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# *Calanus finmarchicus* diapause initiation: new view from traditional life history-based model

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ABSTRACT: Organisms have evolved to optimally align the timing of diapause with the seasonality of environmental conditions in order to maximize their fitness. Observations from the Northwest Atlantic suggest that *Calanus finmarchicus* diapause initiation date varies significantly by geographic location, inconsistent with patterns of seasonal changes of any single environmental factor such as photoperiod, sea surface temperature, or food availability. In the present study, a life history-based model was used to reconcile the apparent inconsistency. The model results suggest that (1) the induction of diapause involves multiple environmental factors as a result of fitness maximization, and (2) in addition to temperature and food condition, predation pressure is another key factor that could affect diapause initiation process. It is further suggested that phenotypic plasticity is likely to be the major source of variation in the timing of diapause initiation for *C. finmarchicus*.

KEY WORDS: *Calanus finmarchicus* · Diapause · Life history · Fitness

## INTRODUCTION

Marine plankton, like other organisms, have evolved various life-history strategies to cope with a seasonally fluctuating environment. Dormancy is one such important life-history strategy that allows plankton populations to survive seasons with adverse environmental conditions, such as low food, extreme temperatures, or high predation pressure. Some zooplankton species can produce benthic resting eggs (Dahms 1995). Other species, mostly open-ocean calanoid copepods including *Calanus finmarchicus*, can migrate to deep water and enter a dormancy (diapause) phase as late-stage copepodites for several months (see reviews in Dahms 1995, Hirche 1996). The timing of dormancy (e.g. initiation and termination) is a critical aspect of this strategy, as organisms have likely evolved to optimally align the timing of diapause with the seasonality of environmental condition in order to maximize their fitness (e.g. Cohen 1970, Taylor 1980, Hairston & Munns 1984, Fiksen 2000).

For *Calanus finmarchicus*, the question of what triggers its diapause initiation is ecologically important, but the answer remains elusive. Johnson et al. (2008) showed that seasonal environmental cues such as photoperiod, sea surface temperature (SST), or food availability alone cannot explain the induction of diapause, although those cues have often been found to induce copepodite diapause or resting egg production in both marine and freshwater copepod species (e.g. Watson & Smallman 1971, Johnson 1980, Marcus 1982, Uye 1985, Hairston et al. 1990, Hairston & Kearns 1995). Johnson et al. (2008) concluded that the induction of diapause must involve the interaction of multiple environmental factors, and further proposed the lipid accumulation window (LAW) hypothesis in an attempt to achieve a mechanistic understanding of how these environmental factors interact.

The LAW hypothesis is plausible in linking environmental factors to the physiological constraint of the diapause process (individuals require sufficient lipid storage for diapause), but it is not able to address the question of whether optimal fitness can

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be achieved if individuals start diapause whenever they are physiologically ready. For instance, the *Calanus finmarchicus* population in the Gulf of Maine is known to have 2 or more generations (Meise & O'Reilly 1996, Durbin et al. 1997, 2000, Miller et al. 2000). Based on the LAW hypothesis, the reason for some of the first-generation individuals not entering diapause remains not very clear. Those first-generation individuals may be capable, and have an option, of shifting energy from active development and reproduction to lipid storage in preparation for diapause. This suggests that factors other than physiological constraint may play a role in the diapause initiation process.

In the present study, it is hypothesized that (1) the induction of diapause indeed involves the interaction of multiple environmental factors, but this is due to fitness maximization rather than physiological constraints; and (2) in addition to temperature and food condition, predation pressure is another key environmental factor that could affect the diapause initiation process. The focus of the present study is on the ultimate cause of selection rather than a direct mechanistic modeling on behavioral responses to environmental cues. The approach used to test the hypotheses is based on the theoretic framework developed for explaining dormancy strategy from a life history theory point of view (e.g. Levins 1968, 1969, Cohen 1970). Although this framework was developed many years ago, new insights can still be gained by using recently observed species-specific vital rates and diapause pattern. The objective here is to reconcile the apparent inconsistency between the observed patterns of diapause onset with induction of diapause by any single observed environmental cue. This would then provide a valuable understanding of the relationship between environment and copepod phenology, and of the possible impact of environmental change on plankton population dynamics in general.

