Oecologia (1989) 80:401–404

Oecologia

To produce many small or few large eggs: a size-independent reproductive tactic of fish

Carlos M. Duarte and Miguel Alcaraz

Instituto de Ciencias del Mar, Consejo Superior de Investigaciones Científicas, Paseo Nacional s/n,
08003 Barcelona, Spain

Summary. We demonstrate here the existence of a range of size-independent reproductive tactics in teleostean fish involving the allocation of a size-dependent reproductive effort between fecundity and egg size. Despite considerable evidence that larger eggs and the larvae hatching from them are more likely to survive than smaller ones, we found no evidence of evolutionary trends towards greater egg sizes. Fish with pelagic eggs tend to spawn many, and therefore small, eggs, whereas demersal spawners tend to produce large, and therefore few, eggs. Maximizing egg number should increase the number of eggs hatching in suitable locations in the patchy pelagic environment and, hence, increase the reproductive success of pelagic spawners. On the other hand, the reproductive success of demersal spawners, which reduce the variance in growing conditions experienced by the off spring, should be more dependent on the survival of the individual larvae, which increases as egg size increases.

Key words: Teleostean fish – Fish eggs – Reproductive tactics – Pelagic-demersal eggs

Early stages (i.e. eggs and larvae) of teleostean fish are subject to great mortality (e.g. Fortier and Leggett 1985; McGurk 1986), such that very large investments in reproductive material are necessary to ensure the persistence of populations. Fish reproductive effort can be measured as the egg mass (or volume) produced per female, and is therefore the product of fecundity (number of eggs produced per female) and egg size. Fecundity alone may not be related to the probability of survival of the individual eggs because egg mortality is scaled to egg size (e.g. McGurk 1986). Therefore, a given reproductive effort allocated to many small, or to few large eggs may yield vastly different recruitment to juveniles (e.g. Ware 1975).

Blueweiss et al. (1978) reported that fish fecundity and egg size increase as the 0.64 power and 0.43 power of body size, respectively. Although these allometric relationships imply that larger fish have greater fecundity and also larger eggs, there are many large fish that spawn small eggs (e.g. *Mola mola*, *Thunnus thynnus*). Thus, while it is generally accepted that fish fecundity is scaled to body size, the statement that egg size increases with increasing body size remains controversial (cf. Miller 1984; Hislop 1984).

Our goal here is to examine the variability in the allocation of the reproductive effort of teleostean fishes between fecundity and egg size. We shall first examine the allometric basis for the variability in fish reproductive effort, fecundity, and egg size. The implications of variability in egg size will be demonstrated by quantifying the relationships between egg size and important components of early survival of fish, such as time to hatching, larval size, and the time from hatching to yolk resorption. We will finally seek patterns that could suggest explanations for the observed variability in the allocation of reproductive effort.

Methods

To obtain the most general description of the relationships in question we gathered data on fish size, fecundity, egg size, time to hatching, larval size, and time from hatching to yolk resorption for as many marine and freshwater teleostean species as possible[1].

Fish and larval length (mm) represented fish size and egg diameter (mm) represented egg size. Standard length was converted to total length by assuming standard length to be 90% of total length. The differences between total and standard length are, however, irrelevant for our analysis since we compare fish ranging over two orders of magnitude in length.

The times (days) from spawning to hatching and from hatching to complete yolk resorption were estimated, when enough data were available, as the time when 50% of the individuals examined hatched or achieved complete yolk resorption, respectively. Because incubation temperature is an important determinant of the time from spawning to hatching (e.g. Ware 1975) we used incubation temperature as a covariate when examining the relationship between egg size and hatching time.

Fecundity was measured as the number of eggs spawned per female. Because of the difficulties in estimating fecundity for fish with serial spawning, we excluded these from our study. Fish reproductive effort was estimated as the product of fecundity and the individual egg mass, estimated from egg dimensions assuming a density of 1.

