3

Life History Tactics

Nearly all cave organisms for which any data are available show some or all of the following characteristics: delayed reproduction, increased longevity, smaller total number of eggs produced, and larger eggs—all features that are commonly associated with what is called K-selection. Since the demonstration by MacArthur (1962) of an analog to Fisher's Fundamental Theorem of Natural Selection in which population size can be maximized by natural selection, models of life history evolution and critiques of such models have been in full flood. Stearns (1977) has pointed out that the models have neglected critical aspects of the evolutionary process and that available empirical data are not extensive enough to distinguish among the various competing models. Because of the delayed maturity and low reproductive rates of cave organisms, it has not usually been possible to accumulate the sort of detailed information on life history parameters that is available for rapidly reproducing species such as *Drosophila*. Life histories of cave organisms should be of interest to modelers because they show the extremes of delayed reproduction and low reproductive rate. On the other hand, even in their current state of controversy, models of life history evolution should be of interest to cave biologists because they provide alternative explanations for the life history characteristics observed.

Two themes run through this chapter. The first is whether the observed life history parameters are adaptive. Consider the following data of Anderson and Watanabe (in Charlesworth 1980) for AR/AR karyotype female *Drosophila pseudoobscura:* the average number of eggs produced by a female was 83.1 under optimal conditions and 2.2 under yeast starvation. The stress imposed by severe food limitation would seem almost inevitably to cause a slowing of growth, a reduction in reproduction, or increased mortality. This is a result of the constraints imposed by lack of available energy and can be called adaptive only in the most trivial sense. This is not to say that cave organisms are slowly starving to death and that their life history traits are not adaptive. Quite the contrary; but a healthy skepticism about universal adaptiveness of life history traits throws those traits that are truly adaptive into bolder relief. The clearest example of this is the large egg size of cave organisms, which is almost certainly adaptive, because larger eggs result in larger offspring that are more resistant to starvation and perhaps to predation.

The second theme of this chapter is that delayed reproduction can be explained by several models, most of which have been recently summarized by Charlesworth (1980). There is no simple correspondence between density dependence of populations and the prediction of delayed reproduction, on the one hand, and density independence of populations and the prediction of accelerated reproduction, on the other. Charlesworth points out that not all forms of density dependence lead to selection for delayed reproduction (or for increasing reproductive effort with age). In particular, a density-dependent mortality factor applied equally to each age class does not result in selection for delayed reproduction. Among the factors that do lead to such selection for delayed reproduction are: (1) density-dependent juvenile survival or fecundity (Charlesworth 1980); (2) density-dependent adult fecundity (Charlesworth 1980); (3) fluctuating juvenile survival (Schaffer 1974a); and (4) long periods in which *r*, the intrinsic rate of increase, is negative (Mertz 1971). Low total reproductive effort, another characteristic often associated with K-selection, may result when juvenile mortality is high (Schaffer 1974b) or when adult mortality is low and *r* is low (Goodman 1974).

The life history models considered in this chapter are limited to those with a clearly defined selective basis. That is, it is assumed that "life histories evolve as a result of gene frequency changes within populations, under the control of natural selection" (Charlesworth 1980, p. 205). Some optimization models of life histories require group selection, and the requirements of others are not clear. I adhere generally to Charlesworth's viewpoint in what follows.

Although there is considerable information on egg numbers and size distributions in the cave biology literature, there are few studies that are detailed enough to allow estimation of life history characteristics. In the rest of this chapter I will consider four of the most complete comparative studies, the first two of which are laboratory studies. By far the most complete laboratory study of terrestrial cave populations is Deleurance-Glaçon's (1963) work on European leiodid cave beetles, supplemented by Peck's (1975a) laboratory study of leiodid populations in North American caves. Rouch's (1968) laboratory studies of aquatic European harpacticoid copepods will then be reviewed. The two most complete field studies are Poulson's (1963, 1969) work on North American amblyopsid fish, and Cooper's (1975) study of North American crayfish.

Leiodid Beetles

Adult cave leiodid beetles are scavengers and saprophages. The most effective baits for them are rotten meat and dung (Peck 1973a, 1975b), and in Mammoth Cave considerable numbers can be found on dung. Although food is generally scarce for the beetles, those species that can utilize mammalian dung at least occasionally have abundant resources. The adults probably have few predators in most caves, occasionally being taken by salamanders (Peck and Richardson 1976), staphylinid beetles, and possibly the larvae of fungus gnats (Peck and Russell 1976). The free-living, active stages of the beetle larvae are carnivorous, but their prey are unknown (Deleurance-Glaçon 1963). Being soft-bodied, the larvae and pupae are more susceptible to predation. Peck (1973a) reports predation by Collembola and mites.

Mortality and fecundity data are available for four species, summarized in Table 3–1. Considering only the three European Bathysciini for the moment, there are large differences in fecundity among the species. For *Isereus colasi* and *I. serullazi,* in line with what we expect for a species with low food availability, egg production is very low. Deleurance-Glaçon states that these species have large eggs, but she gives no measurements. On the other hand, *Speonomus delarouzeei* produces many small eggs, ten times as many as *Isereus*. Direct comparisons with the North American *Ptomaphagus hirtus* are difficult to interpret because of its different phyletic history and different laboratory rearing conditions, but it is intermediate in egg output between the two European genera.

