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REVIEWS

It's a shark-eat-shark world, but does that make for bigger pups? A comparison between oophagous and non-oophagous viviparous sharks

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Abstract Oophagous reproduction (i.e., consumption of unfertilized ova in utero) in sharks has been hypothesized to result in fewer but larger pups relative to those produced by viviparous sharks with different modes of maternal nutrient transfer. We compared pup and litter sizes reported in the literature for 106 shark species with lecithotrophic viviparity, oophagy, and placental viviparity as methods of maternal nutrient transfer during pregnancy. Using a suite of permutational tests, we accounted for the effect of maternal size to test whether oophagous strategies do indeed result in larger pups and smaller litters relative to sharks with lecithotrophic and placental viviparous reproduction. Our results demonstrated that litter size was significantly reduced in species with oophagous reproduction relative to sharks with lecithotrophic and placentally viviparous reproduction. Further, the influence of oophagous reproduction on pup length was more variable, and generally pup length of oophagous species was only larger than sharks with lecithotrophic viviparous reproduction. However, when maternal investment was expressed as litter mass (minimum pup mass by litter size), the effect of oophagy was neutralized. We found further evidence that pup length at birth was directly modulated by litter size and habitat, suggesting pup length at birth may also be adapted to conditions at nursing grounds. Our study supports the hypothesis that both placentally viviparous and lecithotrophic viviparous species maximize their reproductive fitness by allocating nutrients to larger litters of pups, whereas oophagous species maximize reproductive fitness through smaller litters of pups that may be well adapted to their nursing grounds.

Keywords Elasmobranch · Maternal investment · Matrotrophy · Oophagy · Reproductive biology · Vivparity

Introduction

Sharks represent a diverse array of more than 500 species of cartilaginous fishes that have adapted to a

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multitude of climates, habitats, and ecological niches (Weigmann 2016). Sharks are *K*-selected species, as their life histories typically comprise long lifespans with slow development to maturity and low fecundity (Wourms 1977; Dulvy and Forrest 2010). Since sharks do not provide postnatal care to their young, they rely on other reproductive strategies requiring high maternal investment to improve the survivorship of their offspring (Compagno 1984; Cortés 2000). The majority of sharks are viviparous, giving live birth to offspring that are fully developed and prepared for life after parturition (Wourms 1977; Musick and Ellis 2005). Viviparous sharks have evolved a broad range of reproductive modes with variation in nutrient transfer from the female to the developing embryos, with reproductive strategies defined by how embryos are nourished during pregnancy.

Reproductive modes in viviparous sharks exist on a continuum of maternal investment, with lecithotrophy and matrotrophy representing opposite extremes of nutrient transfer during pregnancy (Musick and Ellis 2005; Buddle et al. 2019). All viviparous sharks are initially lecithotrophic, supplying individual embryos with a finite reserve of nutrients via yolk while developing in utero (Wourms 1977). For some viviparous species, lecithotrophy is the sole mechanism for nutrient transfer during the entirety of development (hereafter, "lecithotrophic viviparity"; observed in every extant order of sharks except Heterodontiformes and Lamniformes, Musick and Ellis 2005). Embryos of lecithotrophic viviparous sharks will eventually lose c. $\geq 20\%$ of their initial organic mass by the end of the developmental period as their individual nutrient stores are metabolized (Hamlett et al. 2005; Huveneers et al. 2011). In other cases, multiple mechanisms of nutrient transfer will occur for a single species over the course of embryonic development. For species with matrotrophic viviparity, additional extravitelline nutrients are supplied to their offspring at different stages of gestation (Musick and Ellis 2005; Ostrovsky et al. 2016).

Matrotrophy via embryonic consumption of histotroph is the least recently evolved method of nutrient transfer during pregnancy (Musick and Ellis 2005) wherein embryos receive additional nutrition from uterine secretions (e.g., mucus in muccoid histotrophy and histophagy, Hamlett 1989; egg capsule fluids in embryotrophy, Castro et al. 2016; lipid-rich uterine fluids in lipid histotrophy, Sato et al. 2016). Histotrophy has been observed in species within the superorder Squalomorphii (Hexanchiformes, Squaliformes, Squantiformes, and Pristiophoriformes) and can exist in combination with other forms of matrotrophy, such as within placentally viviparous members of the order Carcharhiniforms (Musick and Ellis 2005), and in the oophagous white shark *Carcharodon carcharias* (order: Lamniformes, see below). The most recently evolved form of matrotrophy in sharks is placental viviparity, where each embryo develops a yolk sac placenta that facilitates nutrient transport from maternal uterine tissues to the embryos after the depletion of their yolk stores (Wourms 1981). The majority of placentally viviparous sharks remain within their egg capsules during development with nutrient transport occurring across the capsule membrane (Buddle et al. 2019, 2021). This reproductive mode has only been observed within five families, all belonging to the order Carcharhiniformes (Wourms and Lombardi 1992; Conrath and Musick 2012).

