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Parent–egg–progeny relationships in teleost fishes: an energetics perspective

Ewa Kamler
The Stanisław Sakowicz Inland Fisheries Institute in Olsztyn, Żabieniec, 05-500, Piaseczno, Poland (Phone: +48-22-7562044; E-mail: kamler@infish.com.pl)

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Abstract

Age-related variations in chemical composition of egg matter were found in females in some studies, but they do not seem to be a universal phenomenon. In contrast, egg size can be well predicted from female age. The relationship has a parabolic shape, but the predicted size decrease of eggs from old females has not always been documented. Female size is an important contributor to egg size, both at intra- and inter-specific levels. Dependence of fecundity on body size has usually been described by a power function. A trade-off between egg number and size is considered in light of life history strategies. During a spawning season egg size may differ between successive batches, but lack of effects of egg batch sequence was reported in some studies. In yolk-feeding fish three discrete periods of elevated mortality are typically observed: shortly after egg activation, during hatching, and at final yolk resorption. The positive relationships between female size, egg size and offspring size/resistance to starvation and predation are a key pathway in parent–egg–progeny relationships. Both maternal and paternal effects contribute to the total survival of offspring, but they operate in different ways and at different times. In contrast to the importance of female size, no paternal size effects were revealed, but density and motility of spermatozoans were decisive. Typically, paternal effects diminish earlier in ontogeny. Major factors governing embryonic survival (fertilisation success and hatching success) differ from factors to which starvation mortality of yolk-feeding larvae is related. Embryonic survival is affected by female age *via* egg matter composition, by egg ripeness and paternal factors such as sperm density and motility. In contrast, starvation mortality of yolk-feeding larvae depends largely on female attributes (age, size and fecundity) *via* egg size, and, in some batch spawners, on egg batch sequence. Among teleost species egg size varies across a wide range (from 0.3 to 85–90 mm in diameter). Species that spawn large eggs are relatively rare. Caloric value of egg dry matter varies within a narrow range of 20–30 J mg^{-1}. Ecosystem and evolutionary components, and reproductive style are factors that contribute to egg endowment and yolk quality. During the last decade considerable progress was made in the methodology and understanding of paternal effect on progeny performance in fishes. This paper reviews these of parent–egg–progeny relationships.

Introduction

The importance of early life history studies in explaining developmental and survival fluctuations in marine fisheries was first realised between 1904 and 1913 as a result of multinational works within ICES Committee A and the Hjort's concept of year-class variation (review by Sinclair, 1997). Early ontogeny plays a vital role in survival with potential to influence the abundance of recruits entering the system (reviews in Smith, 1985, Wootton, 1990, Houde 1994, Chambers and Trippel, 1997, Bunn et al., 2000, Fuiman and Werner, 2002, Tomkiewicz et al., 2003, O'Brien et al., 2003, Schiemer et al., 2003). Firstly, survival rates at early stages are extraordinarily low and variable. For example, only one in 230,000 eggs produced by a marine fish northern anchovy (*Engraulis mordax*) reached adulthood (Smith, 1985). Embryonic survival rate in freshwater walleye (*Sander vitreus*) was 0.37 in Western Lake Erie (Roseman et al., 1996), but only 0.00003 in Spirit Lake, Iowa (Jennings, 1969). Secondly, the relationships between endogenous and exogenous factors, and reproductive characteristics are increasingly important as predictors of egg and larval production of marine fish stocks (Lambert et al., 2003). Lastly, the supply of fish stocking material is one of the major constraints on aquaculture development (reviews in Verreth, 1994, Fuiman and Werner, 2002, Kamler and Wolnicki, 2006).

In wild fish parent–egg–progeny relationships are considered vital in recruitment variability and are incorporated in many respective models (Trippel et al., 1997). In cultured fish, quick prediction of future success or failure in larval rearing based on parent attributes or egg properties is of great importance, especially in species with long embryonic periods and high costs of incubation in hatcheries. Therefore, parent–egg–progeny relationships have received much attention from fish biologists and fishery scientists. Tomkiewicz et al. (2003) reviewed data about offspring production and viability with an explanation of environmental influences. These studies were considered to play a major part in estimating reproductive potential of Northwest Atlantic groundfish stocks. A recent explosion of primary fisheries research literature has resulted from the strong interest in early life stages. An updated review that includes the new literature is required.

Studies in fish energetics evolved in a direction opposite to fish ontogeny. Adults and juveniles were first studied and reviewed; later exogenously feeding larvae became a popular object of study. But there is no synthesis that explores the parent–egg–offspring relationships in fishes. The present review is intended to fill this gap.

This paper will summarise how performance of yolk-feeding fish is associated with female attributes *via* egg properties. I focus here on intrinsic survival potential, thus the remaining major factors contributing to early mortality (such as temperature, food availability and predation) will be mentioned only briefly. An energetics approach will be adopted. In this review paternal effects on fish offspring and processes that occur in marine fish larvae will receive more attention than in my earlier book (Kamler, 1992). Evaluation of selected methods will be given with new approaches highlighted. The main focus will be on new (post 1990) publications that were not available when I wrote the book, but, if necessary, relevant older works will be included as well.

Female attributes affect egg properties

Variation in the fish egg size has been associated with female attributes directly or indirectly through egg number, with egg batch sequence in multi-batch spawners, advancement of spawning season, population origin, latitude, temperature, food availability, and salinity. The problem how female attributes affect egg size (Figure 1) is of practical significance both in fisheries science and aquaculture; it has been intensively studied. Earlier works were extensively reviewed in Nikolsky (1974), Kamler (1992), Chambers and Leggett (1996), Johnston (1997), Trippel et al. (1997) and Chambers (1997).

Female age

The effects of female age on the chemical composition of eggs (as expressed in terms of concentration, mg g^{-1} or %) have been reported for some species. In common carp (*Cyprinus carpio*) hydration (Nikolsky, 1974), sum of protein amino acids in egg dry matter (Vladimirov, 1974), and content of phospholipids and cholesterol in egg dry matter (Kim, 1974) were found to be age-dependent. In vendace (*Coregonus albula*) lipid classes in egg dry matter (Potapova, 1978), and total lipids in dry matter (Wilkońska et al., 1993) were related to female age. Flounder (*Platichthys flesus*) lipid content in ovarian wet matter varied with female age (Shatunovskij, 1963). Female age-related variations of egg matter chemical composition can follow a course: low values in eggs derived from young females, highest values in eggs from females of average age, and again low values in old females (protein, lipids). Other compounds (water, cholesterol) can exhibit a reverse course. However, these variations of egg chemical composition do not seem to be universal. For example, hydration of rainbow trout (*Oncorhynchus mykiss*) eggs (Kamler and Kato, 1983), protein, lipid, carbohydrate and ash in *C. albula* egg dry matter (Kamler et al., 1982), caloric value of *C. albula* egg dry matter (Wilkońska et al., 1993), and sum of “yellow” carotenoids in brown trout (*Salmo trutta*) egg wet matter (Protasowicka and Domagała, 1989) were not related to female age.

Egg size is strongly related to female age (Figure 1). Repeat spawners produce larger eggs than first spawners, thus spawning status of females is a promising predictor of recruitment in

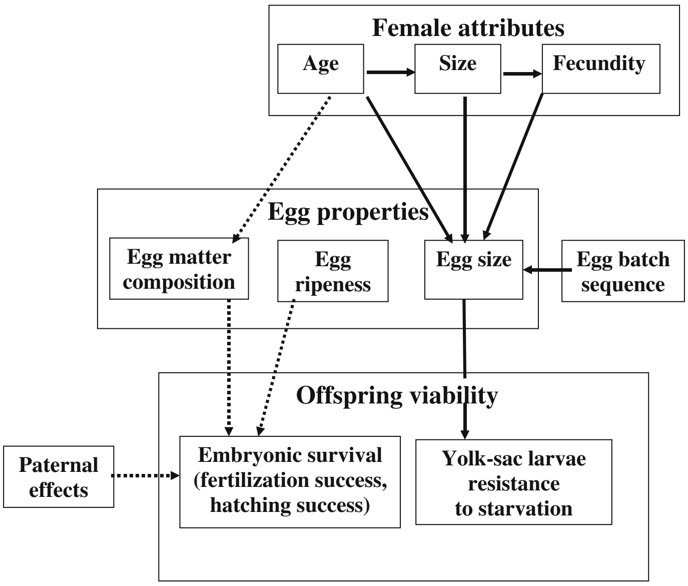

Figure 1. Two groups of parental factors that affect viability of fish progeny. Dotted arrows: effects manifested during embryogenesis; solid arrows: effects manifested in yolk-feeding larvae and later (modified from Keckeis et al. 2000).

