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## ORIGINAL ARTICLE

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# Oil globule size in fish eggs: A matter of biome and reproductive strategy

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## Abstract

Here, on the basis of published information upon over 800 species from 39 orders and 202 families, we analyse how the size of oil globules in fish eggs varies between reproductive guilds and environments with contrasting salinities. About 80% of marine fishes produce eggs with oil globules, the volume of which ( $V_O$ ) never exceeds 9% of the egg reserves and averages 2%. These proportions vary very little between marine fish species producing pelagic or demersal eggs. Fewer freshwater fishes (about 40%) produce eggs with oil globules, but their globules are much larger (mean  $V_O$  of 10%) and their volumes vary considerably between reproductive guilds:  $V_O$  is on average 3–10 times lower in freshwater species with demersal eggs than among freshwater pelagophils and aphrophils (i.e., bubble nesters), where it averages about 40% (range of 23%–69%) of the egg reserves. These results support the idea that oil globules serve to hydrostatic lift in fresh waters, but not or very little in marine waters, where egg buoyancy can be achieved at a lower energy cost through egg hydration. Advantages and constraints of oil globules in fish eggs are discussed in the light of species producing eggs with very large oil globules ( $V_O > 20\%$ ): access to oxygen-rich water layers that are indispensable for egg development vs. smaller size of larvae at first feeding, since the saturated lipids contained in oil globules essentially serve very little to tissue construction.

## KEYWORDS

egg buoyancy, fish, oil globule, reproductive strategy, water salinity

## 1 | INTRODUCTION

In contrast to the situations among other Vertebrates, fishes have evolved a broad range of reproductive strategies, ranging from egg scattering to true viviparity (Balon, 1975, 1981; Breder & Rosen, 1966). Likewise, the dimensions of their eggs are highly contrasting (a 100-fold scale, from <0.2 mm to >20 mm in diameter in some marine mouthbrooders) and they do not intimately reflect the sizes of the parents, as for example many species attaining no more than 1 g at adulthood can produce larger eggs than those of taxa weighing over 500 kg; e.g., the zebrafish (*Danio rerio*, Cyprinidae) vs. the

ocean sunfish (*Mola mola*, Molidae). Another distinctive feature of fish eggs is the presence in many taxa of one or several oil globules (also termed fat or lipid droplets). In contrast to yolk vesicles, which essentially comprise phospholipids and lipoproteins, oil globules exclusively contain saturated fatty acids, cerids and cholesterol esters (Eldridge, Joseph, Taberski, & Seaborn, 1983; Mellinger, 1995; Moodie, Loadman, Wiegand, & Mathias, 1989; Sand & Schlenk, 1969). The numbers and sizes of oil globules in fish eggs vary considerably among species, and they can also change between developmental intervals. Many fish species produce ova with multiple tiny oil globules that coalesce during embryonic development into

a single, larger globule that will be fully absorbed during the larval stage. Nevertheless, these traits show strong consistency within a particular taxon, and before the advent of DNA bar-coding technologies, this information has widely been used, together with egg diameter and yolk structure, in identification keys of fish eggs, especially for the marine ichthyoplankton (e.g., Mito, 1963; Moser et al., 1984; Robertson, 1975; Russell, 1976).

The roles of oil globules in fish eggs have also been explored. It is widely asserted that oil globules serve as concentrated energy stores, as they contain no water and lipids have an energy density about twice as high as proteins or carbohydrates (Jobling, 1995). The contribution of oil globules to egg buoyancy is more debated (Craik & Harvey, 1987; Mellinger, 1994; Riis-Vestergaard, 2002; Sundby & Kristiansen, 2015). The “heavy” components of a fish egg are its yolk proteins and chorionic membrane (density > 1.2 kg/L), whereas lipids are less dense than water (about 0.9 kg/L). The density of the perivitelline space is similar to that of the ambient medium (at 20°C, about 0.998 and 1.025 kg/L, for fresh water and full strength seawater, respectively). By contrast, the yolk and embryo fluids have an almost constant osmolarity independent of ambient salinity, and their density is about the same as that of water at salinity 10–11 (Sundby & Kristiansen, 2015).