There are two possible interpretations of the fecundity differences. First, it could be argued that *Isereus* has been in caves longer than

Table 3–1 Life history characteristics of cave leiodid beetle species for which both mortality and fecundity data are known. Rearing temperature of European species (*Speonomus delarouzeei, Isereus serullazi* and *Isereus colasi*) was 9°C; rearing temperature of American species, *Ptomaphagus hirtus,* was 12.5°C. Assuming a Q_{10} of 2, and multiplying the figures for the European species by a factor of 0.825, the species can be compared at equivalent temperatures. (Data modified from Deleurance-Glaçon 1963 and Peck 1975a.)

	Eggs		Larvae			Pupae		Adults	
Species	No. eggs/ female/yr	Time to hatching (days)	No. instars	Larval duration (days)	% of time feeding	Pupal duration (days)	Pupal duration/ larval duration	Female mortality/yr	Male mortality/yr
Ptomaphagus hirtus	51	18.5	3	42	70	32	0.76	0.42	0.25
Speonomus delarouzeei	131	51	2	167	18	50	0.29	0.33	0.23
Isereus serullazi	13.8	117	1	99	0	116	1.17	—	0.29
Isereus colasi	11.8	117	1	94	0	117	1.24	0.35	—

Speonomus and that *Speonomus* populations are therefore less adapted and less fit. Although this view may be correct, there is no unambiguous evidence to support it. A second hypothesis is that the changes in larval morphology, the suppression of larval feeding period, and the more "regressive" characters of *Isereus* may all be the result of a single selective regime, and that species such as *Speonomus* may be under a different selective regime. *Speonomus delarouzeei* (and *P. hirtus*) may face a lesser food shortage and may have retained the ability to increase rapidly when a rich food source such as mammalian dung is available. Under Mertz's (1971) scheme of classifying species by whether their intrinsic rate of increase is usually positive or usually negative, it may be that r is usually negative for *Isereus* and usually positive for *Speonomus* and *Ptomaphagus*. Deleurance-Glaçon mentions in passing that there are considerable ecological differences among the species, but she gives no particulars. The second hypothesis has no more direct support than the first, but it is at least possible that the life history characteristics of *S. delarouzeei* are adaptive rather than being an inferior version of the *Isereus* life history characteristics. All species listed in Table 3–1, including *S. delarouzeei,* are troglobites (Laneyrie 1967), so there is no possibility of "contamination" by genes from surface populations.

The most apparent pattern in adult mortality is that males consistently have lower rates than females. Time to adult emergence is much shorter for *P. hirtus,* but this is due at least in part to higher rearing temperatures and different food. The time to adult emergence for *S. delarouzeei* (268 days) is less than that of *I. serullazi* (332 days) and *I. colasi* (328 days), which is in line with their fecundity differences.

The most fascinating and unexpected aspect of the *Isereus* life history is the suppression of larval feeding. While a variety of models can explain delayed reproduction (see the beginning of this chapter), suppression of feeding would seem to increase larval mortality, and I know of no model that predicts selection for increased larval mortality. Either suppression of feeding is maladaptive, which is unlikely in view of the extensive morphological changes of the larvae that accompany suppression, or we must look for some explanation that involves selection. I think two factors have led to suppression of larval feeding. First, live prey available to the larvae are probably scarce, so the energy gained by feeding is probably not great. Second, the increase in the pupal period in *Isereus* suggests that the pupal cell protects the organism from predation. For suppression of feeding to be favored, the gain in survivorship from predator escape should exceed the loss from lack of food. As an example of the potentially high mortality rates of immature stages, consider the following life table based on *I. colasi* with an adult longevity of four years of reproduction after the first year of adult life and with constant adult mortality; b_x, represents the number of female eggs produced at age x, and l_x, represents survivorship to age x.

Age	Adult age	l_x	b_x
0	—	1	0
1	0	l_i	0
2	1	$(0.65)l_i$	5.9
3	2	$(0.42)l_i$	5.9
4	3	$(0.27)l_i$	5.9
5	4	$(0.18)l_i$	5.9

If the population size is stable and r is zero, the net reproductive rate

$$R_o = \sum_x l_x b_x \tag{3-1}$$

is 1. For the above life table, $R_o = 1$ when survival to the adult stage, l_i, is 0.11. This at least indicates that high mortality of immature stages is possible.

Harpacticoid Copepods

Harpacticoid copepods are common in the sediments and gravels of many cave streams and pools. As Delamare-Deboutteville points out (quoted by Rouch 1968, p. 13), harpacticoids are "adapted to creep on the substrate or to saunter rapidly among the interstices of the sediments" (my translation). They are common in a wide variety of subsurface habitats besides caves, including sands bordering fresh and salt water. Compared to cave organisms at higher trophic levels, harpacticoids probably suffer high mortality. Their soft-bodied, wormlike morphology is likely to make them susceptible to the vagaries of currents and to the mechanical abrasion of sediments. In addition, many populations suffer predation from groups such as amphipods, isopods, and crayfish. The food of harpacticoids, organic debris and microorganisms, is generally scarcer in caves than in epigean habitats (Poulson 1964, Gittleson and Hoover 1970).

