] and based on a meta-analysis of across 89 shark species and 22 teleost fish species. After reporting the predicted outcomes, we discuss the potential for the maternal risk management model to integrate the evolution of maternal investments and other life history adaptations into a natural selection paradigm.

Methods
Life history data
For our intraspecific analysis of maternal investments in the spinner shark, *Carcharhinus brevipinna,* and the dusky shark, *C. obscurus*, we used published data provided by Nigel Hussey[14] including the length and mass of each pregnant female as well as the length, mass, and number of each near-term pup (Spinner: $N_{female} = 136$; $N_{offspring} = 1276$; Dusky: ($N_{female} = 228$; $N_{offspring} = 2230$). Birth order was determined by the location of placental attachments of near-term pups. Sharks were incidentally caught in beach protection nets in KwaZulu-Natal, South Africa, between 1978 and 2008 and preserved with access permitted by the KwaZulu-Natal Sharks Board[50].

For our interspecific analysis of maternal investments in sharks, we compiled life history data on 117 species spanning twenty-seven taxonomic families and eight orders. Field studies fully documenting life history traits are deficient for the majority of over 540 known shark species[51,52]. Data were aggregated from 41 peer-reviewed scientific articles, field guides, and the IUCN Red List of Threatened Species. We also used online sources including Fishbase with over 59,800 references, Google Scholar, Web of Science, and the Swiss Foundation Shark database (see Appendix A for references and online links). Life history data included reproductive mode ($N = 113$ species); female length at sexual maturity ($N = 112$ species); age at sexual maturity ($N = 45$ species); duration of gestation ($N = 61$ species); offspring length at birth ($N = 92$ species); litter size ($N = 91$ species); and longevity ($N = 80$ species).

For our interspecific analysis of maternal investments in teleost fish, we obtained maternal investment data on 22 marine species including female size (kg), egg diameter, and egg number per spawn from scientific articles and from the same sources listed above (Appendix A). Because sharks and teleost fish are indeterminate growers throughout their lifespan, data on female size varied. The same species may grow to different maximum sizes or reach maturity at different sizes in different habitats[53]. When our sources reported a range of body sizes for sexually mature females and for neonatal pups, we recorded the mean length.

To calculate the percent of energy that shark females invested per litter, we developed a novel fusiform conversion for estimating female mass and pup mass (Fig. 2). We converted shark length (cm) to cone volume (cm^3), and volume to mass (kg) using the equation $V = 2*(cm/3 \pi r^2)/1000$. We assumed that reported body length was measured from the frontal tip to the pre-caudal notch (Fig. 2A); the vertical distance from the base of the dorsal fin to the ventral surface equaled the body width measured from gill to gill (Fig. 2B); and the fusiform body shape scaled consistently across species[54–58]. Although species-specific fin-to-body-mass ratios[59] and partial length-length, mass-mass relationships in the piked spurdog (*Squalus megalops*)[60] have been reported, to our knowledge, this is the first length-volume-mass conversion within and across shark species. Variation in our fusiform conversion accounted for 84% of explained variation in the reported mass of females per species from vetted sources (Fig. 2C; Regression: $R^2 = 0.84$; $p < 0.0001$; $N = 46$ species; Appendix A). For teleost fish, we converted egg diameter (cm) to spherical volume (cm^3) to mass (kg) using the equation $V = (cm/3\pi r^3)/1000$. To estimate the utility of our fusiform conversion, we used the known mean masses of adult females and neonate pups for the spinner shark, *C. brevipinna*, ($N = 136$) and the dusky shark, *C. obscurus* ($N = 228$)[14]. We show that our fusiform conversion overestimated spinner female mass by 4.7% (126 vs 132 kg) and underestimated dusky female mass by 0.3% (280 vs 279 kg). Our fusiform conversion overestimated spinner shark pup size by 4.7% (2.1 vs 2.2 kg) and underestimated dusky shark pup size by 8.7% (4.6 vs 4.2 kg).
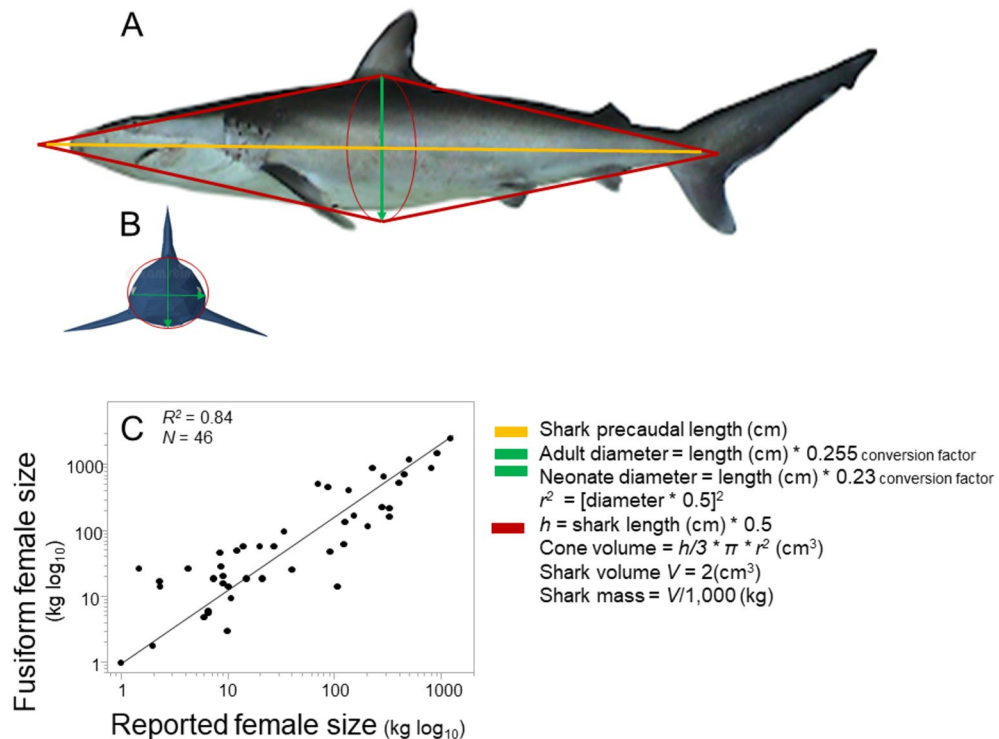
Fig. 2. Estimating interspecific female and offspring mass in sharks using a novel fusiform conversion of length (*cm*) to volume (*V*) to mass (*kg*) using the equation $(h/3 \pi R^2) * 2$ cones/1000. (**A**) We estimated total body volume as two cones connected at the base. (**B**) Moreover, we estimated the height and width of a shark's body from a frontal perspective. (**C**) The fusiform conversion mass of breeding females by the reported mass of females from vetted sources ($N = 46$; Appendix A).