Henceforth, in full strength seawater (salinity 35), positive buoyancy can be produced by egg hydration (and subsequent mechanisms of ionic regulation). In fresh water, the situation changes radically: yolk fluids are denser than the ambient environment, so egg hydration eventually results in negative buoyancy after ionic regulation (Sundby & Kristiansen, 2015); the inflation of the perivitelline space, the density of which is similar to that of the ambient medium, can just make the egg less negatively buoyant, but it produces no upward lift. Apart from situations where eggs are embedded in foams, the sole way of producing an upward lift is increasing the lipid content of the egg, and thus possibly through larger oil globules.

If egg buoyancy were achieved essentially through increased lipid content in fresh waters and through egg hydration in seawater, then one could expect that (a) freshwater fishes would have evolved larger oil globules than seawater fishes, and (b) the sizes of oil globules would vary substantially between species producing demersal or pelagic eggs in fresh waters, whereas there would be little or no variation between reproductive guilds among marine fishes.

Here, we test for these hypotheses by analysing published information on the eggs of over 800 species of freshwater and marine fishes, and we discuss the advantages and penalties associated to the presence of oil globules, in the light of species producing very large oil globules.

## 2 | MATERIAL AND METHODS

Information on the diameters of the oil globule(s), egg and reserves (i.e., yolk + oil globule(s)) were transcribed from scientific articles when explicitly indicated by the authors, otherwise this information

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was derived from photographs therein, using the freeware Image J (Abramoff, Magalhães, & Ram, 2004). Not all fish produce spherical eggs or yolks, and in many instances, eggs have the shape of a “prolate” (elongated) spheroid, so volumes ( $V$ ) were calculated as:  $V = \pi d_a d_b^2 / 6$ , where  $d_a$  and  $d_b$  are the long and short diameters of the structure. When several globules were present, they were measured individually, and their total volume was the sum of individual volumes.

For every scientific article where comprehensive information was available, the egg diameters retained in the database were those of non-fertilized ova. In many instances however, only the diameters of “recently” fertilized eggs were documented. This discrepancy can cause some biases, as egg swelling can take place rapidly and cause a substantial inflation of the perivitelline space (up to four times the egg diameter in some Ostariophysi), thereby leading to some (minor or major) underestimation of the actual proportions of the volume of the oil globule(s) and its contribution to egg buoyancy. Therefore, it was preferred calculating here the ratio ( $V_o$ ) between the volume of the oil globule(s) and the volume of the egg reserves (yolk + oil globule(s)), which remain unchanged during the first hours following egg fertilization.

The species scientific names, taxonomic positions and living biomes were obtained from FishBase (Froese & Pauly, 2016). No more than 20 species in the present database were reported as “estuarine” (i.e., typically spawning in brackish waters), which did not suffice from a statistical perspective to group them in distinct cluster. For the sake of clarity, these species were assigned to fresh or marine waters, depending on the salinity range in which they reproduce by reference to review articles on estuarine assemblages (Albaret, 1999; Elliott et al., 2007).