Matrotrophic oophagy (hereafter, "oophagy") is an adaptation in which developing embryos consume unfertilized ova during gestation after the depletion of its yolk stores. Oophagy is thought to occur in all sharks belonging to the order Lamniformes (Gilmore 1993; Gilmore et al. 2005), as well as in the carcharhiniform family Pseudotriakidae (Yano and Musick 1992; Conrath and Musick 2012) and in the orectolobid tawny nurse shark *Nebrius ferrugineus* (Teshima et al. 1997). Lamnoid oophagy involves continued ovulation during the gestation period, which provides embryos with unfertilized ova during pregnancy which are located and consumed after the embryo exits its egg capsule (Musick and Ellis 2005). In carcharhiniform oophagy, a finite number of ova are provided to each embryo that are contained within its associated egg capsule (Musick and Ellis 2005). Orectolobiform oophagy more closely resembles lamnoid oophagy, with embryonic *N. ferrugineus* having been found to be highly motile in utero, moving between the left and right uterus, likely as a behavioral adaptation to locate ova (Tomita et al. 2019). The embryos of at least one oophagous species, *C. carcharias*, have been observed to engage in lipid histotrophy, the consumption of lipid-rich uterine secretions. This behavior likely precedes the oophagous phase (Sato et al. 2016). Embryos of at least two lamniform species, sand tiger shark *Carcharias taurus* and shortfin mako shark *Isurus oxyrinchus*, have been observed to perform intrauterine cannibalism of their siblings (i.e., adelphophagy) in addition to oophagy (Gilmore 1993; Joung and Hsu 2005). However, adelphophagy is not ubiquitous in Lamniformes. In contrast to the likely opportunistic occurrence of adelphophagy of runts and dead embryos with the benefit of additional nutrients observed in *I. oxyrinchus* (Castro 2013), embryos of *C. taurus* actively hunt and feed on their siblings as adelphophagy is required in order to obtain the nutrients necessary to complete embryonic development before parturition (Gilmore et al. 2005; White 2007). Once the largest *C. taurus* embryo in each uterine horn has reached a size of c. 100 mm and exhausted its yolk reserves, it will begin to depredate its smaller siblings (Gilmore et al. 2005). *C. taurus* embryos have been noted to favor cannibalism over the consumption of unfertilized ova, although once a single embryo remains within a uterine horn it will engage in oophagy (Musick and Ellis 2005).

Oophagous reproductive modes are assumed to benefit sharks by allowing them to invest more energy into fewer, larger offspring. Maternal investment should be optimized to maximize offspring survival while minimizing the energetic cost to the parent (Williams 1966). Therefore, for oophagous species, the potential trade-off between litter size and the amount of nutrients or space the mother is able to provide each embryo during pregnancy may result in larger pups that may have lower predation risk after they are born, while also increasing the potential for pups to select from a wider variety of prey in their environment (Gilmore et al. 2005; Parsons et al. 2008; Oliveira et al. 2010).

To our knowledge, the effect of oophagy on pup size has not been quantified using modern datasets. Currently, more than one-third of shark species are threatened with extinction (Dulvy et al. 2021) and understanding reproduction will be essential to guide conservation strategies and gauge the potential for species recovery. Herein, we tested the hypotheses that oophagous reproduction result in larger pups and smaller litters in a comparison of oophagous viviparous sharks to viviparous sharks that are lecithotrophic or placentally viviparous (Compagno 1977; de Carvalho 1996). We also explored relationships between fecundity, gestation period, and maternal and pup sizes (expressed both in terms of length and mass) to determine how reproductive variables are expressed along a maternal size continuum within each reproductive mode. Additionally, we quantified the relative importance of ecology (e.g., adult habitat utilization) on pup sizes. We predicted that oophagous sharks are born at larger sizes relative to maternal size than viviparous lecithotrophic species, and that oophagous sharks will have smaller litters than sharks using other viviparous strategies.

Methods

Data collection

We reviewed the available peer-reviewed and grey (e.g., books, government reports, theses, and online databases) literature on shark size and reproduction. We limited data collection to shark species belonging to the orders Squaliformes ($n = 16$ spp., c. 12% of extant species), Hexanchiformes ($n = 5$ spp., c. 71% of extant species), Carcharhiniformes ($n = 60$ spp., c. 30% of extant species), Lamniformes ($n = 13$ spp., c. 87% of extant species), and Orectolobiformes ($n = 12$ spp., c. 28% of extant species; Table 1). We selected sharks based on their reproductive mode, with the goal of comparing oophagous species with lecithotrophic (i.e., lower maternal investment) and placentally viviparous (i.e., higher maternal investment) species across a comparable range of body sizes. Although some species of non-oophagous, non-placentally viviparous sharks also contribute a substantial energetic investment toward the production of extravitelline nutrients for their embryos (e.g., embryotrophic tiger sharks, *Galeocerdo cuvier*), others contribute much less and to the degree that these species were initially misidentified as lecithotrophic (Conrath and Musick 2012; Cotton et al. 2015). As there are insufficient available data to reconstruct the broad continuum of maternal energy investment for our analyses, viviparous species thought to rely primarily on any form of histotrophy during embryo development were not considered in this study. Whenever possible, we included replicates (i.e., any additional observation of size or reproductive variables for the same species, regardless of sampling location; range of replicates per species = 1–13, median replicates per species = 2). We recorded the sampling location of each study and classified it into larger geographic regions (hereafter, "ecoregion"; see Supplemental Methods).

Table 1 Categorization of reproductive modes with the corresponding taxonomic orders and families included within each mode

Reproductive Mode	Order	Family (*n* = species)
Oophagy	Carcharhiniformes	Pseudotriakidae (2)
	Lamniformes	Alopiidae (3) Cetorhinidae (1, *Cetorhinus maximus*) Lamnidae (5) Megachasmidae (1, *Megachasma pelagios*) Odontaspididae (2) Pseudocarchariidae (1, *Pseudocarcharias kamoharai*)
	Orectolobiformes	Ginglymostomatidae (1, *Nebrius ferrugineus*)
Lecithotrophic viviparity	Squaliformes	Somniosidae (5) Squaliformes (11)
	Hexanchiformes	Hexanchidae (5)
	Orectolobiformes	Brachaeluridae (2) Ginglymosomatidae (1, *Ginglymostoma cirratum*) Orectolobidae (7) Rhincodontidae (1, *Rhincodon typus*)
Placental viviparity	Carcharhiniformes	Carcharhinidae (48) Hemigaleidae (4) Sphrynidae (6)

From our literature review, we recorded adult female and pup sizes (in meters, m, and kilograms, kg). Specifically, we recorded maximum female length, minimum female length at maturity (the length at which 50% of females belonging to a population are sexually mature [L_{50}]), minimum and maximum pup length, maximum female mass, female mass at maturity, and minimum pup mass. When length values were not associated with an observed mass (i.e., the mass of the specimen was not reported), mass was estimated using minimum pup length, minimum female length at maturity, and maximum female length values in length–weight functions from primary and grey literature. For some species, length–weight functions differ with ecoregions (e.g., pelagic thresher *Alopias pelagicus*); therefore, we used ecoregion-specific length–weight functions to compute mass when we had corresponding lengths from the same ecoregion (see Supplemental Methods for more detail). For species that are widely distributed but data limited (i.e., basking shark *Cetorhinus maximus*, longfin mako shark *I. paucus*, megamouth shark *Megachasma pelagios*, smalltooth sand tiger shark *Odontaspis ferox*, whitenose shark *Nasolamia velox*, sharpnose sevengill shark *Heptranchias perlo*, and whale shark *Rhincodon typus*), it was not possible to obtain biological information regionally, and instead are represented by all known data at the species level (Appendices 1–4).