Statistical relationships between variables were described using least squares regression analysis. Because the direct scatter plots between pairs of variables showed evidence of heteroscedasticity, we calculated double logarithmic regression equations to describe the relationships between these variables. The coefficient of determination (R^2) is used to represent the strength of the relationships, and the standard error of the (log-transformed) estimates ($\mathrm{S.E.}_{\log\ \mathrm{est}}$) to represent the variability about the regression

Offprint requests to: C.M. Duarte

---

[1] A complete data set is available from the senior author upon request

line. Multiple regression analysis was used to account for the influence of incubation temperature on the relationship between incubation time and egg size. Differences between marine and freshwater fish in the relationships obtained were tested using analysis of covariance.

Results and discussion

Relationships between fish size and reproductive characteristics

The data set comprised a total of 383 reports of teleostean reproductive characteristics encompassing 51 species of marine fish and 46 species of freshwater fish ranging widely in length and reproductive characteristics (Table 1). Because different studies considered different variables, sample size differed for the different analyses (Table 1).

Fish reproductive effort (g egg mass fish^{-1}) was strongly related to fish size (mm) (Fig. 1), the relationship being described by the equation:

$$\log(\text{Effort}) = 2.7 \log(\text{Size}) - 2.22 \qquad (1)$$

$$R^2 = 0.89; \quad N = 152; \quad p < 0.0001; \quad \text{S.E.}_{\text{slope}} = 0.07.$$

The slope of this relationship is similar to that found in a previous analysis of reproductive strategies of Canadian freshwater fish (Wooton 1984) and lies within the range of slopes describing the scaling between fish length and weight (Peters 1983), indicating that reproductive effort probably increases linearly with fish weight. The strength of this relationship ($R^2 = 0.89$; Fig. 1) indicates that teleostean fishes of similar sizes have limited ($\text{S.E.}_{\text{log est.}} = 0.50$; ca. threefold) variability in their allocation of energy to reproduction.

The relationship between fish size and fecundity was also highly significant (Fig. 2):

$$\log(\text{Fecundity}) = 2.75 \log(\text{Size}) - 2.18 \qquad (2)$$

$$R^2 = 0.69; \quad N = 220; \quad p < 0.0001; \quad \text{S.E.}_{\text{slope}} = 0.12.$$

The slope and intercept of this relationship did not differ (t-test, $p > 0.10$) from those of the relationship between fish size and reproductive effort, but the variability in the fecundity of fishes with similar sizes was much greater ($\text{S.E.}_{\text{log est}} = 0.90$; ca. sevenfold) than the variability observed in fish reproductive effort (Figs. 1, 2). The greater variability in fecundity of fishes of a given size compared to that in reproductive effort is evidence of the existence of a range of reproductive tactics involving the allocation of a given (size-dependent) reproductive effort between many small, or few large eggs (Wooton 1984). These tactics, however, appear to be species-specific because the within-species variation in fecundity for a given fish size is typically small (e.g. Miller 1984; Hislop 1984).

Table 1. Sample size (N), mean, and range for the variables included in this study: Adult and larval length and egg size in mm, fecundity in 10^3 eggs female^{-1}, incubation temperature in °C, hatching time and time from hatching to yolk resorption in days

Variable	N	Mean	Range
Fish length	293	338	10–2610
Fecundity	230	1836	0.007–57600
Egg size	305	2.3	0.34–8.8
Time to hatching	87	32.7	0.8–240
Incubation temperature	77	14	2–29.6
Larval length	117	10	1.7–38.8
Time to yolk resorption	28	8.9	2–55

