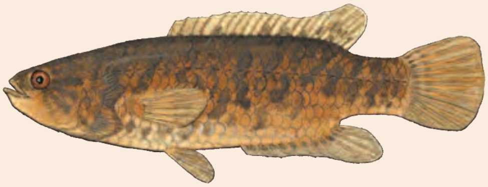
Life-history strategies



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The biological and demographic profile of a population is defined by a set of biological traits such as age or size at first reproduction, fecundity rate, lifespan, mortality rate of each age group, etc. This demographic profile represents a certain adaptation of a population to its environment. The theory of adaptive strategies is based on the assumption that demographic, ecological, ethological and physiological features of a population are co-adapted and modelled by natural selection.

Since environmental changes are continuous, each state of adaptation is only provisional, and the sustainability of a species depends on its aptitude for adapting its demographic strategy to new environmental conditions in order to maintain large populations.

Over the last forty years, several studies have tried to explain the origin of variability of characters among organisms. The various methods of reproduction and their degrees of success in various environments thus formed a basis for theoretical and empirical research referred to as "life history".

Life history studies attempt to explain the trade-off between reproductive and demographic parameters (Stearns, 1983a; Reznick, 1985; Pease & Bull, 1988) in relation to various environmental conditions (Whittaker & Goodman, 1979; Winnemiller & Rose, 1992).

Resource allocation: constraints and compromises

One of the principal ideas of the concept of demographic strategy is that various biological features are interdependent. A fundamental point is the comprehension of how and to what point an organism is willing to invest into each bio-demographic option in order to optimize the use of the resources and their distribution among its various fundamental needs. In other words, each organism has limited time and energy to survive and reproduce. What is thus the ideal resource partition in regards to time and energy for growth, maintenance and reproduction? This allocation of energy among these requirements must be equitable in order to enable the species to optimize the success of its reproduction.

The current theories consider that the evolution of biological features generally involve compromise. An increase in the time (or energy) devoted to an activity will be done at other activities' expense. Thus, for a similar availability of resources, an increase in the investment in gamete production is characterized by reduced growth and accumulation of reserves, which certainly induces a lower survival probability. Conversely, by minimizing the necessary energy for searching and capturing prey, fish will have more energy to devote to growth and metabolism (Hart, 1986). This concept of compromise is particularly important in current theories of evolution concerning biological factors. In such an ecological context, an organism may carry out various possible compromises. The theory makes the assumption that an organism will choose the optimal solution, *i.e.*, that which will provide the best possible adaptation to the conditions of the environment in which it evolves.

The main goal of studying bio-demographic strategies has been to understand the adaptive value of biological factors such as fecundity, age at first reproduction, survival and mortality rates in relation to the conditions of the environment inhabited by these populations. In other words, the selective pressure of the environment moulds the demographic structure of a population and the morphological and physiological characteristics of the individuals. The gamble therefore is to identify the factors and the mechanisms responsible for selecting various combinations of biological or demographic features (Barbault, 1981).

This gives rise to the need to understand the processes behind selection and biological responses in the context of dynamic relationships between populations and environments. It is assumed that biological systems contain sufficiently flexible mechanisms to respond to the fluctuations of the environment. Slobodkin & Rapoport (1974) illustrated the scenario of an organism confronted with an environment in the course of its evolution as a game it plays against nature, where its success is measured by the duration of time it remains in the game. In other words, an individual loses the game when it can no longer reproduce and a population loses the game when it becomes extinct.

At what point are biological characteristics such as fecundity or mortality rates of different ages likely to be modified by the changes in the environment inhabited by an individual? The nature of the adaptive response depends on the scale of time considered compared to the generation time. However there are limits within which adaptations are possible due to constraints that an organism cannot entirely transcend. These constraints may be consequences of the phylogenetic history of the species which resulted in limitations on possible options. Others are of a genetic nature because any evolution requires a certain degree of variability related to the genome. They may also be of a physiological, mechanical, ecological or behavioural nature, enabling organisms to withstand short-term changes in the environment, or of physiological or biochemical nature if these changes persist. In general, fish respond to changes in the environment in two ways:

- by phenotypical plasticity of behavioural and/or physiological nature enabling it to counteract the changes of the environment;
- on a population level, where selection of more competitive genotypes occur vis-a-vis the new environmental conditions.

