

Some Regularities of Fecundity in Animals

A. F. Alimov

Zoological Institute, Russian Academy of Sciences, Universitetskaya nab. 1, St. Petersburg, 199034 Russia

e-mail: alimov@zin.ru

Received December 18, 2014

Abstract—The dependence of descendants' weight on the weight of females in invertebrates and vertebrates can be described by equations of the power function with an exponent close to unity. The specific fecundity of animals decreases with increasing weight in females. A concept of the fecundity rate as the number of offspring produced by one female per year and the fecundity rate coefficient as the fecundity of a female with a weight of 1 g per year are proposed. The fecundity coefficient value is reduced in the course of evolution.

Keywords: fecundity, specific fecundity, fecundity rate

DOI: 10.1134/S207908641506002X

INTRODUCTION

Reproduction is one of the most important functions of the life and development of animals; it ensures the existence of individuals and populations of certain species. The fecundity of animals makes it possible to evaluate their reproductive potential and, therefore, the dynamics of populations of individual species. Individual fecundity refers to the number of offspring per female.

With the use of numerous representatives of the animal world, it was shown that all of the basic functions of organisms (growth rates, respiration, metabolism, nutrition, etc.) are consistently associated with animal weight. Consider how fecundity in animals is related to their weight. The literature on the fecundity of various animals very rarely provides information on the weight of parents and their offspring. Usually, their linear sizes (especially in relation to offspring) are specified. However, many equations showing the relationship between the weight and linear sizes have been calculated for different species. Such equations were not used in this study to determine the weight of individuals by their linear sizes.

RELATIONSHIP BETWEEN THE OFFSPRING AND PARENTAL WEIGHTS

Consider the weight of the offspring and that of mature adult individuals. The offspring weight was assessed as the weight of spawn or laid eggs for fish and crustaceans, respectively; the weight of laid eggs for birds; and the weight of born cubs for mammals.

In this research, I used the results of studies by Zhukov (1965), Ivanova (1985), Khmeleva and Golubev (1984), Khmeleva (1988), Paevskii (1991, 2008), Dol'nik (1995), Alimov and Bogutskaya (2003), Ivanter (2014), Ivanova and Vassilenko (1987), and

Western and Ssemakula (1982). In addition, some information was taken from the multivolume book *Life of Animals (Zhizn' zhivotnykh, 1971)*, the *Biological Encyclopedic Dictionary (Biologicheskii..., 1986)*, and the Internet (especially information on the weight of juvenile small mammals). Hereinafter, the weights of adults (parents) and offspring are designated as Wad and Wo , respectively, for all animals.

The study of 210 specimens belonging to 18 species of freshwater fishes weighing from 9 g to 6 kg (from the bleak to the starlet and pike) showed that the relationship between the weight of females and the egg weight (Fig. 1) can be described by a simple equation:

$$\begin{aligned}\log Wo &= 0.924 \log Wad - 0.836, \\ Wo &= 0.146 Wad^{0.92}, \quad R^2 = 0.86.\end{aligned}\tag{1}$$

The weight of eggs and females was studied in 70 species of birds differing in the weight of mature individuals by 9000 times (the weight of kinglets is approximately 10 g, and the weight of ostriches reaches nearly 90 kg). The weight of the eggs of the studied birds differed by nearly 1200 times (from 1.3 g to 1.5 kg). The data shown in Fig. 2 can be described by the following equation:

$$\begin{aligned}\log Wo &= 0.723 \log Wad - 0.617, \\ Wo &= 0.245 Wad^{0.75}, \quad R^2 = 0.96.\end{aligned}\tag{2}$$

The weight of newborn mammals also depends on the females' weight. This was shown in a case study performed on 50 species of animals belonging to seven orders (Fig. 3). The weight of females of the studied animals differed in nearly 100000 times, varying from 4 g in small insectivores to 60 tons in some whales. In mammals, the relationship between the newborn's weight and the female's weight can be expressed by the equation:

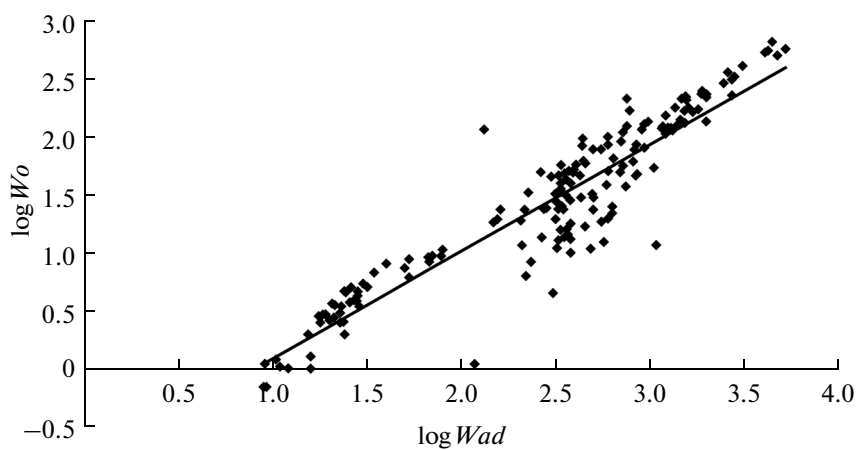


Fig. 1. Dependence of the egg weight logarithm ($\log W_o$) on the logarithm of the weight of females ($\log W_{ad}$) for freshwater fishes.

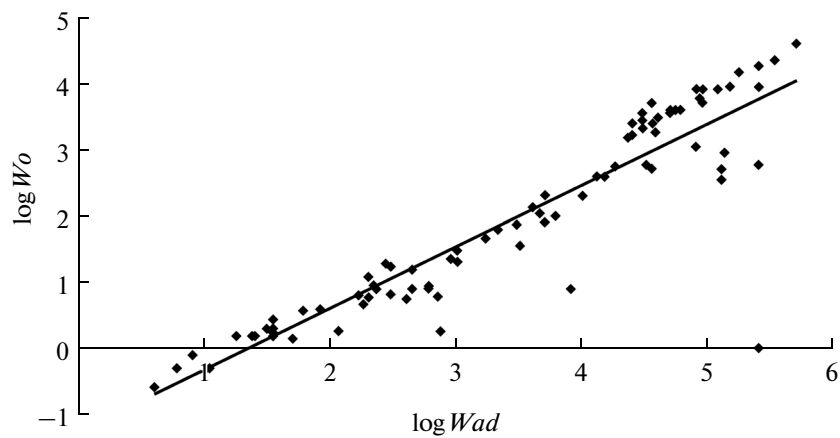


Fig. 2. Dependence of the egg weight logarithm ($\log W_o$) on the logarithm of the weight of females ($\log W_{ad}$) for birds.

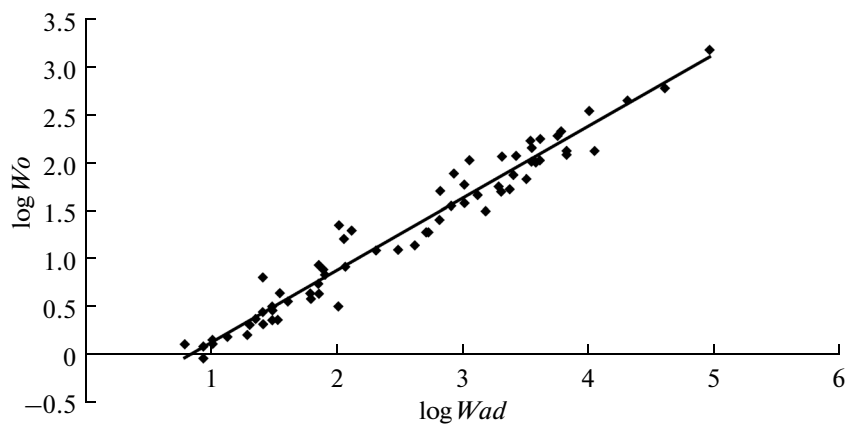


Fig. 3. Dependence of the logarithm of the weight of newborns ($\log W_o$) on the logarithm of the weight of females ($\log W_{ad}$) for different species of mammals.