	Maternal investments and other life history variables in sharks
1	Female size: M (kg)
2	Pup size: m (kg)
3	Litter size: N
4	Pup diversity per litter: mean $kg_{max} - kg_{min}/kg_{min}$ * 100 (%)
5	Litter mass: mN (kg)
6	Age at sexual maturity: (yrs)
7	Gestation: (months or yrs)
8	Interbreeding intervals: (yrs)
9	Lifespan: (yrs)
10	Reproductive period: longevity – age at sexual maturity (yrs)
11	Litter number: reproductive period/interbreeding intervals
12	Offspring number per lifetime: N * litter number
13	Relative maternal investment per pup at hatch or birth: m/M [* 100 = %]
14	Relative maternal investment per litter mass: mN/M [*100 = %]
15	Probability of starvation before reaching sexual maturity: $S = m/M$
16	Probability of predation before reaching sexual maturity: $1 - \omega/N$; where $\omega = 2$

Table 1. The metrics and equations for estimating life history traits. To our knowledge, the equations in lines 13–16 are novel to the maternal risk management model.

Model metrics and equations

Life history metrics and equations are shown in Table 1, Lines 1–12. The equations for relative maternal investments per pup and per litter mass are shown in Lines 13, 14. The predictions linking the probabilities of offspring mortality to the type and intensity of ecological risk factors are shown in Lines 13–16. We use the Gini coefficient to quantify differences in pup size per litter (*i.e.,* offspring diversity). The Gini coefficient measures inequality on a scale of 0 to 1 where 0 represents perfect equality, indicating that all pups received equal energy investments by females; and where 1 represents perfect inequality, indicating that 1 pup received all the energy investments and all others received none (see Gini coefficient equation, Appendix A). We acknowledge that there are uncertainties in our average or median estimates of the life history traits per species. For example, interbreeding intervals in a population of the nurse shark, *Ginglymostoma cirratum*, vary throughout a female's life, with mating typically occurring biennially, but 32% of breeders showing a triennial cycle at least occasionally, reducing estimates of lifetime reproductive output by 11% compared to strict biennial projections[61].

Ecological risk variables in sharks

We used trophic position to approximate spatiotemporal gaps in resource availability. Prey at lower trophic levels are more dense and abundance than prey at higher trophic levels[62]. Hence, the duration of gaps between successful hunts is greater at higher trophic levels. We recorded nursery use data from two scientific sources[63,64] and Fishbase sources. We estimated predation risk using scientific and online source listed above and in Appendix A. We analyzed trophic level as a numeric continuous variable. We analyzed nursery use and predation risk as categorical variables. Species that were reported as nursery users and species that were reported at risk of predation, were categorized as *Yes.* Species that were not reported as nursery users and species that were not reported to be predated were categorized as *Unreported.* We observed that detailed data on life history traits were more commonly available for larger-bodied and coastal sharks, particularly those that are of commercial importance. This has restricted our analysis of other sharks, such as deep-sea shark species.

Statistical analyses

Because the outcomes for maternal investment analyses using length and mass data were equivalent, we reported the results for length and mass, but created figures only for mass. When quantitative data across species did not meet normality and equal variance requirements, we used nonparametric Kruskal–Wallis tests. For our Multifactor ANOVA and Tukey HSD analyses, we transformed female size, pup/egg size, and litter/spawn size variables using log_{10}. We used R 4.2.2 (R Core Team, 2022) to quantify the impact of shark phylogeny[65,66] on the associations between adult female size and pup size, and between adult female size and litter size. For other statistical analyses and accompanying figures, we used JMP® Pro 16 Statistical Software.