marine fish stocks (reviewed in Lambert et al., 2003 and O'Brien et al., 2003). New primary research literature confirms age-induced variation of egg size (Kjesbu et al., 1992 for Atlantic cod (*Gadus morhua*); Brzuska, 1997 for *Cyprinus carpio*; Johnston, 1997 for *Sander vitreus*; Dlaboga et al., 1998 for brook trout (*Salvelinus fontinalis*) and Bartel et al., 2005 for *Salmo trutta*). In European and Chinese races of carp reared in Israeli ponds volume of eggs produced by two year old females was larger by a factor of >2 compared to those produced by 1 year females, but no distinct increase of egg size with spawner's age was seen later (Hulata et al., 1974). Typically, the smallest eggs are produced by first-spawning females, the largest eggs derive from spawners of average age, and the old females produce somewhat smaller eggs (e.g. Kjørsvik et al., 1990; Solemdal et al. 1995; review by Kamler, 1992).

A parabolic relationship was applied with significant results to describe age-dependent variation in egg size (Y) in three freshwater fish species producing relatively large eggs:

$$Y = A + B_{1\tau} - B_2\tau^2 \qquad (1)$$

where τ is female age class, and A, B_1 and B_2 are constants. The equation was used to approximate egg diameter in *Oncorhynchus mykiss* (Bartel, 1971), egg dry weight, protein, lipid or energy contents per egg in *Coregonus albula* (Kamler et al., 1982), egg diameter or energy content per egg in *C. albula* (Wilkońska et al., 1993), and egg dry weight in nase *Chondrostoma nasus* (Keckeis et al., 2000).

Optimal age, i.e. the age at which the largest eggs are produced, is given by:

$$\tau_{\text{opt}} = B_1/2B_2. \qquad (2)$$

Optimal age of *C. albula* computed by Wilkońska et al. (1993) from egg diameter confirmed earlier data by Kamler et al. (1982) based on egg dry weight. Trade-off between elevated maintenance metabolism of a large body of an old female and energy required for egg production, especially at low food supply, has been proposed (Kamler et al., 1982) as an energetic component of the decrease of egg size in old females. However, no egg size decrease in old females was detected, for example, in Siberian sturgeon (*Acipenser baeri*) northern pike (*Esox lucius*) and navaga (*Eleginus navaga*) (Nikolsky, 1974), as well as in *Sander vitreus* (Johnston, 1997), probably because few fish reach an old age (Nikolsky, 1963, Craig, 1982, 1985, Johnston, 1997).

Overall, the youngest females produce the smallest eggs. Why do they not produce fewer large eggs? Mann and Mills (1979) think that a large variation of the size among first-feeding larvae has an adaptive advantage: it would enlarge size range of prey. I question the correctness of that explanation. Small larvae can ingest only a limited range of small prey, whereas large larvae have a wide food size range, from small to large food particles (e.g. data for 20 marine fish species in Last, 1980 and for *Cyprinus carpio* in Bergot and Kestemont, 1995).

A significant ($p < 0.05$), positive correlation between egg size and age at maturation was found for inter-population comparisons of 48 populations belonging to 25 freshwater European fish species (Vila-Gispert and Moreno-Amich, 2002).

A direct relationship between embryonic survival and female age was found in few studies. Reduced viability of embryos developing in eggs that derived from very young females were observed in tench (*Tinca tinca*) (Morawska, 1986), striped bass (*Morone saxatilis*) (Zastrow et al., 1989) and in *Gadus morhua* (Solemdal et al., 1995).

Female size

No effect of female size (fork length) on egg matter composition (as expressed by caloric value, J mg^{-1} dry matter) was found in *Sander vitreus* and white sucker (*Catostomus commersoni*) (Johnston, 1997). No significant effect of female weight was found on chemical composition of egg dry matter (per cent ash, carbon, nitrogen, sulphur and caloric value) in *Chondrostoma nasus* (Keckeis et al., 2000). These are shown in Figure 1: no arrow is drawn between female size and egg matter composition.

Fish body growth is indeterminate, i.e. it does not stop at maturity; in some species body size of adult females grows by an order of magnitude. Female body size is an important contributor to egg size (Figure 1). This relationship has been extensively reported and reviewed (Kamler, 1992). Positive, significant relationships at the intraspecific level have been confirmed by recent primary publications. Examples include: Pacific herring (*Clupea harengus pallasi*) (Hay, 1985; Ware, 1985), *Coregonus albula* (Słomińska et al., 1995), *Salmo trutta* (Ojanguren et al., 1996; Papała et al., 1998; Nicola and Almodóvar, 2002), *Sander vitreus* sampled in 1994 and 1995 and *Catostomus commersoni* in 1994 (Johnston, 1997), *Salmo trutta* and *Esox lucius* (Bonisławska et al., 2000), *Chondrostoma nasus* (Keckeis et al., 2000), an amphidromous goby (*Rhinogobius* sp.) (Tamada and Iwata, 2005), *Salvelinus fontinalis*, arctic charr (*Salvelinus alpinus*), Danube salmon (*Hucho hucho*) and grayling (*Thymallus thymallus*) (Purtscher and Humpesch, 2006). In a tropical catfish vundu (*Heterobranchus longifilis*) heavier females poduced larger oocytes (Nguenga et al., 2004).

At the inter-population level a positive, highly significant correlation ($p < 0.01$) between egg diameter and female size (log standard length) was found for 48 populations belonging to 25 freshwater European fish (Vila-Gispert and Moreno-Amich, 2002). Similar correlations at the inter-specific level were found for Neotropical freshwater fish species ($p < 0.01$, Winemiller, 1989) and North American marine and freshwater fishes (Winemiller and Rose, 1992). Large marine fish species tend to produce larger eggs (Pleuronectiformes, $p < 0.005$, $r^2 = 0.29$, Chambers and Leggett, 1992; 255 marine species, $p < 0.001$, but that relationship had a very low predictive power, $r^2 = 0.04$, Chambers and Leggett, 1996).

Thus, positive relationships between egg size and fish size appear universal. However, the narrow range of female sizes precluded statistical significance of the female size effect on egg size in *Gadus morhua* (Chambers and Waiwood, 1996) and in *Catostomus commersoni* in 1995 (Johnston, 1997). Egg diameter did not depend on *Salvelinus fontinalis* female size: total length and weight (Dlaboga et al., 1998). Further examples of earlier works reporting on inconsistent response of egg size to female size are reviewed in Kamler (1992) and Chambers (1997).

To summarise, a great majority of sources documented positive relationships between egg size and female size, few reported no clear relationship. Chambers (1997) identifies the contributing factors confusing these relationships: the masking effects of egg batch (in batch-spawners), advancement in spawning season, and environmental factors such as temperature. I think that the relationships between egg size and female status are clear in fish species that produce large eggs. Nevertheless, the variance component of egg size attributable to female effect was high: it ranged from 35% in *Gadus morhua* (a batch-spawning species) to 46% in winter flounder (*Pseudopleuronectes americanus*) and 71% in capelin (*Mallotus villosus*) (Chambers et al., 1989, Chambers and Waiwood, 1996; Chambers and Leggett, 1996; Chambers, 1997). Reduced numbers of large fish due to size-selective fisheries, and earlier age at maturity can result in an increased proportion of small (young) spawners, thus to a decline in number and size of spawned eggs (Trippel et al., 1997).