## MATERIALS AND METHODS

The present study adopts an approach used by Bradford & Roff (1997) for calculating the optimal date of diapause egg production in a cricket population. That approach itself is an empirically based extension of the theoretical models of Levins (1968, 1969) and Cohen (1970). The key concept of this approach is that the timing of diapause for a population is optimized such that expected population growth rate (as a measure of fitness) is maximized.

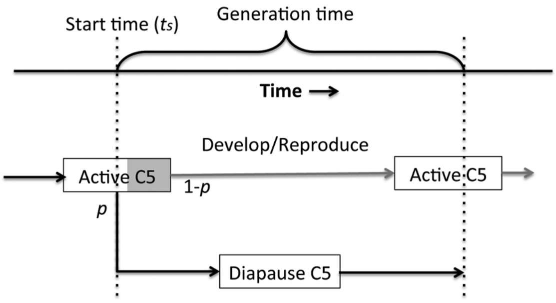

Fig. 1. *Calanus finmarchicus*. Schematic diagram of diapause process. A proportion ($p$) of stage-5 copepodites (C5s) migrate to deep water and start diapause at time $t_s$ while the rest of the C5s continue to develop into adults and reproduce, and their offspring develop to C5s to complete one generation. The value for $p$ is calculated in the model based on fitness maximization (see 'Materials and methods' for details)

For a *Calanus finmarchicus* population, individuals may enter diapause at copepodite stage 5 (C5) as the season progresses. A proportion ($p$) of C5s start diapause at time $t_s$; while the remaining population ($1 - p$) continues to develop into adults and reproduce, and their offspring develop to next-generation C5s (Fig. 1). The total surviving C5s ($N_{C5}$) by the end of the one-generation time period, including both diapausing ($N_{C5d}$) and active C5s ($N_{C5a}$), can be calculated as:

$$N_{C5} = pN_{C5d} + (1-p)N_{C5a},\ 0 \le p \le 1 \tag{1}$$

Partial diapausing can minimize the variance of fitness in stochastic environments, and thus maximize long-term fitness at a population level (e.g. Cohen 1970). The possible mechanisms for partial diapausing are discussed in our 'Discussion' section. The objective here is to find the value of $p$ that can maximize the geometric mean of $N_{C5}$ over different possible environmental conditions (including temperature, food, and mortality as described later in this section):

$$\max_{0 \le p \le 1}\{E[\ln(N_{C5})]\} \tag{2}$$

where $E[\ln(N_{C5})]$ means the expected value.

The geometric mean fitness is commonly used as a criterion of population-level fitness in stochastic environments (e.g. Yoshimura & Clark 1991, see explanation in our 'Discussion' section). For Eq. (1), $N_{C5d}$ can be calculated by assuming a constant mortality rate for diapausing C5s, whereas $N_{C5a}$ can be calculated as the net reproductive rate of a population, defined as the average lifetime number of offspring produced by a member of the population. This rate is often denoted as $R_0$, and can be calculated using the classic life-table approach as:

$$R_0 = \int_0^{\infty} l_x m_x \mathrm{d}x \tag{3}$$

where $l_x$ and $m_x$ are respectively survivorship and fecundity at age $x$. Following a similar approach as in Kiørboe & Hirst (2008), different mortality rates were used for 4 different development stages including egg, nauplii, copepodite, and adult, represented as $\beta_e$, $\beta_n$, $\beta_c$, and $\beta_a$, respectively. Notice that the mortality rate within each development stage is constant at a base temperature, $T_{base}$, of 6°C, and mortality is a function of time (related to temporal change of temperature and represented as a $Q_{10}$ function in this model, with $Q_{10} = 2.2$). For a newly molted individual C5 at time $t_s$, the survivorship at time $t$ is:

$$l(t) = 0.5\underbrace{\mathrm{e}^{\int_{t_s}^{t_s+\delta_3}\beta_c(t)\mathrm{d}t}}_{(S1)}\underbrace{\mathrm{e}^{\int_{t_s+\delta_3}^{t}\beta_a(t)\mathrm{d}t}}_{(S2)}\underbrace{\mathrm{e}^{\int_{t}^{t+\delta_0}\beta_e(t)\mathrm{d}t}}_{(S3)}\underbrace{\mathrm{e}^{\int_{t+\delta_0}^{t+\delta_0+\delta_1}\beta_n(t)dt}}_{(S4)}\underbrace{\mathrm{e}^{\int_{t+\delta_0+\delta_1}^{t+\delta_0+\delta_1+\delta_2}\beta_c(t)\mathrm{d}t}}_{(S5)} \tag{4}$$

