The adaptive timing of diapause – a search for evolutionarily robust strategies in *Calanus finmarchicus*

Ø. Fiksen

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In environments with strong and variable seasonal fluctuations, organisms are selected on the basis of their phenology, such as the timing of diapause, reproduction, or assembling of storage products. A simulation model of the dynamic balance of various phenologies within a population facing density-dependence and varying annual, environmentally determined growth opportunities is presented. The main assumption is that the timing of phenological events is heritable and cued by a single signal (day length). Then, the balance between alternative strategies is regulated by natural selection and reproductive success. The model is developed for the marine copepod *Calanus finmarchicus*, which must decide when to start preparing for diapause by allocating to storage rather than somatic growth, how much storage (lipids) to bring with it during wintering and when to ''wake up'' to complete development and to reproduce. The results show that (1) density-dependence may lead to frequency-dependent resting and emergence strategies, (2) environmental stochasticity causes delayed arousal, (3) the selection procedure creates well-adapted individuals which out-compete others with fixed probabilities of maturing or entering diapause, and (4) that the use of day length as a cue to phenological decisions may be beneficial when growth conditions are persistent within years (e.g. warm/cold years).

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Ø. Fiksen: Department of Fisheries and Marine Biology, University of Bergen, HiB, PO Box 7800, N-5020 Bergen, Norway [tel: +47 55584624; fax: +47 55584450; e-mail: oyvind.fiksen@ifm.uib.no]

Introduction

Phenological traits such as the seasonal timing of arousal in spring and entrance to diapause in summer are highly amenable to evolutionary change, and are therefore likely to be well adapted to local environmental conditions (Miller *et al*., 1991). Most studies on optimal timing of phenology in zooplankton focus on a catastrophic date when winter or other sources of high mortality are likely (e.g. Hairston and Munns, 1984). In a number of zooplankton (and other plants and animals) that rely on energy reserves during overwintering, the problem is more complex. Such organisms have evolved not to an abrupt change in the environment, but to the gradual shift from winter to summer and back to winter. An optimal life schedule in this scenario may depend on the variability of the environment, the internal state and, in density-dependent situations, the schedule of other members of the population.

A model of optimal phenology in *Calanus finmarchicus* using dynamic programming has already been developed (Fiksen and Carlotti, 1998). However, that model was not able to include stochastic annual growth profiles or density-dependence. Here, I develop a very simple genetic algorithm (Holland, 1975; Huse and Giske, 1998) to calculate the optimal seasonal schedule including these features.

The life cycle of *C. finmarchicus* involves a resting phase, usually during the last copepodite stage CV (Miller *et al*., 1991; Hirche, 1996). During this resting phase, which may involve a true diapause (Hirche, 1996), the copepod normally descends to great depth where it resides until late winter or spring. Preparation for diapause also involves accumulation of substantial quantities of storage material (wax esters kept in the fat sac), used as energy reserves during winter and for building gonads in early spring (Hirche, 1996). In some regions, e.g. the North Sea and fjords in the south of

Norway, *C. finmarchicus* pass through two or more generations during one season (Carlotti and Wolf, 1998). The number of generations must be determined by decisions taken during stage CV; if all individuals always enter diapause during CV, then there will never be multiple generations. Mixed strategies may occur where a certain fraction prepares for dormancy and the rest complete development to produce another generation. Ecological models of the population dynamics of *C. finmarchicus* reflect this by imposing fixed probabilities of taking one or the other strategy (Carlotti and Wolf, 1998; Lynch *et al.*, 1998; Miller *et al.*, 1998).

Pelagic environments are highly variable, and the annual profile of growth conditions (food and temperature in surface layers) for omnivorous zooplankton is likely to change from year-to-year. In addition, considerable spatial heterogeneity characterizes oceanic waters; from highly productive front and shelf areas to cold, less productive ocean basins. Consequently, the timing of dormancy preparation and arousal from dormancy will be crucial both to individual fitness and to population dynamics. If the copepod produces two generations in a year when its food resource diminishes earlier than usual, survival through winter may be poor. Alternatively, if the season is longer than average, those producing two (or more) generations are likely to have more offspring (or grand-offspring) entering diapause, and they will also have a shorter period to the next spring bloom.