Additionally, we collected data on shark reproductive biology. We recorded reproductive mode (i.e., oophagic, lecithotrophic, and placentally viviparous), median and maximum litter size, and gestation period (in months). For litter sizes, we avoided recording minimum reported litter size because these values may be artificially biased due to the occurrence of stress-induced abortion during landing (Adams et al. 2018). Because we had relatively fewer observations of gestation period, we averaged gestation period at the species level for analysis.

Lastly, we collected habitat utilization and depth range data for each species. We defined habitat use as neritic (coastal species utilizing areas from the coast up to the continental shelf), oceanic (offshore species utilizing areas beyond the shelf), or both (species utilizing both coastal and oceanic areas). We defined depth range as epipelagic (maximum reported depths are ≤ 200 m), mesopelagic (maximum reported depths are 201–1000 m), and bathypelagic (maximum reported depths are > 1000 m). Habitat utilization and depth range data were obtained from the primary literature, Fish Base (Froese and Pauly 2016), and the International Union for Conservation of Nature (IUCN 2017).

Statistical analyses

All analyses were performed in the statistical computing environment R, ver. 4.1.1 (R Core Development Team 2021). In our analyses, we (1) determined whether pup and litter sizes were independent of maternal size, (2) tested for mean differences in pup and litter size ratios between reproductive modes, and (3) assessed the relative importance of biological (i.e., size and reproductive variables) and environmental variables in regulating pup size ratios using the methods described below.

Because larger shark species tend to produce larger pups and that maternal size can influence litter size (Cortés 2000), we examined the strength of these associations in our dataset. We used Kendall's rank correlation coefficient (τ, used as our data were not normally distributed; Croux and Dehon 2010) and tested for significant associations between pup size, litter size, and female size based on the average values for each species. We also tested for an association in maximum female length and gestation period using Kendall's rank correlation. Significant correlations ($\alpha \leq 0.05$) indicated that pup or litter sizes were not independent of maternal size and thus warranted analysis of size ratios to account for effects of maternal size. Based on our findings, we then generated four ratios of the length of pups relative to the length of the mother (Table 2a), four ratios of litter size relative to the length of the mother (Table 2b), and four ratios of pup mass relative to the mass of the mother (Table 2c) to be used in the next steps of our analyses. For maximum length-based ratios, total length (TL) was used.

Table 2 (a) Length (m) ratios, (b) litter ratios (number of pups), and (c) mass (kg) ratios to represent sizes of pups and litters after adjustment for female size

(a) Length ratio	Definition	Based on
minPL/maxFL	Minimum reported pup length divided by maximum recorded female length	Cortés (2000), Parsons et al. (2008)
maxPL/maxFL	Maximum reported pup length divided by maximum recorded female length	Cortés (2000), Parsons et al. (2008)
minPL/minFLM	Minimum reported pup length divided by female length at maturity (L_{50})	Parsons et al. (2008)
maxPL/minFLM	Maximum reported pup length divided by female length at maturity (L_{50})	Parsons et al. (2008)

(b) Litter ratio	Definition	Based on
medLS/maxFL	Median reported litter size divided by maximum recorded female length	Cortés (2000), Parsons et al. (2008)
maxLS/maxFL	Maximum reported litter size divided by maximum recorded female length	Cortés (2000),Parsons et al. (2008)
medLS/minFLM	Median reported litter size divided by female length at maturity (L_{50})	This study
maxLS/minFLM	Maximum reported litter size divided by female length at maturity (L_{50})	This study

(c) Mass ratio[1]	Definition	Based on
minPM/maxFM	Estimated minimum pup mass at parturition divided by estimated mass for the largest recorded female	This study
minPM/minFMM	Estimated minimum pup mass at parturition divided by estimated mass for minimum female mass at maturity (L_{50})	This study
(minPM × maxLS)/maxFM	Estimated minimum mass of the largest litter size divided by estimated mass of maximum recorded female	This study
(minPM × maxLS)/minFMM	Estimated minimum mass of largest litter size divided by estimated mass for minimum female mass at maturity (L_{50})	This study

[a] When multiple length–weight functions were available for sharks for the same ecoregion, the outputs of the functions were averaged to obtain a single mass estimate for each ecoregion; see Supplemental Methods

Next, we tested whether oophagous reproductive modes (i.e., matrotrophic viviparity with oophagy, as observed in species of Lamniformes, two species of Carcharhiniformes and one species of Orectolobiformes) result in larger pups and smaller litters. We detected severe violations of normality and homogeneity of variances for our size ratios that could not be resolved through transformations. Thus, we employed a permutation-based approach to compare the size ratios between reproductive modes (see Supplemental Methods). This analytical approach creates a custom null distribution for each comparison and allows us to quantify the probability that a difference between reproductive modes would occur if there was no true difference (Hooton 1991). In this analysis, we used the mean difference for each size ratio (comparing oophagy-lecithotrophic viviparity and oophagy-placental viviparity separately) as our critical effect size. For each ratio, we generated 10,000 permutations of our data and calculated *P*-values calculated as follows:

$$P = (\mathrm{b} + 1)/(\mathrm{m} + 1)$$

where b is the number of permutations with a mean difference equal to or more extreme than the critical effect size, and m is the total number of permutations (Phipson and Smyth 2010). Because pup sizes were hypothesized to be larger and litter size presumed to be smaller among species with oophagous reproductive strategies, all *P*-values calculated were one-tailed. We ran analyses with and without species belonging to the family Alopiidae (due to unique tail morphology) and *R. typus* (due to their massive size) to determine if any of our results were influenced (skewed) by body size of these species.