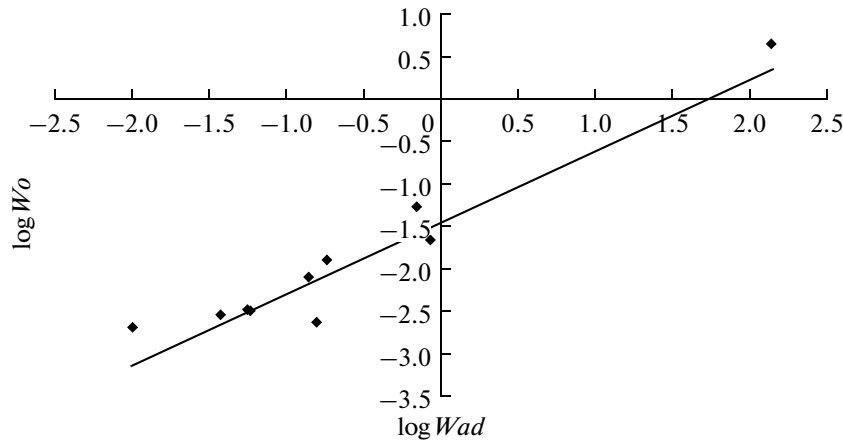


Fig. 4. Dependence of the logarithm of the weight of newly hatched juveniles ($\log W_o$) on the logarithm of the weight of female ($\log W_{ad}$) for different species of crustaceans (according to Khmeleva and Golubev, 1984).

$$\begin{aligned} \log W_o &= 0.996 \log W_{ad} - 1.44, \\ W_o &= 0.036 W_{ad}^{0.996}, \quad R^2 = 0.93. \end{aligned} \quad (3)$$

It should be noted that bears were not included in the above data. The weight of adult bears, both brown and white, reaches 350 kg, whereas the weight of newborn cubs is less than 300–600 g (less than 1% of the female's weight). Such small sizes of bear cubs are due to the fact that they are born in winter in a den, and the female feeds them in the hibernation season. The above data also did not include kangaroos and opossums: their descendants have a very small weight and immediately migrate into the pouch of the female, in which they develop until exiting the pouch.

Analysis of the data (Figs. 1–3) and corresponding equations suggests that, in vertebrates, the weight of newborns or eggs (in fish) increases proportionally to the female's weight. It is important to assess the specific fecundity (i.e., the proportion of the offspring weight to the mother's weight). It can be easily calculated in the range of the studied weights using Eqs. (1)–(3). The egg weight in fish is, on average, 12% (2.2–28%) of the female's weight; the egg weight in birds is, on average, 7% (1.5–22%) of the female's weight; and the newborn weight in mammals is, on average, 5% (2–12%) of the female's weight.

Unfortunately, data on the weight of adults, and especially the egg weight in invertebrates, are very limited. The number of eggs per clutch and the linear size of adults are usually specified. To compare the fecundity of vertebrates and invertebrates, I used the scant (though, apparently, most reliable) data for 12 species belonging to nine orders of crustaceans, including the freshwater crayfish (Fig. 4) (Khmeleva and Golubev, 1984; Ivanov, 1985; Khmeleva, 1988). The following equation was obtained:

$$\begin{aligned} \log W_o &= 0.84 \log W_{ad} - 1.458, \\ W_o &= 0.034 W_{ad}^{0.84}, \quad R^2 = 0.86. \end{aligned} \quad (4)$$

A similar type of equation ($W_o = 0.19 W_{ad}$, weight in micrograms) was obtained for freshwater planktonic crustaceans (Ivanova, 1985).

As can be seen from Fig. 5, the data for crustaceans coincide with the data for vertebrates. This allows us to assume that such a relationship between the weights of adult animals and offspring, most likely, is true for the whole animal world and, for the studied representatives of the animal world, can be described by the following equation:

$$\begin{aligned} \log W_o &= 0.746 \log W_{ad} - 1.205, \\ W_o &= 0.062 W_{ad}^{0.75}, \quad R^2 = 0.74. \end{aligned} \quad (5)$$

The ratio of the weight of eggs or born offspring to the weight of females is often called the reproductive effort. As follows from Eq. (5), the specific fecundity of the studied invertebrates and vertebrates, on average, is close to 6%.

Of course, to assess individual fecundity, a simple comparison of the weights of eggs or newborns with the weight of females is not entirely correct. This is especially true for fish and various invertebrates, because the weight of juvenile fish that have just emerged from eggs is usually unknown for certain species and is unlikely to be known in the near future. It is probably more correct to assess the potential reproductive capacity of different animals, with an accounting of not only the ratio of weights of the parents and the offspring but also the number of offspring per litter, the frequency of litters produced during the year, and the influence of environmental conditions on the change of reproduction of generations. This approach makes it possible to investigate more reliably animal fecundity, which determines the dynamics of abundance of animal populations and communities.