The specific environmental signal that triggers the induction or termination of dormancy is not known (Miller *et al.*, 1991; Hirche, 1996). One possible candidate is photoperiod or day length, which has been demonstrated to be the trigger in many insects (Tauber *et al.*, 1986), although experiments did not show that photoperiod had any effect on arousal in *Calanus* (Miller and Grigg, 1991). Probably, phenological decisions (like preparation for and arousal from diapause and production of storage material) are triggered by a combination of numerous environmental cues (food, predators, temperature, light, internal factors). However, to develop a comprehensible model, it is here assumed that day length is the triggering signal.

Model

Genetic algorithms are characterized by (1) chromosomes or genes, (2) fitness, (3) reproduction, and (4) mutations and crossing-over (Holland, 1975; Sumida *et al.*, 1990; Huse and Giske, 1998). These elements resemble the process of natural selection, and can be utilized to find optimal solutions to complex optimization problems. To develop a genetic algorithm (GA), we need an efficient individual-based model. I have used

the super-individual approach (see Scheffer *et al.*, 1995), where the N_i individuals (the number N_i depends on population size and diversity of strategies) are represented by the super-individual i. All individuals within the super-individual are similar in terms of strategies and states, but die off one by one.

The variables characterizing each individual's (in each super-individual) developmental and physiological status are stage S_i (divided into eggs, NI–NVI, CI–CV, male and female), body weight W_i (µg C), moult cycle fraction L_i E[0, 1] and lipid (wax ester) storage reserves F_i (µg C). The growth and developmental processes are a function of food (for stages>NII) and temperature. When food is available in excess, development and growth follow the Bělehrádek function (e.g. Lynch *et al.*, 1998):

$$D_j = a_j(T+9.11)^{-2.05} \tag{1}$$

where T is temperature (°C), a_j a stage-specific parameter, and D_j is time (days) required to complete stage j. Then, using time-steps of one day, the dynamics of the moult cycle fraction can be calculated (Miller *et al.*, 1998):

$$L_i(d+1) = L_i(d) + \frac{1}{D_j} \tag{2}$$

The value of L_i is reduced by 1 and the value of S_i is increased by 1 each time $L_i \geq 1$.

For the feeding stages, development time may be increased by food shortage. This is included by assuming a type II functional response:

$$f\_lim = \frac{f-5}{75+0.7f}$$

where f is food concentration in µg C l^{-1}, and f_lim is constrained within (0,1). This formulation causes a gradual satiation as food abundance increases and a lower threshold (5), below which no foraging takes place.

The moulting weights w_j are assumed to be fixed for each stage j using the values from Carlotti and Radach (1996). Growth g (in µg C individual^{-1} d^{-1}) is stage-specific:

$$g_j = f\_lim \times \frac{\ln(w_{j+1}/w_j)}{D_j} \tag{3}$$

and a new stage S_i is entered when $w_i > w_j$. In CV, surplus energy may be allocated either to further somatic growth or to the fat sac (see below). Further, only stage CV is allowed to have diapause. During diapause, the copepod does not feed, but takes its metabolic requirements from the stored energy. Exactly what the metabolic activity is (or whether it feeds, Miller *et al.*, 1991) during diapause
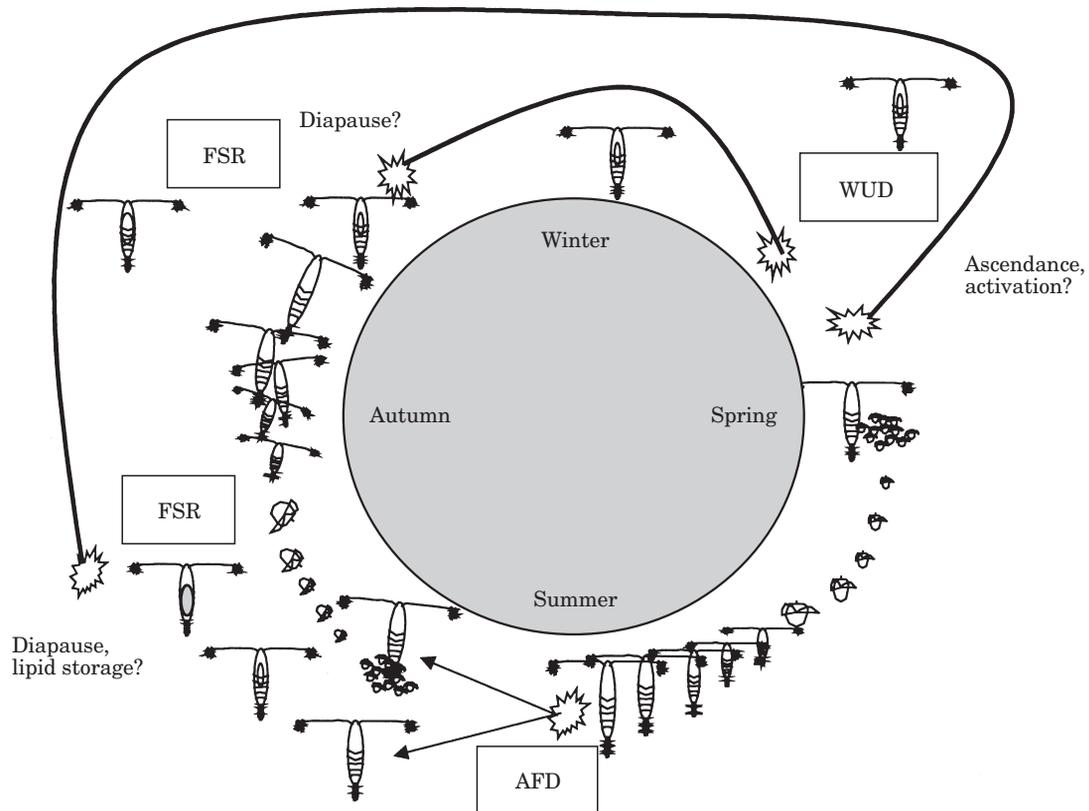
Figure 1. A general overview of how the life cycle alternatives are modelled. Depending on which day the copepods wake up (WUD), switch allocation pattern (AFD), and reach its fat-soma ratio (FSR), the life cycle may consist of one or several generations, and a long or a short diapause.

is not known (Hirche, 1996; but see Ingvarsdottir *et al.*, 1999). I used 0.001 g g^{-1} d^{-1} as a basic value (Carlotti and Wolf, 1998). As noted by Fiksen and Carlotti (1998), multi-year simulations of overwintering zooplankton will be sensitive to this parameter. Mortality rates are stage-specific while the animals are active (with values as in Aksnes and Blindheim, 1996) and fixed at 0.001 d^{-1} in diapause. If the stored energy compartment is exhausted, the mortality rate will increase (starvation) to 0.021 d^{-1}. If the fat sac is not emptied by the time of arousal, the modelled copepod will use a specified fraction each day for structural growth or reproduction.

Females mature when they reach a somatic body weight of 110 µg of carbon (Carlotti and Radach, 1996), and then proceed to grow until they have gained enough matter to produce one batch of 20 eggs. Then they spawn, their body carbon content is reduced accordingly, and the process is repeated. The released eggs are grouped into new super-individuals. If the number of super-individuals exceeds a given level, half the population is removed at random and all abundance estimates are multiplied by two. Similarly, if the number decreases

below that level, each super-individual is duplicated, and the abundance divided by two.