Most of what is known about cave harpacticoid life cycles comes from Rouch's (1968) study of French species. Rouch provides no mortality data, but he does provide detailed information on fecundity of both subsurface and epigean species. In Figure 3–1, egg numbers and egg size are plotted against body size for five cave species, four high-altitude species in streams and ponds, and four ubiquitous low-elevation species in streams and lakes. One of the low-elevation species, *Bryocamptus zschokkei,* is also found in caves, but Rouch reports data only for epigean populations. Besides the ecological classification, Rouch distinguishes three phyletic lines that include both cave and epigean species: *Nitrocella* and *Nitocra* in the Ameridae; *Bryocamptus* in the Canthocamptidae; and *Elaphoidella* in the Canthocamptidae. In a food-poor environment such as caves, one would expect reduced number of eggs per brood and increased egg size. These predictions are in general borne out (Fig. 3–1*A*). All cave species have less than ten eggs per brood, and all low-elevation epigean species have more than ten. This is due in part to the smaller size of the cave species, but in the *Elaphoidella* line, cave species of the same size as epigean species have fewer eggs. Surprisingly, high-altitude species have even fewer eggs, perhaps because of food scarcity in this environment as well. Egg diameters show a similar pattern (Fig. 3–1*B*). The eggs of high-altitude and cave species have larger diameters than those of epigean species, except for the epigean *Canthocamptus staphylinus,* which has a much larger body. There is little doubt that the differences shown by cave species in egg volume and number are the result of adaptation to a food-poor environment.

Although mortality rates are probably density dependent, because of predation, this density dependence does not necessarily lead to delayed reproduction. However, low food supplies may result in density-dependent fecundity, which should lead to delayed reproduction (Charlesworth 1980). Rouch provides data on postembryonic development and adult longevity for one epigean species, *Bryocamptus zschokkei,* and two cave species, *B. pyrenaicus* and *Nitrocella subterranea*. Postembryonic development is 4 weeks for *B. zschokkei,* 10–13 weeks for *B. pyrenaicus,* and 11–16 weeks for *N. subterranea*. Adult longevity is 8.7 months for *B. zschokkei*, 19.6 months for *B. pyrenaicus,* and 14.6 months for *N. subterranea*. While the differences between *Bryocamptus* and *Nitrocella* may be the result of phyletic differences, the differences between *B. zschokkei* and *B. pyrenaicus* are probably caused by selection for delayed reproduction in *B. pyrenaicus*.