Results
Maternal investments

In spinner sharks and dusky sharks, larger females produced larger pups (Fig. 3A; $R^2_{spinner} = 0.12$; p < 0.0001; and $R^2_{dusky} = 0.20$; $P < 0.0001$). The size of spinner and dusky shark females accounted for 12% and 20% of explained variation in mean pup size per litter. Larger females produced larger litters in both species (Fig. 3B; $R^2_{spinner} = 0.39$; $P < 0.0001$; and $R^2_{dusky} = 0.18$; p < 0.0001), with female size accounting for 39% and 18% of explained variation in litter size. Female size was not a significant predictor of relative maternal investments in total litter mass for spinner or dusky sharks (Fig. 3C; $R^2_{spinner} = 0.01$; $P = 0.127$; and $R^2_{dusky} = 0.02$; $P = 0.227$). On average, spinner and
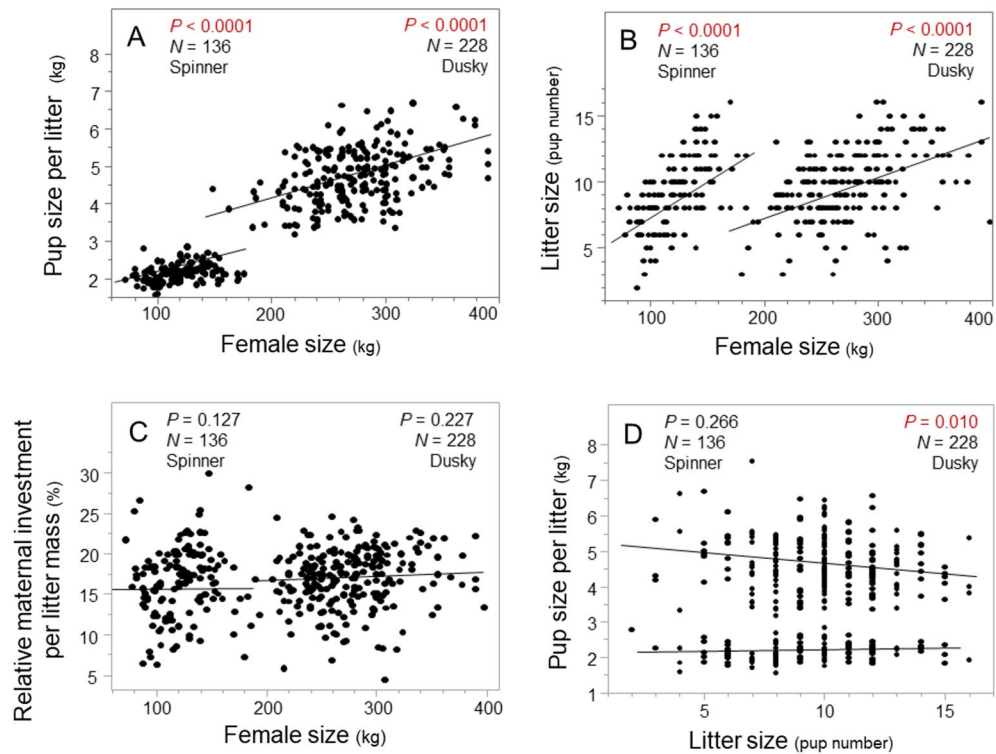
Fig. 3. Comparing maternal investments for spinner and dusky sharks, *C. brevipinna* and *C. obscurus*. (**A**) Pup size by female size in spinner and dusky sharks. (**B**) Litter size by female size in spinner and dusky sharks. (**C**) Relative maternal investment in total litter mass by female size in spinner and dusky sharks. (**D**) Pup size by litter size in spinner and dusky sharks.

dusky shark females invested approximately 16% of their body mass in total litter mass. Litter size was independent of pup size in spinner females (Fig. 3D; Regression: $R^2_{spinner} = 0.010$; $P = 0.266$), but was negatively associated with pup size in dusky shark ($R^2_{dusky} = 0.03$; $P = 0.010$). However, litter size accounted for only 2.9% of variation in pup size, leaving 97% of variation in pup size unexplained. Despite the fact that spinner shark females are approximately half the size of dusky shark females, their maternal investments relative to their body mass were similar. Spinner shark females produced a median 9 pups per litter (range = 2–16). They invested an average of 1.8% of their body size to produce each pup per litter (range = 1.1–3.2%; see Table 1, Line 13 for the equation), and an average of 16.6% of their body size to produce each litter mass (range = 6.3–26.5%; Table 1, Line 14). On average, dusky shark females produced 10 pups per litter (range = 3–16). They invested an average of 1.7% of their body size per pup (range = 1.1–2.9%), and an average of 17.2% of their body size per litter (range = 4.3–32.6%).