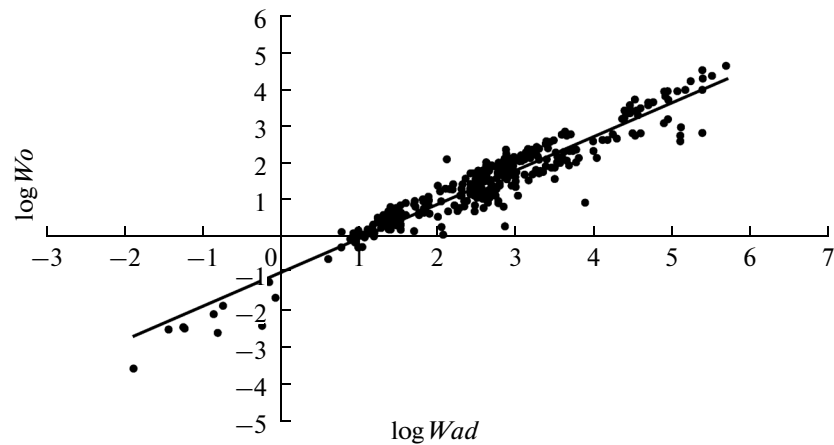


Fig. 5. Dependence of the offspring weight logarithm ($\log W_o$) on the logarithm of the weight of female ($\log W_{ad}$) for all studied animals (see Figs. 1–4).

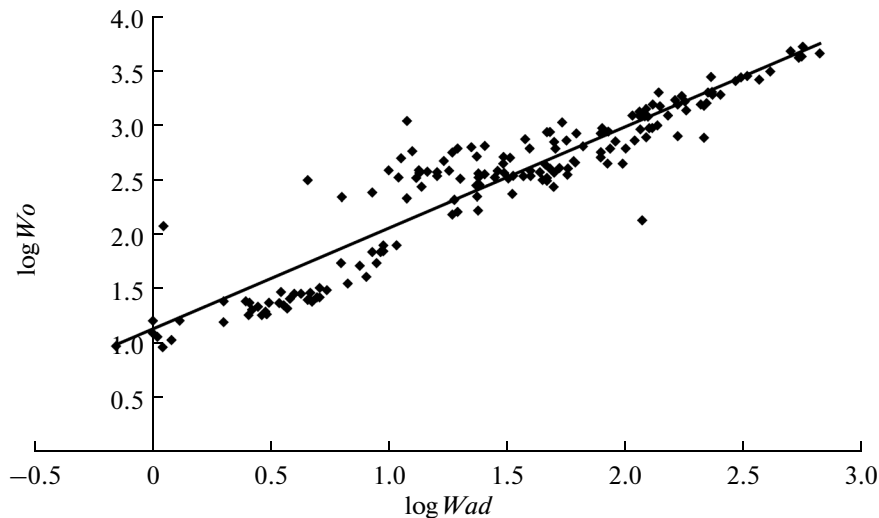


Fig. 6. Weight of eggs spawned per year ($\log M$, g/year) by various species of freshwater fishes.

INTENSITY OF FECUNDITY

Let us consider the weight of offspring produced in one year, taking into account for certain species, the time of onset of maturity, the number of litters per year, and the number of pups or cubs per litter produced by one female: $M = W_o N n$, where M is the weight of the offspring produced in one year (g), N is the number of offspring in a litter, and n is the number of litters produced during one year. The fact that some animals do not breed every year was taken into account. For example, bears and some species of whales breed once in two or three years. The results are shown in Figs. 6–9.

Calculate parameters $a1$ and b by equation $M = a1W_{ad}^b$ for different representative of the animal world:

	$a1$	b
Fish	13.3	0.9
Aves	3.2	0.6
Mammalia	0.8	0.7
Crustacea	30	0.8

Let us call coefficient $a1$ the coefficient of the fecundity intensity in animals, which shows the weight of the offspring produced by one female weighing 1 g per year. Taking into account possible inaccuracies