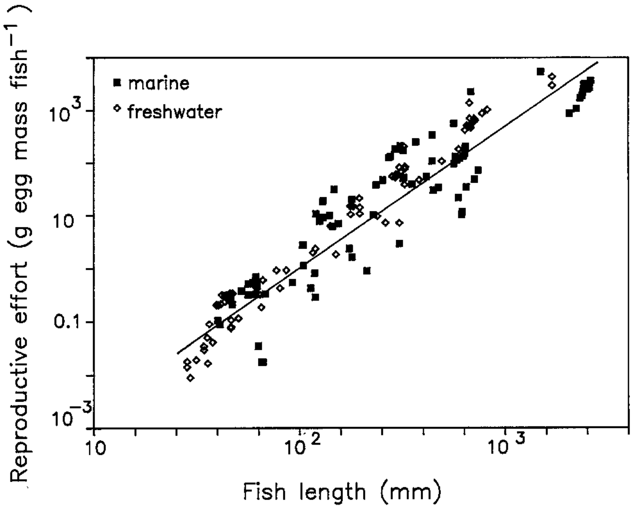

Fig. 1. The relationship between fish length and reproductive effort. The *solid line* represents Eq. 1

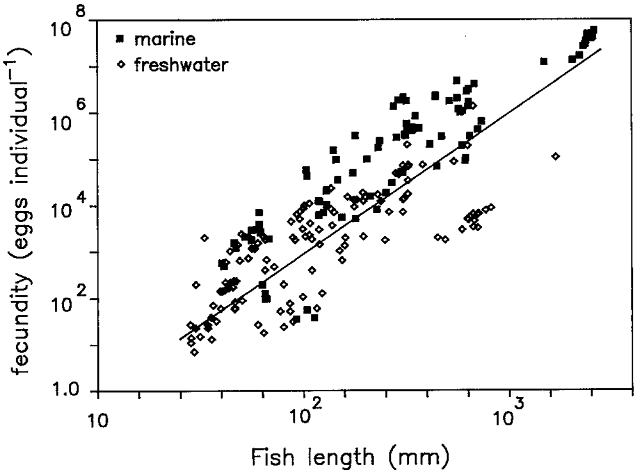

Fig. 2. The relationship between fish length and fecundity. The *solid line* represents Eq. 2

Analysis of covariance showed that the marine and freshwater fish in our data set differed in their scaling of fecundity to body size (Fig. 2), because fecundity varied as the 2.15 power of body size in freshwater fishes whereas it varied as the 2.63 power of marine fish body size (*t*-test, $p < 0.01$). At the same time, most marine teleostean fishes have small (< 1.5 mm) eggs, whereas the freshwater teleosteans in our data set showed a broader range of egg sizes (Fig. 3).

The variability in the allocation of reproductive effort to egg size and fecundity was not influenced by body size (*F*-test; $p > 0.10$), because large fish were not more likely to have large eggs than small fish (Fig. 4; cf. Miller 1984; Hislop 1984). Further examination of the scatter plot between fish length and egg size suggests that the range of egg sizes possible for fishes of a given size is constrained by a lower limit to mature egg size (ca. 0.3 mm diameter) and a size-dependent upper limit to egg size (Fig. 4). Therefore, fish size appears to constrain, rather than determine, the range of egg sizes possible for fishes of any one size. The greater spectrum of egg sizes possible for large fish

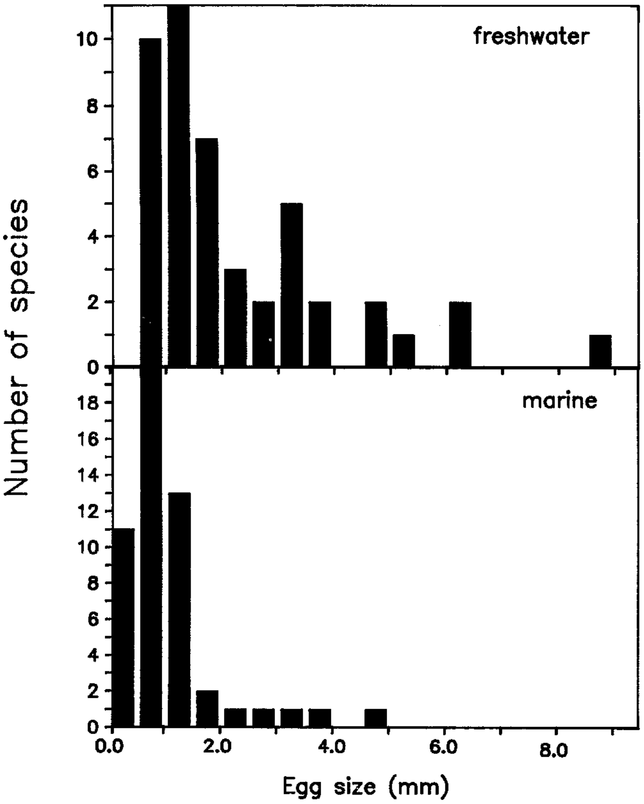

Fig. 3. Frequency distribution of egg size for the marine and freshwater species included in this study

