

THE TIMING OF COPEPOD DIAPAUSE AS AN EVOLUTIONARILY STABLE STRATEGY

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Organisms living in environments that occasionally deteriorate must either move by migration or dispersal to more favorable habitats, or they must become dormant for the inhospitable period. The particular response evolved will depend in part upon the area of the habitat affected and the motility of the resident organisms. For example, at the onset of winter in the temperate zone, most plants become dormant, while many bird species migrate south. At another scale, aphids develop winged dispersing forms in response to local crowding, but make overwintering eggs in response to seasonal climatic changes (Blackman 1974).

For a broad variety of organisms, the physiological and morphological adjustments necessary for dormancy, migration, or dispersal have been studied in some detail, as have the proximate environmental cues that switch these behaviors on and off (e.g., Wareing and Phillips 1970; Dingle 1978; Beck 1980; Flint et al. 1981). Yet it is only comparatively recently that theoretical treatments that attempt to predict either the conditions under which dormancy, migration, or dispersal might be expected to evolve, or the optimal timing of the onset of these behaviors have begun to appear. Cohen (1967) and Levins (1969) were the first to delineate formally conditions favoring dormancy. Levins showed with a simple fitness formulation that as the probability of satisfactory conditions persisting long enough to permit another generation to mature declines, diapause becomes the superior strategy, while Cohen demonstrated that dormancy is favored when the variability in the survival of germinating seeds exceeds some threshold. Later, Cohen (1970) treated insect diapause and found in his model that when population maturation is spread out in time, the optimal fraction of dormant individuals switches sharply from 0 to 1 when the expectation of reproduction falls below the expectation of survival of a dormant adult. As support for the model, Cohen pointed to the many examples of insect populations that switch from nondiapause to diapause at fairly sharp critical day lengths. Recently, Levin et al. (1984) have constructed a model that illustrates the way in which dormancy and dispersal are solutions to the same adaptational problem. They show that as the incidence of dormancy increases, the optimal fraction of dispersing individuals declines, so that when dormancy is high, dispersal is of little advantage unless the dispersing

individuals have very high survival. Similarly, Venable and Lawlor (1980) find that the advantage of delayed seed germination decreases as dispersibility rises.

Taylor (1980) presented a model providing a testable hypothesis for the optimal time to switch to diapause before the onset of harsh environmental conditions. His model is written with insect diapause in mind and assumes that dispersal is not an option. Given that the season ends with a sudden, catastrophic event such as a hard frost, Taylor finds that the optimal time for insects to begin diapause precedes the catastrophe by a period equal to the age of first reproduction plus the time to produce enough offspring such that one survives to adulthood. Although the model was written to describe the behavior of insects, it should apply to any organism producing one or more generations during the favorable season. A population of planktonic freshwater copepods, *Diaptomus sanguineus*, living in a small permanent lake, Bullhead Pond, in Rhode Island, fits this description and provided us with an opportunity to test Taylor's prediction.

Dispersal for these small (ca. 1.0 mm) animals is not a viable adaptive strategy but only an occasional fact of life. They may be transferred infrequently between ponds on the feathers, fur, or in the stomachs of more mobile animals (Thienemann 1950; Maguire 1963; Löffler 1964; Mellors 1975) but they have no other mechanism for movement between habitats. Thus they are left only with diapause as a means of avoiding harsh periods in the environment. The copepods in Bullhead Pond appear in the plankton in autumn, pass through two generations, produce diapausing eggs in the spring and are absent from the water column during the rest of the year. The season ends for *D. sanguineus* when planktivorous sunfish become active in the spring (Hairston et al. 1983, this report). The diapausing eggs, which are resistant to digestion by the fish, reside on the bottom of the pond during the summer and hatch in late autumn when the fish again become quiescent.

We have determined for four seasons the time during the spring that female copepods switch from making subitaneous (immediately hatching) eggs to making diapausing eggs. From field cohort analyses in 6 yr, we have obtained estimates of the time to develop to the age of first reproduction, while the time for a female to lay her first clutch was determined in the laboratory. Finally, the timing of the onset of fish predation was determined from the analyses of copepod mortality in 5 yr.

Taylor's (1980) model of diapause does not describe the effect of year-to-year variation about the catastrophe date on optimal switching time. Given that such variation occurs in our data, we have constructed a computer simulation of the *D. sanguineus* life history to determine how switching time is affected. In general, our simulations support Taylor's conclusions, although variability in catastrophe date tends to make the superior switching time occur somewhat earlier in the season. Our field data show a remarkably good fit to theory.

LIFE HISTORY OF *Diaptomus sanguineus* IN BULLHEAD POND

Diaptomus sanguineus is an herbivorous zooplankter broadly distributed in the United States and Canada (Wilson and Yeatman 1959). In Rhode Island, it occurs in small permanent lakes and temporary pools (Hairston 1980). In Bullhead Pond

(surface area 2.3 ha, maximum depth 4 m) it is typically found in the plankton from November through June. As with other calanoid copepods, its life history consists of an egg stage followed by six naupliar stages (N_1-N_{VI}) and six copepodid stages (C_1-C_{VI}), the last being sexually mature. Insemination occurs by spermatophore transfer after which the fertilized female produces a clutch of eggs that is held in a sac attached to her genital segment. Subitaneous eggs are carried until they hatch while diapausing eggs are dropped after a few days (Watras 1980). Individual females followed in small enclosures in the field produced an average of four clutches each.