where S1, S2, S3, S4, and S5 are the terms for survivorship of C5, adults, eggs, nauplii stages 1 to 6 (N1 to N6), and copepodite stages 1 to 5 (C1 to C5), respectively. Assuming an equal sex ratio, only half of C5s become female. The stage durations are represented as: $\delta_0$ (egg hatching time), $\delta_1$ (duration from N1 to C1), $\delta_2$ (duration from C1 to C5), and $\delta_3$ (duration from C5 to adult). Stage duration ($\delta$) is a function of both temperature and food concentration (except the durations of egg and N1 to N2, which are temperature-dependent only). Following Speirs et al.'s (2005) formulation for food limitation:

$$\delta = a(T(t) + \alpha)^{\beta}/(1 - \mathrm{e}^{(-F(t)/\varphi)}) \tag{5}$$

where the numerator part is for temperature [$T(t)$] dependency following a classic Bělehrádek formulation (Bělehrádek 1935), and the denominator part is for food [$F(t)$] dependency, with the food limitation constant $\varphi$ set to 0.8 mg chl *a* m$^{-3}$ (where chl *a* is chlorophyll *a*) (based on Campbell et al. 2001). In the numerical model implementation, the total life cycle of *Calanus finmarchicus* is broken down to 13 stages (egg, N1 to N6, C1 to C5, and adult), and the aggregated stage duration such as $\delta_2$ and $\delta_3$ can be calculated by summing up the development time of the sub-stages. For *C. finmarchicus*, the Bělehrádek parameters ($a$, $\alpha$, and $\beta$) are from Campbell et al. (2001) directly.

Fecundity is assumed to be a function of food concentration only. The impact of temperature on fecundity has been suggested in earlier studies (Runge 1985, Plourde & Runge 1993, Hirche et al. 1997), but a more recent study (Campbell & Head 2000) in the NW Atlantic region showed no relationship between temperature and fecundity. Instead, fecundity is mainly controlled by food availability. Campbell & Head's (2000) analysis was based on the *in situ* egg production rate measurements across the entire NW Atlantic shelf, and thus is probably more applicable to the present study. A Michaelis-Menten function was used to describe the dependency of fecundity [$m(t)$] on time-varying food concentration [$F(t)$] that females experience:

$$m(t) = \varepsilon_{max}\frac{F(t)}{F(t) + K_F} \tag{6}$$

where $\varepsilon_{max}$ is the maximum egg production rate in food-saturated conditions, and $K_F$ is the half-saturation constant for food limitation on egg production. Values for $\varepsilon_{max}$ and $K_F$ were set to 70 eggs female$^{-1}$ d$^{-1}$ and 1.0 mg chl *a* m$^{-3}$, respectively, based on Campbell & Head (2000). Notice that $m(t) = 0$ if $t < (t_s + \delta_3)$. All model parameters are listed in Table 1.

To test this model, the temperature and food conditions from 3 different habitats along the NW Atlantic shelf were used (Fig. 2), including one in the central Gulf of Maine (GoM), one in the Anticosti Gyre (AG) inside the Gulf of St. Lawrence, and one near-shore site (Stn 27 or S27) on the Newfoundland Shelf. The choice of the study sites was based on the diversity of their geographic locations and diapause timings. The other 2 sites originally in the Johnson et al. (2008) paper, the Halifax station and the Lower St. Lawrence Estuary station, are not included in the present analysis. This is mainly because the Halifax station is known to be very advective, and the Lower St. Lawrence Estuary station is too close to the AG station. The mean temperatures and food concentra-

