Lecithotrophic species and matrotrophic species among poeciliid fishes

[1]Ioan Oroian, [2]Eniko Kovacs

[1] Department of Environmental Engineering and Protection, Faculty of Agriculture, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, Cluj-Napoca, Romania; [2] Faculty of Horticulture, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, Cluj-Napoca, Romania. Corresponding author: I. Oroian, ioan.oroian@usamvcluj.ro

Abstract. Our work aims to address the problem of embryo supply strategies with nutrients in poecilid fishes, as a variation of the reproductive strategy within a phylogenetically and taxonomically related group. Poeciliid fish are divided into two types based on their reproductive strategy: lecithotrophic and matrotrophic species. Lecithotrophic species lay eggs that contain a yolk sac that provides nutrients for the developing embryo. Once the egg is laid, the embryo relies on the yolk sac until it hatches and can feed on its own. Lecithotrophic species do not provide any additional nourishment to their offspring beyond what is already present in the egg. Matrotrophic species, on the other hand, provide additional nourishment to their offspring through a placenta-like structure. The developing embryos are attached to the mother's bloodstream via this structure and are able to receive nutrients directly from her. Matrotrophic species are further divided into two types: histotrophic and hemotrophic. Histotrophic species provide their offspring with nutrients from secretions in the female reproductive tract, while hemotrophic species provide their offspring with nutrients directly from the mother's blood. A high degree of matrotrophy allows the species to carry several broods at different stages of development, a phenomenon known as superfetation. Because the room for developing embryos is limited, viviparity reduces brood size compared to oviparous species. Superfetation can compensate for this loss by keeping embryos at various sizes and stages during development. The greater degree of matrotrophy in a species is linked with a higher degree of placentation, including a thicker maternal follicle, higher degree of vascularization, and larger number of villi in the placenta. The use of placental fish models has expanded our understanding of placental biology beyond mammals and has provided valuable insights into the mechanisms of placental development and function.

Key Words: placenta, lecithotrophic species, matrotrophic species, *Poeciliopsis*.

Introduction. Poeciliid fish are a family of fish that includes guppies, mollies, swordtails, and others (Petrescu-Mag 2007, 2008; Boaru et al 2021). These fish are divided into two types based on their reproductive strategy: lecithotrophic and matrotrophic species (Ponce de Leon & Uribe 2021). Our work aims to address the problem of embryo supply strategies with nutrients in poecilid fishes, as a variation of the reproductive strategy within a phylogenetically and taxonomically related group.

Lecithotrophy and matrotrophy. Lecithotrophic species lay eggs that contain a yolk sac that provides nutrients for the developing embryo. Once the egg is laid, the embryo relies on the yolk sac until it hatches and can feed on its own. Lecithotrophic species do not provide any additional nourishment to their offspring beyond what is already present in the egg (Ponce de Leon & Uribe 2021).

Matrotrophic species, on the other hand, provide additional nourishment to their offspring through a placenta-like structure. The developing embryos are attached to the mother's bloodstream via this structure and are able to receive nutrients directly from her (Ponce de Leon & Uribe 2021). Matrotrophic species are further divided into two types: histotrophic and hemotrophic (Crespi & Semeniuk 2004). Histotrophic species provide their offspring with nutrients from secretions in the female reproductive tract, while hemotrophic species provide their offspring with nutrients directly from the mother's blood (Crespi & Semeniuk 2004). The main difference between lecithotrophic and matrotrophic species of poeciliid fish is the way in which they provide nutrients to their offspring during development.

Matrotrophy and lecithotrophy and are not discrete anatomical traits. Most scientific research quantify matrotrophy using a matrotrophy index (MI) (Kwan et al 2015). MI is a measure used in reproductive biology research to assess the level of maternal investment in offspring development. In the case of poeciliid fish, which are known for their unique reproductive biology that involves maternal provisioning of nutrients to embryos, MI can be calculated using the following formula:

$$MI (\%) = (\text{yolk sac volume} / \text{egg volume}) \times 100$$

To obtain these measurements, researchers can use microscopic imaging techniques such as confocal microscopy or bright-field microscopy to visualize and measure the yolk sac and egg volumes of individual embryos. MI can then be calculated for each individual embryo, and the average MI for a population of embryos can be used as a measure of the overall level of maternal investment in offspring development.