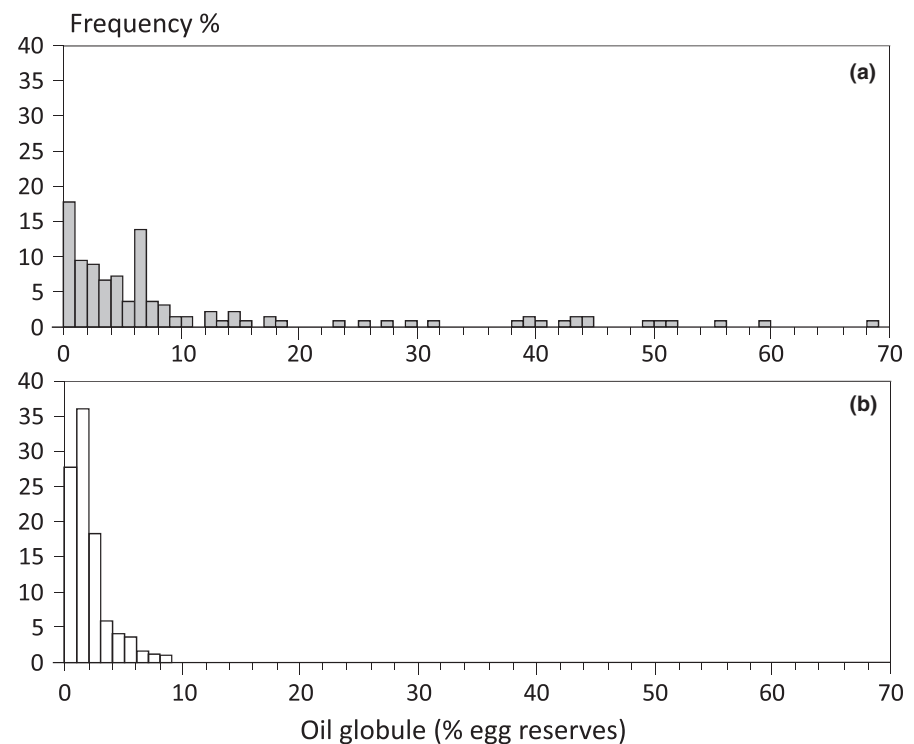
Information on reproductive guilds was obtained from FishBase and additional dedicated publications. Here a simplified scale comprising five broad reproductive guilds (Table 1) was used in preference to comprehensive scales proposed by different authors (Balon, 1975, 1981; Breder & Rosen, 1966), for the sake of statistical representativeness and accuracy of available information. The criteria used here referred to whether eggs are near-neutrally buoyant or demersal, scattered, guarded or brooded by the parents (mouth-brooders and pouch-brooders; Table 1).

In order that every fish species has the very same statistical weight, a single datum was retained in the analyses for every documented species. When several reports were available for a particular species, priority was given to peer-reviewed publications and best documented

**TABLE 1** Proportions (%) of fish species producing eggs with one or several oil globules (OG), as a function of ambient salinity and reproductive guild (on the basis of egg buoyancy and presence or absence of parental care)

Reproductive guild	Egg	Care	Fresh waters		Marine waters	
			N spp.	OG (%)	N spp.	OG (%)
A: Pelagophils	Buoyant	No	54	37.0 b,c	314	80.9 a
B: Aphrophils (bubble nesters)	Buoyant	Yes	18	77.8 a	0	–
C: Scatterers	Demersal	No	166	31.3 c	51	70.6 a
D: Nest spawners	Demersal	Yes	96	49.0 b	71	83.1 a
E: Brooders (mouth/pouch)	Demersal	Yes	17	17.6 c	16	62.5 a,b
Total			351	38.8 b	452	79.5 a

Note. Values sharing at least one script (a, b or c) in common do not differ significantly, whereas other comparisons differ at  $p < 0.05$  (contingency table analyses).



**FIGURE 1** Volume of oil globules (% of egg reserves) in the eggs of freshwater (a,  $N = 136$  spp.) and marine fishes (b,  $N = 359$  spp.). Species producing eggs exhibiting no oil globule(s) are not shown here (see Table 1)

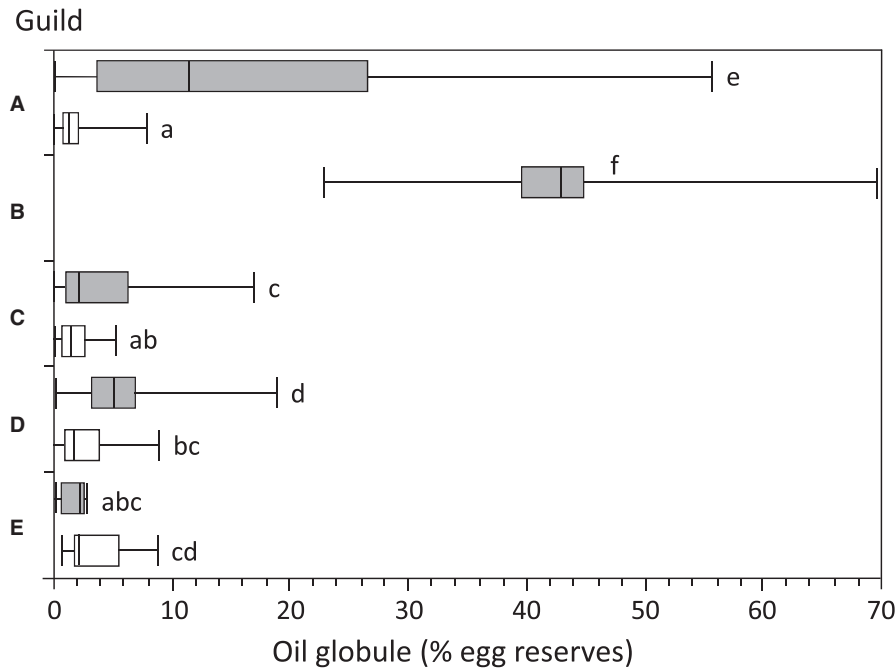
data sets. Between-guild comparisons were achieved with contingency table analyses for the proportions of species with and without oil globules, and with non-parametric Mann–Whitney  $U$ -tests for the volumes of oil globules. Null hypotheses were rejected at  $p < 0.05$ .