Figure 1 shows a cohort analysis for *D. sanguineus* in Bullhead Pond in 1980–1981. Nauplii appeared in the pond in November. At this time there were no adult females carrying eggs, nor had there been for the previous 4 mo, and so these larval copepods must have hatched from diapausing eggs present on the bottom of the pond. The first cohort matured in February and March and produced eggs, all of which hatched immediately. The second cohort matured in April and May and produced a pulse of eggs from which there was no immediate issue. These were found to be diapausing eggs by a method described below. This sequence of events was repeated in all 5 yr (1978–1982) that we have studied the pond. Two generations appeared in every year, initiated by the hatching of diapausing eggs in the autumn and terminating with increased fish activity and the production of diapausing eggs in the spring. The generation time of the first cohort was greater than that of the second cohort in each season because copepod development rates are temperature dependent (Edmondson et al. 1962).

COMPUTER SIMULATION

Rationales.—A FORTRAN program was designed to simulate 100 seasons of competition between populations of diaptomid copepods that switched from making subitaneous eggs to making diapausing eggs at different times before the end of each season. The model, as it is written, does not mimic directly the action of natural selection in a sexually reproducing diploid population such as *Diaptomus sanguineus*, although it would be closer to reality for an asexual species. Our objective here is simply to determine which diapause strategy performs best under the specified set of environmental conditions. Figure 2 is a schematic diagram of the operation of the simulation. Populations, consisting of individuals that shared a common reproductive strategy, were described by a series of difference equations stepped at constant time intervals (the equivalent of 0.08 times the time from egg to first reproduction in this simulation) as in a population projection matrix (Leslie 1945). The number of eggs at any given time, $n_{0,t}$, was obtained from the number of individuals in each reproductive age class in the previous time period and the quantity of eggs, F , each produced:

$$n_{0,t} = F(n_{i,t-1} + n_{i+1,t-1} + \cdots + n_{m-1,t-1} + n_{m,t-1}).$$

The abundance of each of the older life history stages was calculated as the proportion of individuals, P_i , surviving from the previous stage:

$$n_{i,t} = P_i n_{i-1,t-1} \quad (i > 0).$$

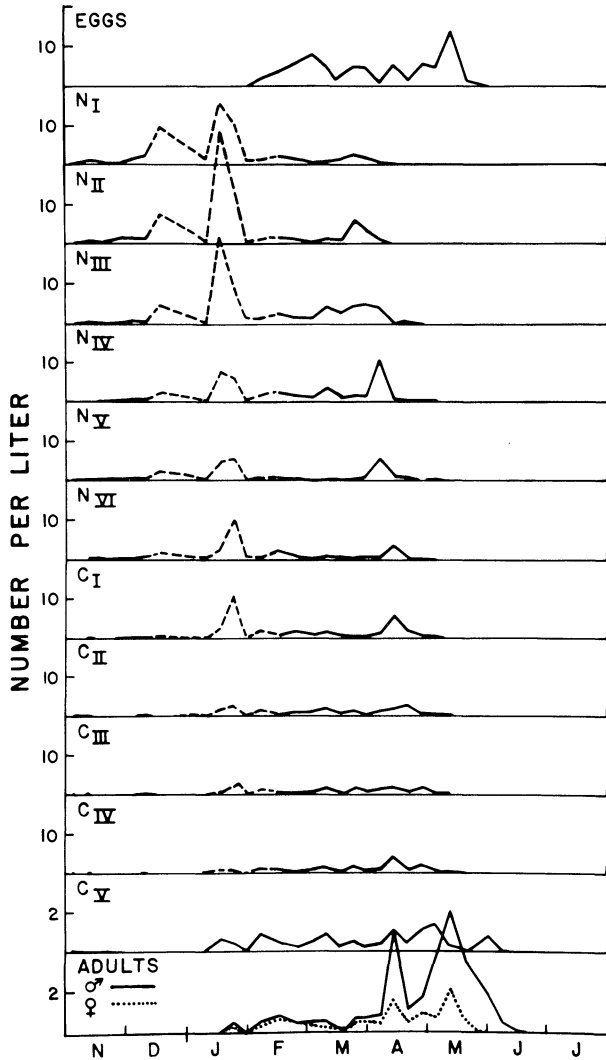


FIG. 1.—Cohort analysis for *Diaptomus sanguineus* in Bullhead Pond in 1980–1981, showing 2 distinct generations. Samples were taken in winter through the ice with a hand pump (dashed line) and at other times with a Clarke-Bumpus plankton sampler (solid line). Note scale change for C_V and adults.

Initial survivorship values were set at 1.0 for immature instars and 0.9 for adults. When modified by competition as described below, survival to the adult stage was comparable to that measured in Bullhead Pond (Hairston et al. 1983).

Mature females produced four clutches of eggs in successive time steps. Each clutch consisted of a maximum of either 20 subitaneous eggs or 10 diapausing eggs, and was reduced by competition as described below. The number of clutches and the numbers of eggs per clutch of each type were typical values