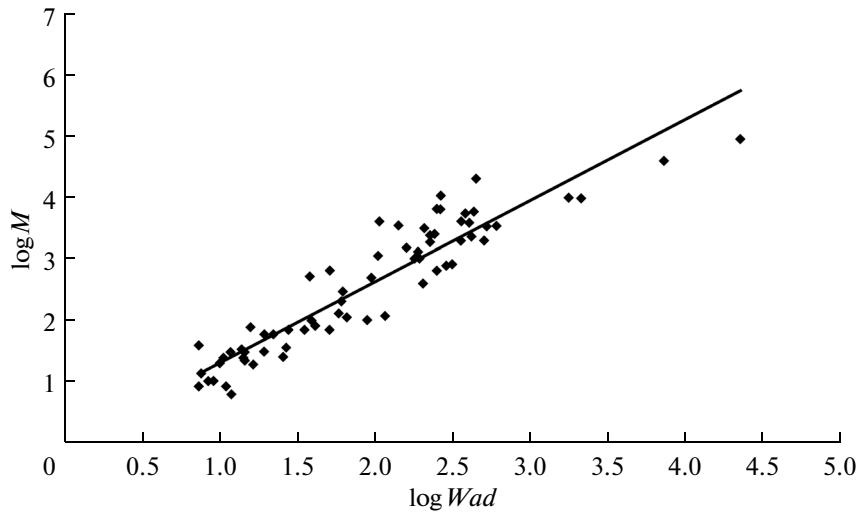


Fig. 7. Weight of eggs laid per year ($\log M$, g/year) by different species of birds.

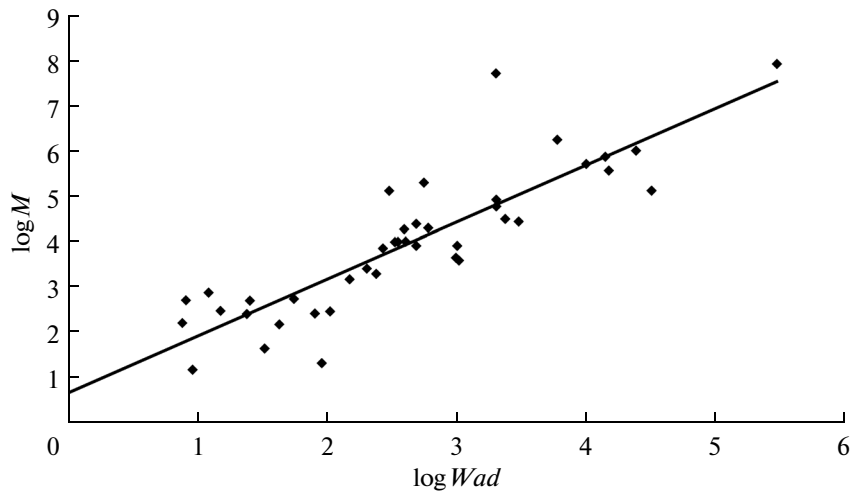


Fig. 8. Weight of offspring born per year ($\log M$, g/year) by females of different mammal species.

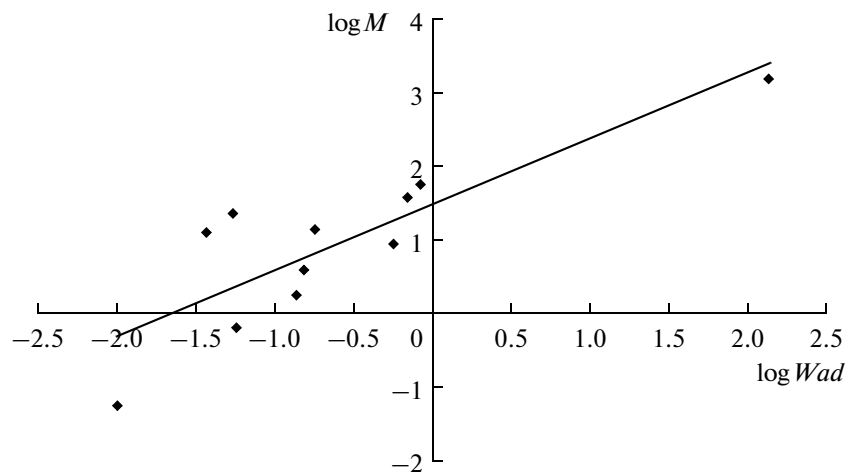


Fig. 9. Weight of eggs laid per year ($\log M$, g/year) by females of crustacean different species.