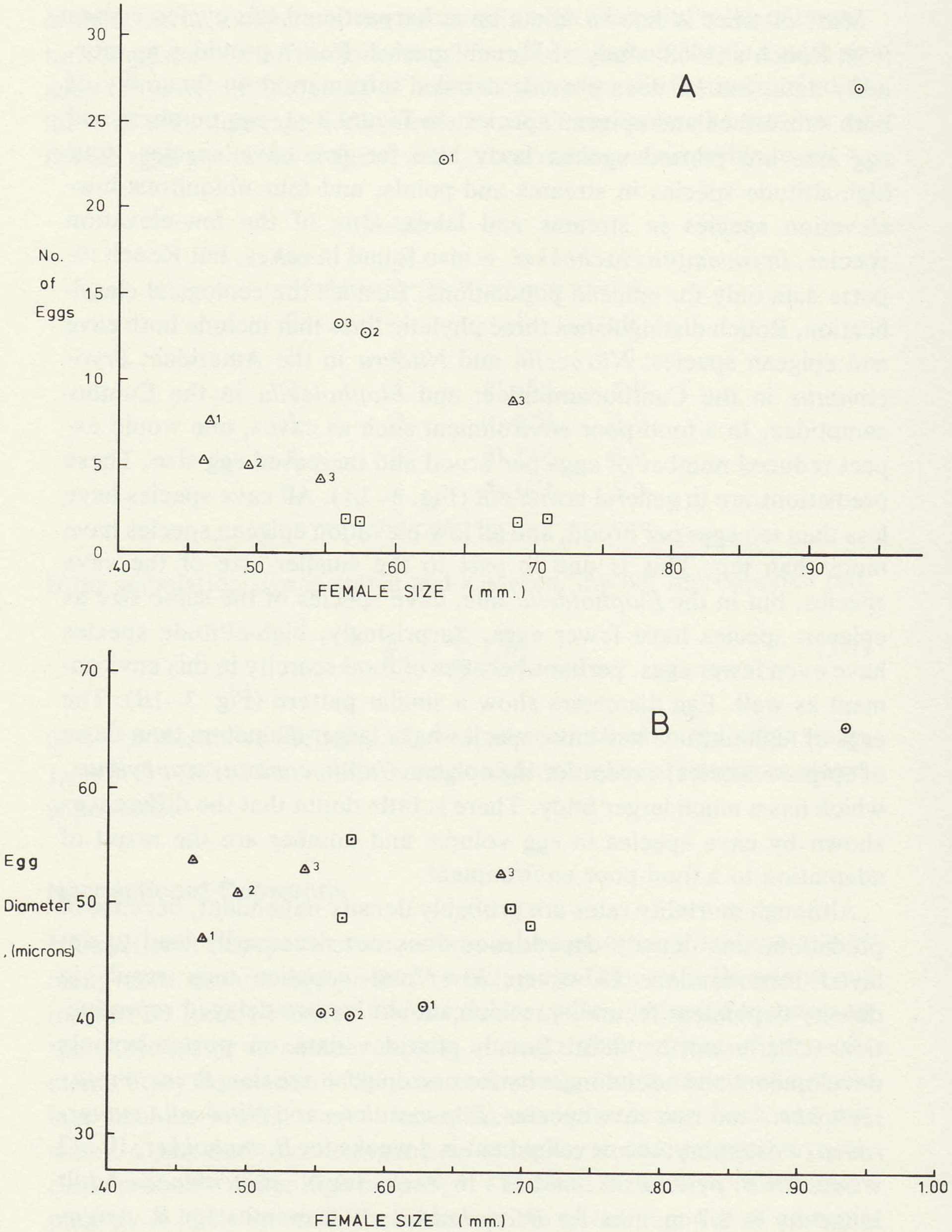

Figure 3–1 (*A*) Female size plotted against number of eggs for European harpacticoids. (*B*) Female size plotted against egg diameter. Squares are species in high-altitude streams and ponds, triangles are cave species, and circles are low-altitude epigean species. The three phyletic lines labeled are: 1, *Nitrocella* and *Nitocra;* 2, *Bryocamptus,* and 3, *Elaphoidella*. (Data from Rouch 1968.)

Rouch's data on egg number and egg diameter can be used to estimate reproductive effort. Compared to other cave organisms, in these species adult mortality and *r* are high, so reduced reproductive effort is less likely (Goodman 1974). As indicated in Figure 3–2, there is no difference between cave and low-altitude epigean species in reproductive effort per brood except for the epigean *Canthocamptus staphylinus,* whose reproductive effort is nearly an order of magnitude higher than that of any other species. High-altitude epigean species show some indication of reduced reproductive effort. If the number of broods is taken into account, cave species have lower reproductive effort, but the females are smaller as well (Table 3–2). Given the small number of species, there is no conclusive evidence for reduced lifetime reproductive effort.

Amblyopsid Fish

In addition to the modifications in morphology and physiology discussed in chapter 2, Poulson (1963, 1969) has provided considerable in-

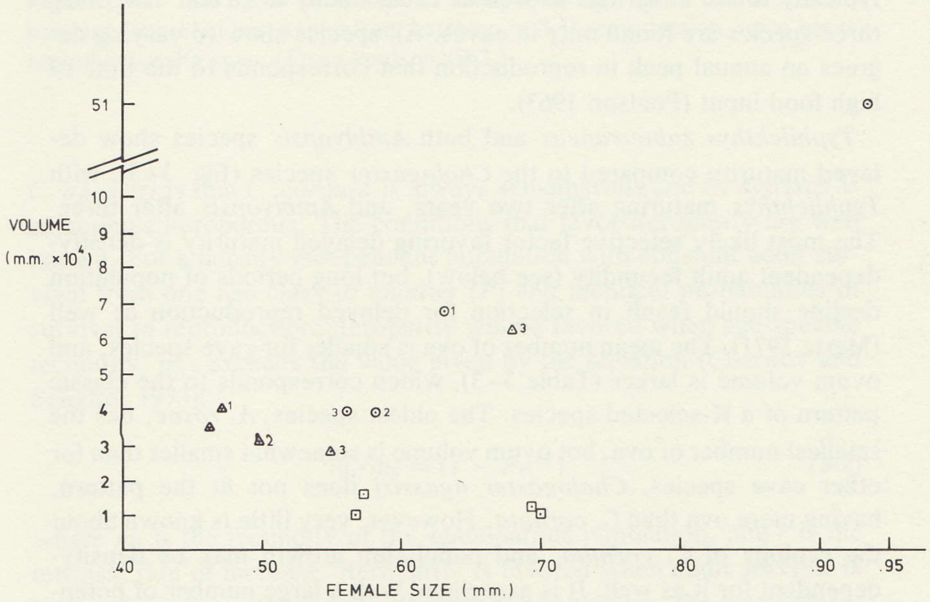

Figure 3–2 Reproductive effort per brood, measured as total egg mass volume plotted against female size. Labels as in Fig. 3–1. (Data modified from Rouch 1968.)

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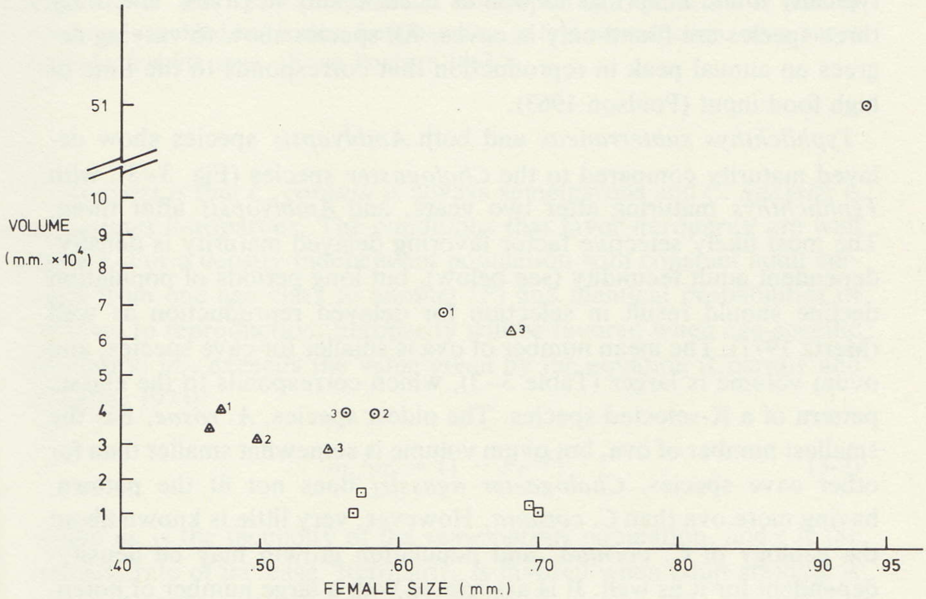