The difference between this model and other models of the life cycle of *C. finmarchicus* is that a few "genes" are added to each individual. These are (1) the time (day of the year, day length) at which a resting CV should wake up from diapause and initialize the maturation process (the "wake-up-day", WUD); (2) the day of the year when it should shift allocation pattern from somatic growth to fat reserves (the "allocation-to-fat-day", AFD), and (3) the fat/somatic tissue ratio required before diapause (the "fat-soma-ratio", FSR). These decision rules are specified for each super-individual, and the traits are inherited by the offspring produced by the present individuals. All the rules are effectuated during the CV stage. During this stage, the genes will control the diapause strategy and the pattern of energy allocation between soma and storage. If the copepod is in stage CV, it will check the current day length or its present fat/soma ratio against the inherited rules (WUD, AFD, FSR) and behave accordingly. In all other stages, it will follow fixed, predetermined schedules (Figure 1).
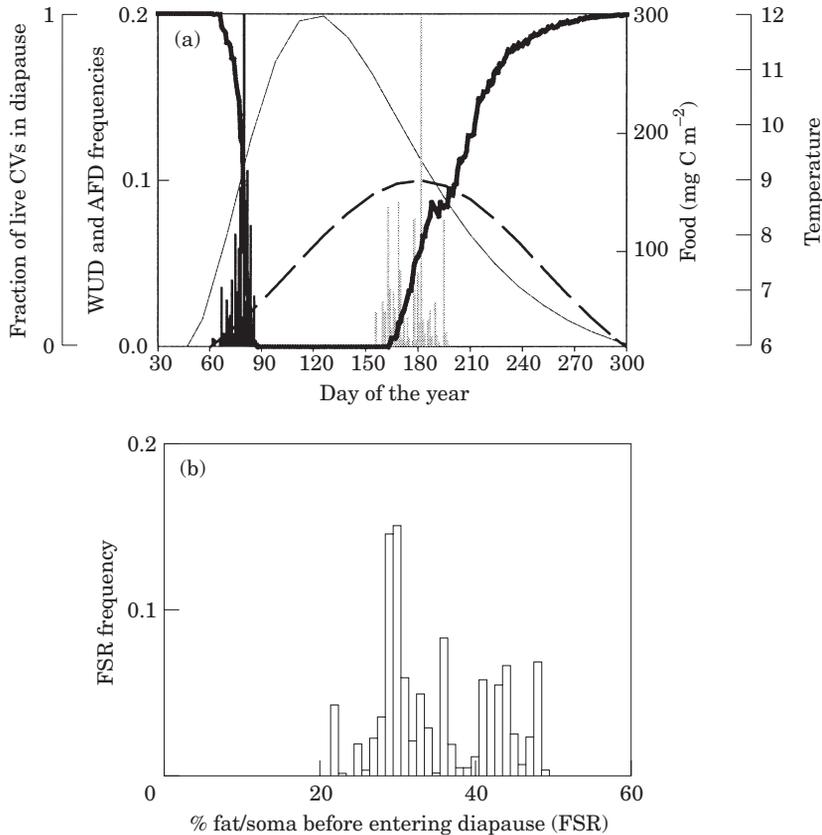
Figure 2. (a) Food (thin line) and temperature (broken line) during one year in the simulation with stable environment and no density-dependence ($\lambda=0$). The resulting "allele" frequencies of the genes WUD (black bars), AFD (grey bars) after 50 years are imposed. The thick line shows the fraction of CVs in diapause for each day during the last year. (b) The frequency of fat-soma ratios FSR in the population after 50 years.

During simulations, the frequency distribution of the strategies and combinations of strategies in the super-individuals are subject to natural selection. The rules of behaviour are transferred across generations, and those with higher-than-average reproductive success will tend to increase their proportions in the population (gene pool), so that fitness is intrinsically determined. In nature, genetic variability in a population is maintained through immigration, crossing over and mutations. Here, I have ensured a continuous supply of variance (invading strategies) by adding a small level of stochasticity during the transfer of genetic information from parents to offspring. The offspring get a random normal variate from $N(\mu,\sigma^2)$, where μ is the value of the mother and $\sigma^2=9$ d for the AFD and WUD genes and $\sigma^2=0.04$ for the FSR gene. Crossing-over (new, random combinations of the genes) was not included in the model version presented here. Initially, the copepods are given a random mixture of reasonable "gene frequencies".

Annual variability in environmental conditions drives the selection of strategies in the population. Here, a model environment is created in which food F_d (mg C m^{-3}) and temperature T_d at day d display a log-normal and a Gaussian annual cycle, respectively. The maximum level and day of the year when the maximum is reached are both drawn from normal deviates. The dynamics of the food resource depend on the standing stock F_d, maximum growth rate ν, carrying capacity K_d at day d, and grazing from zooplankton:

$$F_{d+1} = F_d + \nu F_d \left(1 - \frac{F_d}{K_d}\right) - \sum_i N_i w_i \lambda \qquad (4)$$