Since reproductive mode could consistently explain differences in litter size ratios but not pup size ratios (see Results), we then quantified the relative importance of biological and environmental variables on pup size at birth. To employ a conservative approach in our analyses, we used the ratio of minimum pup length and maximum female length (Table 2a) as the dependent variable. Because we found evidence that litter size was regulated by oophagy, we selected the maximum litter size and maximum female length ratio (Table 2b) as a biological explanatory variable. Additionally, we included depth and habitat as ecological explanatory variables. To simplify these analyses by reducing degrees of freedom, we reduced the number of depth categories to two (epipelagic: depth $\leq$ 200 m; meso/bathypelagic: depth $>$ 200 m). We did not consider gestation period here, as we detected significant correlations with maximum female length (see Results). We included all two- and three-way interactions among possible explanatory variables in our analyses. We used bootstrapped stepwise linear regressions in the R package *bootStepAIC* (Rizopoulos 2009) with 10,000 bootstrap samples (sampled with replacement) to fit the linear models. We summarized the percentage of times each variable was selected as an independent predictor in our most parsimonious model for each bootstrap sample, as well as the mean parameter estimates with confidence intervals.

Results

Description of data

On average, minimum pup length (m) was greatest for oophagous species ($\bar{x} \pm$ SE: 0.99 ± 0.05 m, $n = 55$ observations of 16 species) followed by placentally viviparous ($\bar{x} \pm$ SE: 0.54 ± 0.01 m, $n = 240$ observations of 58 species) and lecithotrophic species ($\bar{x} \pm$ SE: 0.30 ± 0.01 m, $n = 86$ observations of 32 species; Fig. 1a). Conversely, maximum litter size (pups per litter) was smallest among species with oophagy ($\bar{x} \pm$ SE: 5.63 ± 0.64 pups, $n = 49$ observations of 14 species), with placentally viviparous ($\bar{x} \pm$ SE: 14.0 ± 1.00 pups, $n = 200$ observations of 56 species) and lecithotrophic species ($\bar{x} \pm$ SE: 40.8 ± 9.12 pups, $n = 71$ observations of 27 species) having larger litters (Fig. 1b). When considering maximum female length (m), oophagous species were on average larger ($\bar{x} \pm$ SE: 3.98 ± 0.24 m, $n = 55$ observations of 16 species) than placentally viviparous ($\bar{x} \pm$ SE: 2.17 ± 0.06 m, $n = 241$ observations of 58 species) and lecithotrophic species ($\bar{x} \pm$ SE: 2.75 ± 0.46 m, $n = 86$ observations of 32 species; Fig. 1c). However, maximum female mass (kg) of lecithotrophic species were greater ($\bar{x} \pm$ SE: 6267.1 ± 2525.7 kg, $n = 45$ observations of 21 species) than both oophagous ($\bar{x} \pm$ SE: 809.0 ± 302.2 kg, $n = 25$ observations of 11

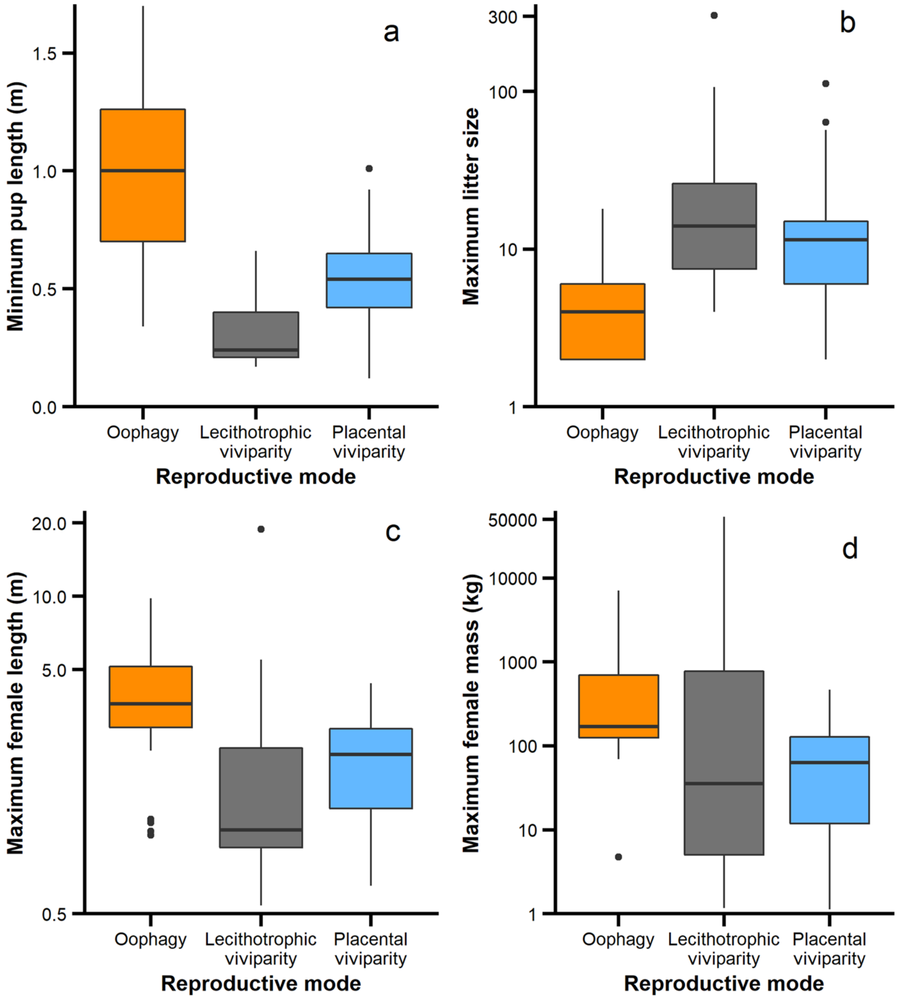

Fig. 1 Morphometric measure of (**a**) minimum pup length (m), (**b**) maximum litter size ($\log_{10}$ scale), (**c**) maximum female length (m, $\log_{10}$ scale), and maximum female mass (kg, $\log_{10}$ scale) for 16 oophagous (orange), 32 lecithotrophic species (grey), and 58 placentally viviparous (blue) species

species) and placentally viviparous sharks ($\bar{x} \pm$ SE: 88.7 ± 7.4 kg, $n = 158$ observations of 46 species; Fig. 1d).