During successive generations their descendants form a larger proportion in the population whose genetic pool thus becomes modified by natural selection.

A priority: assurance of descent

The reproductive success of individuals is determined by the manner in which they reallocate time and energy investments as a response to changes occurring in the environment, due to their effects on survival and reproduction. This search for compromise between various biological requirements is aimed at optimizing the selective value ("fitness"), *i.e.*, the relative contribution of an individual to future generations. Individuals that possess the highest fitness are those that produce the greatest number of descendants compared to less adapted individuals within the population. The individuals that provide the greatest proportion of descendants are also those that have the greatest influence on hereditary characters in this population (Begon *et al.*, 1996). Survival, fecundity and the generation time are the principal components of "fitness" (Winemiller & Rose, 1992).

Major types of demographic strategies: theory and empiricism

Theoretical studies and their predictions

The majority of theoretical studies are based on the postulate that natural selection tends to optimize reproductive effort of each age so that fitness (*i.e.*, "selective value, reproductive success and/or sustainability of descent") of individuals and the population at large is optimized. In order for this to happen, natural selection would act by adjusting certain parameters (fecundity, age and size at first maturation, etc.) depending on prevailing ecological conditions, thus constituting a "vital strategy".

Theoretical studies are based on mathematical models which analyse methods by which fitness is maximized. Most of these mathematical models use "r", which is the "Malthusian parameter" as a measure of fitness, and apply the assumption that age distribution is stable.

Cole (1954) commended the use of mathematical models in the study of the evolution of life strategies. He also asserted the need for a simple demographic procedure which consists of varying one parameter and considering the others to be fixed in order to evaluate the consequences of a variation of this parameter.

One of the basic hypotheses shared by all theorists relates to the cost of reproduction (the most recent include Reznick, 1985; Winkler & Wallin, 1987; Stearns, 1992; and Blondel, 1995).

Every organism had a fixed quantity of a limited resource at its disposal which it must distribute between reproduction, growth and maintenance. This theory is very important for species that have an indefinite growth.

The question lies in understanding what would be, for different organisms, the optimal investment in reproduction in a given environmental condition. Two major approaches have been applied to life history studies (Stearns, 1977):

- "deterministic models" (Cole, 1954; Mc Arthur & Wilson, 1967; Southwood *et al.*, 1974), which predict that organisms exposed to high mortalities regardless of their initial density experience large fluctuations in population density or repeated episodes of colonization, evolving towards earlier maturation, larger ranges, increased reproductive effort and a shorter life-span than organisms exposed to a density-dependent mortality or a constant population density.
- "stochastic models" (Murphy, 1968; Schaffer, 1974b) which predict the evolution of the same combination of traits, although for different reasons. When environmental variability involves a highly variable juvenile mortality, the following combination of traits would emerge: late maturation, decreased reproductive effort and increased longevity.

Fitness and variation of reproductive effort with age

Increase of reproductive effort with age leads in theory to better reproductive performance for each age (Gadgil & Bossert, 1970). This effort however also leads to a reduction in survival and growth, and thus to a consequent reduction in the contribution to reproduction in successive ages. That said, many authors (review by Giesel, 1976) consider that, except for animals with unlimited growth such as fish, the reproductive effort increases to a peak then decreases with age.

Fitness and parental investment in offspring

How much energy should be invested in caring for young? If the energy allocated per offspring increases:

- the number of offspring produced decreases;
- the size of offspring at birth increases;
- the individual fitness of offspring increases.

Fitness and iteroparity/semelparity

Semelparity is the reproductive strategy where individuals reproduce only once during their lifetime, while iteroparity refers to several reproductions during one lifetime.