Within a litter, maternal investments in pup size for spinner and dusky sharks were labile. Pup sizes per litter tended toward a broad uniform distribution rather than a normal or skewed distribution (Fig. 3). In spinner shark litters, the difference in size between the smallest and largest pups per litter averaged 19% (range: 15% to 23%; Fig. 4A-C). Birth order was not a significant predictor of pup size in spinner sharks (Kruskal–Wallis test: $\chi^2 = 14.39$; $P = 0.937$; $N = 1276$). The male:female sex ratio in spinner sharks was 1:1. In dusky sharks, the mean difference in pup size between the smallest and largest per litter was 27% (range: 22% to 32%; Fig. 4D-F). Birth order was not a significant predictor of pup size in dusky sharks (Kruskal–Wallis test: $\chi^2 = 14.14$; $P = 0.896$; $N = 2230$). The male:female sex ratio in offspring was 1:1. For spinner and dusky shark females, investments per pup per litter differed, but the differences were small (GI = 0.038 and 0.025) relative to differences in egg size per clutch by loggerhead sea turtles (GI = 0.137) and a fire ant queen's offspring (GI = 0.910).
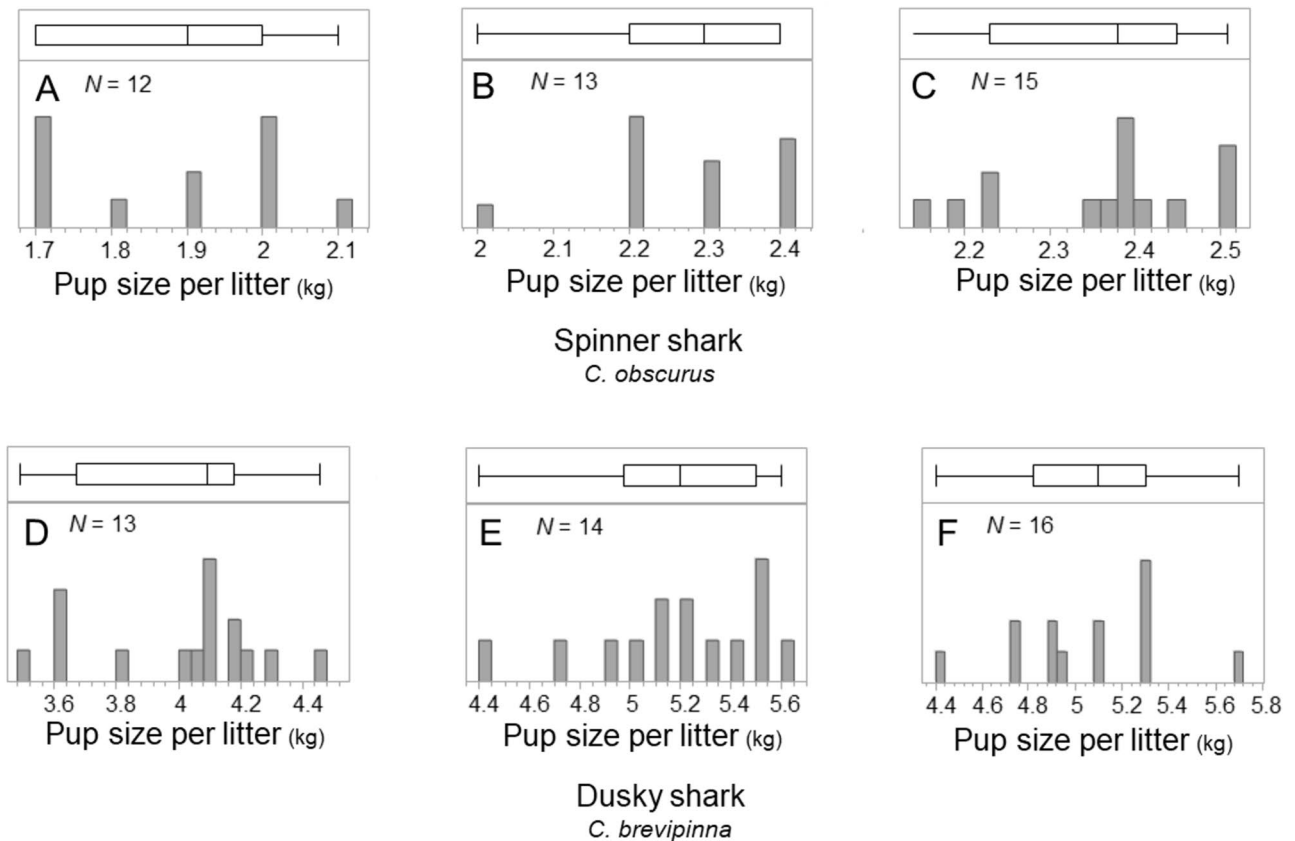
Spinner shark
C. obscurus

Dusky shark
C. brevipinna

Fig. 4. Distributions of pup size per shark litter. (**A**–**C**) Pup sizes per litter in spinner sharks. (**D**–**F**) Pup sizes per litter in dusky sharks. The median is denoted as a vertical line within the box. The box defines two interquartile ranges from the median. The whiskers show the full range of pup size data.