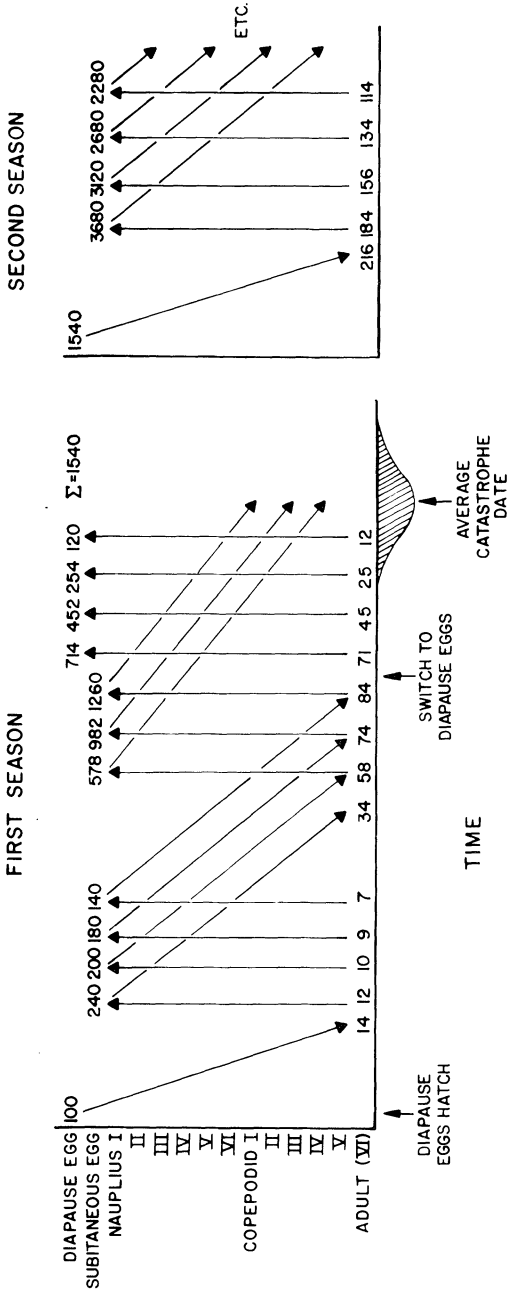


FIG. 2.—Schematic diagram of the computer simulation of the life history of *Diaptomus sanguineus*. In this illustration the model starts with 100 diapause eggs which hatch, and experience mortality as they mature to adults. Each adult produces up to four clutches. Only subitaneous (immediately hatching) eggs are produced until the switching date, after which only diapausing clutches are produced. The season ends with a catastrophe. All diapausing clutches are summed and start the next season. See text for other details.

obtained from our field and laboratory data for *D. sanguineus*. A unique "switching time," assigned to each population, determined when reproductive females switched from producing subitaneous eggs to producing diapausing eggs. Each season ended with a catastrophe which was generated as a random deviate drawn from a normal distribution with mean and standard deviation chosen to bracket those found in Bullhead Pond. The cumulative sum of diapausing eggs produced up to the time of the catastrophe, decremented by a small amount of density-independent mortality (0.005 per day), determined the initial population size in the next season.

Competition within and between populations was accomplished by allowing the total abundance of all individuals, N_t , to affect the survivorship and egg production of each life history stage:

$$P_{i,t} = \frac{P_i}{1 + a \cdot N_t}$$

$$F_t = \frac{F}{1 + b \cdot N_t}$$

where a and b are density feedback coefficients chosen so that equilibrium sizes attained by the populations approximated those seen naturally in Bullhead Pond. Within broad limits, initial parameter values, while they affected the rate of approach to equilibrium, and equilibrium population size, did not influence which strategy was superior.

Superior competitors excluded others because on average they left more diapausing eggs at the end of each season. Superiority was determined first by competing two strategies with equal starting population sizes of one half the equilibrium abundance, and noting which strategy increased over time and which decreased. Secondly, strategies that had increased were started at low population sizes and competed against inferior strategies initiated at the equilibrium abundance. This allowed us to determine which strategies could establish themselves from a low initial population size, and once established prevent invasion by other strategies; that is, which strategies were evolutionarily stable (ESS, *sensu* Maynard Smith 1976).

A population started at low abundance has a finite probability of becoming extinct immediately even if in the long run it possesses a superior strategy for survival and competition in a variable environment. Therefore, in simulations with variance about the time of the catastrophe greater than zero, 5 to 10 runs were made with different seeds initiating the random number generator. This allowed us to distinguish long-term effects of unpredictability in catastrophe from short-term effects.

Levin et al. (1984) have discussed the complications that can arise from attempting to define an ESS from a simulation such as the one presented here. They point out that there may exist strategies that cannot invade others, but cannot be invaded themselves. The authors nevertheless find value in the approach when it is used with proper caution. We encountered some of the difficulties they describe. Under any specific set of parameter values, we found up to four classes of

strategies: those that always outcompeted all others or at least did so more often than other strategies; those that occasionally outcompeted others (depending on the particular sequence of randomly generated catastrophe dates); those that coexisted with others but never outcompeted them; and those that always lost in competition. As will be seen in the next section, we were usually unable to define a single ESS, but rather delineated a suite of strategies of varying competitive abilities. For lack of a better term, we call these an *ESS suite*.

Results and predictions.—We initially compared the ESS suite for time to switch to diapause, obtained from the simulation, with Taylor's (1980) result. To do this, we set the standard deviation about the mean catastrophe date to zero. It became obvious that the starting age distribution had an important effect. When each season was initiated with populations of diapausing eggs that hatched simultaneously, periods of time occurred between generations in which there were no reproducing females; all reproduction from preceding generations had already taken place while individuals in following generations had not yet matured. For a wide range of switching times, the same number of diapausing eggs were produced. Within certain boundaries then, there was no unique ESS for switching time.

On the other hand, when the hatching of diapausing eggs was broadly spread out in time, successive generations overlapped and reproduction was continuous within a population. Under these conditions a unique ESS for switching time was obtained, and was always a period of time exactly equal to the age of maturity plus the time to produce the first clutch of eggs. For the sake of brevity, we will call this *one generation*, although it is slightly less than the usual definition of the time to reach the mean age of reproduction. Our result is independent of the point in the season at which the catastrophe occurs (except in the trivial case in which the catastrophe comes before the first generation matures), and agrees with Taylor's prediction that the optimal time to begin diapause precedes the catastrophe by the age of first reproduction plus the time to produce enough offspring such that one survives to adulthood since in our simulation the first clutch contains 20 eggs, at least one of which always survives to maturity. The result is intuitively satisfying since copepods that switch to making diapausing eggs with less than one generation to go before the catastrophe will have offspring that fail to mature, while individuals that switch with more than one generation to go could have made offspring that would have matured and made diapausing eggs of their own.