The existence of organisms presenting such varied reproductive strategies aroused the curiosity of scientists studying the evolution of vital cycles such as Cole (1954), who tried to determine why iteroparity, although apparently advantageous, is not common in organisms. In a relatively stable environment, iteroparity would be the least effective manner to increase the intrinsic growth rate of a population (and thus its fitness), but in a variable and unstable environment, where chances of reproductive success are weak, iteroparity supports fitness. Iteroparity is also more advantageous for species which attain their first sexual maturity later than others and which produce small offspring.

Structures of mortality per age group were incorporated thereafter in the theory. A invariable environment or high juvenile mortality would generate an evolutionary pressure for multiple reproduction (iteroparity) whereas a variable or high adult mortality would imply few reproductions or even only one reproduction (semelparity) (Murphy, 1968).

Fitness and age at first sexual maturity

The ascent to sexual maturity represents a critical phase in the life of an individual. Initially, resource and time are allocated uniquely to survival and growth and are thereafter subjected to trade-offs between reproduction, growth and survival (Wootton, 1979).

The age of first spawning is one of the most important life history traits because it constitutes one of the main evolutionary adjustments imposed by natural selection (Cole, 1954; Roff, 1984). A decrease in the age at first maturity can significantly increase fitness by maximizing the number of offspring produced at early ages. In fact, the age of first spawning is the parameter that has the greatest impact on fitness (Noakes & Balon, 1982). If there is juvenile survival due to environment variability, reproductive performance decreases and first maturity is delayed. Conversely, if environment variability acts against adult survival, the reproductive effort increases and the first breeding occurs earlier (Schaffer, 1974b).

Fitness and resource availability

In theory, for a population limited by resource, a resource increase must lead to an increase of reproductive effort at all ages for iteroparous organisms and a decrease in the age of first maturity for semelparous organisms (Gadgil & Bossert, 1970).

Boyce (1979) presents a model that analyses the effects of seasonal changes in resource availability on the evolution of life histories. In a constant environment, natural selection favours the population whose individuals have a high growth rate (r) if the resource is abundant, and a low need of food if the resource is limited. In a seasonal (*i.e.,* variable) environment, the population that has the best fitness maximizes the ratio between benefits (growth) during favourable periods and loss (decrease) during unfavourable conditions. The model shows that, whatever the life cycle, the growth rate of the population (r) and carrying capacity (K) decrease when the environmental variability increases. Thus, when seasonality tends to decrease the chances of reproductive success, natural selection favours individuals that present a low reproductive effort and allocate a more significant part of their resource to other functions (e.g. growth). In return, this scenario increases survival chances for future reproduction (Schaffer, 1974a and b; Boyce, 1979).

Fitness and fecundity

With regard to the reproductive strategies, most mathematical models use "r" as the fitness index. Thus, they are based on the hypothesis of a stable age distribution, which is never the case in the field. If we consider the effects of the interaction between age and fertility on fitness, it is observed that populations with closer age and fertility distributions will have the largest rate of increase and the largest reproductive success in the long term (Giesel, 1976). Thus, populations with a majority of old individuals should breed later and should have a late fertility. Conversely, those with a "young" age distribution should have an early fertility distribution.

Phenotypical plasticity in the life history theory

Although very few theories take phenotypic plasticity (the ability to respond quickly) to environmental variability into account, a majority of authors agree that it is one of the determinants of life histories and that it contributes to increase fitness. Whether the conditions are favourable or not, it allows organisms to maximize reproduction. Thus progeny will be perpetuated against environmental heterogeneity.

A single genotype may show several potential phenotypes if it is exposed to environmental conditions included in its reaction range (Stearns & Koella, 1986; Blondel, 1995). Although geneticists and ecologists recognize the importance played by ranges of reactions in their theories, there are only very few predictions on the shape and position of reaction ranges. Stearns & Koella (1986) propose a model in which ranges of reaction for the age and size of first maturity have been calculated. Thus, they vary the growth rate and calculate an optimal age of first maturity for each growth rate (the fitness estimator). This model distinguishes the genetic and phenotypic components of the variation of age and maturity size:

- shape and position of the curve in the size/age space reflects the evolutionary response (genetic) to selection;
- location of the point (representing maturation) on the curve reflects the phenotypic response of an individual to a growth variation.