Across 89 shark species, larger females produced larger pups per litter (Fig. 5A; $R^2_{mass} = 0.83$; p < 0.0001; $R^2_{length} = 0.74$; $P < 0.0001$). Female size accounted for 83% of explained variation in mean pup size per litter. In contrast, litter size and the percent of maternal investments in litter mass were independent of female size (Fig. 5B; $R^2_{mass} = 0.00$; $P = 0.536$; $R^2_{length} = 0.02$; $P = 0.154$; Fig. 5C; $R^2_{mass} = 0.03$; $P = 0.080$; $R^2_{length} = 0.02$; $P = 0.162$). Moreover, pup size per litter was independent of litter size (Fig. 5D; $R^2_{mass} = 0.01$; $P = 0.331$; $R^2_{length} = 0.004$; $P = 0.553$). Median maternal investments across species were remarkably similar to those seen in female spinner and dusky sharks, but were broader in range. Using the median for these 89 shark species, females produced 11 pups (range = 1 to 300), invested 1.67% of their energy per pup (range = 0.07–8.0%), and invested 16.9% of their energy to produce each litter (range = 0.57–47.1%).

Species phylogeny accounted for 75% of explained variation in the positive relationship between female size and pup size (Regression: $R^2 = 0.75$; $F_{1,71} = 209.8$; $P < 0.0001$). However, species phylogeny accounted for less than 1% of the of explained variation in the independent relationship between female size and litter size ($R^2 = 0.005$; $F_{1,70} = 0.360$; $P = 0.550$).

In contrast to sharks, larger breeding teleost females did not invest in larger egg size (Fig. 6A; Regression: $R^2_{mass} = 0.00$; $P = 0.778$; $R^2_{length} = 0.00$; $P = 0.953$). Instead, larger teleost females invested in larger spawn size, i.e., a larger number of eggs (Fig. 6B; Regression: $R^2_{mass} = 0.76$; $P < 0.0001$; $R^2_{length} = 0.66$; $P < 0.0001$). In agreement with sharks, the relative maternal investment in spawn mass (egg size * egg number) was independent of female size (Fig. 6C; Regression; $R^2_{mass} = 0.00$; $P = 0.689$; $R^2_{length} = 0.02$; $P = 0.529$). Moreover, maternal investments in spawn size and egg size were independent (Fig. 6D; Regression; $R^2_{mass} = 0.01$; $P = 0.563$; $R^2_{length} = 0.00$; $P = 0.918$). Teleost females produced a median 132,000 eggs per spawn (range = 133–6,138,000), invested 0.00001% of their energy resources to produce each egg (range = 0.0000004–0.0001%), and invested 2.8% of their energy in spawn mass (range = 0.1–21.7%).
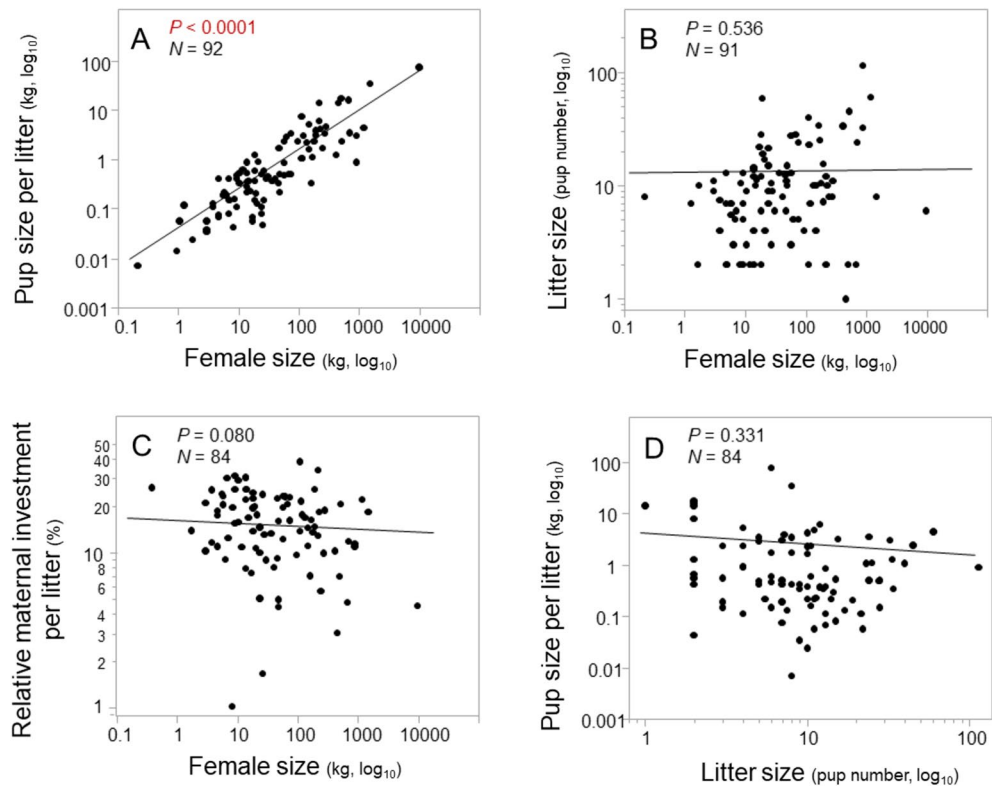
Fig. 5. Maternal investments across shark species. (**A**) Pup size by female size. (**B**) Litter size by female size. (**C**) Percent maternal investment per litter mass by female size. (**D**) Pup size by litter size.