Figure 3–2 Reproductive effort per brood, measured as total egg mass volume plotted against female size. Labels as in Fig. 3–1. (Data modified from Rouch 1968.)

Table 3–2 Lifetime reproductive effort for epigean *Bryocamptus zschokkei* and cave *B. pyrenaicus* and *Nitrocella subterranea*. (From Rouch 1968.)

Species	Habitat	Mean length of female (mm)	Egg vol./brood (mm^3)	No. broods	Total egg vol. (mm^3)
Bryocamptus zschokkei	Epigean	0.63	6.9×10^{-4}	14	9.7×10^{-3}
Bryocamptus pyrenaicus	Cave	0.47	4×10^{-4}	16.7	6.7×10^{-3}
Nitrocella subterranea	Cave	0.50	3×10^{-4}	9.2	1.2×10^{-3}

formation on life cycle modifications of cave amblyopsid fish. Fecundity and longevity data are summarized in Figure 3–3 and Table 3–3, in which the species are listed by increasing evolutionary time in caves. *Amblyopsis* is also a separate phyletic line, albeit closely related, and has been in caves the longest time. *Chologaster cornuta,* found in swamps and small streams in the Coastal Plain, can be considered the base line for comparing varying levels of cave adaptation. *C. agassizi* is typically found in springs as well as occasionally in caves. The other three species are found only in caves. All species show to varying degrees an annual peak in reproduction that corresponds to the time of high food input (Poulson 1963).

Typhlichthys subterraneus and both *Amblyopsis* species show delayed maturity compared to the *Chologaster* species (Fig. 3–3), with *Typhlichthys* maturing after two years, and *Amblyopsis* after three. The most likely selective factor favoring delayed maturity is density-dependent adult fecundity (see below), but long periods of population decline should result in selection for delayed reproduction as well (Mertz 1971). The mean number of ova is smaller for cave species, and ovum volume is larger (Table 3–3), which corresponds to the classic pattern of a K-selected species. The oldest species, *A. rosae,* has the smallest number of ova, but ovum volume is somewhat smaller than for other cave species. *Chologaster agassizi* does not fit the pattern, having more ova than *C. cornuta*. However, very little is known about the ecology of *C. cornuta,* and population growth may be density-dependent for it as well. It is associated with a large number of potential predators and competitors (Poulson 1963).

Reproductive life span presents a more complicated pattern. The major difference in life cycle between *C. cornuta,* the swamp fish, and

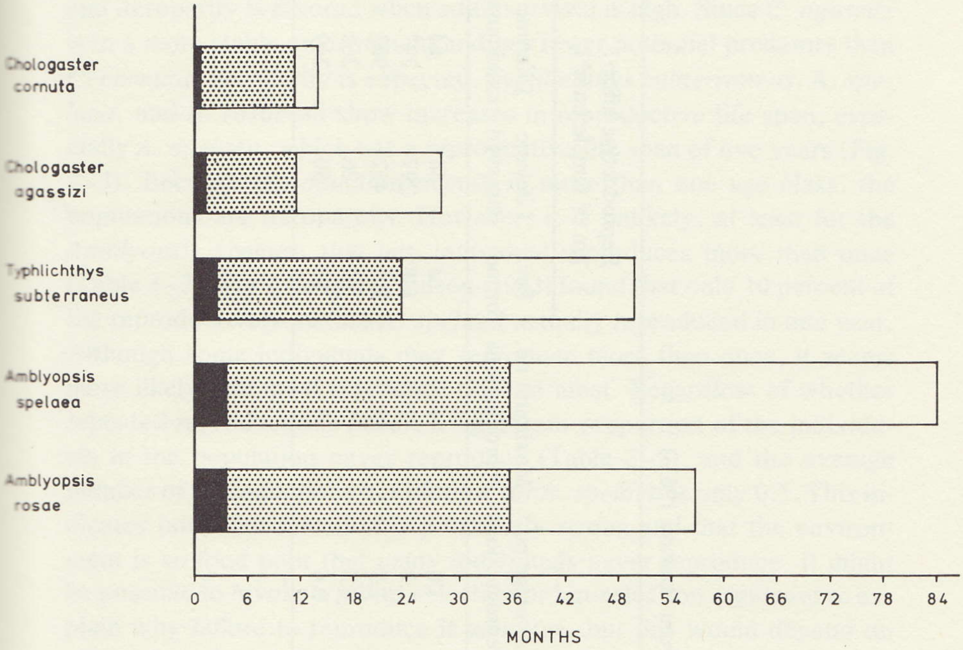

Figure 3–3 Life spans of species of amblyopsid fish. Black bar is time to hatching, speckled bar is time from hatching to first reproduction, open bar is reproductive life span. (From Poulson 1963.)