Discussion about the "r-K" selection

The terms 'r' and 'K' refer to the parameters of the logistic growth curve of a population, where 'r' is the slope (population growth rate) and 'K' the upper asymptote (carrying capacity of the environment for the population).

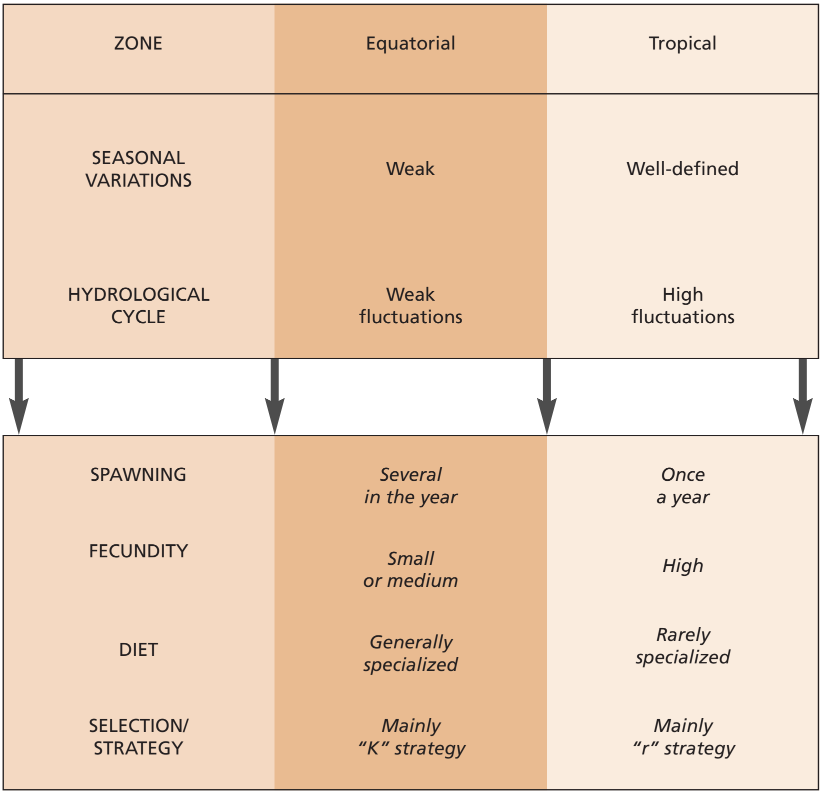
Species possessing short lifespans and high rates of reproduction are said to have evolved in "density-independent" conditions which would support a high growth rate (r), this is referred to as "r" selection. Conversely, species that have a long lifespan and a low rate of reproduction have evolved in "density-dependent" conditions which support the carrying capacity of high densities of individuals, *i.e.*, "K" selection.

The characteristics of “r” selection are: early maturation, high individual growth rate, high relative fecundity, small size offspring, increased effort on reproduction and short lifespan. Organisms in this selection evolve in variable environments with abundant resources.

“K” selection is characterized by: late maturation, low individual growth rate, low relative fecundity, decreased effort in reproduction, large sized offspring and long life expectancy. This occurs for organisms occupying environments dominated by trophic and spatial competition (figure 9.1).

The theory of “demographic strategies” was initially highly successful because it was simple, practical and accorded a good explanation for regulation of populations. According to Southwood *et al.* (1974), the habitat as a unit is the framework in which evolutionary pressures are exerted. The ecological strategy for “r strategists” is to be small sized and opportunistic. They possess an enormous capacity for adaptation and a very low level of extinction and thus have a high potential for selection. The “K strategists” on the other hand tend to be extremely adapted to their habitat, acquire large sizes and thus lose their plasticity for selection. If their habitat changes because of environmental variations on a large temporal scale, their population is threatened with extinction.