In reality, the hatching of diapausing eggs of *D. sanguineus* is spread out over several weeks (fig. 1). To reflect this, we ran simulations with a starting population age structure distributed among the naupliar stages as follows: 0.1 N_I , 0.2 N_{II} , 0.4 N_{III} , 0.2 N_{IV} , and 0.1 N_V ; a distribution resembling that seen in November 1982. The outcome (fig. 3A) is intermediate between discrete nonoverlapping generations and simple continuous reproduction. When the catastrophe occurred early in the season there were periods in which a range of switching times was competitively equivalent, and other periods in which populations switching to diapause one generation before the catastrophe were superior to all others. As the time of the catastrophe was moved later in the season, generations started to overlap and reproduction became continuous, leading to a single ESS for switching time.

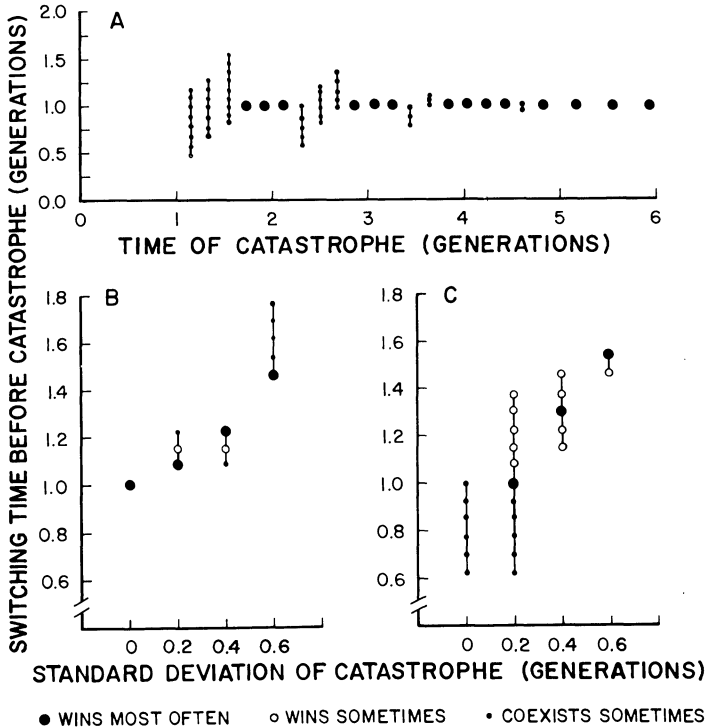


FIG. 3.—Results of computer simulation of the timing of copepod diapause. A, ESS as a function of the time of the catastrophe in the season; standard deviation about the catastrophe date is zero. B, ESS for catastrophe occurring after 2.1 generations as a function of standard deviation about the catastrophe date. C, ESS for catastrophe occurring after 2.3 generations as a function of standard deviation about the catastrophe date. See text for further explanation.

Similarly, F. Taylor (personal communication) finds that age structures producing well-defined cohorts, as well as discrete generations, may lead to very broad plateaus in the fitness functions for a range of switching times.

The principal object in writing the simulation was to investigate the effect of a variable catastrophe date on the ESS for the time to switch to diapausing egg production. This variability might arise from any of a number of causes. Certainly the date on which the fish become active and the environment becomes uninhabitable for copepods varies from year to year, depending largely on local weather. In addition, there may be variation between years in the time at which diapausing eggs hatch and in the duration of a generation. These would have the same effect in the model as true variation in catastrophe date since their ultimate effects would be to alter the length of time and hence the amount of reproduction possible before a catastrophe.

In 1981, the *D. sanguineus* population in Bullhead Pond disappeared after two complete generations (fig. 1). Thus the catastrophe occurred at or shortly after this period of time. We investigated the effects of increasing variability about the

catastrophe date on the ESS for switching time for a number of catastrophe dates ranging from 1.9 to 2.9 times the length of a generation. Figures 3B and 3C give representative results. In both examples, as the standard deviation for catastrophe date increased, so did the center of the ESS suite for switching time. This occurred because there is a rising chance that the catastrophe will occur before many or all individuals in a population have made diapausing eggs. Thus populations playing it safer by switching earlier have a competitive advantage. For reasons given above, catastrophes between 1.9 and 2.1 times the generation time in figure 3A had a unique ESS. As the standard deviation increased (fig. 3B), catastrophe dates were included that lacked a single ESS for switching time and so ESS suites of increasing width as well as increasing absolute value were obtained. In contrast, catastrophes between 2.2 and 2.7 times the generation time resulted in a broad range of competitively equivalent switching times. As the standard deviation about the catastrophe date increased (e.g., fig. 3C) the width of the ESS suites for switching time first increased with the inclusion of other competitively equivalent strategies (fig. 3A), and then decreased as catastrophe dates with the unique one-generation ESS for switching time were also included.

TESTING THE MODEL

Four pieces of information are needed to test the predictions of either Taylor's (1980) model of diapause, or our computer simulation. These are: (1) the time during the reproductive season of the copepods that their mortality first becomes heavily influenced by fish feeding activity (the mean and standard deviation of the catastrophe date); (2) the time during the season that female copepods switch from making subitaneous eggs to diapausing eggs; (3) the duration of a copepod generation from egg to sexually mature female; and (4) the time it takes for a mature female to mate and produce her first egg sac.