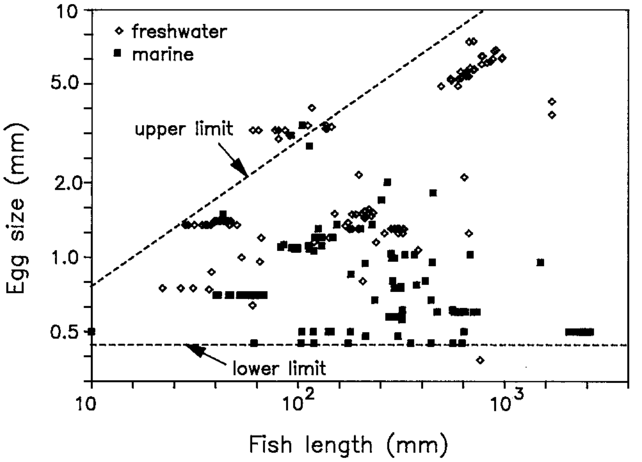

Fig. 4. The relationship between fish length and egg size. *Broken lines* represent the upper and lower limits to egg size suggested by the scatter plot

imply that a greater range of tactics in the partition of reproductive effort between fecundity and egg size is available to large fish.

Effects of egg size on early survival of fish

Evidence of the importance of egg size for early fish survival is derived from the relationship between egg size and larval size (mm; Fig. 5):

$$\log(\text{Larval size}) = 0.51 + 0.99 \log(\text{Egg size}) \qquad (3)$$

$R^2 = 0.90$; $N = 106$; $p < 0.0001$; $\text{S.E.}_{\text{slope}} = 0.03$

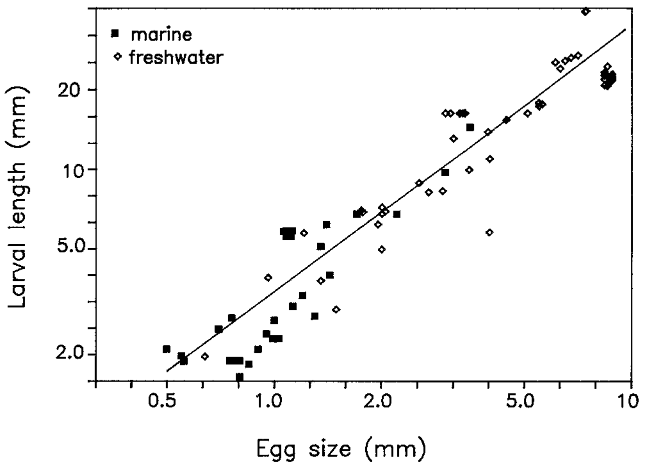

Fig. 5. The relationship between egg size and larval length. The solid line represents Eq. 3

which demonstrates that larval size is largely determined by egg size ($\text{S.E.}_{\text{log est}} = 0.12$; ca. 1.3-fold) and that larval size increases linearly with egg size (Ho: slope = 1; t-test, $p > 0.10$). Further, although the time to hatching (days) changes linearly with both egg size and temperature (Fig. 6a)

$$\log(\text{Hatching time}) = 1.8 + 0.98 \log(\text{Egg size}) - 1.01 \log T \qquad (4)$$

$R^2 = 0.83$; $N = 72$; $p < 0.0001$

egg size appears to be more important (partial $F = 297$) than incubation temperature (partial $F = 40$) in determining the duration of the incubation period (Fig. 6a). Equation 4 is slightly different from that recently published by Pauly and Pullin (1988) for marine fish with pelagic eggs, probably because of the much smaller range of egg sizes in their analysis.