Fecundity

Relationships between egg number (absolute fecundity) and female body size (Figure 1) has been shown in many studies (reviews in Nikolsky, 1963; Wootton, 1979; Opuszyński, 1983; Wootton, 1990; Kamler, 1992; Jobling, 1995; Trippel et al., 1997). Female size explained a large part of variance in individual fecundity, for example 92% in *Pseudopleuronectes americanus* (Buckley et al., 1991); 72% in *Coregonus albula* (Sarvala et al., 1992); 25% in *Oncorhynchus mykiss*, 66% in *Salvelinus fontinalis*, 69% in *Salmo trutta*, 74% in *Salvelinus alpinus* (Purtscher and Humpesch, 2006); 18–88% in gudgeon (*Gobio gobio*), 50% in *Esox lucius*, 74% in burbot (*Lota lota*), and 71–98% in roach (*Rutilus rutilus*), (Bańbura and Koszaliński, 1991). A power function was used to describe dependence of egg number (E.n.) on lenght (L):

$$\text{E.n.} = aL^b \tag{3}$$

The b coefficient usually clusters around 3 (Wootton, 1979), but both a and b vary between species (Purtscher and Humpesh, 2006), and, within a species - in different food supply and temperature levels (reviewed for *Clupea harengus pallasi* in Hay, 1985). Lambert et al. (2003) reviewed studies on factors influencing fecundity in gadoid fish species, and considered interactions and interdependences among the factors. Major factors were food supply and temperature. The indicators of nutritional status, condition factor and hepatosomatic index may be predictive of potential fecundity (Lambert et al., 2003).

A trade-off between number and size of eggs is one of the trade-offs that are central to life history theory (Stearns, 1992; Einum and Fleming, 2000). Across 44 Ivory Coast freshwater fish species (Albaret, 1982), 42 teleosts (Elgar, 1990) and six mouth-brooding cichlids (Goldschmidt and Witte, 1990) the species that produced smaller eggs had higher fecundity. In Antarctic fishes a tendency is observed to increase egg size and decrease fecundity towards more southern, colder waters (Knox, 1994). Also from intraspecific comparisons negative relationships between absolute fecundity and egg size have been observed (Blaxter, 1969; Mann and Mills, 1985; Sarvala and Helminen, 1995; Dujmic, 1997; Jonsson and Jonsson, 1999; Nicola and Almodóvar, 2002; see also review in Hutchings, 1997). In Chinook salmon (*Oncorhynchus tshawytscha*) negative relationships between relative fecundity and egg size were found to have similar shaped curves in 1996, 1999, 2000 and 2001 (Heath et al., 2003). In *Coregonus albula* egg weight explained 15% (wet wt) or 23% (dry wt) of the variance in fecundity (Sarvala et al., 1992). In *Salmo trutta*, *Oncorhynchus mykiss* and *Thymallus thymallus* higly significant ($p < 0.001$) relationships were found between fecundity and volume of individual eggs; the latter explained 11, 24 and 34% of the variance in fecundity (Purtscher and Humpesch, 2006). Phenotypic selection for egg size is stabilized at an optimal size that maximizes maternal reproductive success (Einum and Fleming, 2000); Atlantic salmon (*Salmo salar*) egg optimal size derived from their experiment coincided well with the mean egg size observed in a native population.

However, from studies on *Oncorhynchus mykiss* (Bartel, 1971), the convict cichlid (*Cichlasoma nigrofasciatum*) (Townshend and Wootton, 1984), *Salvelinus alpinus* and *Salvelinus fontinalis* (Purtscher and Humpesch, 2006) the expected trade-off was not detected. In only 12 cases of 21 listed by Stearns (1992, Appendix 2e from plants to man) higher offspring number was associated with smaller offspring size.

Winemiller (1992) postulated an interplay between maternal age at maturity, fecundity, and egg size (i.e. survivorship of progeny). Among these components three life history strategies are possible: the "opportunistic" strategy with early maturity, low fecundity and small progeny size, the "equilibrium" strategy with late maturity, low fecundity and large size, and the "periodic" strategy with late maturity, high fecundity but low progeny size. Thus, the trade-off between egg number and size can be clouded by several side-effects.

An anthropogenic impact on the relationship between egg number and size was observed in conservation programmes. In studies on genetic evolutionary response of *Oncorhynchus tshawytscha* to captive breeding a rapid unintentional selection on increased fecundity at the expense of egg size with no change of female body size was found (Heath et al., 2003). In the hatchery mean egg mass decreased from 270 to 200 between 1988 and 2001. That had implications for rivers in which declining wild populations were supplemented with hatchery-reared fish. Significant decrease of egg volume over several years was found in Quinsam River and Robertson Creek in which supplementation effort (the number of females spawned in the hatchery divided by the total number of adult females) was high, 43 and 28%, respectively. However, no significant decline in egg volume was observed in Nanaimo and Nahmint Rivers in which supplementation effort was low (16 and 4%).

Batch sequence contributes to egg size

Spawning in batches over a period of several weeks is considered one factor that increases chances for larvae to encounter optimal feeding conditions (the match-mismatch hypothesis, Cushing, 1975, 1990). High negative correlations ($p < 0.01$) were reported between egg size and length of breeding season, and between egg size and number of spawnings per year for 25 European freshwater fish species (Vila-Gispert and Moreno-Amich, 2002) and for North American marine and freshwater fish species (Winemiller and Rose, 1992).

Batch sequence (Figure 1) is a factor contributing to egg size. In a multiple batch spawner *Gadus morhua*, 26% of the observed variance in egg size resulted from batches-within-females (Chambers and Waiwood, 1996). Mean egg size decreased in successive batches laid by an individual female during spawning season: Atlantic mackerel (*Scomber scombrus*) (Ware, 1977); *G. morhua* (Kjesbu, 1989; Kjesbu et al., 1996); killifish (*Fundulus heteroclitus*) (Hsiao et al., 1994); *Rhinogobius* sp. (Tamada and Iwata, 2005); earlier works were reviewed in Mann and Mills (1979). Such a pattern could reflect the depletion of energy resources by repeated spawnings. Chambers and Waiwood (1996) found a significant decline of egg diameter in successive spawned batches in 5 of 10 captive, individually monitored females, but this effect was not detectable when eggs were pooled from all 10 females. In multiple-spawning fish egg size may initially increase with successive spawnings to a maximum value and later decrease. The latter pattern was observed for egg diameter in Amur loach (*Misgurnus anguillicaudatus*) (Suzuki, 1983) and egg dry weight in the orange throat darter (*Etheostoma spectabile*) (Marsh, 1984). *Tinca tinca* egg dry weight and energy content (J egg^{-1}) tended to be largest in the middle of the breeding season and smaller early and late in the season, but this result was not significant (Kamler and Stachowiak, 1992). Thus, the earlier conclusion of Żuromska and Markowska (1984) was confirmed, i.e., that the quality of *T. tinca* eggs remained unchanged between batches. On the other hand, in *Cichlasoma nigrofasciatum* egg diameter, wet and dry weight increased in successive batches (Townshend and Wootton, 1984).

Thus, batch sequence within a reproductive season may be or may be not a component of egg size variance. Besides depletion of energetic resources, an asynchronous spawning activity of large and small females, as well as temperature change within a spawning season may contribute to egg size variation between successive batches (Kjesbu et al., 1996; Tamada and Iwata, 2005). We still have to wait for more research before a synthesis of batch sequence effects on egg size is possible.

Factors that determine offspring viability

Parental effect on early life history traits is a product of extrinsic and intrinsic factors. The former are primarily the supply with nutrients and temperature encountered by spawning individuals. In this chapter I will focus mostly on paternal and maternal effects.

Variations in offspring viability

Three distinct periods of elevated mortality, separated by the periods of low mortality, are typically observed during fish endogenous feeding periods. Two periods occur during embryogenesis, the third occurs in yolk-sac larvae. The first burst of mortality is shortly after egg fertilisation (early mortality, EM (%) = 100 minus fertilisation success). The second occurs during hatching (mortality post-hatch, MPH (%) = 100 minus hatching success); i.e., the mortality cumulated from day 0 (fertilisation) to the last day of the hatching period. The third period of elevated mortality is starvation mortality (SM) when yolk reserves are depleted under absence of external food (see for example Ivlev, 1961 for data from 12 species; Viljanen and Koho, 1991, and Wilkońska et al., 1994 for *Coregonus albula*; Keckeis et al., 2000 for *Chondrostoma nasus*). Early mortality and post-hatch mortality are inter-related, while starvation mortality is not correlated with the other two (Żuromska and Markowska, 1984 for *Tinca tinca*; Keckeis et al., 2000 for *C. nasus*).

Paternal effects

Determinations of fish spermatozoan properties have been done to assess paternal effects on embryonic survival (Figure 1). In teleosts spermatozoans are immobile in non-diluted seminal fluid. The triggering factors for spermatozoan motility are dilution of the inhibitory seminal fluid, pH, oxygen concentration and osmotic shock (decrease of osmotic pressure in fresh water or increase in sea water) (reviewed in Cosson et al., 1999). The major energy source is ATP. The spermatozoans stop swimming when ATP level declines to 50–20% of its initial level (Billard et al., 1995).