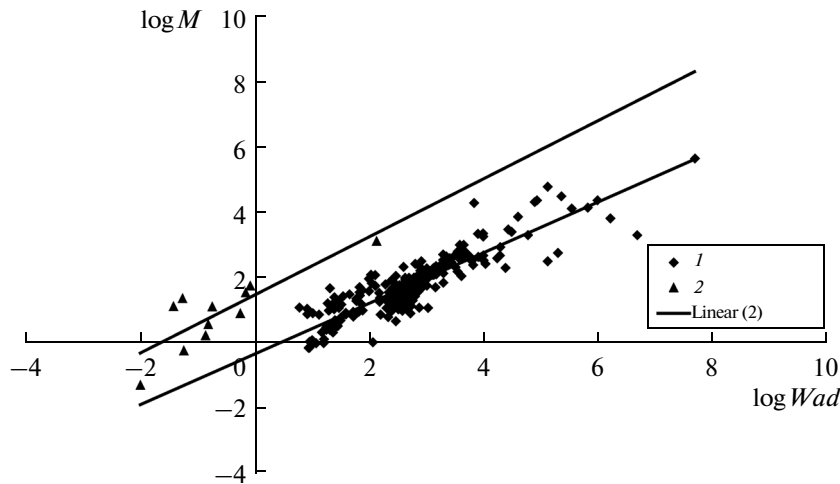


Fig. 10. Weight of offspring ($\log M$) produced per year by females of different weight ($\log W_{ad}$) of (1) vertebrates and (2) crustaceans.

and rounding rules, we can take the value of coefficient b in the studied animals at a first approximation to be 1. The values of coefficient aI show that the highest and lowest intensity of fecundity are observed in crustaceans and mammals, respectively (Fig. 10).

I accepted the idea of A.I. Zotin and A.A. Zotin (1999) based on the hypotheses proposed by Ivlev (1959) and Dolnik (1968), according to which arogenesis is associated with an increased energy metabolism in the organism. The metabolism intensity, in turn, is related to the organism. The metabolism intensity in different organisms is compared using the metabolic rate factor. It served as a basis for the quantitative characterization of progressive evolution. A.I. Zotin and A.A. Zotin have introduced the orderliness coefficient (Cr), which is calculated using the metabolic rate factor. The orderliness coefficient shows the degree of closeness to equilibrium, i.e., the progressive evolution itself. It was assumed that the value of the exponent in the equations for the dependence of the metabolic rate on the weight is 0.75 for all organisms, and the metabolic rate factors were recalculated for various representatives of the animal world.

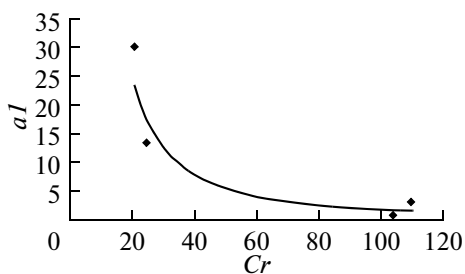


Fig. 11. Correlation between the fecundity rate coefficient (aI) and the orderliness coefficient (Cr) in the studied animals.

Later, I took the values of these coefficients for different organisms from the book by A.I. Zotin and A.A. Zotin (1999). Using the coefficients of the intensity of fecundity (aI) and orderliness (Cr), I attempted to assess how the fecundity of the studied animals changed in the course of evolution and found that it decreased (Fig. 11). Since the data used are fairly limited, the curve in the figure was not calculated and shows only a possible trend in changes. However, the values for poikilothermic (crustaceans and fishes) and homeothermic (birds and mammals) animals, as could be expected, are located in opposite parts of the curve.

The reproductive capacity of animals is closely related to the dynamics of abundance of their populations. The instantaneous rate of an increase in the abundance of individuals in a population (r_m , time^{-1}) of animals is in inverse proportion to their definitive weight (W_{\max}) (Fenchil, 1974; Alimov, 1989): $r_m = k W_{\max}^{-b1}$, where k is the instantaneous rate of an increase in abundance at a weight $W_{\max} = 1$.

For example, for fish $r_m = k W_{\max}^{-0.26}$, the specific rate of an increase in the abundance of their population directly depends on the relative fecundity of animals and inversely depends on their definitive weight (Alimov and Bogutskaya, 2003). To ensure a high population abundance, more offspring per unit weight of animals should be produced. Since the specific production (the rate of the biomass turnover in a population) and the metabolic rate in animals are in inverse proportion to their weight, the relatively high fecundity, which is ensured by the high metabolic rate, determined a high biomass turnover rate.