The time to yolk resorption (days) is also linearly scaled to egg size (Fig. 6b)

$$\log(\text{Yolk duration}) = 0.66 + 1.12 \log(\text{Egg size}) \qquad (5)$$

$R^2 = 0.75$; $N = 24$; $p < 0.0001$; $\text{S.E.}_{\text{slope}} = 0.13$

These relationships support the statement that increased egg size should increase the potential for survival of the individual fish, because the large larvae they produce are subject to lower mortality (McGurk 1986), are able to feed on larger prey, and swim faster; and because longer yolk duration should increase larval resistance to starvation and, thereby, increase its probability of encountering a favorable environment. Thus, we could expect fish to exhibit an evolutionary trend towards increased egg size. Existing information, however, provides no evidence of such pattern in the size of fish eggs, because some primitive teleosteans (e.g. *Latimeria*, sturgeon) have large eggs, whereas some relatively advanced fish (e.g. flatfish) spawn small eggs. The contradiction between the apparent greater fitness associated with large eggs and the lack of clear evolutionary patterns in egg size is not unique to teleostean fishes (cf. Capineri 1979), and suggests that the survival potential of individual eggs is not the most important factor controlling the success of fish reproduction.

The differences in reproductive strategies between marine and freshwater teleostean fishes in our data set, indicated by differences in egg size and the scaling of fecundity

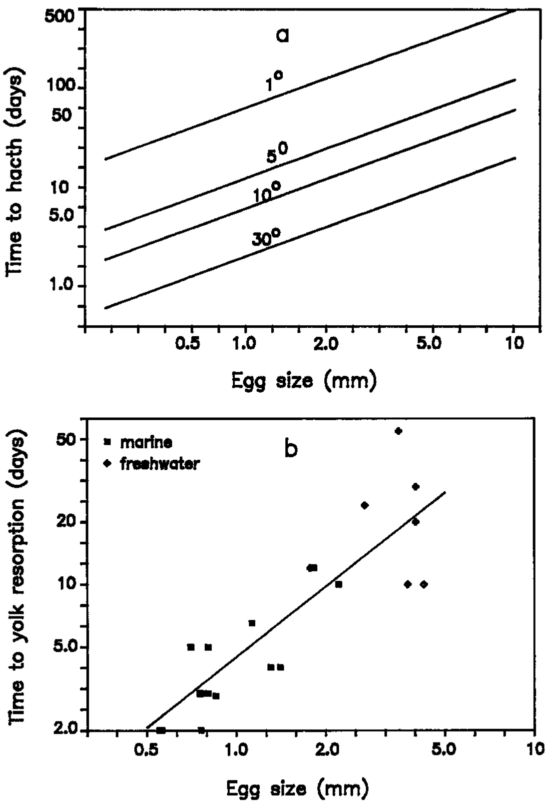

Fig. 6. **a** Times from spawning to hatching predicted for different incubation temperatures and egg sizes from Eq. 4, and **b** the relationship between egg size and the time from hatching to yolk resorption; the *solid line* represents Eq. 5

to fish size, may ultimately reflect differences in the physical dimensions of these environments. Because the littoral zone is much smaller relative to the pelagic zone in the ocean than in freshwater, the proportion of fish with a pelagic habit is greater in the sea. The efficient colonization of the open ocean by fish involves the production of pelagic eggs. Thus, there are a number of marine teleostean fishes that have pelagic eggs whereas most freshwater and some marine fish have demersal eggs.

The location and trophic conditions of early development of teleostean fishes with pelagic eggs are subject to an important stochastic component due to the temporal variability of mesoscale oceanic circulation and the patchy nature of the marine environment. Fish spawning demersal eggs, in contrast, have greater control over the habitat characteristics that their offspring will experience (e.g., temperature, presence or absence of vegetation), which should reduce the variability in the growing conditions experienced by their offspring.