Copepod mortality and fish activity.—The eggs of *Diaptomus sanguineus* are darkly pigmented. When 10 to 20 of these are attached to the urosome of a female copepod, it becomes distinctly visible, representing an approximate 1.2-fold increase in exposed surface area of the animal. Elsewhere, we have shown that sunfish perceive females carrying eggs at 1.3 times the distance that they detect nongravid females (Hairston et al. 1983). Since sunfish search roughly hemispherical volumes for their planktonic prey (O'Brien et al. 1976; Luecke and O'Brien 1981), this linear difference in visibility translates to a doubling of the vulnerability of gravid females to predation. Ultimately, when Bullhead Pond warms in the spring and the sunfish begin to feed, increased *D. sanguineus* mortality is reflected as a sharp rise in adult copepod sex ratio. We measured the timing of the spring increase in sunfish activity using 24-h live-trap samples as described by Hairston et al. (1983). Figure 4 shows activity measurements for 4 yr as well as the increases in sex ratio for 5 yr.

The date on which the sex ratio began its dramatic increase was taken as the time of the catastrophe for that year. This date was established in the following way. The change in copepod sex ratio may be described by the equation:

$$\frac{d}{dt} \left(\frac{M}{F} \right) = \frac{M}{F} (d_f - d_m)$$

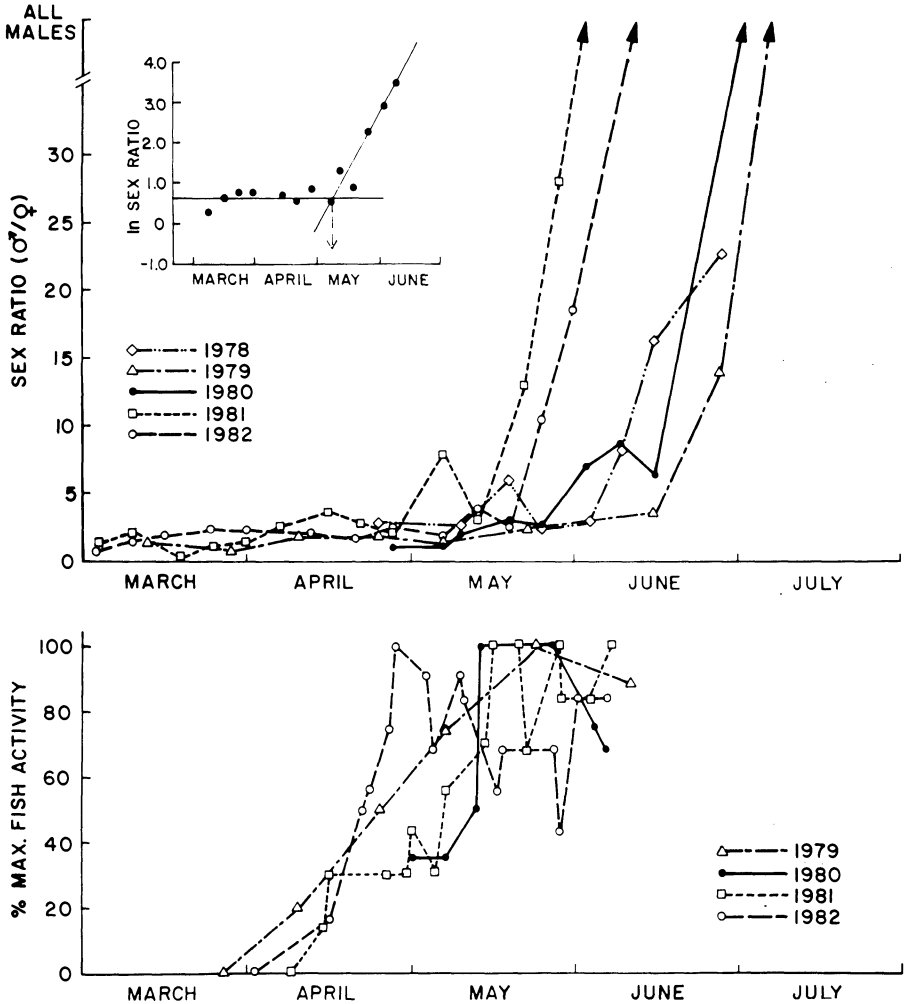


FIG. 4.—Timing of catastrophe. *Top*, Increase in copepod sex ratio as an indication of the onset of fish predation on highly visible gravid females. *Inset*, Natural log of sex ratio, illustrating statistical technique for obtaining catastrophe date. *Bottom*, Change in fish activity in spring as pond temperatures increase.

where M and F are the abundances of males and females and d_m and d_f are their respective mortality rates. A plot of the natural logarithm of sex ratio against time has a slope equal to the difference in mortality of the two sexes:

$$\ln \left(\frac{M}{F} \right)_t = \ln \left(\frac{M}{F} \right)_0 + (d_f - d_m) \cdot t.$$

Because the relative rates of male and female mortality change when fish start to feed, there is a distinct change in the slope of this line at that point. The inset in figure 4 gives an example of this analysis for data from 1982. Analyses of variance

were run on successively larger groups of data, starting from the right-hand side of the graph, until the F values peaked and started to decline. Two regression lines were drawn; one through the delineated data and the other through the remaining data on the left of the plot. The date corresponding to the intersection of these two lines was taken as the time of the onset of predation, or the catastrophe date.

An estimate of the catastrophe date was obtained from each of the 5 yr for which we have data. In all cases, the slopes of the regression lines after the onset of predation were significantly greater than zero ($P < .01$) while those before the start of predation were not. The catastrophe dates estimated by this method are 25 May 1978, 9 May 1979, 6 May 1980, 18 April 1981, and 8 May 1982. The mean date is 7 May \pm 13 days (1 SD).

Generation time.—The duration of egg development, the time for a female to mature, and the time for a mature female to mate and produce her first clutch compose what we call here, *one generation*. For copepods, the first two phenomena are known to be temperature dependent (e.g., Edmondson et al. 1962; McLaren 1974), and the third very likely is also. This means that the relevant generation time for testing the model is one specific to the temperatures prevailing in the environment during the period directly preceding the catastrophe. For *D. sanguineus* in Bullhead Pond in spring, this is essentially the length of the second of the two generations produced in each season (see fig. 1).