Table 1. List of model parameters

| Symbol | Definition | Value |
|---|---|---|
| $\beta_e$ | Egg mortality rate at $T_{base}$ | 0.04 d$^{-1}$ |
| $\beta_n$ | Nauplii mortality rate at $T_{base}$ | 0.07 d$^{-1}$ |
| $\beta_c$ | Copepodite mortality rate at $T_{base}$ | 0.04 d$^{-1}$ |
| $\beta_a$ | Adult mortality rate at $T_{base}$ | 0.05 d$^{-1}$ |
| $T_{base}$ | Base temperature in $Q_{10}$ function | 6°C |
| $Q_{10}$ | $Q_{10}$ coefficient | 2.2 |
| $\varphi$ | Food limitation constant on development | 0.8 mg chl *a* m$^{-3}$ |
| $\varepsilon_{max}$ | Maximum egg production rate | 70 eggs female$^{-1}$ d$^{-1}$ |
| $K_F$ | Half-saturation constant for food limitation on egg production | 1.0 mg chl *a* m$^{-3}$ |

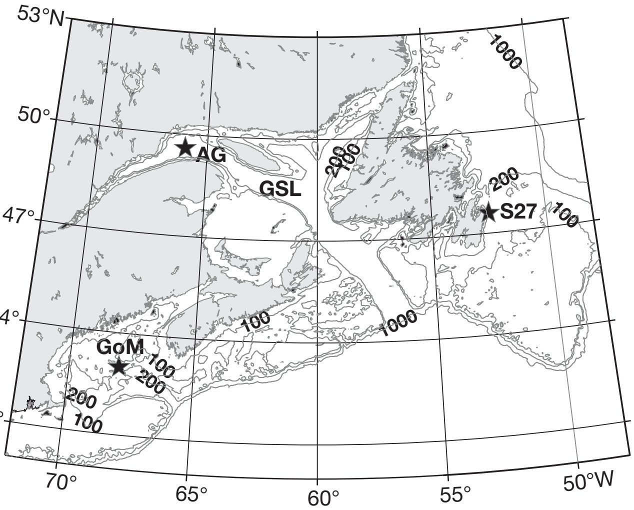

Fig. 2. Study region showing 3 sites (stars) in the NW Atlantic. GoM: central Gulf of Maine; AG: Anticosti Gyre in the Gulf of St. Lawrence (GSL); S27: Stn 27 on the Newfoundland Shelf. Numbers = depth (m)

tions for the selected 3 sites are shown in Fig. 3 (data sources are noted in the caption). To mimic stochastic environment conditions, the model allows temperature and food to vary around their mean with a standard deviation of 10% (for temperature) and 30% (for food) of their mean each day (assuming a normal distribution). A total of 100 model runs were conducted for each site, with the daily temperature and food concentration values randomly picked from the normal distributions. In addition, mortality rate in the model was treated in a similar way (with a standard deviation of 30% of its mean base mortality), such that the environmental uncertainty in predation pressure could be approximately accounted for.

## RESULTS

Observation data suggest that *Calanus finmarchicus* diapause initiation date varies significantly by geographic location: late spring for the GoM site, and late summer–early fall for the 2 northern sites, AG and S27 (Fig. 4, gray bars). It is worth noting that the