All active *Calanus* except eggs and the first naupliar stages feed on the resource (assuming a specific ingestion rate λ for all stages) and will become food-limited at high densities. Carrying capacity is described by the log-normal function

$$K_d = a\exp\{-0.5[\ln(d/d_0)/b]^2\}$$

and temperature by a Gaussian function

$$T_d = T_0 + a_1\exp\{-0.5[(d-d_0)b_1]^2\}$$
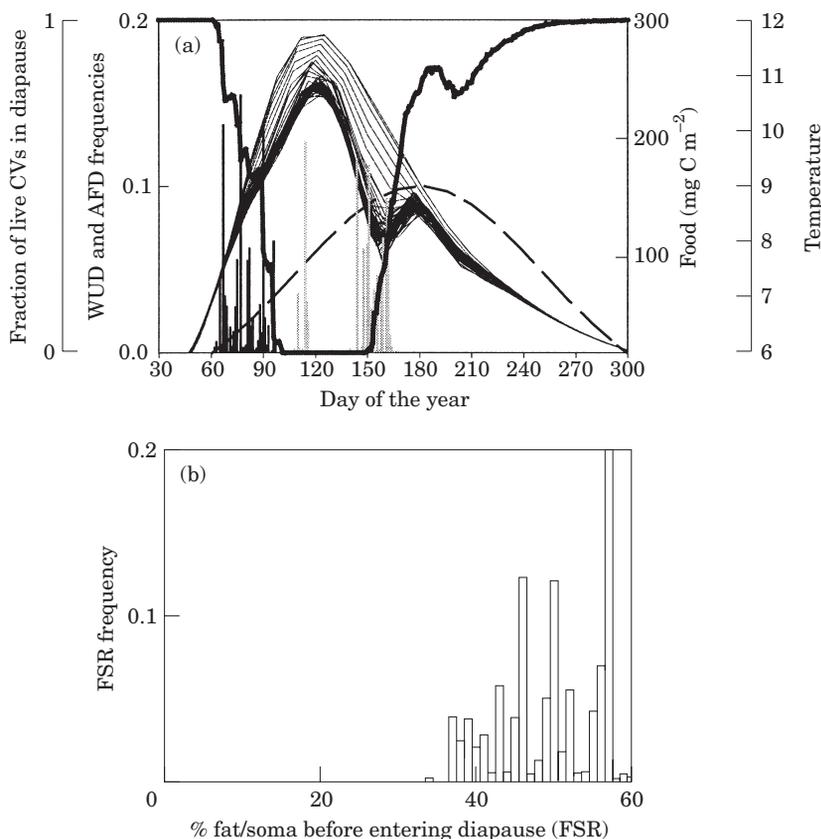
Figure 3. Stable environment with density-dependent food dynamics ($\lambda = 0.5$). All graphs are as in Figure 2. The food concentration is plotted for all 50 years and shows a progression from initially ungrazed food stock at low zooplankton abundance to "top-down" controlled dynamics as the zooplankton population reaches its equilibrium.

where d is day of the year, and a, a_1, d_0, d_1, b, and b_1 are drawn by chance from standard normal populations with specified means and deviations.

Results

Stable environment without density-dependence

A simulation with the same environment each year, no density-dependence, and the life cycle moulded through natural selection, mutations and reproduction of successful strategies are presented in Figure 2. The surviving individuals contain WUD and AFD genes within a narrow range, while the spread is larger in the FSR gene. The food and temperature profiles combined with the distribution of life-history strategies in the population cause a gradual transition to diapause, all from the second generation.

Stable environment with density-dependence

Density-dependence is introduced by setting $\lambda = 0.5$ (Equation 4). At large abundances of *C. finmarchicus*, a game situation occurs where the copepods are "playing the field" (Maynard Smith, 1982). The simulation is initialized with a low *Calanus* abundance, and as the population grows and reaches its equilibrium the resource dynamics become more influenced by grazing and the food is driven below its ungrazed carrying capacity (Figure 3). Late in summer, increasing proportions of the population enter diapause, the grazing pressure is relieved and the resource recovers slightly. If too many individuals emerge early in spring, or stay active too long in late summer and autumn, the low carrying capacity at the fringe of the productive season will make it profitable to shift out of the population centre. This process will eventually lead to evolutionarily stable frequencies that involve different phenologies with equal fitness.