CONCLUSIONS

In conclusion, it should be said that the dependence of the offspring weight on the weight of females in invertebrates and vertebrates can be described by power-function equations with an exponent close to unity. The specific animal fecundity decreases with increasing weight in females. Given the obvious lack of data on the invertebrate fecundity, such studies should be performed in the future. The notion of fecundity intensity (the number of offspring produced by one female per year) and the coefficient of fecundity intensity (the fecundity of a female weighing 1 g per year) is proposed. The banal idea that mammals and birds are evolutionarily more advanced than, for example, crustaceans was expressed quantitatively, and an attempt to find a correlation of this fact with fecundity was made. The fecundity intensity increases in the course of evolution. It is important to study the relationship between the rate of increase in the abundance of populations of different animals and their fecundity rate, with special attention paid to the specific fecundity features in *k*- and *r*-strategists.

I do not lay claim to complete coverage of the literature on animal fecundity. This paper should be considered as a first step in the quantitative analysis of data on the animal fecundity and the search for common patterns.

REFERENCES

- Alimov, A.F., *Vvedenie v produktsionnuyu gidrobiologiyu* (Introduction to Production Hydrobiology), Leningrad: Gidrometeoizdat, 1989.
- Alimov, A.F. and Bogutskaya, N.G., The regularities in relationships between fecundity, body mass and growth rate of fishes, *Zh. Obshch. Biol.*, 2003, vol. 64, no. 2, pp. 112–127.
- Biologicheskii entsiklopedicheskii slovar'* (Biological Encyclopedic Dictionary), Moscow: Sovetskaya Entsiklopediya, 1986.
- Dol'nik, V.R., Energy metabolism and evolution of the animals, *Usp. Sovrem. Biol.*, 1968, vol. 66, no. 5, pp. 276–293.
- Dol'nik, V.R., *Resursy energii i vremeni u ptits v prirode* (Energy and Time Resources of the Birds in Nature), St. Petersburg: Nauka, 1995.
- Fenchil, T., Intrinsic rate of natural increase: the relationship with body size, *Oecologia*, 1974, vol. 14, no. 14, pp. 317–326.
- Ivanova, M.B., *Produktsiya planktonnykh rakoobraznykh v presnykh vodakh* (Production of Crustacean Plankton in Fresh Waters), Leningrad: Zool. Inst., Akad. Nauk SSSR, 1985.
- Ivanova, M.B. and Vassilenko, S.V., Relationship between number of eggs, brood weight, and female body weight in Crustacea, *Int. Rev. Gesamt. Hydrobiol. Hydrogr.*, 1987, vol. 72, no. 2, pp. 147–169.
- Ivanter, E.V., *Teriologiya* (Theriology), Petrozavodsk: Petrozavodsk. Gos. Univ., 2014.
- Ivlev, V.S., Assessment of evolutionary significance of the levels of energy metabolism, *Zh. Obshch. Biol.*, 1959, vol. 20, no. 6, pp. 94–103.
- Khmeleva, N.N., *Zakonomernosti razmnozheniya rakoobraznykh* (The Regularities of Reproduction of Crustacean), Minsk: Nauka Tekhnika, 1988.
- Khmeleva, N.N. and Golubev, A.P., *Produktsiya kormovykh i promyslovykh rakoobraznykh* (Production of Fodder and Fishery Crustacean), Minsk: Nauka Tekhnika, 1984.
- Paevskii, V.A., Comparative demography of the birds. Modern status and general results, *Ekologiya*, 1991, no. 4, pp. 73–78.
- Paevskii, V.A., *Demograficheskaya struktura i populyatsionnaya dinamika pevchikh ptits* (Demographic Structure and Population Dynamics of Oscines), Moscow: KMK, 2008.
- Western, D. and Ssemakula, J., Life history patterns in birds and mammals and their evolutionary interpretation, *Oecologia* (Berlin), 1982, vol. 54, no. 3, pp. 281–290.
- Zhizn' zhivotnykh* (Life of Animals), Moscow: Prosveshchenie, 1971, vols. 3, 5, 6.
- Zhukov, P.I., *Ryby Belorussii* (Fishes of Belorussia), Minsk: Nauka Tekhnika, 1965.
- Zotin, A.I. and Zotin, A.A., *Napravlenie, skorost' i mekhanizmy progressivnoi evolyutsii* (Direction, Rate, and Mechanisms of Progressive Evolution), Moscow: Nauka, 1999.

Translated by M. Batrukova