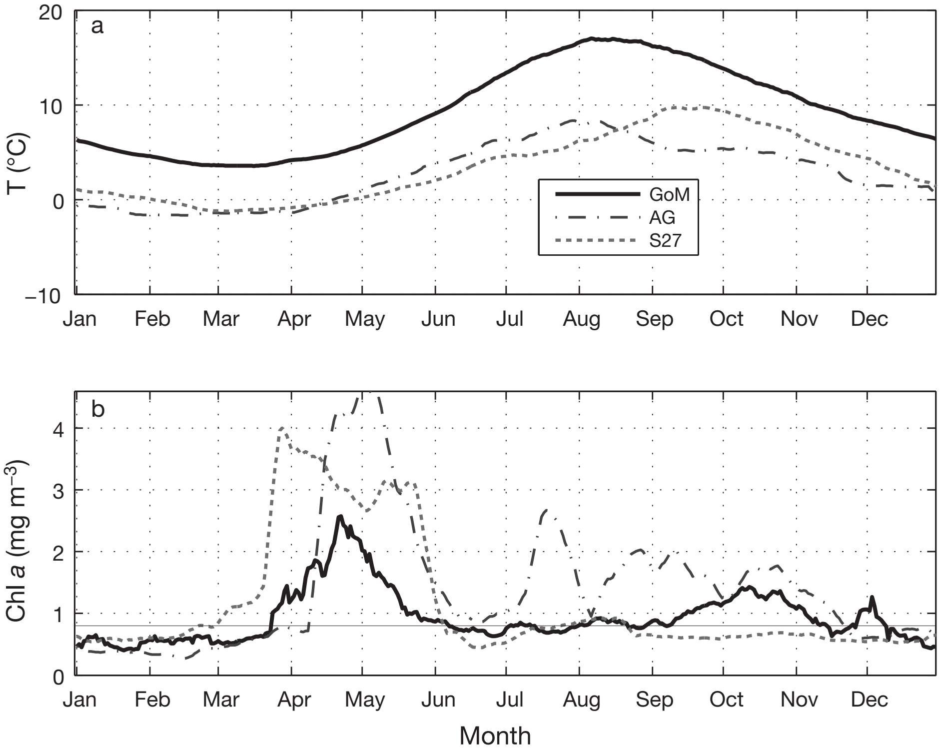

Fig. 3. (a) Mean temperature and (b) chlorophyll *a* (chl *a*) concentration observed at the 3 sites (see Fig. 2 for locations and abbreviations). Sea surface temperature and ocean color data from satellite are used for the GoM site, and *in situ* observation from the Canadian Atlantic Zone Monitoring Program (AZMP; www.meds-sdmm.dfo-mpo.gc.ca/isdm-gdsi/azmp-pmza/index-eng.html) are used for both AG and S27 sites. The straight horizontal line in (b) represents the food limitation constant φ in Eq. (5)

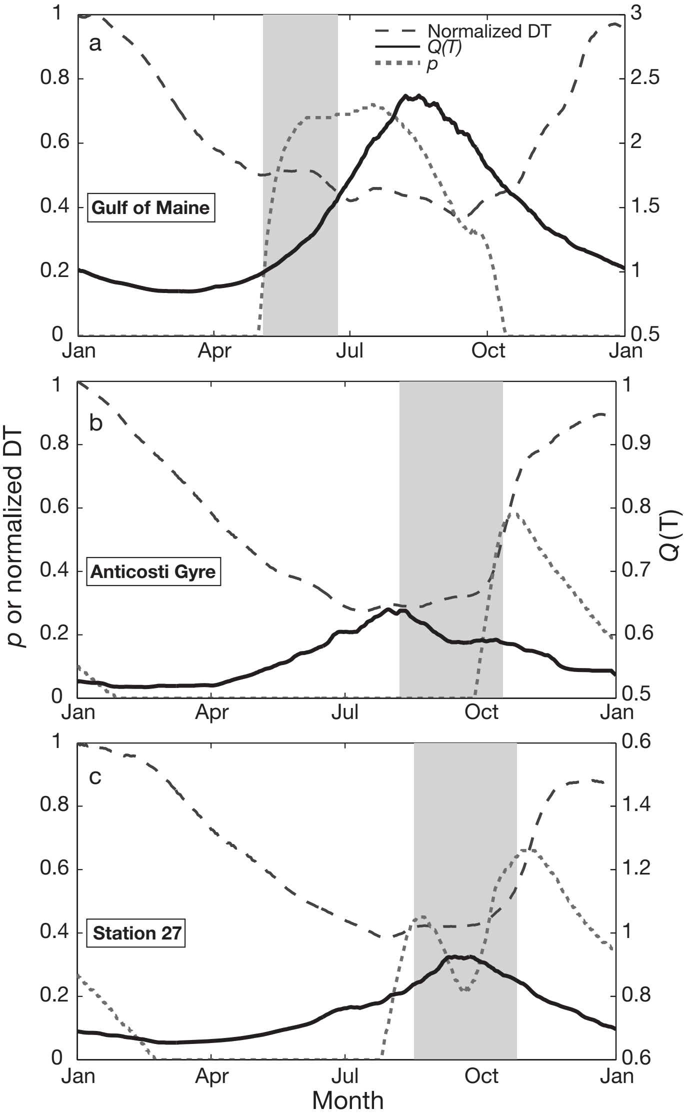

Fig. 4. *Calanus finmarchicus*. Diapause timing and environmental factors at the sites (a) Gulf of Maine, (b) Anticosti Gyre, and (c) Stn 27. *p*: model-computed diapause proportion; normalized DT: development time (DT) normalized to maximal DT at each site; *Q*(T): mortality coefficient as a function of temperature. Gray bar: observed time period of diapause initiation (see 'Results' for how this is derived)