FIGURE 9.1.
Responses of species to global environmental conditions: comparison between equatorial and tropical African fishes



ZONE	Equatorial	Tropical
SEASONAL VARIATIONS	Weak	Well-defined
HYDROLOGICAL CYCLE	Weak fluctuations	High fluctuations

SPAWNING	*Several in the year*	*Once a year*
FECUNDITY	*Small or medium*	*High*
DIET	*Generally specialized*	*Rarely specialized*
SELECTION/ STRATEGY	*Mainly “K” strategy*	*Mainly “r” strategy*

However, various authors consider the r-K continuum of Pianka (1970), on which most of the theories on life histories is based, to be very limited and inadequate in accounting for the diversity of the life histories observed (review by Stearns, 1992 and Blondel, 1995). In most cases, the carrying capacity of the environment (K) and the mode of regulation of the concerned population (limited by resource or predation) are unknown, which makes the parameters observed compatible with several hypotheses (Wilbur *et al.,* 1974; Stearns, 1992).

Even when it is used as a simple classification method for life histories, the r-K dichotomy is unable to justify over 50% of the case studies (Wilbur *et al.*, 1974; Stearns, 1977; Stearns, 1992). As a result of the focus on the effects of "density-dependence" of r and K selections, other important biological constraints of life cycles are masked. These include: environmental variability, predator-prey relationships, factors of mortality per age group (Wilbur *et al.*, 1974; Michod, 1979), and also fecundity per age group (Stearns, 1983b). In spite of this, the r-K selection concept has made it possible to draw the attention of researchers to certain aspects of life histories and to formulate considerations in terms of evolution (Noakes & Balon, 1982).

Due to the drawbacks of the r-K continuum in dealing with evolutionary diversity of life histories, various authors such as Southwood (1977), Whittaker & Goodman (1979) and Winnemiller (1992) have proposed additional themes to the Pianka (1970) model.

In place of "r" and "K" strategies, Balon (1985, 1990) distinguishes two major types of ontogenetic models. First is the indirect development model, which involves generally small eggs produced in large number that give rise to young, partially developed larvae of small size, with a low volume of vitellus, which is insufficient to produce the final phenotype. The second is the direct development ("precocial") model in which fish produce a restricted number of eggs of large size with a great quantity of vitellus, enabling embryonic development up to an advanced stage.

This presents two major types of strategies: indirect development, which consists of producing a great number of eggs which will be subjected to a high mortality, but which frees the parents for other activities after spawning; and direct development, which consists of investing in the survival of a small number of individuals, an activity that requires a prolonged energy investment by the parents.

Empirical models

The multiplicity of selective forces which act on life histories and the diversity of responses by organisms have made it impossible for any demographic strategy to account for the diversity of the life histories (Southwood, 1988; Stearns, 1992; Blondel, 1995).

Due to this difficulty, scientists have turned to single or multi-dimensional empirical models. The Winemiller & Rose (1992) model of reproductive strategies, for example, identifies three strategies of reproduction along a three-dimensional continuum (table 9.I). These strategies form a triangular

Periodic	Opportunistic	Equilibrium
Optimizations of fecundity at the expense of the juveniles' survival	Optimization of the growth rate of the population by the generation time reduction	Optimization of the survival of eggs and young by parental care practice
Late maturity at a medium or large size Small and numerous eggs Single seasonal breeding	Early maturity at a small size Small or medium eggs Numerous breeding	Late maturity at a small or medium size Few large eggs Multiple breeding
Reproduction synchronized with most favourable periods for survival of the young	Fish living in little predictable environments or pioneer species able to repopulate quickly after disturbance	Fish living in relatively stable environments; highly developed parental care
Alestidae (*Alestes*) Mormyridae (*Mormyrus*) Siluriformes Cyprinidae	Cyprinodontiformes Small Alestidae Small Cichlidae	Cichlidae Mormyridae Anabantidae
Females generally larger than males, without significant differences in colouration	Males more coloured than females	Males generally larger and more coloured than females.

TABLE 9.I.
Biological characteristics of species belonging to the three major categories of demographic strategies (see figure 9.2).

continuum (figure 9.2) whose tips are characterized by the optimization of one demographic component at the expense of the other two.