Estimates of instar durations were obtained from cohort analyses of field populations such as the one presented in figure 1. We have suitable data for 3 yr in Bullhead Pond. In addition we have 3 yr of data for a *D. sanguineus* population in nearby Little Bullhead Pond. In the analysis presented below we used all six data sets. To eliminate some of the variability introduced by uncertainty in distinguishing earlier naupliar stages from each other, and by sampling error, we combined data from successive pairs of instars. We integrated the areas under the plots of numbers versus time (see fig. 1) for each instar using a digitizer. Then, taking the mean pulse time, M_n , of each instar, we found the period between successive pulses, $M_n - M_{n-1}$. Rigler and Cooley (1974) have shown that this is related to the development time, D_n , of instar n by the equation: $M_n - M_{n-1} = 1/2 (D_n + D_{n-1})$. A series of such calculations using mean pulse times from pairs of instars gives development times for all instars but one (one more unknown than equations). We obtained the development time of the first pair of instars independently from laboratory rearing experiments carried out at natural temperature and light conditions, and then solved for all other development times. The results are: naupliar stages I and II ($N_I + II$) 1.5 days; $N_{III} + IV$ 3.6 days; $N_V + VI$ 5.4 days; copepodid stages I and II ($C_I + II$) 6.0 days; $C_{III} + IV$ 7.4 days; and C_V 3.0 days. The total development time from hatching to adult is the sum of these or 26.9 days.

We did not estimate egg development time from the cohort analysis because estimates of egg abundance are confounded by the mixture of subitaneous and diapausing eggs present in the population in late March and early April. Laboratory data indicate that at the temperatures prevailing in March, eggs took about 4 days from their first appearance in the egg sac to hatching. This estimate comes from a direct determination of egg duration at 15° C and extrapolating back to 10°

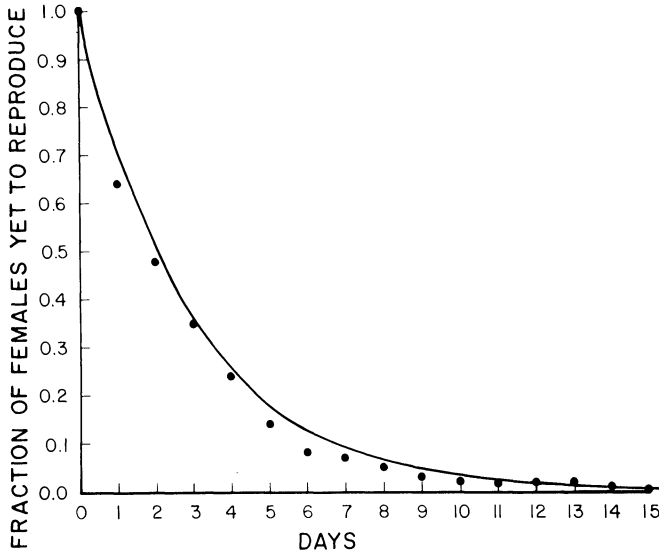


FIG. 5.—Estimate of interclutch interval for *Diaptomus sanguineus*. The slope of least square fit, forced through 1.0 at day zero, of $\ln y = 1 - bx$ is $b = 0.34$.

C, the temperature of Bullhead Pond at the end of March, using the relationships given for three species of diaptomid copepods by Edmondson et al. (1962) and one species studied by Watras and Haney (1980).

The time from maturation to first reproduction is a function of several processes including the rate of physiological development of females and males, nutritional quality of the environment, water temperature, and the probability of encounter of the two sexes (Watras and Haney 1980; Watras 1980). Any estimate therefore will be something of an approximation. The information we have comes from a laboratory experiment in which gravid females and mature males were placed as pairs in plastic tissue culture dishes containing 15 ml of 75 μm -mesh filtered pond water (i.e., natural food was present) and maintained at temperature and light conditions existing in Bullhead Pond. The time between the hatching of the first clutch and the production of the next egg sac was recorded. Females apparently could not store sperm since those placed in dishes without males either produced no second clutch or extruded nonviable oocytes (see also Watras and Haney 1980). The results show a simple logarithmic relationship between time and the cumulative probability of clutch production (fig. 5). There is apparently a constant probability of reproduction on any given day. The time for a female to be mated and to produce a clutch is then the inverse of the slope (0.34) or 2.9 days. This estimate clearly has a great deal of variability associated with it since many females produced clutches within one day while others took as long as 14 days.

Since females arriving at the adult instar might take longer than the normal interclutch interval to produce their first egg sac, and because natural densities of males and females (fig. 1) are substantially below the effective density in the tissue

culture dishes (67 per liter), our estimate of the time to first reproduction is conservative. It depends, however, on the relative importance of the probability of males locating females and the probability of mating after encounter. Watras and Haney (1980) have suggested for *Diaptomus leptopus* that the interclutch interval must be quite short (1.4 days maximum).

Adding the three components of generation time, we obtain an estimate of: 4 days as egg + 26.9 days in immature instars + 2.9 days to first reproduction = 33.8 days.

Timing of the switch to diapause.—The subitaneous eggs of *D. sanguineus* are difficult to distinguish from its diapausing eggs by light microscopy. This is true for other species of *Diaptomus* including *D. stagnalis* (Brewer 1964), *D. minutus* and *D. spatulocrenatus* (Cooley 1978), and *D. leptopus* (Watras 1980). We employed the standard technique for identifying egg types. Females carrying egg sacs were isolated from live plankton collections, and placed in tissue culture dishes with 75 μm -mesh filtered pond water. The course of egg hatching was followed for a minimum of 2 wk. Subitaneous eggs hatched within this period while diapausing eggs were defined as those that did not. All eggs within a single clutch were either subitaneous or diapausing; mixed clutches were never observed. We are confident that eggs that did not hatch were not dead, because 95% could be hatched 4 mo later by subjecting them to a low oxygen shock. Furthermore, groups of eggs isolated in this manner, sectioned, and viewed under transmission electron microscopy showed distinct morphological differences. Notably, the walls around subitaneous eggs were thin and contained no internal structure while those of diapausing eggs were thick and ridged with internal striations (Hairston and Olds 1984).