C. agassizi is that *C. cornuta* is always semelparous and *C. agassizi* is sometimes iteroparous. The conditions that favor iteroparity are well known. For a density-independent population with constant adult survival from one age class to another (P) and identical probabilities of survival to reproduction, iteroparity will be favored when age-specific fecundity, m_i, exceeds the value given by the equation (Charnov and Schaffer 1973):

$$m_i/m_s = (1 - Pe^{-r}) \tag{3-2}$$

where m_s is the fecundity of the semelparous population, and r is the intrinsic rate of increase. Iteroparity is favored when adult survival is high and r is low. For density-dependent populations, the equation reduces to (Charlesworth 1980):

$$m_i/m_s = (1 - P) \tag{3-3}$$

Table 3–3 Reproductive effort of amblyopsid

(Data modified from Poulson 1963.)

Species	Habitat	Mean no. ova per female	vum vol. mm³)	Female wt. (gm)	Average no. reproductions	Maximum no. reproductions	Reproductive effort/ gm of female (mm³) Per brood	Lifetime observed	Lifetime maximum
Chologaster cornuta	Swamp	98.0	0.61	0.93	1.0	1	64	64	64
Chologaster agassizi	Spring	152.1	2.80	2.87	2.0	2	148	297	297
Typhlichthys subterraneus	Cave	49.8	5.20	0.86	1.5	3	301	452	903
Amblyopsis spelaea	Cave	69.5	5.20	6.88	0.5	5	52	26	260
Amblyopsis rosae	Cave	23.0	4.50	1.25	0.6	3	83	50	249

and iteroparity is favored when adult survival is high. Since *C. agassizi* is in a more stable environment and has fewer potential predators than *C. cornuta,* iteroparity is expected. *Typhlichthys subterraneus, A. spelaea,* and *A. rosae* all show increases in reproductive life span, especially *A. spelaea,* which has a reproductive life span of five years (Fig. 3–3). Because reproduction occurs in more than one age class, the populations are iteroparous. However, it is unlikely, at least for the *Amblyopsis* species, that any individual reproduces more than once (Table 3–3). For example, Poulson (1963) found that only 10 percent of the reproductively mature *A. spelaea* actually reproduced in one year. Although some individuals may reproduce more than once, it seems more likely that most reproduce once at most. Regardless of whether repeated reproductions occur, a significant proportion of the individuals in the population never reproduce (Table 3–3), and the average number of reproductions per lifetime for *A. spelaea* is only 0.5. This indicates both that selection is potentially strong and that the environment is so food poor that many individuals never reproduce. It might be possible to invoke a group-selection or kin-selection argument to explain why failure to reproduce is adaptive, but this would depend on either shared rearing of young or high population extinction rates, for both of which there is no evidence. It seems most likely that many of the fish are simply slowly starving to death or are unable to obtain enough food to reproduce.

Table 3–3 gives estimates of reproductive effort. Whether one considers per-brood reproductive effort or maximum or observed lifetime reproductive effort, the same pattern emerges. In the *Chologaster-Typhlichthys* line, reproductive effort increases with increasing cave adaptation. On the other hand, *Amblyopsis* shows a reduced reproductive effort compared to both *T. subterraneus* and *C. agassizi.* Since reproductive effort should be low when adult mortality and *r* are low (Goodman 1974), why does *T. subterraneus* show a high reproductive effort? It is clear from the data in Table 3–3 and Figure 3–3 that the maximum potential rate of increase for *T. subterraneus* is higher than for either *A. spelaea* or *A. rosae,* but this simply changes the question to why *r* is higher for *T. subterraneus.* There are some habitat differences between the species. In particular, *T. subterraneus* can occur in smaller streams than *Amblyopsis,* and these smaller streams may have greater food supplies. However, even where *T. subterraneus* occurs in large, food-poor streams, it maintains a high reproductive effort (Poulson 1963). Based on available information, it would seem that the life cycle of *T. subterraneus* is not as adapted to cave conditions as that of *Amblyopsis,* presumably because *T. subterraneus* has been in caves a shorter time.

Poulson also provides evidence for density-dependent population growth. As shown in Figure 3–4, the age distributions of all of the cave species are skewed toward larger age classes. Assuming a stable age distribution, this is most likely to result from density-dependent factors. More direct evidence of density dependence comes from Poulson's (1969) study of *A. spelaea* in Upper Twin Cave, Indiana (Table 3–4). In a five-year study he found that total metabolic demand of the population varied less than either biomass or numbers of individuals. For food-limited populations, total metabolic demand should more accurately reflect carrying capacity than either numbers or biomass. A plot of the log of metabolic demand at time $t + 1$ against the log of metabolic demand at time t can be used to assess density dependence in a manner analogous to Tanner's (1966) use of population size. With density dependence, the slope should be less than 1, which it is for the *A. spelaea* population (slope = −0.66, S.D. = 0.54).