Fig. 6. Maternal investments in egg size and number per spawn in teleost fish. (**A**) Egg size per spawn by female size per species. (**B**) Egg number per spawn by female size per species. (**C**) Percent maternal investment per spawn mass. (**D**) Egg size by egg number per species.

Fig. 7. Maternal investments by ecological-risk factors in sharks. (**A**) Female size by trophic position. (**B**) Pup size by trophic position. (**C**) Litter size by trophic position. (**D**) Female size by nursery use. (**E**) Pup size by nursery use. (**F**) Litter size by nursery use. (**G**) Female size by predation. (**H**) Pup size by predation. (**I**) Litter size by predation. The shaded areas around the regression slopes represent confidence intervals (0.95). For independent categorical variables, "I" bars represent the $\log_{10}$ mean $\pm \log_{10}$ SE. Lines visually represent changes between the means.
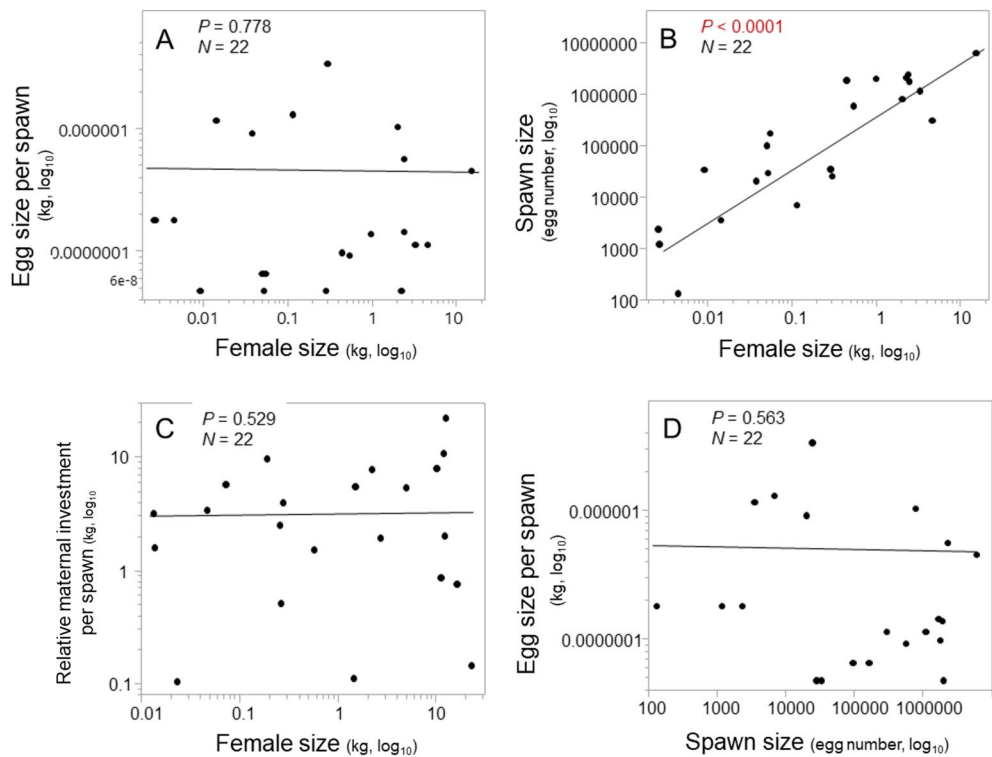
Maternal investments by ecological risk factors in sharks

Trophic position, our proxy for spatiotemporal gaps in prey availability, was a positive predictor of female size and pup size, but not litter size (Fig. 7A–C; Mixed model: $F_{1,1,1,1,1,1,\text{female size}} = 8.03$, $P = 0.006$; $F_{1,1,1,1,1,1,\text{pup size}} = 10.68$, $P = 0.001$; $F_{1,1,1,1,1,1,\text{litter size}} = 0.13$, $P = 0.717$). Nursery use was a positive predictor of pup size, but not female size or litter size (Fig. 7D–F; Mixed model: $F_{1,1,1,1,1,1,\text{female size}} = 2.09$, $P = 0.151$; $F_{1,1,1,1,1,1,\text{pup size}} = 8.01$, $P = 0.006$; $F_{1,1,1,1,1,1,\text{litter size}} = 0.01$, $P = 0.916$). Predation was a positive predictor of litter size, but not adult female size or pup size (Fig. 7G–I); Mixed model: $F_{1,1,1,1,1,1,1,\text{female size}} = 1.75$, $P = 0.189$; $F_{1,1,1,1,1,1,1,\text{pup size}} = 0.54$, $P = 0.463$; $F_{1,1,1,1,1,1,1,\text{litter size}} = 4.48$, $P = 0.037$). Interactive effects for trophic position x predation were not significant ($P_{\text{female size}} = 0.619$; $P_{\text{pup size}} = 0.762$; $P_{\text{litter size}} = 0.088$). Interactive effects for trophic position x nursery use were not significant ($P_{\text{female size}} = 0.844$; $P_{\text{pup size}} = 0.702$; $P_{\text{litter size}} = 0.893$); Interactive effects for nursery use x predation were not significant ($P_{\text{female size}} = 0.770$; $P_{\text{pup size}} = 0.615$; $P_{\text{litter size}} = 0.590$). Interactive effects for Trophic position x nursery use x predation were not significant ($P_{\text{female size}} = 0.300$; $P_{\text{pup size}} = 0.176$; $P_{\text{litter size}} = 0.372$).

