3. DIAPAUSE IN CRUSTACEANS: PECULIARITIES OF INDUCTION

3.1 INTRODUCTION

Crustaceans, the most important group of invertebrates in aquatic food webs, occupy a place similar to that of the insects in terrestrial environments. Being the best-studied group, crustaceans were selected for a detailed description of the peculiarities and mechanisms of diapause in aquatic animals.

3.2 DIAPAUSE IN CRUSTACEAN LIFE CYCLES

The annual cycle of crustaceans, which evolved under the pressure of environmental conditions and is normally fixed genetically, reflects the average conditions to which populations have been exposed over a long period of time. Diapause occurs during harsh periods, while active growth and reproduction occur during favorable times. Unfavorable factors may be different in different seasons. For example, high temperatures and lack of food are both unfavorable for the cyclopoid Cyclops vicinus and lead to a summer and winter diapause, induced by different signal factors (Alekseev et al. 2001). The fact that crustaceans respond to different external perturbations by the same adaptation (diapause) demonstrates its plasticity and effectiveness.

Regarding the seasonal cycle as an alternation of periods of active development with diapause, and combining these periods with different seasons, one can find different schemes of relationships.

3.2.1 Monocyclic Species

This group usually consists of species with a diapause, whose duration considerably exceeds the period of active development, or of species with a heterogonic life cycle in which gamogenesis occurs after a period of population growth by female parthenogenesis. This rather large group can be subdivided according to the seasons of active reproduction.

Spring species. They usually only reproduce during the spring (sometimes under ice) peak of phytoplankton vegetation and are in diapause during the rest of the year (Fig. 3.1).

Winter species. In temperate climates, these are presumably glacial relicts from Arctic basins. The main factor limiting their distribution is a higher water temperature. Diapause may last from 6 to 11 months, as in the cyclopoid C. insignis, which reproduces almost exclusively under ice and is in diapause from April to December (Monchenko 1974).

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**Summer species.** They include many pelagic and littoral cladocerans. One good example is the cladoceran *Bosmina longirostris*. At the latitude of London, it hatches from ephippia in the beginning of May and completes its cycle by producing winter ephippia in October (Fryer 1993).

Many crustaceans from high latitudes have a monocyclic development (even those who have several cycles in water basins at lower latitudes), associated with a short period of asexual reproduction like in *Daphnia middendorffiana* (Stross & Chisholm 1975). Monocyclic development in southern regions may be also caused by peculiarities of the basin; for example, in temporary water bodies in which there is only time for one cycle.

### 3.2.2 Bicyclic and Polycyclic Species

A bicyclic and polycyclic development permits more possibilities for life cycle optimization than in monocyclic species. The total duration of diapause in this case may be either comparable to that of active growth and reproduction, or be even shorter.

Bicyclic development, which is interrupted by diapause between cycles, is a strategy usually peculiar to species that develop in spring and fall. The temperature optimum of these species is within an interval of comparatively low temperatures – up to +15°C. One example is the Palearctic cyclopoid *C. vicinus*. Summer diapause, which is between spring and summer peaks of reproduction, is advantageous if summer oxygen depletion occurs in the hypolimnion. The copepod migrates into this

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**Figure 3.1. Role of diapause in shaping the annual cycles of crustaceans.**

- **A.** Monocyclic species of summer type: a sequence of generations is interrupted by a facultative winter diapause (*Bosmina longirostris* at London latitude: Fryer 1993).
- **B.** Complicated life cycle with two or more diapauses in the same specimens (*Cyclops scutifer* in Norwegian lakes: Elgmork 1985).
- **C.** Polycyclic species (*Daphnia magna* from shallow pools in England: Ferrari & Hebert 1982).
- **D.** Bicyclic species with summer oligopause and winter diapause (*Daphnia longispina* in a foresty lake in North Russia: Alekseev, 1990).
- **E.** Monocyclic species of winter type (*Cyclops insignis* in Ukraine: Monchenko 1974).
- **F.** Bicyclic species with summer and winter diapauses (*Cyclops vicinus* in Sevan Lake, Caucasus area: Alekseev et al. 2001).