### 3 | RESULTS

The present database comprises 803 fish species, from 39 orders and 202 families, of which 452 marine species and 351 freshwater species (see Supporting Information Appendix S1). The proportions of taxa producing eggs with one or several oil globules amount to 79.5% in marine waters and 38.8% in fresh waters ( $\chi^2 = 138.27$ ,  $p < 0.0001$ ; Table 1). This difference is largely explained by the absence of oil globules in the eggs of almost all Ostariophysi

(Characiformes, Cypriniformes, Gonorynchiformes, Gymnotiformes and Siluriformes), which altogether account for about 60% of fish diversity in fresh waters, but are very rare in marine environments (Supporting information Table S1). Within a particular biome, the proportions of species with oil globule(s) do not vary substantially across reproductive guilds (Table 1), except for freshwater aphrophils (“bubble nesters”), which are dominated by Perciformes, a group where most (>85%) species produce eggs with one or several oil globules (Supporting information Table S1).

The ratio between the volumes of the oil globules and egg reserves ( $V_O$ ) among fishes ranges from <0.1% to over 65% (Figure 1). Values of  $V_O < 1\%$  may sound extremely low to many scientists familiar with fish eggs, but it should be reminded that for an oil globule attaining 20% of the yolk diameter, the corresponding value of  $V_O$  is 0.8%. In marine fishes,  $V_O$  is low (on average 2% and always <9%) and



**FIGURE 2** Volume of oil globules (% of egg reserves) in relation to reproductive guilds in freshwater (grey-shaded bars) and marine fishes (open bars). Species exhibiting no oil globule(s) are not shown here (see Table 1). Guilds: A: Pelagophils (without any parental care); B: Aphrophils (bubble nesters); C: Scatterers with demersal eggs and no parental care; D: Nest spawners with demersal eggs; E: Brooders (mouth/pouch) brooders. In every category, the central vertical line is the median ( $P_{50}$ ) of the data range, the horizontal bar is the interquartile ( $P_{25}$ – $P_{75}$ ) range, and whiskers encompass the entire data range. Numbers of species producing eggs with oil globule(s) as in Table 1. Categories sharing at least one script (a–f) in common do not differ, whereas other comparisons differ at  $p < 0.05$  (Mann–Whitney U-tests)

varies little between reproductive guilds, as in every guild there is a preponderance of species producing eggs with small oil globules and no species with very large oil globules (Figures 1 and 2). By contrast,  $V_O$  is much higher in freshwater fishes (mean of 10%) and it varies considerably between guilds, being 3–10 times lower in species with demersal eggs than among pelagophils and aphrophils. This difference largely originates from the variable occurrence of freshwater species producing eggs with very large oil globules ( $V_O > 10\%$  of egg reserves, i.e., about 50% of egg diameter) among different reproductive guilds: in freshwater fishes producing eggs with oil globules, very large oil globules are found systematically among aphrophils (14 of 14 spp.), frequent among pelagophils (12 of 20 spp.), but rare in other guilds with demersal eggs (7 of 102 spp.; Table 1; Figure 2).

Based on the present literature coverage, eggs with very large oil globules ( $V_O > 10\%$ ) can be found in 33 freshwater species belonging to four orders, namely the Clupeiformes (1 sp.), Osteoglossiformes (1 sp.), Symbranchiformes (2 spp.) and Perciformes (29 spp.). Among Perciformes with very large oil globules, about 60% belong the Anabantoidei (i.e., Anabantidae [climbing perches], Helostomatidae and Osphronemidae [gouramis], 11 spp.) or their sister group (Channidae [snakeheads], 6 spp.).