Members of the same genus, genus *Poeciliopsis* for instance, show various reproductive life history adaptations (Georgescu et al 2020). *Poeciliopsis monacha* Miller, 1960 (the headwater livebearer), *Poeciliopsis lucida* Miller, 1960 (the clearfin livebearer), and *Poeciliopsis prolifica* Miller, 1960 (the blackstripe livebearer) form part of the same clade within genus *Poeciliopsis* (wikipedia.org). However, their modes of maternal provisioning vary greatly. *P. monacha* is considered true lecithotrophic because it does not really provide any resources for its offspring after egg fertilization (wikipedia.org). We can say that the pregnant female is basically a swimming egg sac. *P. lucida* shows an intermediate degree of matrotrophy, meaning that to a certain extent the offspring's metabolism can actually affect the mother's metabolism, allowing for increased nutrient exchange (wikipedia.org). The last one, *P. prolifica* is believed to be highly matrotrophic, and almost all of the nutrients and materials needed for the embryo development are supplied to the oocyte after it has been fertilized (wikipedia.org). This degree of matrotrophy allows the species to carry several broods at different stages of development, a phenomenon known as superfetation (wikipedia.org; Saleh-Subaie et al 2021). Because the room for developing embryos is limited, viviparity reduces brood size compared to oviparous species. Superfetation can compensate for this loss by keeping embryos at various sizes and stages during development (Thibault & Schulz 1978; Saleh-Subaie et al 2021) (Figure 1).

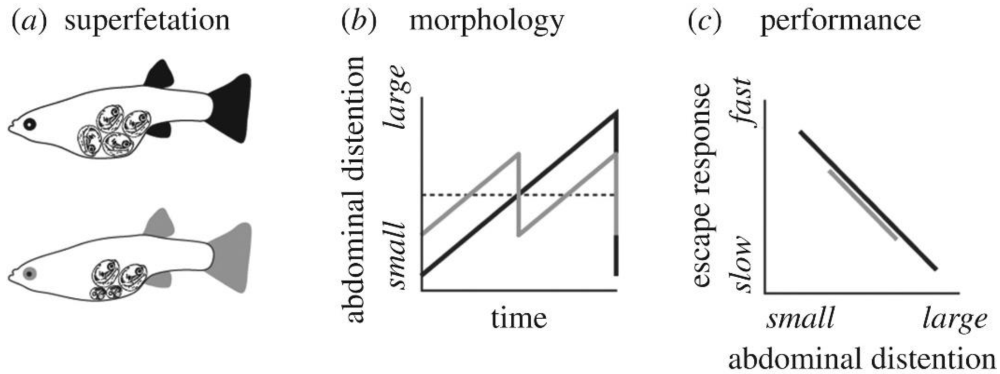

Figure 1. The hypothesized effect of superfetation and pregnancy on swimming performance and morphology in livebearing fishes (Fleuren et al 2019). (a) Two hypothetical livebearing fish species that differ in the presence of superfetation: no superfetation (i.e. one brood; fish with dark fins) and two overlapping broods (fish with grey fins). All other aspects of reproduction (e.g. female length, offspring developmental time, offspring size at birth, lifetime fecundity) are assumed to be equal. (b) Predicted change in female body shape through time for the two hypothetical species. An increase from one litter (dark line) to two overlapping litters (grey line) results in a more frequent production of smaller litters. This decreases the amplitude around the mean reproductive

burden (dashed line), effectively reducing the peak abdominal distention during pregnancy (Pollux et al 2009; Thibault & Schulz 1978). (c) Predicted decline in escape performance with an increase in abdominal distention: both lines have equal slopes and intercepts and differ only in the range of body thickness (x-axis). For heuristic purposes the temporal patterns in (b) and (c) are depicted as linear, because the exact relationships between body shape and time, and body shape and performance, respectively, are unknown (Shrader & Travis 2005).