We plotted maternal investments for 89 shark species and 22 teleost fish species (Fig. 8). The probability of starvation was eight orders-of-magnitude greater for sharks than teleost fish (median = $1.67e-2_{\text{sharks}}$ vs $6.9e-10_{\text{teleosts}}$). In contrast, the probability of predation was eight orders of magnitude greater for teleost fish than sharks (median = $8.000e-1_{\text{sharks}}$ vs $9.9998e-9_{\text{teleosts}}$). To ensure replacement fitness, the average shark invested 5.4 million times more energy per pup than the average teleost fish invested per egg (median: 0.54 kg per pup vs 0.0000001 kg per egg). On the other hand, the average teleost fish produced 12,000 times more offspring than the average shark per reproductive event (median: 132,000 eggs per spawn vs 11 pups per litter).
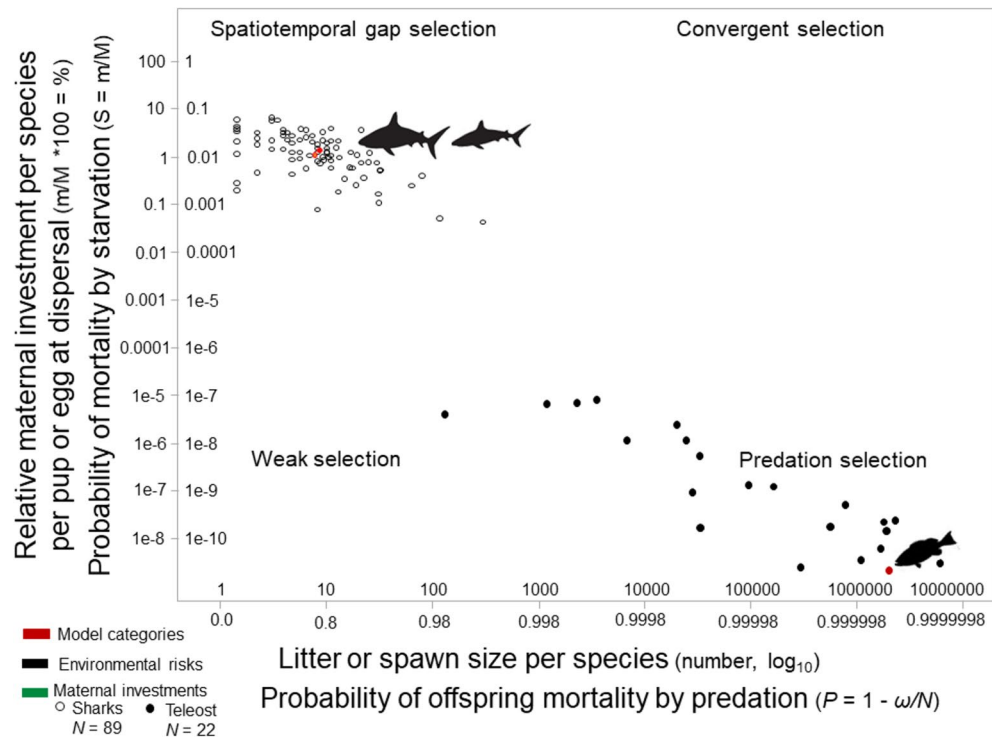
Fig. 8. The maternal risk management model's predicted probabilities of mortality in sharks and teleost fish. The "y" axis represents the relative maternal investment per pup and egg at dispersal (m/M). The "x" axis represents litter size and spawn size per species (N). Clear circles represent shark species ($N = 89$); black circles represent teleost fish species ($N = 22$). Silhouettes and red circles indicate spinner and dusky sharks, *C. brevipinna, C. obscurus*, and the greasy grouper, *Epinephelus tauvina*.

Discussion

Across 89 shark species, we show that maternal investments in pup size and litter size were independent investment traits. Likewise, across 22 teleost fish species, maternal investments in egg size and spawn size were independent. Our findings agree with other interspecific metadata studies in teleosts[67–69], birds[70], reptiles[71–73], and humans[29]. Among 136 breeding spinner shark females, pup size and litter size were independent maternal investment traits. Among 228 breeding dusky shark females, the relationship between pup size and litter size was negative, suggesting an investment trade-off. However, this negative relationship does not meet the zero sum trade-off required by life history models as litter size accounted for less than 3% of variation in pup size, leaving more than 97% of this relationship unexplained. Rather than interpreting this negative relationship as an investment trade-off[14], we offer an alternative interpretation. Maternal investments by the spinner shark and the dusky shark arise from species-specific differences in the intensity of ecological risk factors.