## 4 | DISCUSSION

The present study supports the working hypothesis that oil globules serve to provide egg buoyancy in fresh water and little or not in

seawater: indeed, oil globules are much larger in freshwater fishes with pelagic eggs than in those with demersal eggs and than in marine fishes, among which there is little difference between reproductive guilds. The idea that egg buoyancy in seawater is achieved chiefly through egg hydration is further attested indirectly by the high water contents of marine pelagic eggs in comparison to those of freshwater eggs (about 80%–92% vs. about 60%–80%; Kamler, 1992; Riis-Vestergaard, 2002).

It cannot be excluded that part of the difference documented here between freshwater and marine fish eggs is of taxonomic origin, as most groups of fishes with very large oil globules comprise no marine members (e.g., the Anabantoidei and Channidae; see also Supporting Information Tables S1 and S2). Nevertheless, differences between biomes are also conspicuous among several taxonomic groups occurring both in marine and fresh waters, as for example, among the family Sciaenidae (Perciformes). In the freshwater pelagophil *Aplodinotus grunniens*  $V_O$  amounts to 49.7% (Hernández-Gómez, Perera-García, Valenzuela, Duran, & Mendoza-Carranza, 2013), whereas in marine sciaenids with similar reproductive habits,  $V_O$  ranges from 0.6% to 3.7% (17 spp.; Supporting information Table S2).

By reference to Sundby and Kristiansen (2015, equation 2) it can be assumed that the minimal fractional volumes of oil globules needed to make a fish egg positively buoyant in fresh waters would range from about 20% to about 30%, depending essentially on the respective fractional volume of the egg chorion, which has the highest density (about 1.2 kg/L) of all egg components, and can amount to about 1%–5% of the egg volume (Sundby & Kristiansen, 2015). The results of the present study largely concur with this functional

hypothesis, as all fish eggs that are reported here to be “genuinely” positively buoyant in fresh waters (i.e., without the “assistance” of air bubbles or other means), indeed exhibit large oil globules that contribute to at least 23% of the egg reserves (i.e., in all aphrophils and some pelagophils, such as the freshwater drum *A. grunniens*; Figure 2; Supporting Information Tables S1 and S2).

The production of floating eggs is unusual in freshwater fishes, and it can be viewed as hazardous at first sight, because such eggs can be damaged by rainfalls, dispersed by eddies, exposed to steep thermal gradients or subjected to predation by both aquatic and aerial predators. By contrast, this reproductive strategy can be a major advantage in deoxygenated environments, where the oxygen concentration is systematically much higher at the air-water interface than in deeper water layers, and especially wherever floating eggs are protected by bubble nests or surrounding vegetation (Hostache & Mol, 1998). There is broad evidence that all freshwater aphrophils also have evolved air-breathing capacities. These capacities probably enabled the parents to minimize the energy expenditures and duration of air-breathing excursions during which they might be forced to leave their eggs without any protection if these eggs had been demersal.

The production of eggs with very large oil globules can thus be advantageous to secure positive buoyancy and access to oxygen in hypoxic fresh waters, but this reproductive strategy probably imposes several constraints and trade-offs for the parents and offspring.

It is generally assumed that the key elements of reproductive strategies in fishes refer to spawning frequency, egg number and egg size, which should be further equated with the capacity of the female parent to acquire energy from its environment (e.g., McBride et al., 2015). The energy density of fish eggs has rarely been taken into account in this general equation, especially for comparative analyses in an interspecific perspective. This is presumably because information on the composition of fish eggs is restricted to a few tens of species (Eldridge et al., 1983; Mellinger, 1995), many of which are marine pelagophils, that produce eggs with a high water content and small oil globules, if any (Riis-Vestergaard, 2002; present study). To our knowledge, there has been no single detailed experimental study on the composition and energy density of the eggs of freshwater aphrophils. Nevertheless, it can be hypothesized that their energy density is higher than in any other fish egg, for at least two reasons: (a) freshwater fishes generally produce eggs with a lower water content than those of marine fishes (Kamler, 1992), and (b) in freshwater aphrophils, the volume of oil globules containing high-energy lipids averages about 40% of the egg reserves, thus about 20 times as much as in the eggs of marine fishes (present study). These traits can make the energy density in the eggs of freshwater aphrophils about 2–3 times as high as in those of other freshwater fishes devoid of oil globule(s), and at least 4–6 times as high as in the eggs of marine fishes (by reference to the synthetic equation provided by Riis-Vestergaard, 2002). These very large ratios might suggest that the production by freshwater aphrophil fishes of eggs with a very high energy content, for reasons supposedly “aiming” to facilitating their development in oxygen-rich water layers, might impose additional constraints on the issues of energy acquisition and allocation