Correlations

There were strong, positive correlations between minimum pup length and maximum female length, which were significant for all three reproductive modes (oophagy: $\tau = 0.70$, $P < 0.001$, $n = 16$; placental viviparity: $\tau = 0.67$, $P < 0.001$, $n = 58$; lecithotrophy: $\tau = 0.64$, $P < 0.001$, $n = 32$; Fig. 2a), and which were nearly identical to the values for minimum pup length and minimum length at maturity (oophagy: $\tau = 0.73$, $P < 0.001$, $n = 15$; placental viviparity: $\tau = 0.68$, $P < 0.001$, $n = 52$; lecithotrophy: $\tau = 0.56$, $P < 0.001$, $n = 30$; Fig. 2b). There was no significant correlation between minimum pup length and maximum female mass for oophagous species ($\tau = 0.35$, $P = 0.16$, $n = 11$), although significant relationships were found for placentally viviparous ($\tau = 0.68$, $P < 0.001$, $n = 46$) and lecithotrophic species ($\tau = 0.72$, $P < 0.001$, $n = 21$; Fig. 2c).

When examining litter size ratios, we found significant correlations between maximum litter size and maximum female length for lecithotrophic ($\tau = 0.74$, $P < 0.001$, $n = 27$) and placentally viviparous species ($\tau = 0.43$, $P < 0.001$, $n = 56$) but not for oophagous species ($\tau = 0.19$, $P = 0.37$, $n = 14$; Fig. 2d), with similar results when considering minimum length at maturity (lecithotrophy: $\tau = 0.77$, $P < 0.001$, $n = 26$; placental viviparity: $\tau = 0.36$, $P < 0.001$, $n = 52$; oophagy: $\tau = 0.26$, $P = 0.24$, $n = 13$; Fig. 2e). When considering the correlation

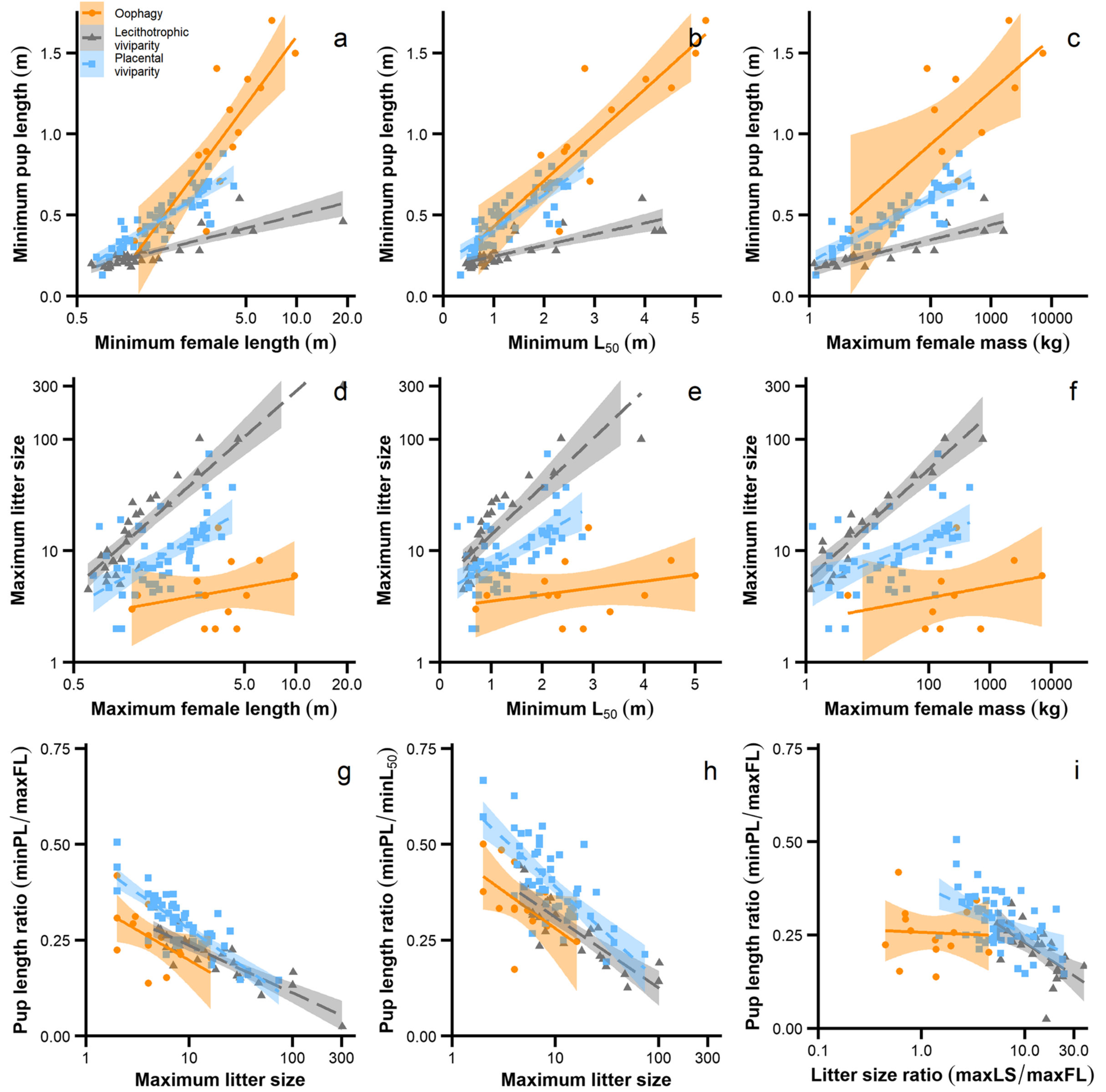

Fig. 2 Relationships (and standard errors) between (**a–c**) minimum pup length and maximum female sizes, (**d–f**) maximum litter size and maximum female sizes, (**g–i**) pup size ratios and litter sizes for 16 oophagous (orange), 32 lecithotrophic (grey), and 58 placentally viviparous (blue) species