Positive effects of sperm density and sperm motility on egg fertilisation rates were observed in *Cyprinus carpio* (Kołdras and Mejza, 1983). A positive effect of the number of spermatozoans per egg on European catfish (*Silurus glanis*) fertilisation success was found. A good level of hatching was found with 800 spermatozoans egg^{-1}, but the best result was with 8000 spermatozoans egg^{-1} (Linhart et al., 1997). In contrast, *Gadus morhua* fertilisation rates were not significantly correlated neither with the proportion of the motile spermatozoans, nor with spermatocrit (a measure of the percentage of the total volume of milt occupied by spermatozoa, i.e. a correlate of sperm density) (Trippel and Neilson, 1992). Bream (*Abramis brama*) egg fertilisability did not depend on sperm density and motility, but was positively correlated with aspartate aminotransferase (AspAT) and acid phosphatase (AP) activities in sperm (Glogowski et al., 1997). In sperm competition trials among different *Salmo salar* males, Gage et al. (2004) identified parentage by using polymorphic microsatellite markers. Sperm velocity was a key factor for fertilisation success, which was not related to spermatozoa number or total length, and longevity was a spermatozoal trait inversely related with competition success. Survival of *Oncorhynchus mykiss* embryos at the eyed stage was significantly affected by $>50\%$ replacement of fishmeal by cottonseed meal in diet fed to broodstock males for two years prior to maturation (Rinchard et al., 2001).

Advances in our knowledge of the teleost male gametes have been summarised recently. Cosson et al. (1999) presented factors affecting the motility of fish spermatozoa. Works on fish testicular physiology, induction of sperm motility, and sperm quality were reviewed by Coward et al., (2002). Trippel (2003) synthesised results of field and laboratory studies on male reproductive potential in marine fish. Trippel and Neilson (1992) reviewed results for seven species; the majority of observations indicated a positive effect of sperm density and motility on successful fertilisation, while variability in hatching success of *Gadus morhua* was unrelated to male size and age (Trippel and Morgan, 1994). Thus, the paternal effect probably operates mostly in very early ontogeny.

Maternal effects

Egg matter composition is one among the factors influencing embryonic survival (Figure 1). A negative relationship between embryonic survival and hydration of unswollen eggs was found in *Oncorhynchus mykiss* (Satia et al., 1974; Kato and Kamler, 1983) and in *Chondrostoma nasus* (Keckeis et al., 2000). Increase of protein percentage in *Cyprinus carpio* egg wet matter resulted in an increase of fertilisation success and hatching success; this effect was stronger at low protein levels (ca. 14–17 %) than in higher ones ($>17\%$) (Semenov et al., 1974). Positive correlations between egg fertilisability and percentage of undeformed hatched individuals, on the one hand, and the concentration of total protein amino acids in egg dry matter, on the other hand, was reported for *C. carpio* by Vladimirov (1974). Also, total protein concentration and concentration of sulphydryl groups (–SH) in *C. carpio* eggs at gastrulation positively influenced fertilisation and hatchability (reviewed in Konovalov, 1984).

In *Coregonus albula* per cent of normal hatch correlated positively with egg lipid percentage in dry matter, but per cent of total hatch was negatively related to carotenoid level ($\mu g\ g^{-1}$) (Dabrowski et al., 1987). In Red Sea bream (*Pagrus major*) developing eggs an elevated phospholipid content and elevated free tyrosine were observed in eggs of high hatching success and were proposed as criteria for egg quality (Seoka et al., 1997b). In contrast, hatchability of *O. mykiss* eggs was not influenced by caloric value of egg dry matter (Kato and Kamler, 1983). Similarly, in *Chondrostoma nasus* early mortality (EM) and mortality post-hatch (MPH) were not related with caloric value of dry matter, nor with ash, carbon, nitrogen, and sulphur percentages in dry matter, but a combined effect of N and S was detected: $EM = 22\,368 - 1867{*}N - 29\,070{*}S + 2426.8{*}N{*}S$, $r^2 = 0.50$, $p = 0.01$. Nitrogen and sulphur are bound in protein; the interaction between them suggests that early mortality, although independent of protein concentration, was related to protein composition (Keckeis et al., 2000). One of the most prominent reasons for early life stage mortality in salmonids throughout the North American Great Lakes and the Baltic Sea is a thiamine deficit in eggs. A suggested explanation is high thiaminase activity in main food items of salmon (McDonald et al., 1998). In summary, the majority of existing data supports the conclusions that embryonic survival depends on egg matter composition.

Relationship between embryonic survival and egg ripeness (Figure 1) is of importance for fish culture. Egg quality of captive fish is usually inferior when compared with wild fish; mechanical damage during handling, stress, and over-ripening of ovulated but not oviposited eggs are the major contributing factors (reviewed in Brooks et al., 1997; Lambert and Thorsen, 2003). Eggs retained in the abdominal cavity have no oxygen supply and after a certain time degeneration takes place. For example, over-ripe eggs of *Abramis brama* retained for 7–8 h had a reduced oxygen consumption rate, oxidative phosphorylation (P/O coefficient) and ATPase activity. These were paralleled by decreasing protein amino acids content and increase of free amino acids, cholesterol and free fatty acids as well as by an enhanced embryonic mortality at the morula, gastrula and tail-bud stages (Zhukinskij et al., 1981). Gosh (1985) in her review of the literature concerning metabolic changes in fish eggs during over-ripening suggested that this process is associated with an accumulation of metabolic inhibitors.

The problem of egg over-ripening has been explored in many species: pink salmon (*Oncorhynchus masu*) (Kawajiri, 1927); *Misgurnus anguillicaudatus* (Suzuki, 1975); grass carp (*Ctenopharyngodon idella*) Nedyalkov (1981); *Gadus morhua* (Kjørsvik and Lønning, 1983); *O. mykiss* (Springate et al., 1984); turbot (*Scophthalmus maximus*), McEvoy (Barton) (1984); cyprinids (Billard et al., 1986); Alantic halibut (*Hippoglossus hippoglossus*), (Bromage et al., 1994); *Tinca tinca* (Linhart and Billard, 1995a);*Cyprinus carpio* (Linhart et al., 1995); snapper (*Pagrus auratus*) (Hobby and Pankhurst, 1997); *Silurus glanis* (Linhart and Billard, 1995b and Linhart et al., 1997). For example, total hatching percentage of *S. glanis* ovulated ova decreased with prolongation of retention time at 22–24 °C in the ovarian cavity (h between ovulation and fertilisation) (0 h – 74.5%, 2 h – 77.5%, 4 h – 54.2%* and 6 h – 37.9%*), while the percentage of deformed larvae increased (8.2%, 8.6%, 17.9%* and 50.0%*, respectively) (results significant from the controls are marked with an *) (Linhart and Billard, 1995b). Thus, in *S. glanis* a window for successful fertilisation was about 2 h (Linhart and Billard, 1995b), whereas in *H. hippoglossus* it was 4–6 h (Bromage et al., 1994), in *C. carpio* at about 20 °C *in vitro* successful fertilisation occured after 4–6 h of retention (Linhart et al., 1995; Rothbard et al., 1996), but in *O. mykiss* held at 10°C *in vitro* successful fertilization could be performed after 4–6 days (Springate et al., 1984).

Intra-specific comparisons demonstrated that high retention temperatures accelerated over-ripening of eggs (Kawajiri, 1927; Suzuki, 1975; Billard et al., 1986). In *Silurus glanis* at incubation temperatures of 8 and 25 °C, that strongly deviated from optimal temperatures, egg storage had stronger negative effect on hatching success and increased per cent of deformed larvae than at incubation temperatures within the optimum range (Linhart and Billard, 1995b; see also Billard et al., 1986; Rothbard et al., 1996). In the ornamental (koi) carp, *Cyprinus carpio*, the latter authors quantified separately the effect of the egg ripeness in the female abdominal cavity and reduction of spawned egg viability during external storage in ovarian fluid. The eggs that were stripped shortly after ovulation and preserved in water or other solutions lost their fertilisability almost immediately (Billard et al., 1986, Linhart et al., 1995, Linhart and Billard 1995b) which suggests autoactivation without any sperm contribution (Billard et al., 1986).