estimation of the diapause initiation date is somewhat arbitrary, mainly due to the difficulties in separating the surface-active C5s from the deep diapausing C5s in the bottom-to-surface net-tow samples. For the AG and S27 sites, the initiation dates were extracted directly from Johnson et al. (2008), where the initiation date was defined as the date when the proportion of C5s in the population rose to half the overall maximum, calculated as each year's maximum C5 proportion averaged over all years at that station. For the GoM site, the same proxy was calculated using the data collected from NOAA's Marine Resources Monitoring, Assessment, and Prediction (MARMAP) and Ecosystem Monitoring (ECOMON) surveys (program details and sampling protocol can be found in: Sherman 1980, Meise & O'Reilly 1996, Kane 2007). Although the data source for the GoM site is different from the 2 northern sites, the proxy only uses local population structure information (i.e. stage ratio), and therefore the diapause timing estimation is site-independent. Overall, the data clearly indicate the significant regional difference in the timing of *C. finmarchicus* diapause initiation.

The model-computed diapause initiation dates show significant timing differences as suggested by the observation, especially between the GoM site and the 2 northern sites. The population in the GoM site (Fig. 4a) starts diapause in late spring–early summer, as shown by the increase in diapause proportion *p* from 0 at the beginning of May to ~0.7 at the end of May. The value for *p* remains high during summertime, but starts to drop by the end of August, then returns to 0 in October. In contrast, both northern sites have their *p* peaks in fall. For the AG site (Fig. 4b), the majority of the population (60%) start diapause in October; whereas for the S27 site (Fig. 4c), the model shows that ~45% of the population initiated diapause in August (earlier than the observed date), followed by a major peak ($p = 0.66$) by the end of October. Both AG and S27 have a small proportion (<25%) of the population initiating diapause at the beginning of the year. In general, the modeled diapause initial timing matches well with the observation on a seasonal time scale for all 3 sites. In particular, the model captures the observed large timing difference in diapause initiation between GoM and the 2 northern sites.

The model suggests different environmental controls for diapause initiation at the 3 sites. For the GoM site (Fig. 4, upper panel), diapause is induced mainly by the quick increase in mortality, indicated by $Q(T)$ ($= Q_{10}^{[(T - T_{base})/10]}$), from spring to summer, even though the total development time (represented as normalized development time in Fig. 4) is expected to be low as a result of warm temperature in summer. Food limitation in summer appears to be a secondary effect, since the development time continues to decrease from spring to summer, yet the majority of C5s still start diapause due to the expected high mortality in summer. This is not likely the case for the 2 northern sites, where the majority of the population starts diapausing even as the expected mortality decreases and water temperature starts to cool down in late fall. On the other hand, the increase in $p$ coincides with the lengthening of development time resulting from decreasing temperature and low food concentration. The situation is slightly more complicated for the S27 site, where the first smaller peak of $p$ is largely due to the increased mortality rate, followed by a major peak caused by the lengthening of development time. In other words, diapause can sometimes be induced by a combination of multiple environmental factors and it is difficult to assess the relative contribution of each factor, especially if these 2 peaks are close to each other.

## DISCUSSION

### Environmental causes of diapause initiation

The lack of an apparent single universal environmental cause for diapause initiation in different habitats has been noticed for many other copepod species. For example, Johnson (2004) found that the timing of *Calanus pacificus* diapause initiation in the Southern California Bight was not consistent with the timing of changing photoperiod or warming temperature, and also was not related to food availability alone. Similarly, for copepod species that produce resting eggs as a dormancy strategy, their response in the timing of resting egg production to environmental cues may also vary among populations from different geographic regions (e.g. Marcus 1984, Avery 2005). This has also been observed for freshwater copepod species even within the same geographic region but in different isolated habitats (e.g. Hairston & Olds 1987). From a fitness point of view, this is not surprising, as different habitats may have unique cues for the upcoming adverse environment; and an organism's life-history strategy needs to adapt to local environmental conditions to achieve optimal fitness. The model used here is capable of capturing the essence of this process and linking the seemingly uncorrelated environmental condition with diapause dynamics. The model results suggest that the relative importance of one environmental condition versus the other might alternate in different habitats, resulting in no single universal cue for diapause, as indicated by the observation data. However, questions remain with regard to the physiological and genetic aspects of the diapause response to environmental factors, which is further discussed below.