between maximum litter size and maximum female mass, we again found the strongest correlations for lecithotrophic ($\tau = 0.82$, $P < 0.001$, $n = 18$) and placentally viviparous species ($\tau = 0.30$, $P = 0.004$, $n = 43$) but not for oophagous species ($\tau = 0.39$, $P = 0.14$, $n = 10$; Fig. 2f).

When considering a possible relationship of minimum pup length/maximum female length and maximum litter size, we found strong, negative correlations across all reproductive modes (lecithotrophy: $\tau = -0.67$, $P < 0.001$, $n = 27$; placental viviparity: $\tau = -0.59$, $P < 0.001$, $n = 56$; oophagy: $\tau = -0.49$, $P = 0.02$, $n = 14$; Fig. 2g) which was also similar when considering minimum pup length/minimum length at maturity (lecithotrophy: $\tau = -0.71$, $P < 0.001$, $n = 26$; placental viviparity: $\tau = -0.49$, $P < 0.001$, $n = 52$; oophagy: $\tau = -0.58$, $P = 0.008$, $n = 13$; Fig. 2h). The effect of maternal length on pup length and litter sizes (i.e., minimum pup length/maximum female length and maximum litter size/maximum female length) were negatively correlated for lecithotrophic ($\tau = -0.51$, $P < 0.001$, $n = 27$) and placentally viviparous species ($\tau = -0.27$, $P = 0.003$, $n = 56$), but not for oophagous species ($\tau = -0.08$, $P = 0.75$, $n = 14$; Fig. 2i).

For all reproductive modes, we found significant correlations of mean gestation period and maximum female length. For both oophagous and placentally viviparous species, gestation period was greater for larger females (oophagy: $\tau = 0.65$, $P = 0.03$, $n = 8$; placental viviparity: $\tau = 0.21$, $P = 0.04$, $n = 48$), though the opposite was true for lecithotrophic species ($\tau = -0.49$, $P = 0.04$, $n = 11$).

Permutational analysis

We found that pups length ratios of oophagous species were consistently larger than species with lecithotrophic reproductive modes (Fig. 3a). When compared to placentally viviparous species, pup length ratios of oophagous species were greater only when length ratios were based on maximum pup length and female length at maturity (Fig. 3a). In fact, by accounting for maternal length, some mean length ratios of species with oophagous reproductive modes were exceeded by those of placentally viviparous species, although these differences were non-significant (Table 3a). When assessing litter size ratios, we found that all significantly differed between reproductive modes (Fig. 3b), with oophagous species having smaller litters than those of species with other reproductive modes for all comparisons (Table 3b). For mass ratios, we found some mixed results; the minimum pup mass/maximum female mass ratio significantly differed between the oophagous and non-oophagous reproductive modes, though this was less apparent when maternal size was expressed as minimum mass at maturity (Fig. 3c, Table 3c). When reproductive output was expressed as litter mass (minimum pup mass × maximum litter size), we found no effect of reproductive mode when controlling for maximum female mass; however, we did detect significantly greater litter mass in placentally viviparous species over oophagous species when accounting for female mass at maturity (Fig. 3c, Table 3c).

The exclusion of the family Alopiidae nor *R. typus* did not change the significance levels of any of our permutation comparisons.

Bootstrap modelling

The stepwise bootstrap modelling exercise most frequently selected the maximum litter size ratio (maximum litter size/maximum female length) and habitat as the two variables that best explained the minimum pup length/maximum female length ratio (Table 4). The most parsimonious model

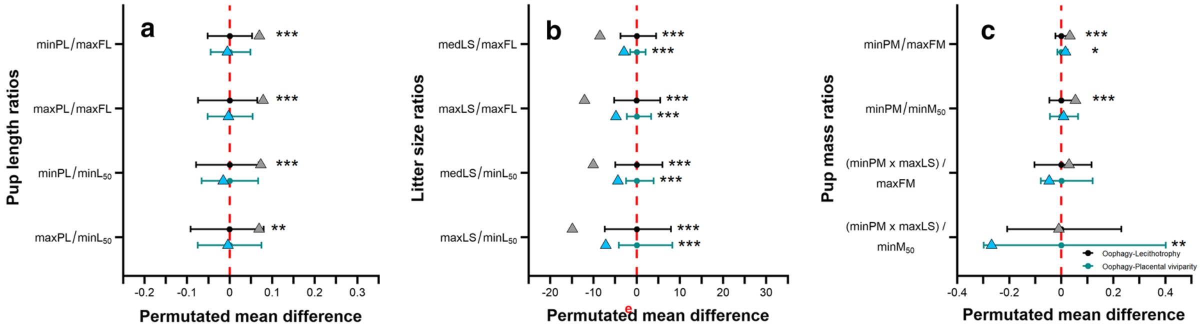

Fig. 3 Permutational mean differences for oophagous and lecithotrophic (black points and error bars) and oophagous and placentally viviparous (blue points and error bars) species for each of the (**a**) pup length ratios, (**b**) litter size ratios, and (**c**) pup mass ratios analyzed. Error bars represent the range of permutational mean differences. Triangles represent the observed mean difference between reproductive modes. Asterisks indicate significance: $^{*}P < 0.05$, $^{**}P < 0.01$, $^{***}P < 0.001$