No effect of egg size on embryonic survival (Figure 1) was found in *Pseudopleuronectes americanus* (Buckley et al., 1991), *Sander vitreus* and *Catostomus commersoni* (Johnston 1997), and *Chondrostoma nasus* (Keckeis et al., 2000).

However, egg size is regarded as a key feature in fish early history. Egg size may be expressed as egg diameter, egg volume, wet weight, dry weight, energy content per egg or else the content of a key substance (e.g. carbon, nitrogen, protein) per egg. In this sequence these indices are increasingly relevant as information about the resources supplied to an embryo, but they are also increasingly difficult to measure. Most data on egg size are expressed in egg diameter. However, the shape of many fish eggs deviate from a sphere, some species produce eggs with thick, gelatinous chorion, and the width of perivitelline space varies across species. For example, in *Oncorhynchus mykiss* the volume of perivitelline space (as compared to the total egg volume at the end of swelling) was only 7% (recomputed from Kamler and Kato, 1983). But in *Ctenopharyngodon idella* the diameter of unswollen eggs was about 1 mm (0.7–1.5 mm), and increased to 6 mm after swelling (Billard et al., 1986), which suggests that the perivitelline space accounted for approximately 99% of volume of the swollen egg. Comparative value of egg wet weight is biased by interspecific variability of hydration (i.e., % water in wet matter) of unswollen eggs, e.g. 56%

in *Oncorhynchus* spp, 74% in eggs of sea spawners (excluding *Anguilla* and *Trachurus*) (reviewed in Kamler, 1992 and Thorsen et al., 2003). Comparisons of egg dry weight are weakened by interspecific variability in the composition of egg dry matter; for example the difference in caloric values of 1 mg dry matter between most contrasting species was about twofold (Wootton, 1979).

There are several studies that demonstrated a positive effect of egg size on fish offspring performance. In the Lake Saimaa system *Coregonus albula* from Lake Haukivesi had smaller ($p < 0.05$) egg size (diameter 1.71 ± 0.05 mm ($\pm$SD) and dry weight 0.57 ± 0.09 mg) than eggs from Lake Orivesi (1.81 ± 0.09 mm and 0.65 ± 0.08 mm, respectively). Differences in egg size were mirrored by a significant difference in total length of newly hatched larvae (Viljanen and Koho, 1991). Growth of yolk-feeding lake whitefish (*Coregonus clupeaformis*) increased with egg size expressed in terms of lipid content (Brown and Taylor, 1992). Highly significant effect of egg size on *Salmo salar* size at the initiation of external feeding and after 20 days of strongly limited feeding was found by Einum (2003), while larval size was independent on paternal body size. Largest eggs of *Sander vitreus* had high levels of ($n-3$) polyunsaturated fatty acids (PUFA) in yolk plus blastoderm. Larvae hatched from these eggs had faster rate of formation of hypural bones and greater body length on days 1 and 13 after hatching, ingested more food, and had lower levels of deformities and mortality (Moodie et al., 1989).

Length of newly hatched *Gadus morhua* larvae significantly increased with egg diameter, but only 6% of the length variance could be explained by egg size (Pepin et al., 1997). Egg size (egg diameter, dry weight and energy content per egg) had a significant positive effect on growth rate in dry weight of *G. morhua* larvae (R^2 32–48%, Browman et al., 2003). Positive effect of egg mass on early juvenile survival in *Oncorhynchys tshawytscha* was quantified by curves of similar shape during four consecutive years, 1996–1999 (Heath et al., 2003). In *Salmo salar* two groups of eggs (small and large ones) were collected from each of eight females and fertilised with sperm from one male. Larger ($p < 0.001$) juveniles emerged from nests with larger eggs, the positive effect of egg size on body size persisted 28 ($p < 0.001$) and 107 ($p < 0.02$) days after emergence (Einum and Fleming, 2000). Difference between weight of early larvae from two New Zealand populations of *Oncorhynchus tshawytscha* was consistent with the difference in egg size, but fish weight difference decreased with time and disappeared after one year rearing in shared conditions (Kinnison et al., 1998).

A large set of data appeared in the last decade, concerning changes in resistance to starvation with egg size. Eggs and larvae from the Isąg Lake were the largest among three *C. albula* populations studied, and larval resistance to starvation was the highest in that lake (Słomińska et al., 1995). Larvae of *Mallotus villosus* from eggs with large yolk reserves had longer post-hatching life span when faced with no access to food (Chambers et al., 1989). A highly significant ($p = 0.005$), non-linear relationship between time to 50% starvation mortality (TSM50) of *Chondrostoma nasus* larvae at the final steps of yolk sac resorption and egg energy content (J egg^{-1}) was found; 47% of the total TSM50 variance was attributable to egg size (Keckeis et al., 2000). In the Lake Biwa system a fluvial-lacustrine population of *Rhinogobius* sp. was exposed to risk of larval starvation and produced larger eggs than a lacustrine population in which larvae experienced more favourable food conditions (Maruyama et al., 2003). Tamada and Iwata (2005) conducted laboratory experiments involving newly hatched *Rhinogobius* sp. larvae to investigate relationships between resistance to 72-h starvation and egg volume. They found a significant positive correlation. Body length, body weight, visual range and survival were functions of yolk supply at hatching in *Gadus morhua* larvae fed a fixed external food concentration; the benefit of better endowment with yolk was long-lasting (Fiksen and Folkvord, 1999). Large yolk reserves in newly hatched Antarctic fish larvae help them to survive the starvation periods in years when the retreat of the pack-ice is delayed (Radtke et al., 1989).

The benefits for a larva to be large have been well documented. It is commonly accepted that starvation and predation are the two most important causes of mortality in fish early life and are size-dependent (Hempel, 1965; reviews in Miller et al., 1988; Kamler, 1992; Fuiman and Magurran, 1994; Houde, 1994, 1996; Chambers and Trippel, 1997). Large larvae have a higher resistance to starvation (Rosenberg and Haugen, 1982; Miller et al., 1988;

Trippel et al., 1997; Keckeis et al., 2000). Sizes of vimba (*Vimba vimba*), European chub (*Leuciscus cephalus)*, dace (*L. leuciscus*), ide (*L. idus*), barbel (*Barbus barbus*) and *Chondrostoma nasus* larvae at the onset of external feeding ability were 2, 2, 3, 3, 9.5 and 10 mg wet weight, respectively. The respective 50% larval survivals were 9.2, 10.9, 11.1, 11.4, 12.1 and 14.4 days of delayed first feeding at 20°C (Kujawa, 2004). Greater success of large *Gadus morhua* larvae in establishing external feeding was shown by Knutsen and Tilseth (1985). Predation of larvae was maximized by larval large size, while predation on larvae was minimized (Ware, 1975; Houde and Schekter, 1980; Hunter, 1981; Keckeis and Schiemer, 1992; Letcher and Bengtson 1993; Fuiman, 1994; Flore et al., 2001). With a simulation model of field situations Winemiller and Rose (1993) have demonstrated that larval growth and survival rates of small number of large larvae or, alternatively, large number of small larvae, may be modified by prey density and patchiness of distribution.

Swimming performance is an important component of successful food acquisition. Direct links between larval swimming variables (move distance and duration, swim speed, pause duration, turn angles and per cent of activity) and female attributes (body size, ration size and "thermal history") were evaluated in *Gadus morhua*. The response was weak and inconsisent, it was probably masked by a high degree of variability in the variables (Browman et al., 2003).

An adaptive character of the maternal effect was demonstrated in a study by Tamada and Iwata (2005) on an amphidromous fish *Rhinogobius* sp. colleced from different stations along the Aizu River. Younger and smaller female spawners were found in the lower course of the river (2 km from the sea), whereas females inhabiting the upper reaches (8 and 12 km from the sea) were progressively older and larger. A highly significant, positive relationship ($p < 0.0001$) was found between egg volume and female standard length. In newly hatched larvae resistance to starvation was experimentally assessed. Percentage of survival a 72-h starvation was positively related ($p < 0.05$) to egg size. Thus, survival of larvae hatched from larger eggs in the upper part of the river is maximised to compensate for risk of starvation (and possibly predation) during their longer migration to the sea (Tamada and Iwata, 2005).