The importance of predation (mortality) in initiating diapause of *Calanus finmarchicus* is suggested by the present study, but was not explicitly considered by Johnson et al. (2008). An earlier study by Kaartvedt (2000) on *C. finmarchicus* in the Norwegian Sea provided some evidence that the increase in mortality risk due to the arrival of migrating fish during summer is the major driving force for the seasonal descent of *C. finmarchicus.* From a life-history strategy point of view, the diapause response to predation pressure is practical: copepods have almost no chance to escape from relatively large fish if encountered, so they rely on prevention of the threat rather than active attempts to escape, mainly through diel or seasonal migrations to refuge habitats such as deep water layers (Pasternak et al. 2006). From a physiological point of view, the chemical stimuli (e.g. fish exudates) released into the environment by a predator could play a significant role in the induction of prey diapause, and this has been tested for *Daphnia* sp. in freshwater systems (e.g. lusarczyk 1995, 1999, Pijanowska & Stolpe 1996). Additional evidence from studies on freshwater copepods is available on linking diapause response with predation pressure of either invertebrates (Hairston 1987) or vertebrates (Nilssen 1977, Hairston & Olds 1987, Hairston 1987, Hairston et al. 1990). It is possible that copepod species like *C. finmarchicus* have a similar response to predation, although invertebrates rather than fish might be the dominant predator in marine systems. Certainly, the stimuli are not necessarily limited to fish exudates only. Alarm substances from injured conspecifics might be another chemical stimulus (e.g. lusarczyk 1999); or a simple increased encounter rate with predators (through mechanical or visual cues; Bollens et al. 1994) could be a strong signal of intensified predation pressure.

### Role of lipids

The role of lipids in triggering the diapause process deserves special attention. Irigoien (2004) presented a very interesting hypothesis on this topic, suggesting that the production of the hormones regulating molting and diapause is controlled by (or related to) the lipid level (fatty acids and sterols) in the copepods. In other words, diapause could be triggered by the accumulation of lipids. A key question to this hypothesis is: what controls the accumulation of lipids in the first place? This also leads to another question: why do some individuals start accumulating lipids and enter diapause while others stay active and continue to spend energy on development and molting? It has been suggested that this 'decision' process could start in the C4 stage (Johnson et al. 2008), maybe triggered by lipid content at that stage, but no evidence is yet available to support this argument. A recent genetics study by Tarrant et al. (2010) showed that genes associated with lipid synthesis, transport, and storage were upregulated (more highly expressed) in active copepods when compared to diapausing ones, but this still does not address the question of what triggered the gene upregulation in the first place.

That being said, there is no doubt that lipids play an important role throughout the entire diapause process, due to the energy requirement during diapause and the subsequent arousal and reproduction period (Jónasdóttir 1999, Irigoien 2004, Saumweber & Durbin 2006). The question now becomes: can and should we include lipid as a state in the model, such that the influence of lipid status on the diapause initiation process can be evaluated? This would require the model to keep track of the bioenergetics of *Calanus finmarchicus*, starting from eggs to the C4 stage. The model can become complex very quickly, with a dramatic increase in model parameters and associated uncertainty (see a recent example by Maps et al. 2010). More importantly, at the C4 or C5 stage, an assumption has to be made on when and at what proportion the energy allocation needs to switch from development and molting to lipid storage. This very assumption is closely related to the key problem that the present study intends to address.

The approach in the present study is to avoid this problem by not keeping track of the history of individual bioenergetics. Instead, the focus is on the consequence of diapause decision in terms of fitness maximization, and then to derive (inversely) the optimal diapausing time. The inherent assumption in this approach is that individuals need to be physiologically ready (e.g. store enough lipids) prior to diapause. If the environmental conditions in a region do not allow the accumulation of enough lipids within one generation, then the residing population is probably unlikely to persist, unless there is continuous population supply from surrounding regions via an advection process.