The simulation with density-dependence gave a range of spring emergence strategies with similar fitness, and an earlier switch of allocation routes. The load of reserves (FSR) increased compared to the density-independent situation. The fraction of early (about day 115) AFD strategists does not result in animals with
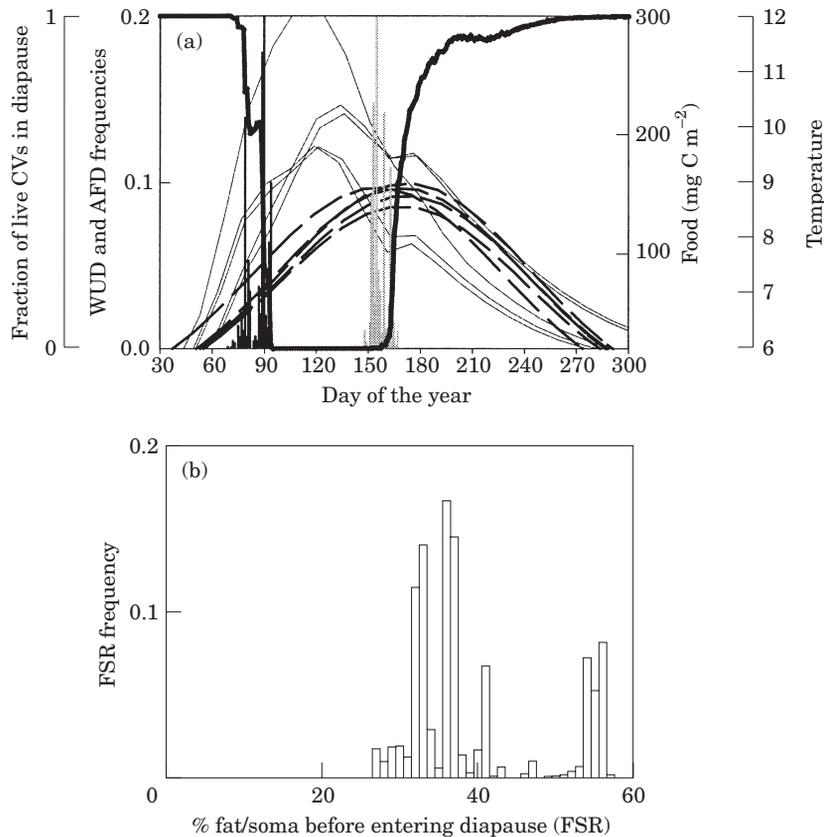
Figure 4. Simulations with a variable environment (carrying capacity of the food and temperature) and density-dependent resource dynamics. Only a few years of food and temperature are displayed, but otherwise the plots are as in Figures 2 and 3.

correspondingly early entrance of diapause (Figure 3). This is because such animals have a late WUD (see below), and therefore are very young when they pass their AFD. They also have high FSR, so they need more time to fill their fat sacs. In this scenario, two generations are evident and the first is clearly the dominant (about 80% of the population in this scenario, see fraction of CV in diapause in Figure 3).

Variable environment with density-dependence

Next, an environment where the carrying capacity of the food resource varies stochastically between years is applied. Temperature also varies on an annual basis, independent of food. The environment and corresponding growth opportunities differ significantly between years in these simulations (Figure 4).

Although the inherited switch of allocation pathways (AFD) is limited to a range of about 14 d (Figure 4), individuals will continue to enter diapause for an extended period of time. Individuals with the same genotype can display a wide range in date of diapause entry, depending on the FSR gene and where in the

generation cycle the copepod is when the AFD gene ''activates''. As eggs are laid in batches during the whole of spring and summer, individuals will be distributed across all stages when they pass their specific allocation-to-fat day (AFD). The eggs laid by the first generation enter diapause between day 150 and day 180 (ca. 90% of the population, but this depends on the environmental situation in the final year), while the second generation needs more time to fill its fat reserves (days 180–260).