Paternal vs. maternal effects

Complex laboratory studies of parental effects (i.e. paternal and maternal) on offspring viability in *Tinca tinca* under the absence of predators revealed three ontogenetic periods with different responses (Żuromska and Markowska, 1984). Sperm quality was decisive for fertilisation success and hatching success, while egg size had no such effect. Effect of egg quality first manifested between embryo formation and hatching, but at that time egg effect was weaker than the effect of sperm. In contrast, size and viability (expressed as percentage of non-deformed larvae) of 4-day-old larvae was dependent on egg size (dry weight and energy content per egg, J egg^{-1}), but not on sperm quality (Żuromska and Markowska, 1984). The problem of paternal *vs.* maternal effects was further studied in three independent experiments on *Coregonus albula*. Survival till hatching depended on sperm quality, whereas egg quality determined the size and viability of larvae (Wilkońska and Żuromska, 1988). Sperm quality did not affect significantly larval size, while egg size always had a positive, significant effect on larval size, and survival time of starving larvae depended on egg or larval dry weight (Wilkońska et al., 1993, 1994, 1995).

The positive correlation between salmonid female size and egg size has been modelled by Hendry et al. (2001). They assumed a reduced survival of offspring from larger eggs when ambient oxygen is low, because as an egg becomes larger, its volume (to which oxygen consumption is proportional) increases more rapidly than its surface (to which oxygen diffusion into the egg is proportional). However, soon thereafter that assumption was contradicted by results of an experiment where large eggs survival was higher in low oxygen conditions (Einum et al., 2002). Then the original model was re-analysed (Hendry and Day, 2003). In the new version the positive correlation between female size and egg size was found to arise as a result of several combinations of different effects. Large eggs have an advantage in the incubation milieu in which oxygen content is reduced as the result of larger egg clutches spawned by larger females (Hendry and Day, 2003).

I think that further explanation of the advantage of larger eggs should include metabolic constraints during fish embryogenesis. Oxygen consumption rate is very low at the beginning of embryogenesis, in eggs incubated in water partly anaerobic conditions normally prevail (reviewed in Kamler, 1992). Large eggs (wet weight 20 mg, Kamler et al., 1998) of a litophilous rheophilic cyprinid *Chondrostoma nasus* were exposed between egg activation and gastrula to a strongly reduced oxygen content (10% of air saturation) (Keckeis et al., 1996). From these eggs 93.4% of the hatched larvae were viable. Anaerobic glycolysis is less efficient than aerobic metabolism by a factor of nearly 20 (Hochachka and Somero, 1973). Thus, larger yolk resources will be less depleted after a period of non-effective resource use at low environmental oxygen.

To summarize the problem of parent–egg–progeny relationships in fishes, three conclusions can be made. Firstly, key pathways include positive relationships between female size, egg size and offspring size/resistance to starvation and predation (Figure 1). For example, among 143 published field and laboratory data sets on different predictors of variation in egg and larval quality, reviewed for North Atlantic fish by Lambert et al. (2003), 38 data sets focused on that pathway. Most of the latter (84%) revealed positive, significant relationships. In the remaining, statistically non-significant effects were detected, but no contradicting results were found. Direct relationships between female attributes and larval performance have been rarely documented. Large (> 15 kg) *Morone saxatilis* females produced larvae larger than those produced by smaller (< 4 kg) females, these differences were manifest at 5 and 25 dys post-hatch, but larval survival to 25 days was not related to female size (Monteleone and Houde, 1990). Usually the direct relationships have been weaker than an indirect link through egg quality (Lambert et al., 2003).

Secondly, both maternal and paternal effects contribute to the total survival of offspring (Figure 1). Probably this is why the mortality of fish embryos and larvae is higher than expected from egg size-based theory alone (Houde, 1997). Paternal and maternal contributions to the total variation of progeny operate in different ways and at different times. In contrast to the importance of female size, no paternal size effects were revealed, but density and motility of spermatozoans are decisive. In most studies male effects extinguished earlier in ontogeny. Works on paternal effect had been less advanced, but a considerable progress in the study of the quality of male gametes has been done in the last few decades.

Thirdly, major factors governing embryonic survival (fertilisation success and hatching success) differ from factors to which starvation mortality of yolk-feeding larvae is related. Embryonic survival is affected by female age *via* egg matter composition, by egg ripeness and paternal factors (sperm density and motility; dotted arrows in Figure 1). In contrast, starvation mortality of yolk-feeding larvae depends largely on female attributes (age, size and fecundity) *via* egg size, and, in some batch spawners, on egg batch sequence (solid arrows in Figure 1).

Thus, the "bigger is better" paradigm applies well to egg size, but is not ubiquitous. Viability of yolk-feeding larvae at the onset of external feeding is strongly size-dependent, but factors other than egg size may be decisive in embryogenesis (Figure 1). Not only egg size *per se* is important, but also the size relative to a norm for a spawners' age group (*Oncorhynchus mykiss*, Kamler and Kato, 1983) or for a population (*Sander vitreus*, Moodie et al., 1989). Another few examples of deviation from the "bigger is better" paradigm are reviewed in Chambers and Trippel (1997) and Brooks et al. (1997).

Size-selective predation

Size-selective predation is another factor regulating offspring size. During natural incubation in the sea *Gadus morhua* egg diameter increased by 0.002 mm day^{-1}, and that of plaice (*Pleuronectes platessa*) by 0.003 mm day^{-1}. That was explained by the greater mortality of smaller eggs, resulting from size-selective predation (Rijnsdorp and Jaworski, 1990). Last (1980) demonstrated that both, small and large predators can prey on small food items, while large particles are available only for large predators. Moreover, small predators are more numerous than larger ones.

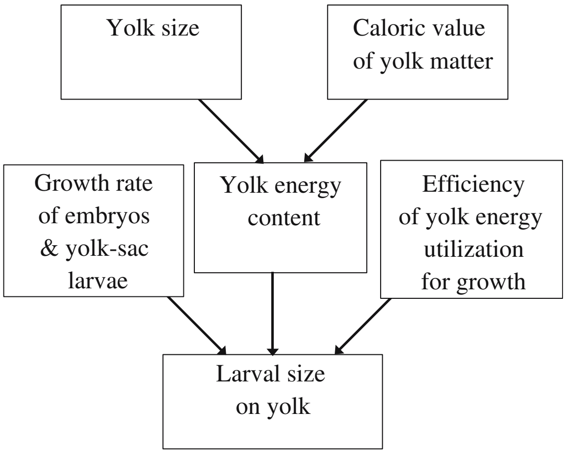

Figure 2. Factors contributing to larval size on yolk (modified from Kamler and Keckeis, 2000).

What makes a yolk-dependent larva large?

The main intrinsic factors contributing to the larval body size attained from yolk are: growth rate of embryos and yolk-feeding larvae, efficiency with which yolk energy is converted to body tissues and yolk energy content (Figure 2). Growth rate of embryos and yolk-feeding larvae, and efficiency of yolk energy utilization for growth will be considered in another review (Kamler, unpubl.). In this chapter I will focus on the yolk energy content. It results from yolk size and caloric value of yolk (Figure 2). In several fish species the initial yolk energy reserves are allocated between lipoprotein yolk and oil globule(s). Examples are pelagic marine species, of which 75% have oil globules (Ahlstrom and Moser, 1980), *Lota lota* (the only gadiform fish in fresh waters, Kujawa et al., 2002), perch (*Perca fluviatilis*; Korzelecka et al., 1998) and salmonid fishes.

Yolk (egg) size

In *Salmo salar* yolk constituted 82.1% of the total egg dry matter (Hamor and Garside, 1977), in *Gadus morhua* about 80% (Finn et al., 1995a), and in *Chondrostoma nasus* 79% (Kamler et al., 1996). The contribution of *C. nasus* yolk energy to total egg energy was a little higher, 81%, because yolk is the component richest in energy. Caloric values (J mg^{-1} dry matter) of *C. nasus* yolk, intact egg, egg cases and perivitelline fluid were 29.6 > 28.4 > 26.1 > 25.2 respectively ($p < 0.05$) (Kamler et al., 1998). Thus, yolk is the main component of an egg, and the majority of studies did not distinguish between particular egg components, therefore the further considerations will be done on total eggs.