Poeciliopsis elongata (Günther, 1866) (elongate toothcarp), *Poeciliopsis turneri* Miller, 1975 (the blackspotted livebearer), and *Poeciliopsis presidionis* (Jordan & Culver, 1895) (the Sinaloa livebearer) form another clade that could be considered an outgroup to the *P. monacha, P. lucida*, and *P. prolifica* clade (wikipedia.org). All these three species are very highly matrotrophic. The matrotrophy is so evident in these three species that Turner (1940) described the follicular cells of *P. turneri* as pseudoplacenta, pseudochorion, and pseudoallantois (wikipedia.org). The greater degree of matrotrophy in a species is linked with a higher degree of placentation, including a thicker maternal follicle, higher degree of vascularization, and larger number of villi in the placenta (Kwan et al 2015).

The placenta is thought to have evolved as an adaptation to the low-nutrient environments in which they live, as it allows for more efficient transfer of nutrients from the mother to the offspring (Petrescu-Mag et al 2019). However, the reason for placental evolution in Poeciliids is controversial, and involves two major groups of hypotheses, adaptive and conflict hypotheses (Furness et al 2021). Adaptive hypotheses, including the locomotor hypothesis (Thibault & Schulz 1978), Trexler-DeAngelis model (Trexler & DeAngelis 2003; Riesch et al 2013), and life-history facilitation (Pires et al 2011; Furness et al 2021), broadly suggest that the placenta evolved to facilitate the evolution of another advantageous trait in the fish’s environment (wikipedia.org). The conflict hypothesis suggests the placenta is a nonadaptive byproduct of genetic "tug-o-war" between the mother and the offspring for resources (Crespi & Semeniuk 2004).

Research relevance. Placental fish models, such as the viviparous fish species, are important for research because they have evolved convergent reproductive strategies with placental mammals. These fish have developed specialized organs that support the growth and development of their embryos, which share similarities with the mammalian placenta. This makes them valuable models for studying the evolution of placentation and the mechanisms of placental development.

In addition to their reproductive biology, placental fish models also have other advantages for research. They have a short generation time, allowing for rapid genetic studies and experiments. They are also easy to maintain and breed in the laboratory, making them cost-effective and efficient models for research.

Placental fish models have been used to study a range of topics including embryonic development, maternal-fetal interactions, nutrient transport, and the effects of environmental toxins on pregnancy outcomes. Studies in these fish have helped to identify genes and pathways involved in placental development and function, and have provided insights into the evolution of reproductive strategies in vertebrates.

Conclusions. Poeciliid fish are divided into two types based on their reproductive strategy: lecithotrophic and matrotrophic species. Lecithotrophic species lay eggs that contain a yolk sac that provides nutrients for the developing embryo. Once the egg is laid, the embryo relies on the yolk sac until it hatches and can feed on its own. Lecithotrophic species do not provide any additional nourishment to their offspring beyond what is already present in the egg.

Matrotrophic species, on the other hand, provide additional nourishment to their offspring through a placenta-like structure. The developing embryos are attached to the mother's bloodstream via this structure and are able to receive nutrients directly from her. Matrotrophic species are further divided into two types: histotrophic and hemotrophic. Histotrophic species provide their offspring with nutrients from secretions in the female reproductive tract, while hemotrophic species provide their offspring with nutrients directly from the mother's blood.

A high degree of matrotrophy allows the species to carry several broods at different stages of development, a phenomenon known as superfetation. Because the room for developing embryos is limited, viviparity reduces brood size compared to oviparous species. Superfetation can compensate for this loss by keeping embryos at various sizes and stages during development. The greater degree of matrotrophy in a species is linked with a higher degree of placentation, including a thicker maternal follicle, higher degree of vascularization, and larger number of villi in the placenta.

The use of placental fish models has expanded our understanding of placental biology beyond mammals and has provided valuable insights into the mechanisms of placental development and function.

Conflict of interest. The authors declare no conflict of interest.

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Authors:
Ioan Oroian, Department of Environmental Engineering and Protection, Faculty of Agriculture, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, Calea Mănăștur 3-5, 400372 Cluj-Napoca, Romania, e-mail: ioan.oroian@usamvcluj.ro
Eniko Kovacs, Faculty of Horticulture, University of Agricultural Sciences and Veterinary Medicine Cluj-Napoca, Calea Mănăștur 3-5, 400372 Cluj-Napoca, Romania, e-mail: eniko.kovacs@usamvcluj.ro

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