Comparing scenarios

After selection, the alleles may combine in specific patterns within each individual, such that, for example, late AFD combines with low FSR or early WUD. However, such trends were not very conspicuous in the simulations presented above (Figure 5). Some combinations dominate the population, but there are always variations attributable to mutations and the persistence of different strategies with equal or similar fitness (Figure 5). If anything, there seems to be a correlation between late AFD and low FSR in all scenarios, and between late WUD and late AFD in the stable,
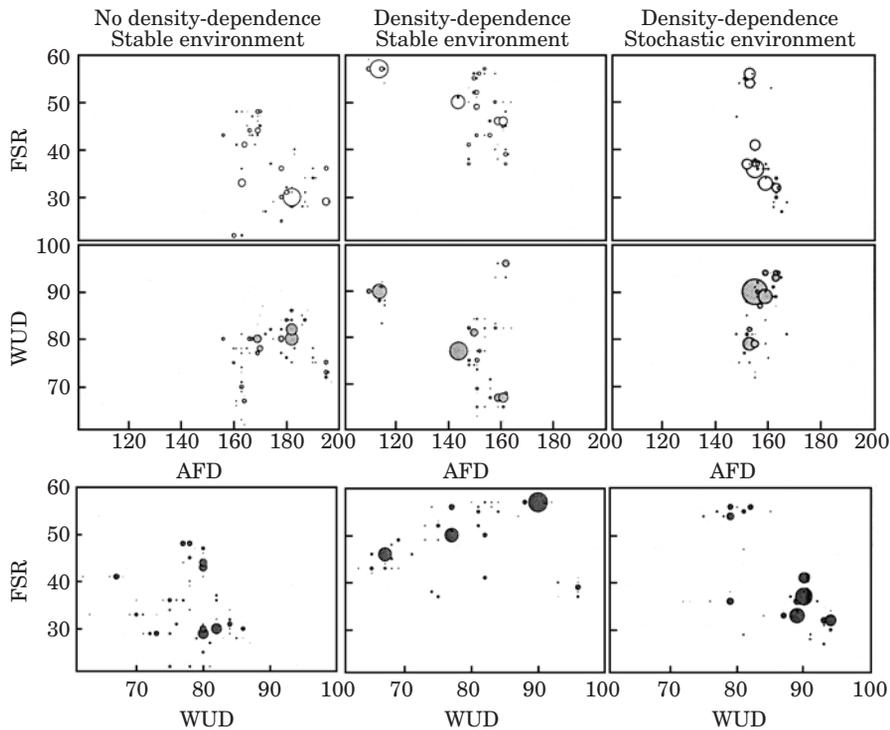
Figure 5. Combination of alleles at the three loci for the simulations presented in Figures 2–4. Bubble sizes indicate the fraction of individuals in the population containing the particular allele combination after 50 years.

density-dependent scenario. In the latter scenario, a correlation between late WUD and high FSR may also exist. That scenario also has the highest level of competition between individuals, and it may therefore be expected that the strategies become more specialized and divergent.

The process of adaptation in the three scenarios is illustrated in Figure 6. Initially, I drew reasonable values at random for each gene in all individuals. Through selection, mutations, and reproduction, the average values change and eventually stabilize, and variation is reduced to reflect mutation rates and the coexistence of multiple strategies. In the deterministic case with no density feedback, copepods wake up early (and simultaneously, see Figure 2), build fat late and have a low FSR. If density-dependence is included, they wake up early (but spread out, Figure 3), have early AFD and gather much fat before diapause. In the stochastic scenario, they wake up late and have intermediate storage strategies. This corresponds to two generations in the first scenario, and mainly one generation in the density-dependent scenarios.

Fixed probability of entering diapause in CIV–CV?

Some simulations were performed where, initially, 50% of the population have a fixed probability for diapause

or reproduction at the transition from stage CIV to stage CV (Figure 7). It is evident that the strategy of simply taking on one or the other strategy with fixed probabilities is suboptimal, and eliminated from the population within a few years.

Discussion

Earlier models of phenology in zooplankton (e.g. Hairston and Munns, 1984) and some purely theoretical models (e.g. McNamara, 1994; Iwasa and Levin, 1995), have focused on how organisms deal with "catastrophic dates" or environmental disturbances which are lethal to all active (not in diapause) individuals. The model of Fiksen and Carlotti (1998) predicted that optimal phenology depends on the internal state of *C. finmarchicus*, but it does not consider density-dependence or environmental variability. However, the problem facing many organisms is gradually changing growth and mortality conditions, with highly variable prospects for the future. The present model, using evolution itself as a model frame, shows that optimal phenology may depend on the action of others and on the variability of the environment.