These differences imply that larval mortality of pelagic spawners should be most influenced by the stochasticity of the habitat where hatching occurs, whereas the mortality of larvae hatched from demersal eggs should be influenced to a greater extent by the potential survival of the individual larvae. A trade-off towards maximizing the quantity of eggs produced should increase fitness of pelagic spawners, whereas increasing the survival capabilities of the individual larvae (e.g. producing larger eggs) should maximize the number of larvae surviving from demersal eggs. Because reproductive effort is constrained by fish size, spawning many eggs implies spawning small eggs and spawning large eggs implies, in turn, spawning few eggs. Further, spawning small eggs also reduces the time from spawning to hatching (Eq. 4, Fig. 5a; Ware 1975), which should reduce the distance between spawning and hatching locations of pelagic eggs, thereby decreasing the uncertainty about the hatching location.

These considerations suggest that the variability in reproductive allocation between egg size and fecundity is ultimately determined by the degree of parental control upon the growth conditions experienced by the larvae. Large eggs in marine fish are typically found in fish with demersal eggs inhabiting estuarine (Dando 1984) or littoral environments (e.g. Belonidae). The larger eggs of fish spawning demersal eggs may be one step in the trend towards increasing egg size as the degree of parental care increases (Balon 1984), because the production of demersal eggs has been considered as a preliminary step towards the development of parental care (Potts 1984).

In summary, our analysis suggests that differences in the allocation of reproductive effort between fecundity and egg size among teleostean fishes are independent of their evolutionary history, and depend on the habitats they occupy. The production of many, and consequently small, propagules by pelagic spawners appears to be a necessity for colonizing the pelagic environment.

References

Balon EK (1984) Patterns in the evolution of reproductive styles in fishes. pp. 35–54. In G.W. Potts, and R.J. Wooton (Eds.) Fish reproduction: strategies and tactics. Academic

Blueweiss L, Fox H, Kudzma V, Nakashima D, Peters RH, Sams S (1978) Relationships between body size and some life history parameters. Oecologia 37:257–272

Capineri JL (1979) Quantitative variation in plants and insects: effect of propagule size on ecological plasticity. Am Nat 114:350–361

Dando PR (1984) Reproduction in estuarine fish. In: Potts GW, Wooton RJ (eds) Fish reproduction: strategies and tactics. Academic Press, Oxford, pp 155–170

Fortier L, Leggett WC (1985) A drift study of larval fish survival. Mar Ecol Prog Ser 25:245–257

Hislop JRG (1984) A comparison of the reproductive tactics and strategies of cod, haddock, whiting and Norway pout in the Northern Sea. In: Potts GW, Wooton RJ (eds) Fish reproduction: strategies and tactics. Academic Press, Oxford, pp 311–330

McGurk MD (1986) Natural mortality of marine pelagic fish eggs and larvae: role of spatial patchiness. Mar Ecol Prog Ser 34:227–242

Miller PJ (1984) The tokology of gobioid fishes. In: Potts GW, Wooton RJ (eds) Fish reproduction: strategies and tactics. Academic Press, Oxford, pp 119–154

Pauly D, Pullin RSV (1988) Hatching time in spherical, pelagic, marine fish eggs in response to temperature and egg size. Env Biol Fish 22:261–271

Peters RH (1983) The ecological implications of body size. Cambridge University Press, Cambridge

Potts GW (1984) Parental behavior in temperate marine teleosts with special reference to the development of nest structures. In: Potts GW, Wooton RJ (eds) Fish reproduction: strategies and tactics. Academic Press, Oxford, pp 223–244

Ware DM (1975) Relation between egg size, growth, and natural mortality of larval fish. J Fish Res Board Can 32:2503–2512

Wooton RJ (1984) Introduction: Strategies and tactics in fish reproduction. In: Potts GW, Wooton RJ (eds) Fish reproduction: strategies and tactics. Academic Press, Oxford, pp 1–12

Received October 20, 1988