### Plasticity and fitness

The habitat of *Calanus finmarchicus* in shelf and open-ocean systems is usually highly dispersive. Populations can be transported from one habitat to another within the generation time scale, and this leads to the question of whether the changes in the response of diapause initiation to environmental conditions is due to genetic variance or phenotypic plasticity. Avery (2005) found that for *Acartia hudsonica* populations in relatively enclosed estuarine systems, phenotypic plasticity allows the population to produce a different percentage of resting eggs in different environments, and the phenotypic plasticity has a genetic component (genotypes vary in the phenotypic expression of egg dormancy depending on the environment). Marcus (1984) also hypothesized that genetic variation might be a major contributor for resting-egg-producing *Labidocera aestiva* in 4 embayments along the northeast US coast. However, the habitats that *C. finmarchicus* resides in are usually more dispersive than the relatively isolated estuaries or embayments. Thus it is expected that phenotypic plasticity is probably the major source of variation in its diapause response to the environment, as the population in the Gulf of Maine is probably connected with the populations from the Scotian Shelf (or further upstream in the Gulf of St. Lawrence) and from deep slope waters (Lynch et al. 1998, Johnson et al. 2006).

The phenotypic plasticity, either in continuous (reaction norm) or discontinuous (polyphenism) form, is a result of local adaption to the environmental variations (Sterns 1989, Nijhout 2003). If *Calanus finmarchicus* can respond to different environmental conditions locally, as my model results suggested, then it would mean that there might be multiple environment cues that work together either in an additive or synergistic manner, which has been suggested for the diapause induction of some insect or copepod species (e.g. Saunders 1971, Watson & Smallman 1971, Hairston & Kearns 1995). It is worth noting that the environmental cues (token stimulus) are different from the ultimate cause of selection (selective environment) (Mayr 1961, Norrbin 1996, Nijhout 2003), and that my model results reflect more on the ultimate cause, although it can help derive possible environmental cues.

One of the key assumptions in the present study is that *Calanus finmarchicus* has a strategy of reducing the risk of catastrophic failure in adverse environmental conditions. Since the diapause for *C. finmarchicus* occurs at the C5 stage, its risk-reducing strategy is likely to be different from the bet-hedging strategy used by egg-diapausing species who can produce either diapausing or non-diapausing eggs (e.g. Hairston & Olds 1987, Bradford & Roff 1993). Instead, *C. finmarchicus* may have a combination of both developmental plasticity (adaptive response to predictive environmental signals) and random phenotypic variation resulting from a strategy known as adaptive coin-flipping (Cooper & Kaplan 1982). Due to the random phenotypic variation component involved in the strategy of a genotype, the measurement of fitness needs to reflect the reproductive outcomes of all individuals with that genotype (e.g. Yoshimura & Clark 1991). The geometric mean of the population growth rate has been used as a standard criterion for evaluating the fitness of genotypes (e.g. Dempster 1955, Cohen 1966, Lewontin & Cohen 1969). This fitness measure is thus being used for the present study.

## Model limitation

The model presented here can be applied to other marine species, including other *Calanus* species, and species that use resting egg for their diapause strategy (e.g. *Acartia* spp. or *Centropages hamatus*). It is worth noting that this model has limitations. For instance, egg production is not related to adult size in the model, although numerous studies have suggested otherwise for many copepod species (e.g. Runge 1985, Durbin et al. 1992, Campbell & Head 2000). Also, the mortality term in the model is very difficult to estimate. The use of a temperature-dependent mortality formulation is mainly based on empirical evidence that (1) predators have a higher predation rate as temperature increases, (2) predator abundance increases in warm seasons (e.g. Sullivan & Meise 1996), and (3) visual predators exert higher predation pressure on prey in warm seasons due to the increase in daylight length. A recent study by Plourde et al. (2009, their Fig. 10a) across the NW Atlantic shelf supports the idea that mortality is usually higher when temperature is higher, although factors other than temperature may determine local or short-term variability in mortality. This kind of variability has been partially accounted for by randomly varying mortality rates in the model. Furthermore, some of the variability in vital rates and environmental condition is difficult to quantify, so simplifications have been made in the model. Finally, the difference in energy cost for individuals with early versus late diapause initiation is not considered in the model. Individuals entering diapause late need less energy to make it through adverse conditions, and therefore need less time preparing for diapause in the C5 stage. Future studies are needed to improve the model by alleviating some of these limitations. Despite the limitations, this modeling study provides new thoughts on the environmental causes of *Calanus finmarchicus* diapause and hopefully can stimulate further experimental and theoretical studies on this interesting and important problem.

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