The model is built on the assumption that *Calanus* uses day length or some other signal (or mixture of signals) to recognize the seasonal cycle. If the copepod
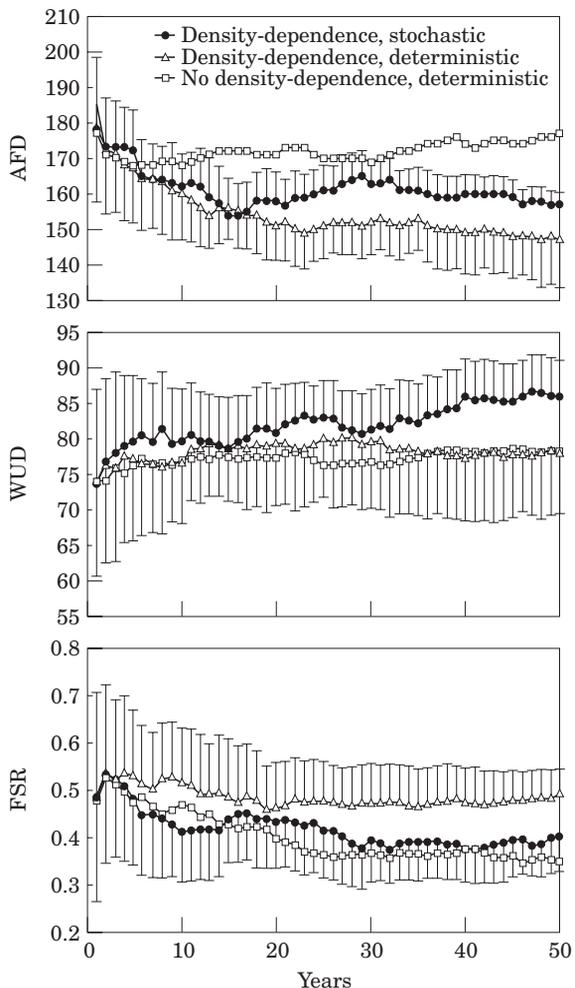
Figure 6. Average population values of the strategy-genes plotted at the end of each year. The error bars show ± 1 s.d. for two of the simulations. The change in successful strategies is most intense during the first years.

Figure 7. The frequency at the end of each year of individuals with fixed probabilities (from 0.1 to 1) of entering diapause in CV for (a) a stable and (b) a stochastic environment.

does not base its phenology on information about "external time" (daylight; Miller and Grigg, 1991), but on "internal time" (some internal clock), then the model is easily reformulated by plugging in, for instance, the speed of the clock as "genetic" information instead of day length. If the diapause decisions are made as a function of food, predators, temperature, or some mixture of these, then the problem is much more difficult to model. The model suggests that use of day length as a signal to decide whether to enter diapause or to mature is a robust strategy when growth conditions within each year are correlated. Slow development will make it profitable to prepare for diapause, because it is likely that offspring also will be delayed and therefore run a high risk of arrested growth and enhanced mortality during autumn and winter. Rapid growth will have

opposite effects, and production of a second generation may be profitable. If the switch date is associated with a given day length, more individuals will produce a second generation in warm years and enter diapause in cold years.

Recent models often use fixed or time-varying probabilities to decide whether a CV prepares for diapause or reproduction (Carlotti and Wolf, 1998; Lynch et al., 1998; Miller et al., 1998). The fixed strategy seems to be suboptimal in the present setting (Figure 7), but obviously the conservative strategy of making just one generation is fairly successful in a variable environment. In a sufficiently variable environment, the conservative strategy is likely to be the long-term winner.

It appears that genetic algorithms provide a promising method for studying adaptation (e.g. Sumida et al., 1990; Forrest, 1993). The current model may be improved, or made more realistic, by adding more (or different) genes, environmental cues, or spatial dimensions. This would require some mechanism to balance the weight of the signals, for instance through neural networks (e.g. Ezoe and Iwasa, 1997; Huse and Giske, 1998). With these additions, the relative importance of food availability, population size, day length, and internal state could be assessed within a single model

to find evolutionarily stable emergence and resting strategies.

Acknowledgements

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