Equilibrium strategies correspond to the "K" strategies of MacArthur and Wilson. These species optimize juvenile survival by a larger investment during egg (vitellus) production and practice parental care. These strategies are often developed by sedentary populations living in stable environments such as the Cichlids of the large East African Lakes. Others include Ariidae and Arapaimidae;

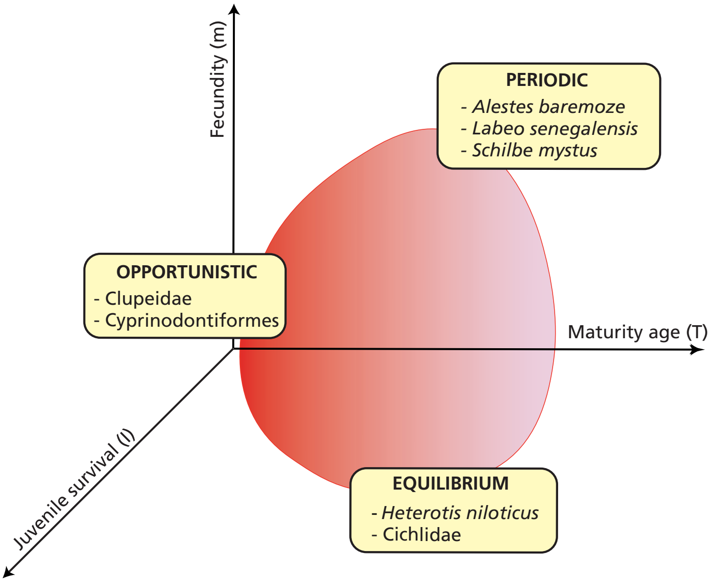


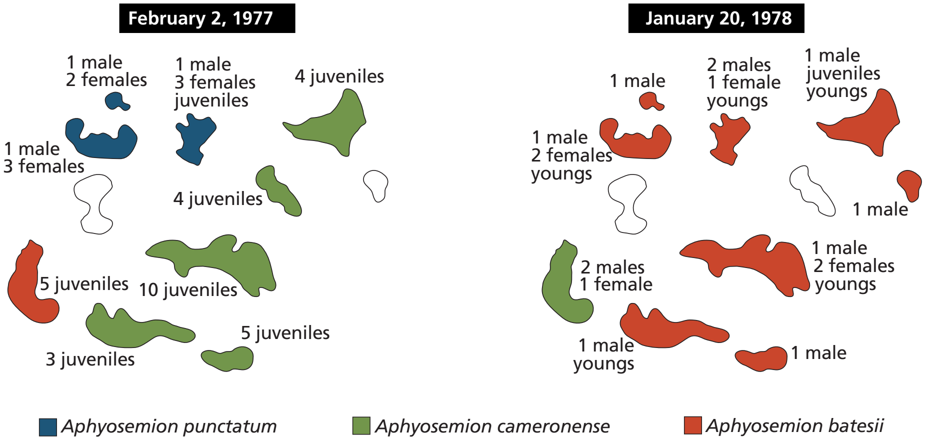
FIGURE 9.2.
Major types of demographic strategies in fish (modified from Winemiller & Rose, 1992).

APLOCHEILIDAE OF THE IVINDO BASIN

Eight species belonging to five genera appear to use the same niche. All are sympatric and diurnal, occupy the same habitat, and feed mainly on small insects that fall from surrounding trees. Many of these species can lay drought-resistant eggs[1], which allow them to colonize temporary environments. These low-fecundity species are characterized by their ability to release specific pheromones that inhibit the reproduction of other species. Thus, the first species to colonize a new environment also prevents other species from establishing themselves there. Coexistence, theoretically impossible, can only take place when disturbances sweep the entire system clean, forcing a redistribution of species. This occurs, for instance, following floods or the passage of an elephant herd (Brosset, 1982). The first species to reach a new pool of water will occupy the space and prevent other species from developing there (figure 9.3). Disturbances occur frequently enough that each of the species manages to be the first in a given space at one time or another; otherwise extinction would occur. This example shows how essential the temporal dimension is, as system diversity and the survival of the different species depend on the high frequency of disturbances.

FIGURE 9.3.

Aplocheilidae from Gabon: sharing space by mutual exclusion of the different species in confined spaces (elephant track) (redrawn from Brosset, 1982).