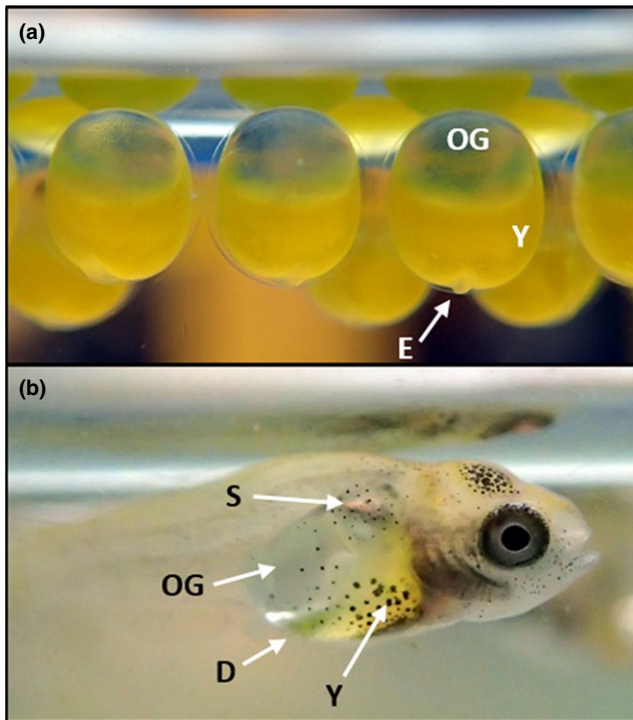
by the female parent, possibly at the expense of its fecundity or spawning frequency, but again, detailed information on this topic is still tremendously lacking. It is worth noticing that freshwater aphrophil fishes comprise species with contrasting feeding habits, namely the herbivorous gouramis and the carnivorous snakeheads, which have strikingly different capacities (and strategies) for collecting energy from the ambient environment, while they both produce eggs with a high energy density, in view of the large dimensions of their oil globule(s). These considerations raise additional questions and perspectives as regards the issues of energy acquisition and allocation by the female fish parent in the context of reproductive strategies, which remain to be elucidated in the course of future research.

Fish body length at hatching or at the start of exogenous feeding is a key to individual survival and recruitment, as longer larvae with faster swimming speed have greater capacities to evade predators, their larger mouth dimensions facilitates the use of a broader spectrum of food resources and their greater resistance to food shortage is also better, owing to their larger energy reserves (McGurk, 1986; Miller, Crowder, Rice, & Marschall, 1988; Ware, 1975). This “bigger-is-better” conundrum has been proved invalid in several instances (e.g., Litvak & Leggett, 1992; Paradis, Pepin, & Brown, 1996), but it remains relevant for the vast majority of fish species (Leggett & Deblois, 1994). It is generally admitted that the size of fish hatchlings or first-feeding larvae is intimately dictated by egg size (e.g., Miller et al., 1988). Nevertheless, this assertion is slightly reductionist, as it overlooks issues pertaining to the energy density or composition of fish eggs. In particular, the oil globules of fish eggs are essentially made of saturated fatty acids, which are deemed to serve primarily to metabolic purposes and very little to tissue construction, because the developing embryo chiefly needs proteins and phospholipids, which are present in the yolk but not in the oil globule(s) (Eldridge et al., 1983; Mellinger, 1995; Moodie et al., 1989; Riis-Vestergaard, 2002; Sand & Schlenk, 1969; Sundby & Kristiansen, 2015). This (almost) exclusive metabolic use of the energy contained in the oil globule(s) of fish eggs has been empirically supported by several findings:

1. during egg incubation and first developmental stages *extra ovo*, the volume of the oil globule(s) remains almost unchanged;
2. after the yolk has been fully absorbed, remnants of the oil globule(s) are systematically observed;
3. in the medaka *Oryzias latipes*, eggs from which the oil droplets had been mechanically removed under experimental conditions produced viable developmental patterns and eventually larval body sizes similar to those observed in individuals hatched from intact eggs (Iwamatsu, Muramatsu, & Kobayashi, 2008).
4. once the yolk has been fully absorbed, the body length of a larva deprived of exogenous food remains unchanged until the end of the absorption of the oil globule, even in species possessing very large oil globules (e.g., the giant gourami, *Osphronemus goramy*, Osphronemidae; authors' unpublished observations);

The late absorption of the egg oil globule(s) and (almost) exclusive use for metabolic purposes has at least two major consequences,





**FIGURE 3** (a) Recently fertilized eggs of an aphrophil, the giant gourami (*Osphronemus goramy*, Osphronemidae), showing a very large oil globule ( $V_O$  of  $41\% \pm 2\%$ ). (b) Larva of giant gourami 9 days after hatching, still possessing a very large oil globule, which makes the larva positively buoyant. D: digestive tract; E: embryo; OG: oil globule; S: swimbladder; Y: yolk

especially for aphrophils that produce eggs with larger oil globules than any other fishes.

- First, the yolk-sac larvae hatched from aphrophil eggs remain positively buoyant and float at the surface of the water for a while (Vierke, 1975; Dzerzhinskiy, 2016; authors' unpublished observations; Figure 3), which can be advantageous in deoxygenated waters, but at the expense of a higher predation risk, and this might have been the reason why this reproductive strategy co-evolved with parental care.
- The second consequence echoes directly to the “bigger-is-better” conundrum: if the energy contained in the oil globule(s) exclusively or primarily serves purposes other than tissue construction, then it can be anticipated that the larvae issued from eggs with very large oil globule(s) be smaller than those issued from eggs of similar dimensions but devoid of oil globule(s). In order to test empirically for this supposedly common-sense hypothesis, we calculated the ratios between the total body lengths of fish larvae at the start of exogenous feeding and the diameters of the eggs from which they hatched. For the sake of consistency, this comparison was restricted to freshwater fishes, as the water content of marine fish eggs is generally (much) higher. In eggs of freshwater fishes with  $V_O > 20\%$ , this ratio is about  $3.5 \pm 0.5$  (mean  $\pm$  SD, 8 spp., Akatsu, Ogasawara, & Yasuda, 1977; Parameswaran & Murugesan, 1976; Morioka, Ito, Kitamura, & Vongvichith, 2009; Morioka, Ito, & Kitamura, 2010; Morioka,

Chanthasone, Phommachan, & Vongvichith, 2012; Morioka, Vongvichith, Phommachan, & Chantasone, 2013), whereas in other freshwater fishes producing eggs with no or small oil globule(s), this ratio is about 40% higher (mean  $\pm$  SD of  $5.0 \pm 1.1$ ; Mann-Whitney U-test;  $p < 0.0001$ ; 107 spp., authors' unpublished data).

The penalty brought about by the presence of very large oil globules in terms of larval size at the time of first feeding might account for why the “large oil globule strategy” has not evolved in marine environments, where egg buoyancy can be achieved at a presumably lower energy cost through egg hydration. This functional hypothesis is further amplified by the fact that the eggs of many marine fish species—especially those of pelagophils—have a small diameter, which imposes major constraints on larval size, mouth dimensions and access to exogenous food. Nevertheless, it is clear-cut that the current knowledge on the reproductive strategies of fishes is still impaired by the paucity of data upon egg composition, energy density and its pathways, for metabolic or developmental purposes. Further experimental research on these topics is needed before any truly supported conclusion can be drawn. To this respect, freshwater aphrophils, which have evolved extreme life history strategies in terms of oil globule(s) dimensions, and thus egg composition and energy density (and their aftermath in terms of energy acquisition by the female parent), can be an excellent template for a better understanding of the evolution of life history strategies among fishes.

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## SUPPORTING INFORMATION

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