Finally, there is evidence that mean density and, by implication, carrying capacity, increases over evolutionary time as expected if *K*-selection is occurring. Poulson (1969) gives the following figures for

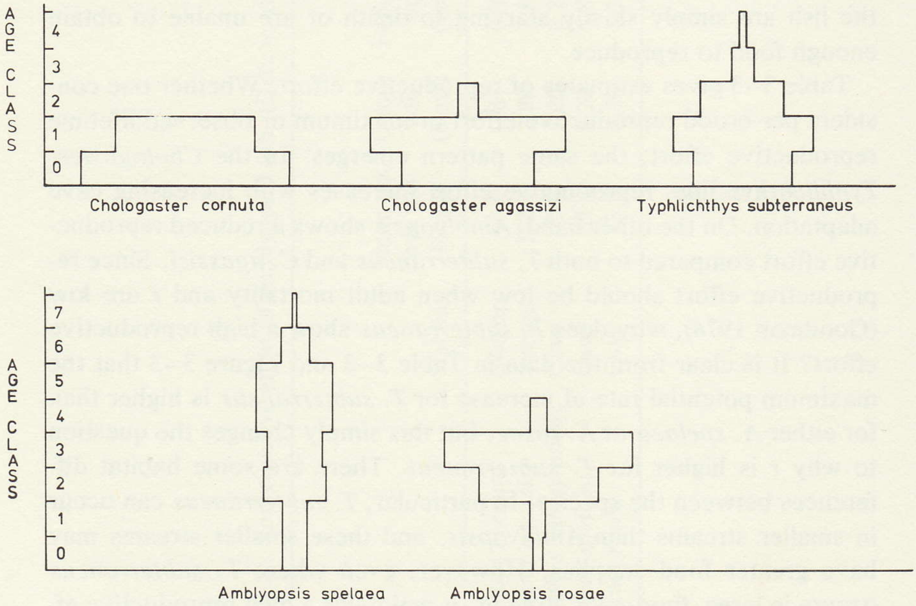

Figure 3–4 Age structure of five species of amblyopsid fish. (Modified from Poulson 1963.)

Table 3–4 Population characteristics of *Amblyopsis spelaea* in Upper Twin Cave, Indiana. The population was sampled once a year for five years. (Modified from Poulson 1969.)

	Total no. fish	Total weight (gm)	Total metabolic rate (cc O_2/day)
Mean	111	421	162
Coefficient of variation $\left(\frac{\sigma^2}{\bar{X}}\right)$	303	402	128
Range	84–130	363–455	149–180

number of fish per hectare in caves: *C. agassizi,* 50; *T. subterraneus,* 265; *A. spelaea,* 520; *A. rosae,* 1500.

Orconectes australis australis Crayfish

In the most extensive field study to date of the life cycles of cave organisms, Cooper (1975) analyzed crayfish populations in Shelta Cave, Alabama, over a period of 6 years. Because the *Orconectes australis australis* population in that cave represents the extreme in longevity and delayed reproduction, it is an appropriate final example.

Shelta Cave consists of several large, connected galleries with lakes. A very rich aquatic fauna is present, including three species of cave-limited crayfish (one *Orconectes* and two *Aviticambarus*), and two predators on young crayfish: the fish *Typhlichthys subterraneus* and the salamander *Gyrinophilus palleucus*. The most common crayfish was *O. australis australis,* with a population estimated at around 1,000 (Copper 1975). Over the course of the six years, Cooper marked over 900 *Orconectes* with codes unique to each individual, most of which were retained through molts. Because of a high recapture rate of marked individuals, Cooper was able to estimate growth rates of a rather large number. By summing up the times taken for each growth increment, one can calculate longevities (Table 3–5). Using the average rate of growth, Cooper found that the average time taken to reach the maximum carapace length of 47 mm was 176 years. Using the maximum growth rate observed for each size interval, the life span was 37 years. No life span can even be calculated by using the minimum growth rate, because some crayfish shrank in size! Cooper himself urges caution in interpreting these figures, but they are most remarkable, especially

Table 3–5 Growth rates and longevity in *Orconectes australis australis*. Rates are expressed in mm per month. The smallest size class (15.7 mm) is approximately that of newly hatched individuals. (From Cooper 1975.)

No. samples	Change in carapace length (mm)	Size increment (mm)	Max. rate	Months	Av. rate	Months
3	5.6 to 10.7	5.1	0.24	21.3	0.12	42.5
*	10.7 to 16.2	5.5	0.31	17.7	0.17	32.4
3	16.2 to 21.0	4.8	0.38	12.6	0.22	21.8
6	21.0 to 30.2	9.2	0.14	65.7	0.09	102.2
31	30.2 to 39.2	9.0	0.13	69.2	0.04	225.0
13	39.2 to 47.0	7.8	0.03	260.0	0.0005	1,695.7
Total months				446.5		2,119.6

* Rates determined by interpolation from adjoining size classes.

since the data are the most extensive available and the most carefully taken. The most reasonable interpretation of the growth rates given in the table is that the average growth rates in fact represent the actual growth rates of the population during the time it was sampled, and that the maximum growth rates approach growth rates under optimal conditions, at least for Shelta Cave.

Size at first reproduction can be estimated in several ways. Females are sexually mature when the carapace is 38–39 mm long, but the carapaces of the only successfully reproducing females were between 45 and 47 mm long. One smaller individual (carapace length 38 cm) had the remnants of an unsuccessful clutch. Translated into age, sexual maturity is reached in 35 years under average conditions, and in 16 years under optimal conditions. The age of reproduction occurs at 105 years for individuals with average growth rates and at 29 years for individuals with maximum growth rates.