Table 3 Observed mean (and 95% confidence intervals) of (a) pup length ratios, (b) litter size ratios, and (c) pup mass ratios of each reproductive mode for 16 oophagous, 32 lecithotrophic, and 58 placentally viviparous species

(a) Length ratio	Oophagy	Lecithotrophic viviparity	Placental viviparity
minPL/maxFL	0.27 (0.25–0.29)	0.20 (0.18–0.21)	0.27 (0.26–0.28)
maxPL/maxFL	0.31 (0.28–0.33)	0.23 (0.21–0.25)	0.31 (0.30–0.32)
minPL/minFLM	0.35 (0.32–0.38)	0.28 (0.25–0.30)	0.36 (0.35–0.38)
maxPL/minFLM	0.39 (0.36–0.43)	0.33 (0.30–0.35)	0.40 (0.38–0.42)
(b) Litter ratio	**Oophagy**	**Lecithotrophic viviparity**	**Placental viviparity**
medLS/maxFL	1.28 (1.02–1.56)	9.83 (8.43–11.23)	4.26 (3.82–4.70)
maxLS/maxFL	1.66 (1.29–2.03)	13.79 (12.20–15.37)	6.47 (5.76–7.17)
medLS/minFLM	1.85 (1.47–2.22)	11.94 (10.24–13.64)	6.21 (5.45–6.98)
maxLS/minFLM	2.45 (1.91–2.99)	17.38 (15.35–19.41)	9.63 (8.38–10.87)
(c) Mass ratio	**Oophagy**	**Lecithotrophic viviparity**	**Placental viviparity**
minPM/maxFM	0.04 (0.02–0.06)	0.01 (0.00–0.01)	0.02 (0.02–0.03)
minPM/minFMM	0.07 (0.04–0.11)	0.02 (0.01–0.03)	0.07 (0.06–0.08)
(minPM × maxLS) / maxFM	0.14 (0.05–0.23)	0.11 (0.08–0.14)	0.19 (0.17–0.20)
(minPM × maxLS) / maxFMM	0.28 (0.14–0.41)	0.29 (0.20–0.37)	0.55 (0.49–0.61)

Table 4 Percentage of times different global model parameters were included in bootstrapped models (out of 10,000 bootstrap samples) and percentage of times they were significant in linear models assessing the minimum pup size/maximum female size ratios of 14 oophagous (from 16 ecoregions), 23 lecithotrophic (from 17 ecoregions), and 55 placentally viviparous (from 20 ecoregions) species

Parameter (% of bootstraps wherein selected)	Level	Significance (% of models in which parameter is significant)
Litter ratio (100%)		83.4%
Habitat (91.4%)	Neritic	54.4%
	Oceanic	29.7%
Depth (75.6%)	Meso/bathypelagic	22.5%
Litter ratio × Depth (57.3%)	Litter ratio × Meso/bathypelagic	40.0%
Habitat × Depth (43.8%)	Neritic × Meso/bathypelagic	24.1%
	Oceanic × Meso/bathypelagic	32.7%
Litter ratio × Habitat (43.0%)	Litter ratio × Neritic	25.3%
	Litter ratio × Oceanic	15.3%
Litter ratio × Habitat × Depth (22.6%)	Litter ratio × Neritic × Meso/bathypelagic	9.0%
	Litter ratio × Oceanic × Meso/bathypelagic	16.1%

The reference levels of the parameters Habitat and Depth were set to ‘both’ and ‘epipelagic,’ respectively

identified included the maximum litter size/maximum female length ratio and habitat. Larger litter size ratios reduced pup length ratio, and larger pup length ratios were associated with neritic habitats (Table 5).

Discussion

Oophagous reproduction has been hypothesized to increase individual fitness (relative to non-oophagous reproductive modes) by allowing sharks to invest

Table 5 Results of bootstrapped stepwise linear regressions, including parameter estimates and their standard error (SE) and 95% confidence intervals (CI)

Parameter [Level]	Estimate	SE	Lower CI	Upper CI
Intercept	0.273	0.015		0.287
Litter ratio	−0.005	0.001	−0.007	−0.004
Habitat [Neritic]	0.043	0.015	0.030	0.063
Habitat [Oceanic]	0.025	0.023	0.004	0.041

The reference level for Habitat was 'both.'

more energy into fewer, larger offspring (Gilmore et al. 2005; Parsons et al. 2008; Oliveira et al. 2010). The results presented herein demonstrate, when we expressed individual pup length as a proportion of adult body length, oophagous species are born significantly larger than viviparous lecithotrophic species. In addition, relative pup size at birth was similar among the oophagous species of Lamniformes, the carcharhinid family Pseudotriakidae, and the orectolobiform *N. ferrugineus*. This result indicates that oophagy confers similar energetic benefits to developing embryos despite arising independently within evolutionarily distinct lineages of sharks (Conrath and Musick 2012; Naylor et al. 2012; Fig. S1) and despite oophagous carcharhinid sharks providing only a finite number of unfertilized ova to each embryo compared to Lamniformes and *N. ferrugineus* which provide them throughout the gestation period. Herein, we also provide updated quantitative support that oophagy favors fewer offspring facilitated via increased nutritional investment toward a relatively small number of when compared to both placentally viviparous and lecithotrophic viviparous strategies (Wourms 1977; Gilmore 1993; Gilmore et al. 2005; Parsons et al. 2008; Table 3b). Interestingly, when maternal investment is expressed in terms of whole litter mass, but not length, as a proportion of female mass, the distinction between oophagous and lecithotrophic species is neutralized. This suggests that total energetic investment per litter is ultimately similar between reproductive modes.