We followed the course of egg production in Bullhead Pond for 4 yr. In 1979, the types of eggs carried by 20 females were determined every other week, while in 1981, 1982, and 1983, groups of 24 females were isolated weekly. The switch to diapause occurred over a fairly brief period at the end of March and early April in all 4 yr (fig. 6). We know from following the sequence of clutches produced by individual females in 1981 and 1982 that each copepod switched the type of eggs it carried and there was not a change in the type of female that matured during this period.

To test our model, we needed to choose a date for the time of the switch to diapause. This must necessarily be somewhat arbitrary, and in the absence of any other criterion, we have used the date on which 50% of the gravid females were carrying diapausing eggs. A subtle bias is introduced in this way since, depending on the age structure of the population, a fraction of the eggs carried on any given date would actually have been produced previously. Females only switch from making subitaneous eggs to diapausing eggs (no reverses are seen), so those making subitaneous eggs tend to be overrepresented, and the true date that the population reaches 50% comes slightly earlier than our estimate would indicate. The error is certainly less than the egg development time (4 days) and is probably closer to half that value.

The dates on which 50% of *D. sanguineus* collected from Bullhead Pond carried diapausing eggs, extrapolated from the data plotted in figure 6, are 23 March 1979,

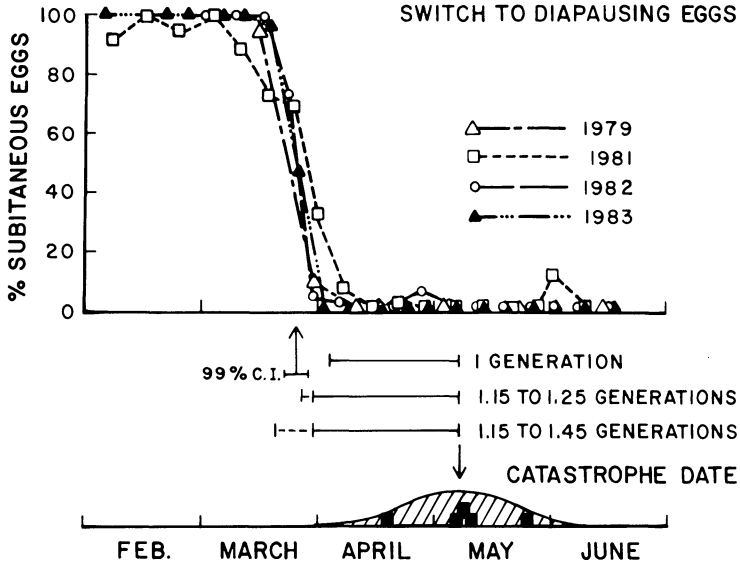


FIG. 6.—*Bottom*, The mean and standard deviation of the catastrophe date (boxes give the times of the onset of fish predation calculated from data in fig. 4). *Center*, the length of a *D. sanguineus* generation (see text) and the period of the superior switching times taken from figs. 3B and 3C. *Top*, The timing of the switch from subitaneous (immediately hatching) eggs to diapausing eggs for *Diaptomus sanguineus*. Arrows indicate mean switching date with 99% confidence limits, and mean catastrophe date.

27 March 1981, 24 March 1982, and 24 March 1983. The mean switching date is 25 March.

The test.—The time from 25 March (the switching date) to 7 May (the mean catastrophe date) is 43 days or 1.3 times the generation time of 33.8 days. This exceeds Taylor's (1980) prediction (based on a constant time of catastrophe) that copepods should switch to diapause one generation before the catastrophe. Taylor's model predicts that optimum switching time should become more conservative if survival to reproduction is so low that a female must produce more than one clutch to replace herself. But *D. sanguineus* in Bullhead Pond does not experience especially heavy postjuvenile mortality, and life table calculations show that reproductive rates (r) of zero or greater are obtained with the first clutch (Hairston et al. 1983).

In our simulation the value of the ESS suite for switching time increases as year-to-year variation in the timing of the catastrophe goes up (fig. 3). In figure 4 and its accompanying discussion in the text, we estimated the standard deviation around the onset of fish predation to be 13 days; about 40% of the generation time. In figure 3B this translates to an ESS suite for switching time of 1.15 to 1.25 times the generation time; considerably closer to the value observed for *D. sanguineus*. If generation time is longer than we have estimated, or catastrophe date more variable, then the fit is still better. Because of the effects of nonoverlapping generations and random variation in catastrophe date seen in the predictions of

the simulation, it is possible that a range of switching times is equally adaptive for *D. sanguineus* in Bullhead Pond. The value observed of 1.3 generations falls at the center of the range of 1.15 to 1.45 seen in figure 3C.

Expressed as Julian date, *D. sanguineus* switched to diapause on day 83.8 ± 2.9 (99% confidence limits). The two predictions from our model are for switching dates between days 84 and 88 (with day 84 winning most often) or days 78 and 88 (with day 83 winning most often), well within the 99% confidence limits of the switching date we observed (fig. 6). The model predicts that a range of switching dates may be competitively equivalent, and the *D. sanguineus* in Bullhead Pond appear to substantiate this. On average 50% of the females started producing diapausing eggs between 1.15 and 1.45 generations before the increase in fish activity, and 90% switched between 1.0 and 1.6 generations before the catastrophe.