During the entire study Cooper (1975) found only two reproducing females, one with 54 attached young and one with 78 attached young, which are low figures compared to most epigean species. However, he also found indirect evidence that reproducing females sequester themselves. The proportion of large females in the population was observed to drop during the winter. Assuming a constant sex ratio for the whole population, the sex ratio of the observed population can be used to estimate the fraction of large females reproducing. At a maximum, the fraction of large females reproducing is 0.67 and some of these reproductions are probably unsuccessful, because of egg resorption, for example.

Given delayed maturity and relatively small clutch sizes, the question is whether the population can maintain itself ($R_0 \geq 1$) under the conditions Cooper observed. To answer this, one needs mortality estimates (see equation 3-1), which can be figured from the decline in frequency of marked individuals in Cooper's last sample, taken 20 months after the last marking. Assuming that a constant fraction of the population dies each month, irrespective of age, the monthly adult mortality rate is 0.020. This is an overestimate of mortality because some emigration may have occurred. More important, it is an underestimate because it neglects juvenile mortality, since few juveniles are marked. Juvenile mortality is higher than adult mortality because juveniles are preyed upon by *Typhlichthys subterraneus* and *Gyrinophilus palleucus*.

The estimate of mortality rate, with the caveat that it is too low, can be compared to mortality rates required to produce a nondeclining population for several idealized populations of *O. australis australis*. Four such populations were considered, differing in age of reproduction of females (Table 3–6). For simplicity, males were not considered. The ages of reproduction in the table correspond to the observed ages of reproduction *and* to reproductive maturity both for populations of indi-

Table 3–6 Maximum mortality to maintain a nondecreasing population of *Orconectes australis australis* in Shelta Cave, assuming constant mortality for four idealized populations differing in age of reproduction. Clutch size is assumed to be 40 female eggs; CL = carapace length.

Population growth conditions	Age of reproduction (yrs)	Maximum mortality		Observed mortality	
		Month	Year	Month	Year
Maximum, reproduce at 39.2 mm CL	15	.026	.218	.030	.333
Maximum, reproduce at 45 mm CL	29	.011	.119	.030	.333
Average, reproduce at 39.2 mm CL	35	.009	.100	.030	.333
Average, reproduce at 45 mm CL	105	.003	.034	.030	.333

viduals with average growth rates and for populations with maximum growth rates. All individuals are assumed to reproduce once and to produce forty female eggs. Individuals may reproduce more than once, but because considerable mortality probably accompanies reproduction, additional reproductions would be rare and would add relatively little to the growth rate. To compensate for this, clutch size is put somewhat higher than observed. Regardless of these details, a clear pattern emerges. In all cases, observed mortality is much higher than the mortality required to maintain population size. Therefore, the population in Shelta Cave is probably declining, albeit slowly, corresponding to Mertz's idealized population in which r is usually negative with occasional bursts of positive r. The delayed maturity is most likely the result of selection to slow the rate of decline in a population that is generally declining.

Summary

The life history patterns of fish and crayfish species, which are higher up in the food web and relatively free of predators, are easier to interpret than the patterns of lower species. Both fish and crayfish show signs of severe food limitation. Many individuals of the cave-limited species, with the exception of *Typhlichthys subterraneus,* fail to reproduce even once. At least for the crayfish studied by Cooper, there was evidence of failed reproduction and of egg resorption. But there was also strong evidence of an adaptive response to severe food limitation. Fewer, larger offspring were produced, and reproduction was delayed. The only incongruity was in the pattern of reproductive effort in the amblyopsid fish. With low adult mortality and low population growth rates, reproductive effort should be low. Two predictions can be made in this regard. First, the *Amblyopsis* line, which has apparently been in caves longer than the *Chologaster-Typhlichthys* line, should have a lower reproductive effort. Second, within the *Chologaster-Typhlichthys* line, reproductive effort should decline with increasing cave adaptation. The first prediction was confirmed by the data, but the second was not. Although there is considerable room for doubt, it is probably true that *Typhlichthys* is less adapted to the cave environment than the *Amblyopsis* species because *Typhlichthys* has had less time to adapt.

Some of the leiodid beetles, especially *Isereus serullazi* and *I. colasi,* show the classic pattern of delayed reproduction, with the unexpected twist of suppressed larval feeding. Although there is no comparable data available for surface-dwelling species, the life history patterns of *Ptomaphagus hirtus* and *Spenomus delarouzeei* are clearly less modified than those of *Isereus*. This may be caused by differences in the length of time these species have been in caves; it is just as likely that niche differences have allowed *Ptomaphagus* and *Speonomus* to exploit a more abundant food supply, such as mammalian feces. This is unlike the situation with fish and crayfish, where there is no obvious alternative food source that is at all abundant.

Compared to closely related surface species, all cave harpacticoids have fewer but larger eggs, indicating food scarcity. However, the differences are not extreme. Harpacticoid species from high-elevation surface habitats have even fewer and larger eggs than the cave species. On a per-brood basis, there is no indication of reduced reproductive effort for cave harpacticoids, which is consistent with the conjecture that their rate of increase is higher than that of many other cave groups and thus less likely to show reduced reproductive effort.