Dusky sharks are nomadic hunters at depths up to 80 m in mid-pelagic polar-regions during summer months and in mid-pelagic equatorial-regions during winter months[74]. In contrast, spinner sharks hunt at depths of 10 to 30 m along coastal and continental shelf environments[75]. The maternal risk management model allows us to reverse engineer a hypothetical cause and effect for the convergence in litter size, but a divergence in pup size between the two species. The female body size and pup size of dusky sharks increased to nearly twice the size of spinner sharks as a replacement fitness adaptation to their seasonal migratory life style. Larger prey and larger schools of prey were available, but at a cost of extended gaps between prey and exposure to colder polar waters[74]. In short, we speculate that the dusky shark's negative pup-size/litter-size investment relationship is a reproductive trait in response to a lower risk of pup mortality by predation relative to a pup's risk of starvation while hunting for prey in polar waters.

We acknowledge that our ecological risk metrics are approximations that are not fully independent measures of starvation and predation risks. For example, some juvenile sharks show morphological traits that improve swimming abilities that enhance an individuals' anti-predatory performance and its hunting abilities[76]. Studies have demonstrated that when starved, juvenile and adult sharks enter a state of metabolic depression to conserve energy[77–79]. This adaptation, while beneficial in the short term, may have detrimental long-term effects on health and survival. Research indicates undernourished sharks exhibit reduced growth rates, lower body mass, and compromised body condition[80]. Undernourishment may affect their ability to compete for mates, evade predators, and efficiently capture prey. Females with insufficient food intake may produce fewer and lower quality pups, leading to reduced pup survival rates[81]. Nutritional insecurity in sharks has implications for trait evolution, population replacement, and the long-term viability of shark species.

Perhaps the most striking finding of our study is the difference in the risks of predation and starvation between shark pups and teleost fish eggs (Fig. 8). The ecological challenge for teleost eggs and larvae is that they are at a similar trophic level to the eggs and larvae of carnivorous invertebrates such as nauplii and calanoid copepods[82] and to filter feeders. Consequently, to ensure replacement fitness in high predation environments, the average teleost female in our study produced 132,000 eggs, 12,000 times more offspring than the average shark. The ecological challenge for sharks is that they occupy higher trophic positions and, depending on species, may often experience extended gaps between successful hunts[53]. To ensure replacement fitness in an environment with gaps in prey availability or successful prey capture, the average shark in our study invested 5.4 million times more energy per pup than the average teleost fish invested per egg.

From a natural selection perspective, offspring represent crude experiments out of which two may survive to sexual maturity to replace each breeding female and her mate(s). If we focus our field research on expanding our knowledge of life history traits, we can better understand the local ecological risk factors, predation, starvation, and mass mortality events, that affect offspring mortality rates within and across populations.

Currently, the maternal risk management model does not adequately account for the ontogenetic changes in habitat and diet that occur as sharks grow from juveniles to adults. This knowledge gap between life stages complicates our understanding of starvation risks in juveniles, as they typically hunt smaller prey than adults. Ontogenetic shifts in diet may be related to changes in foraging ability and the expansion of habitat use associated with reduced predation risk as juveniles grow[83–85].

Similarly, this model does not fully address other factors that may contribute to relative predation risk in juvenile sharks, including pupping or egg-laying habitat selection by breeders or nursery use by offspring. Historically, nursery use is thought to be driven by increased resource availability and reduced risk of predation[86,87]. However, there are studies suggesting that all nursery use may not have the same drivers, or that neither resource availability nor reduced risk of predation appears to shape habitat use within nurseries[88]. Finally, the model does not address environmental risks and constraints such as temperature, dissolved oxygen levels, depth, or salinity[89,90] which may select for avoidance of inter- and intraspecific competition and morphological and physiological differences between juveniles and adults[85]. This is an important area for future model development as data availability improves.

Until we resolve deficiencies in available data and current understanding of life histories, particularly the environmental and ecological risk factors that challenge the survival of each generation of offspring within and across species, our grasp of the interconnected interactions of ecology and evolution remains incomplete. In conclusion, we invite consideration of the maternal risk management model as a new tool to increase our understanding of the complex environmental and ecological risk factors that have shaped the diversity of species for more than 3.7 billion years of life on our planet[91–93].

Data availability
The datasets used and analyzed during this study are available in Excel format from the corresponding author upon reasonable request.

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Author contributions

DD collected the shark data, analyzed the data, completed all graphics, wrote the first draft and read the final draft. CM added four columns of shark data, strengthened the Methods and Discussion sections and competed line edits to the final draft. AG competed the phylogeny analysis in sharks and read the final draft. MLG edited an early draft and read the final draft. DLC conceived the study, supervised the project, finalized data analysis and figures, and wrote the final draft. All authors reviewed the manuscript prior to submission.

Competing interests

The authors declare no competing interests.

Additional information

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