Egg size varies among teleost species across a wide range from below 0.3 mm in diameter (shiner perch (*Cymatogaster aggregata*), Wallace and Selman, 1981) to 85–90 mm and over 300 g in weight (coelacanth (*Latimeria chalumnae*), Anthony and Millot, 1972, Balon, 1990). Similarly large eggs (65–97 mm) can be found among Elasmobranchii (Blaxter, 1969; Opuszyński, 1983). Compilation of the frequency distribution of egg size among teleost species shows a significant positively skewed (i.e. skewed to the right) distribution of egg diameters (Figure 3a) and even higher skewness in egg volumes (Figure 3b). Earlier compilations of egg size distribution (diameters: Ware,1975; Wootton, 1979; Coburn, 1986; Miller et al., 1988; Chambers and Leggett, 1996; volume: Bagenal, 1971; wet weight: Kamler, 1992) showed the same tendency. Positively skewed distributions were also reported for total length at hatching of 66 species of freshwater and marine fishes (Miller et al., 1988) and for length at metamorphosis of 129 flatfish species (Chambers and Leggett, 1992). It was also observed at an intraspecific level for length of 29 leptocephali of an anguilliform European conger (*Conger conger*; Correia et al., 2002). Overall, a decrease in number of species with increasing size, i.e. skewness to the right, is the principal feature of body size distributions among sets of related taxa (Hemmingsen, 1934; Hutchinson and MacArthur 1959; Trammer, 1999). Positive skewness of egg size distribution means that species that spawn large eggs are relatively rare.

Variation of egg size has ecosystem, evolutionary and behavioral components. Large eggs are observed in the species with long incubation periods at low temperature. Examples are salmonids among freshwater fishes, and polar species among marine fish. Average egg diameter of the Antarctic fishes is 2.8 mm, and egg size increases towards higher latitudes, i.e. colder waters (Knox, 1994). An analysis of 85 data sets from 59 marine fish species revealed that polar pelagic spawners produced larger and fewer eggs than boreal pelagic spawners, but this difference was not observed in demersal (substrate) spawners, which produce few

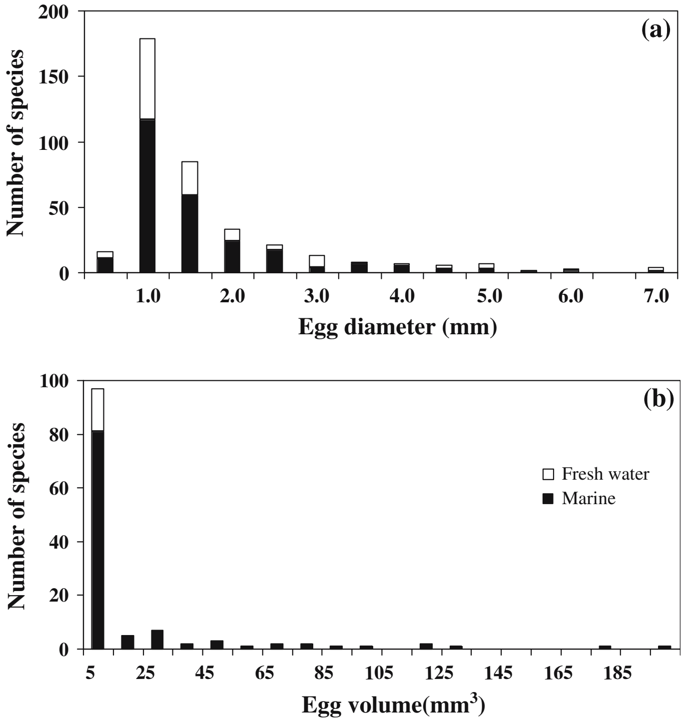

Figure 3. Frequency distribution of teleost fish egg size: interspecific comparisons. (a) egg diameter in 254 marine (sk = 2.636, $t = 4.412$, $p < 0.001$) and 130 freshwater (sk = 2.923, $t = 4.892$, $p < 0.001$) fish species, compiled from: Shirota (1970), Ware (1975), Wootton (1979), Peňáz et al. (1981), Peňáz (1983), Coburn (1986), Verreth (1994), Halačka and Lusk (1995) and Christiansen et al. (1998); (b) egg volume in 105 marine (sk = 4.169, $t = 7.774$, $p < 0.001$) and 27 freshwater (sk = 4.264, $t = 8.326$, $p < 0.001$) fish species, compiled from: Bagenal (1971) and Christiansen et al. (1998). Each species is represented by one value, an intraspecific variation is not represented here.

large eggs irrespective of the zoogeographical region (Christiansen et al., 1998). Pelagic eggs are generally smaller than demersal eggs (Kendall et al., 1984; Chambers, 1997). Typically, marine fish spawn pelagic eggs that range 0.6–4.0 mm in diameter (reviewed in Blaxter, 1988 and Bunn et al., 2000), while most of freshwater eggs are demersal. "Old" species (Acipenseridae, *Latimeria chalumnae* and Elasmobranchii) that have more geological time to develop tend to produce large eggs. Specialization of fish reproductive styles from non-guarders through guarders to egg bearers is accompanied with an increase of egg size (Balon, 1991). Thus, several factors co-determine the variation of egg size (Marshall, 1953).

Caloric value

Caloric value of egg dry matter (Table 1) varies within a range of about 20–30 J mg^{-1}, a very narrow range as compared to size variability. There is a tendency for large eggs (e.g. *S. trutta* and *O. mykiss* about 10–30 mg dry weight egg^{-1}) to have high caloric value, whereas small eggs (e.g. *T. tinca* and *G. morhua*, about 0.1 mg dry weight egg^{-1}) tend to have a low caloric value, but there is not always a correlation between these two variables. High caloric value (30 J mg^{-1}) eggs are found in European eel *Anguilla anguilla* whose larvae have high energy demands for traveling from spawning grounds, and in Atlantic bluefin tuna (*Thunnus thynnus*), but in remaining marine species low caloric values (19.5–25.3 J mg^{-1}) were observed (Table 1; see also Wootton, 1979). Lithophilous salmonids (data sets 4–10 in Table 1) have egg matter rich in energy (26.5–29.5 J mg^{-1}). In phytophilous cyprinids (12–15 in Table 1) lower caloric values (25–27 J mg^{-1}) are observed. Interestingly, in a lithophilous cyprinid *Chondrostoma nasus* the egg caloric value of 28.6 J mg^{-1} is similar to that of litophilous salmonids rather than to phytophilous cyprinids.

Table 1. Caloric values of freshly spawned fish eggs (E) or mature ovaries (MO)

Species		Caloric value (J mg^{-1}dry weight)				Source
		Mean	95% conf. lim.	Range	Method*	
1. *Clupea harengus pallasi*	E, s	25.2	–	–	B	Eldridge et al., (1977)
2. *Sardinops caerulea*	MO, s	22.6	21.9–23.2	–	B	Lasker (1962)
3. *Anguilla anguilla*	MO, s	30.1	–	–	C†	Epler et al., (1981)
4. *Salmo trutta m. trutta*	E, f	27.5	–	25.2–30.4	B	Kamler (1987)
5. *Oncorhynchus nerka*	MO, f	27.5	–	–	B	Nishiyama (1970)
6. *O. mykiss*	E, f	29.5	–	–	C†	Suyama and Ogino (1958)
7. *O. mykiss*	E, f	27.8	27.6–28.1	25.9–28.8	B	Kato and Kamler (1983)
8. *O. mykiss*	E, f	26.5	–	24.3–27.6	B	Paaver et al., (1988)
9. *Coregonus albula*	E, f	27.0	–	23.8–35.3	B	Kamler et al., (1982)
10. *C. albula*	E, f	27.5	–	–	B	Wilkońska et al., (1993)
11. *Esox lucius*	MO, f	24.1	–	–	B	Diana and Mackay (1979)
12. *Tinca tinca*	E, f	25.5	25.2–25.7	23.4–27.3	B	Kamler and Stachowiak (1992)
13. *Cyprinus carpio*	E, f	25.2	24.8–25.5	23.4–26.4	B	Kamler (1972, 1976); Kamler and Malczewski (1982)
14. *C. carpio*	E, f	26.1	–	–	B	Peňáz et al., (1976)
15. *Eupallasella perenurus*	E, f	26.8	25.5–28.1	26.7–26.9	C	Kamiński et al., (unpubl.)
16. *Chondrostoma nasus*	E, f	28.6	28.5–28.7	28.3–29.1	C	Keckeis et al., (2000)
17. *Catostomus commersoni*	E, f	25.0†	–	23.7–26.5	B	Johnston (1997)
18. *Pagrus major*	E, s	25.3	–	–	C†	Seoka et al., (1997a)
19. *Clarias gariepinus*	E, f	27.9	–	27.8–28.1	C	Kamler et al., (1994)
20. *Sander vitreus*	E, f	26.6†	–	23.6–28.8	B	Johnston (1997)
21. *Gadus morhua*	E, s	19.5	–	–	B	Finn et al., (1995b)
22. *Oryzias latipes*	E, f	23.6	–	–	B	Hirshfield (1980)
23. *Morone saxatilis*	E, f	30.9	28.5–33.3	26.2–34.5	B†	Eldridge et al., (1982)
24. *Micropterus salmoides*	E, f	25.1	23.0–27.1	–	B	Laurence (1969)
25. *Lepomis macrochirus*	E, f	21.3	–	–	B	Cummins and Wuycheck (1971)
26. *L. macrochirus*	E, f	24.4	–	22.4–26.4	B	Toetz (1966)
27. *Thunnus thynnus*	E, s	30.1	–	–	C†	Takii et al., (1997)
28. *Tilapia mossambica*	E, f	26.2	–	–	?	Mironova (1977)
29. *Cottus bairdi*	E, f	22.7	22.3–23.1	21.1–24.7	B	Docker et al., (1986)
30. *Hippoglossus hippoglossus*	E, s	24.9	24.1–25.8	–	B	Finn et al., (1991)