DISCUSSION

Given the constraint that diapause in *Diatomus sanguineus* can only occur in the egg stage, there are two ways that a population might switch from the production of subitaneous eggs to diapausing eggs. One is a seasonal change in the type of female that matures, so that those growing up early in the year make only subitaneous eggs while those maturing after the switching date make only diapausing eggs. The second possibility, and that followed by *D. sanguineus* in Bullhead Pond, is that individual females make subitaneous eggs before the switching date and diapausing eggs after it. There are several reasons why the latter strategy would seem superior. The most important of these is that individual females making eggs at or near the switching date can maximize their own fitness by starting to make diapausing clutches when the expectation of egg maturation falls below the expectation of survival during diapause (Cohen's 1970 result). Were these copepods not able to switch individually, the population result might be the same (females maturing during, or subsequent to, the ESS suite of switching times would make diapausing eggs) but individuals stuck making subitaneous eggs too late in the season would lose fitness. Second, Taylor (1980) explicitly considered in his model the time from the induction of diapause in the "sensitive stage" to the start of the diapausing stage. He found that if the switching time were defined as the point of the induction of diapause (rather than the start of diapause itself), the optimum time before the catastrophe to switch was simply moved back to one generation plus the induction period. For *D. sanguineus*, in which the type of eggs produced by a female can change from one clutch to the next, the sensitive stage can precede the switching time by no more than the interclutch interval (4 days here). This is a shorter time period than if females were induced to make diapausing eggs sometime before they matured. Given that there is variability in the development time of females and in the time to first reproduction, shortening the interval between the environmental cue for diapause and diapause itself, permits a more precise adaptation. Finally, if in a population of *D. sanguineus* with well-defined cohorts, females grow up to produce only one type of egg, and if the switching date falls between cohorts, as it does in Bullhead Pond, the population

switch to diapause would lag significantly behind the optimum. There would be an overrepresentation in the population of females still making subitaneous eggs while females making diapausing eggs would not have matured yet. Females able to change the type of eggs they produce would have a competitive advantage because they would track the optimum switching date more closely.

The observations that *D. sanguineus* switches to making diapausing eggs at or near the ESS suite of times, and does so in an arguably superior manner, leads naturally to the question of how the copepods do it. Marcus (1980, 1982) has shown for the marine calanoid copepod *Labidocera aestiva*, which diapauses in the fall, that the production of diapausing eggs is induced by day lengths of 8 h while 18-h days induce subitaneous egg production. She proposed, referring to Taylor (1980), that the switch occurred approximately one copepod generation before the autumnal decline in temperature made the water uninhabitable. The induction of diapause or dormancy by photoperiod, or photoperiod and temperature together, is a common phenomenon in insects (Beck 1980), vertebrates (Flint et al. 1981; Lyman et al. 1982), and many plants (Harper 1977), and it would not be surprising to find that it also applied here. A cue like photoperiod, that is consistent between years, might well explain the low variation in switching date seen in figure 6. In a related study, we have shown that the cue inducing diapause is not specific to Bullhead Pond. Females transferred to enclosures in a small fishless temporary pond started diapause at the same time as control animals maintained in Bullhead Pond itself (Hairston and Olds 1984).

In examining copepod diapause with the computer simulation we have found that if catastrophe date is extremely variable ($SD > 0.5$ generations), the ESS is no longer one with a particular switching date or dates. Rather the superior life history is for maturing copepods to follow some bet-hedging strategy that allows copepods to make additional generations if conditions permit, but to remain in the system if an early catastrophe occurs. Under most conditions, the superior strategy is for females to make their first clutch subitaneous eggs that ensure a maximum contribution to r , and all later clutches diapausing eggs (Hairston et al. 1984). In a highly variable environment a population switching to diapause on a particular date every year will either experience a catastrophe preceding the switch and therefore become extinct, or will switch too early to take advantage of particularly long seasons when they occur. Walton (1982) has observed cycling from subitaneous to diapausing eggs as a cohort matures in *D. birgei* in a temporary pond in Virginia and our preliminary data from temporary ponds in Rhode Island suggest that the same may be true for *D. sanguineus*.

Traditionally, diapause has been thought of as an adaptation to avoid physically harsh conditions in the environment (e.g., Ricklefs 1979; Varley et al. 1973) or, as in *Daphnia* populations, to competition for food (Slobodkin 1954; Hutchinson 1967). Southwood (1978) pointed out that habitats may also become unfavorable because of the development of natural enemies. Strickler and Twombly (1975) were the first to propose diapause as a predator avoidance mechanism in copepods, and Nilssen (1978, 1980) has since interpreted his data on the late stage copepodid diapause of cyclopid copepods in this light. Our study is the first to

show a close connection between the timing of the onset of predation and the timing of diapause.

SUMMARY

Diaptomus sanguineus, a small freshwater copepod, avoids periods of intense fish predation by producing diapausing eggs. We developed a computer simulation of the copepod's life history and used it to compete populations that switched to diapause at different intervals of time before the onset of fish predation (the catastrophe). With no variation about the catastrophe date, the evolutionarily stable strategy (ESS) is one in which the switch to diapause comes exactly one generation before the catastrophe, as Taylor (1980) has shown analytically. With increasing variation about the catastrophe date, the ESS becomes one of switching to diapause at time intervals increasingly greater than one generation. Using field data on copepod mortality rates from 5 yr, we have estimated the mean and variance about the catastrophe date. Using field and laboratory data, we have estimated the copepod generation time and the timing of the switch to diapause. We find, in close agreement with simulation-derived ESSs, that *D. sanguineus* starts making diapausing eggs 1.3 generations before the major onset of fish-induced mortality.

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