Differences in relative size at birth as a function of maternal body size has been previously detected in placentally viviparous species from the family Carcharhinidae, in which smaller species had offspring that were 40–60% of maternal body length and larger species had pups that were 20–40% of maternal length (Parsons et al. 2008), contrasting the positive relationship between female body length and fecundity. Our results support the conclusion that the interaction between female length and litter size is a driver of relative pup length for non-oophagous species. However, maximum litter size as a function of maximum female length was a poor predictor of relative pup length for oophagous species, which have a weaker relationship between female body length and litter size. For example, although we identified that oophagous species with smaller bodies had lower fecundity and greater relative pup length at birth compared to large-bodied oophagous species, we found several exceptions. Large-bodied (≥ 4.5 m) oophagous Lamniformes species such as *C. carcharias* have relatively large litters compared to some other members of their order, but other large-bodied species such as *O. ferox*, and *C. maximus* have reduced fecundity relative to their size, but similar relative pup lengths (*C. carcharias*: mean 0.21 vs. *O. ferox* and *C. maximus*: range 0.15–0.22%). In contrast, the comparatively smaller (2.9–3.8 m) *I. oxyrinchus* has the largest litter sizes observed within the order (i.e., more pups per meter of female), yet relative pup length for this species is also similar (c. 0.19–0.24). This suggests that there is not a trade-off between uterine space and relative pup length in oophagous sharks and pup length is likely to be modulated by different factors.

It is possible that in some cases, reduced fecundity in oophagous species may be compensated for by increased reproductive frequency. Oophagous Lamniformes have a broad range of gestation periods (from 9 months up to 25 months) and temporal patterns of pregnancy also vary among oophagous sharks (i.e., combined gestation and resting period; Gilmore et al. 2005; Castro 2009). For example, highly fecund *I. oxyrinchus* in the eastern Pacific are thought to have a three-year reproductive cycle comprising a lengthy gestation period of up to 23–25 months and a one-year period of rest (Joung and Hsu 2005). In contrast, Alopiids such as the common thresher *Alopias vulpinus* have small litters of typically 2–4 pups per reproductive cycle but may have gestation periods as short as 9–12 months (e.g., Gubanov 1972; Natanson and Gervelis 2013) with a one-year rest. Other threshers, such as *A. superciliosus* and *A. pelagicus*, forgo reproductive seasonality entirely, with females possibly becoming pregnant again immediately after parturition (Chen et al. 1997; Liu et al. 1999; Das

2016) potentially as an adaptation to maximize lifetime reproductive output for these species. When the maximum litter sizes of these sharks are compared, their average annual fecundity (maximum litter size/reproductive periodicity) is similar, with *A. vulpinus*, *A. pelagicus*, and *A. superciliosus* giving birth to an estimated two pups per year and I. oxyrinchus producing an average of 3.7 pups per year (Appendix 4). However, differing patterns of reproductive periodicity may also exist within single species; for example, populations of *C. taurus* residing in the northwest Atlantic have been observed to reproduce annually (litters of two pups per year; Gilmore 1993), whereas evidence of a biennial reproductive cycle (average of one pup per year) for this species has been collected in the southwest Atlantic (Lucifora et al. 2002), southeast Atlantic (Dicken 2006), and southwest Pacific (Bansemer and Bennett 2009), suggesting that variability in reproductive periodicity may be influenced by regional adaptation.

Ecological effects on pup length at birth

Our analyses provide evidence that there may be an influence of habitat in the trade-off between litter size and embryonic nourishment during pregnancy. For example, neritic habitats were associated with greater pup length compared to viviparous shark species that had smaller pups in oceanic environments. Larger pups may have a competitive advantage in more sheltered, eutrophic coastal environments than sharks born in the open ocean (e.g., Gilmore et al. 2005). In addition, it is also likely that our model was influenced by the relative abundance of small-bodied placentally viviparous sharks that occupy coastal environments (Castro 1993) which have larger pups relative to their maximum body length than larger-bodied, oceanic species.

Conservation implications

Globally, shark populations are in decline (Baum et al. 2003; Davidson et al. 2016; Dulvy et al. 2021), largely due to ineffective protective measures (Robbins et al. 2006), unsustainable shark-targeted fisheries (de Mitcheson et al. 2018), and mortality through incidental bycatch (Campana et al. 2009). Understanding reproductive potential is an essential component to developing effective conservation strategies with realistic recovery goals (Wheeler et al. 2020). Although some reproductive variables, such as fecundity, pup size, and size at maturity, are easily quantified through direct observation, other measures such as reproductive periodicity and gestation period are more difficult to ascertain; for many species these values are simply unknown. Moreover, our current knowledge of the reproductive habits of sharks is primarily assessed via bycatch monitoring (e.g., Joung and Chen 1995; Beerkircher et al. 2002; Pajuelo et al. 2018), shark fisheries and derbies (e.g., Campana et al. 2005, White 2007), and opportunistic sampling of pregnant females or neonates (e.g., Joung et al. 1996; Cliff et al. 1990) which may limit access to reproductive information about more protected or elusive species. Encouragingly, novel research focusing on non-lethal sampling technology such as steroid hormone analysis (e.g., Awruch et al. 2014; Fujinami et al. 2017; Verkamp et al. 2022), and ultrasonography (e.g., Anderson 2018; Sulikowski et al. 2016) may facilitate improved estimates of these measures without the need for removal of reproductive animals from the population.

Conclusion

Our study supports the hypothesis that placentally viviparous carcharhinids maximize their reproductive fitness by allocating nutrients to larger litters of pups, whereas oophagous species have achieved success in their environments by using the opposite approach, and both forms of matrotrophic viviparity resulted in larger pups on average than lecithotrophic viviparity. As additional life history data become available for viviparous sharks, the differences between reproductive strategies should be examined at a higher resolution such as incorporating as fine-scale habitat use (e.g., temperature, latitude). Future research should continue to elucidate how sharks select and use nursery habitats and how reproductive periodicity varies with environmental features.

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Availability of data All data used in our analyses are made available within our appendices.

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Declarations

Conflict of interest All authors certify that they have no conflicts of interest to declare for this project.

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