Based on 30 data sets from 25 species spawning in fresh waters (f) or in the sea (s) (modified from Kamler, 1992).
*B, caloric value measured directly in a bomb calorimeter; C, computed by the author(s) from chemical composition.† caloric values computed from the data reported by author(s).

Increased mean egg size in a sequence: marine pelagophilous, marine bottom spawning, freshwater pelagophilous, freshwater phytophilous and freshwater lithophilous, 0.06, 0.29, 0.46., 0.63 and 14.59 mg dry weight egg^{-1}, was paralleled by an increase of caloric value, 21.3, 21.9, 22.6, 23.7 and 25.0 J mg^{-1} dry matter, respectively (Faustov and Zotin, 1967). Percentage of lipids in egg matter increased with egg size, but hydration decreased (Balon, 1977, 1990). In five another groups of fishes, sea spawners (excluding *Anguilla* and*Trachurus*), Cyprinidae, Acipenseridae, *Salmo* and *Oncorhynchus*) an increase of egg wet weight (1.3, 1.5, 24.5, 80.0 and 186.0 mg, respectively) was accompanied by an increase of the caloric value of egg wet matter (6.0, 8.2, 11.7, 11.2 and 12.2 J mg^{-1} wet matter, respectively), and, at the same time, by decrease of hydration (74, 68, 56, 60 and 56% wet weight, respectively) (Kamler, 1992). Thus, all three possible ways may be used to maximize energy reserves in fish eggs.

Recent methodological progress

Fish gametes, embryos and early larvae are small biological elements. Recent progress in their study has been due to advanced techniques and miniaturisation of methods.

To assess fertilising ability of spermatozoans, their swimming speed and swimming potential need to be assessed. Fish spermatozoans are very small and their flagellae beat at a high frequency, up to 200 Hz, but only for a short time, (seconds to minutes) (Cosson et al., 1997, 1999). Thus, the *in vivo* observations of spermatozoans require special procedures (Cosson et al., 1999). New techniques that offer more subtle description of the fertilising ability of fish spermatozoans have been reported. A video recorder of enlarged images of spermatozoans against a haemacytometer grid pattern in the background was used for measuring spermatozoan swimming speed (Trippel and Neilson, 1992). A high speed video combined with microscopy and a computer-assisted sperm analysis was developed for assessing the spermatozoan swimming potential (Cosson et al., 1997, 1999).

An advanced experimental design allowing offspring traits to be partitioned among paternal and maternal effects is known as the North Carolina Design II (Lynch and Walsh, 1998; Huuskonen et al., 2003). Two female × two male factorial fertilisations form a block from which four families are produced. Paternal and maternal effects are separately studied in 4n families derived from several (*n*) blocks.

Promising technique of miniaturised and individualised egg incubation gives an insight into inter-individual variability during fish earliest ontogeny. Thorsen et al. (2003) monitored individually quality of marine fish eggs. Eggs were inspected under a binocular microscope during incubation of single eggs at controlled temperature in small cell culture multidishes containing 24 wells of 2 cm^3 water each. In *Cyprinus carpio* larvae individually reared in pure water Ługowska (2005) documented withdrawal of body deformities that resulted from egg incubation in solutions of copper and cadmium.

The CHNS Analyser seems to be a method that can be applied for assessing elemental composition of animal tissues. Percentages of carbon (C), hydrogen (H), nitrogen (N) and sulphur (S) in dry matter are directly measured. Caloric value can be computed from these data after a separate determination of ash (A). Oxygen fraction (O) is computed from:

$$O = 100 - (C + H + N + S + A) \tag{4}$$

Then caloric value of dry matter is computed from the C, H, O and S fractions with a formula given by the Analyser's programme. The reliability of that procedure had been positively tested in a pilot trial with direct bomb determinations used as a reference (Kamler et al., 1994). Protein fraction can be computed using the nitrogen-protein conversion factor of 5.78 appropriate for aquatic organisms (Gnaiger and Bitterlich, 1984).

Multiple advantages of the CHNS method are noteworthy.

- The measurements are done in a short time.
- In case of material of animal origin the sample size can be as small as 3–5 mg dry matter, that makes the method especially suitable for determinations in which a shortage of material occurs (for example, fish embryonic tissues separated from yolk).
- Precision of the CHNS method (replicability of results) is typically very high. For example, coefficients of variation (sample standard deviation as per cent of mean) in triplicate determinations of initial *Tinca tinca* eggs and larvae at final yolk resorption were: for carbon 0.06 and 0.12%, respectively, for nitrogen 0.17 and 0.33%, and for caloric value 0.25 and 0.12%, respectively (Kamler et al., 1995).
- Reliability of that method was tested comparing results obtained for spawn of 20 *Chondrostoma nasus* females using two sets of measurements. In one, performed at the Institute of Ecology, Poland, spawn of each female was measured in a Carlo Erba (1108) elemental CHNS-O automatic analyser with sulfanilamide as a reference. In another, performed at the Vienna University, Austria, individual eggs of the same females were measured separately in a Carlo Erba NA 1500 nitrogen analyser (the version for N and C determinations), acetanilide served as a reference. A close concordance of the carbon percentages in dry matter measured with these two procedures ($P > 0.05$) indicates that both assays resulted in good estimates of the same. Discrepances between nitrogen percentages were significant, but low (from 0.006 to 0.731% N in dry

matter) compared to the overall mean level of nitrogen in these samples, 11.9% N in dry matter (Keckeis et al., 2000).

Thus, elemental analysis can be recommended for determination of main elements, energy and protein contents in early fish stages.

Conclusions

Substantial advances in recent years have been made in understanding of fish intrinsic survival potential during early ontogeny. Results of these studies played a part in explanation of the paternal and maternal effects on fish offspring. Both, paternal and maternal factors contribute to total viability, but they operate at different time and in different ways.

Paternal effects are produced very early in ontogeny. No paternal size-effects were manifest, but spermatozoan density and motility are decisive. Maternal effects contribute to embryonic survival, which responds to egg ripeness and female age *via* egg matter composition.

Maternal size-effects reveal later. The key pathway in the parent–egg–progeny relationship are the positive relations between female size, egg size and larval size, the later resulting in variability of larval resistance to starvation and predation.

Reproductive style, and evolutionary and ecosystemal components are the factors contributing to yolk endowment with energy. Of two components of the latter, yolk size in newly laid teleost fish eggs varies across a wide range, whereas caloric value of yolk remains within a relatively narrow range.

Recent methodological progress in studies of fish reproductive parameters and yolk-feeding developmental stages is noteworthy. It includes optimisation of assessment of spermatozoan fertilization ability, advanced experimental designs in partitioning among paternal and maternal effects, miniaturization and individualization of observation techniques, and application of the CHN – a reliable method in studies of chemical composition of biological materials.

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