NOTE 1

[1] This diapause, of variable duration [a period of five years has been reported (Munro *et al.*, 1990)], may be occasional and have no effect on egg survival. For some species, however, egg desiccation is a necessary step for future development. This drought resistance is well-known to aquarium enthusiasts, who take advantage of it to swap material by post.

Periodic types of strategies are implemented in environments where seasonal and spatial variability are relatively predictable, and in which selection supports individuals who reproduce when the conditions of the environment are most favourable to the survival of the juveniles. The eggs are numerous and of small size, and maturation is delayed to a time when abundant egg production is maximized. Moreover, the large size of the adults enables them to survive during unfavourable periods for reproduction, and to store energy necessary for gonad development. This type of strategy is often associated with species that undertake long distance migrations for reproduction as it enables them to spawn for instance in seasonally flooded zones. Alestidae (*Alestes baremoze*) has developed this type of strategy which corresponds to type-“r” strategy

Finally, opportunist type strategies are implemented by species that favour the reduction of generation time in order to colonize environments much faster and to maximize population growth rate. Early maturation, small size, several but small spawns (which in the final analysis correspond to increased fecundity) characterize this type of strategy. It also corresponds partly to the “r”-type strategy or the abovementioned indirect mode of development. Some species, especially within Cypriniformes, Alestidae and certain Cyprinidae, are adapted to diapause or dormancy which enables them to survive highly unfavourable conditions during a particular stage of development in their life (see box “Aplocheilidae of the Ivindo basin (Gabon)”).

The identification of these three major types of strategies does not imply that all species can be classified in one or the other. Many fish have developed several intermediate strategies between these extremes. However, there are compromises between certain biological features which are not viable and which are eliminated by natural selection. Therefore, late maturation, low fecundity and low parental investment are a poor combination and such populations would be eliminated rapidly because they are not highly apt to compete. In the same way, physical and physiological constraints are such that it is not possible to consider that compromises between the biological characteristics would lead to “super-fish” that would reproduce early, possess high fecundity and a long lifespan (figure 9.4).

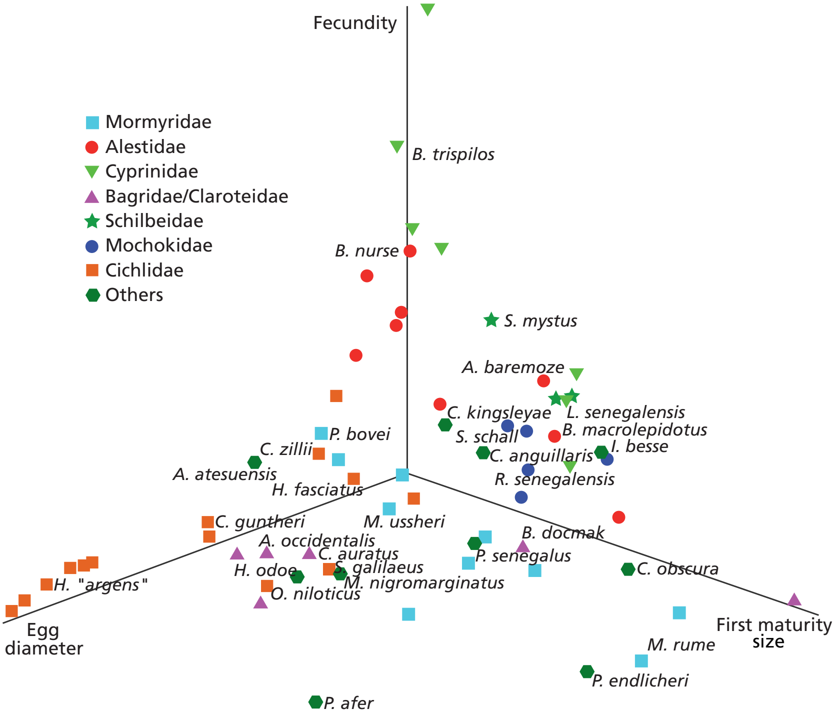


FIGURE 9.4.
Demographic strategies of some African fish species.

Scientific editors

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The Inland Water Fishes of Africa

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