Diel vertical migration of zooplankton: optimum migrating schedule based on energy accumulation

TATSUKI SEKINO* and NORIO YAMAMURA
Center for Ecological Research, Kyoto University, 509-3 Otsuka Hirano Kami-Tanakami Otsu Shiga 520-2113 Japan
(*author for correspondence, e-mail: sekino@ecology.kyoto-u.ac.jp)

Abstract. Zooplankton perform diel vertical migration (DVM) to avoid predators at the upper water layer, but often stay in the upper water layer throughout the day seeking food in spite of the presence of predators. This difference in migrating behavior has been explained by differences in environmental conditions or genetic differences. We examined theoretically how nutritious conditions of zooplankton individuals relate to determining different migrating behavior. A simple optimization model, maximizing the population growth rate, demonstrates that zooplankton individuals change their migrating behavior depending on the amount of accumulated energy. Such energy accumulation and its investment in reproduction are repeated every reproductive cycle. Therefore, unless the reproductive cycle is synchronized among individuals, different migrating behaviors will be observed within a population even if no genetic differences exist. Our model demonstrates that such coexistence of the two migrating behaviors is possible in natural *Daphnia* populations, and suggests that internal conditions of zooplankton individuals may be important as a factor for determining migrating behavior of zooplankton.

Key words: *Daphnia*, DVM, nutritional status, predation, reproductive cycle, thermal structure

Table 1. Glossary of symbols

Symbol	Interpretation	Unit
r	growth rate of a given *Daphnia* population	day^{-1}
i	number of days staying in the upper water layer	days
T	number of days for a reproductive cycle	days
T_s	number of days for a reproductive cycle when a given individual stays in the upper water layer during whole reproductive cycle	days
T_m	number of days for a reproductive cycle when a given individual performs DVM during whole reproductive cycle	days
T_0	number of days before maturation	days
g_m	expanding rate of period of a reproductive cycle due to DVM (equal to T_m/T_s)	
N	number of eggs produced in a reproductive cycle	eggs

Table 1. (Continued)

Symbol	Interpretation	Unit
N_0	number of eggs produced in the 1st reproductive cycle	eggs
k	number of eggs produced per unit energy	eggs $\cdot$ J^{-1}
a_s	daily accumulated energy when staying in the upper water layer	J $\cdot$ day^{-1}
a_m	daily accumulated energy when performing DVM	J $\cdot$ day^{-1}
S	survival probability over a single reproductive cycle	cycle^{-1}
S_0	survival probability for maturation	
s_s	daily survival probability when staying in the upper water layer	day^{-1}
s_m	daily survival probability when performing DVM	day^{-1}

Introduction

Diel vertical migration (DVM) is a general phenomenon in marine and fresh water zooplankton. Usually, zooplankton ascend to the upper water layer at dusk after staying in a deeper layer during daytime, and then descend again at dawn (Cushing, 1951; Hutchinson, 1967). Several hypotheses have been proposed to explain DVM (Kerfoot, 1985; Lampert, 1989, 1993). Among these, the 'predator avoidance hypothesis' has received most support from various researchers (Zaret and Suffern, 1976; Stich and Lampert, 1981; Wright *et al.*, 1980). This hypothesis states that zooplankton stay in the deeper water layer with little light and low food levels to avoid visually searching predators such as fish during daytime, but migrate to the food-rich upper water layer to gain food during nighttime.

Huntley and Brooks (1982) reported that when the food supply was limited, the zooplankton stayed in the upper water layer throughout the day despite the presence of predators. This suggests that whether zooplankton perform DVM or stay in the upper water layer throughout the day is a result of the trade-off between the necessity to avoid visually searching predators and the necessity to gain food (Johnsen and Jakobsen, 1987; Lampert, 1989). Therefore, it has been proposed that seasonal changes in the trade-off between predation pressure and food abundance can cause seasonal changes between the two migrating behaviors. Apart from these seasonal changes, inter- or intraspecifically both migrating behaviors have been observed simultaneously within lakes (Stich and Lampert, 1981; Weider, 1984; Guisande *et al.*, 1991). Since prey body size influences visibility to predators (Zaret and Kerfoot, 1975; Brooks and Dodson, 1965; Wright *et al.*, 1980), it has been supposed that a genetic difference in body size causes a difference in vulnerability to predation, resulting in a differentiation of migrating behavior (De Meester *et al.*, 1995). However, Sekino and Yoshioka (1995) reported that both migrating behaviors, coexisted within a population of *Daphnia galeata*, but could not be explained by

differences in body size. They suggest that difference in the nutritional status may be important to explain the migrating behavior.

Zooplankton invest most of their accumulated energy for reproduction after maturation (Tessier and Goulden, 1982). Thus, zooplankton with more accumulated energy can produce more offspring and have a higher potential reproductive fitness. In this respect, zooplankton which stay in the upper water layer throughout the day have an advantage over those which perform DVM. Zooplankton eaten by predators, however, lose all accumulated energy and further reproductive potential. If the expected loss is larger than the net energy gain, zooplankton may move to the deeper layer to avoid predators at the expense of energy gain. Assuming that environmental conditions are constant, the net energy gain is proportional to the time period spent in the upper water layer, whereas the expected loss of accumulated energy due to predation increases with increasing amount of accumulated energy. Therefore, it is expected that zooplankton begin to perform DVM when the amount of accumulated energy exceeds a certain threshold. Since energy accumulation and reproductive investment are repeated (Tessier and Goulden, 1982), zooplankton may alter their migrating behavior according to their reproductive cycle. If the reproductive cycle is not synchronized within a population, different migrating behaviors will be observed within the population because the amount of accumulated energy exceeds the threshold in some individuals but not in others.

Several theoretical models about the DVM of zooplankton have been proposed in previous studies. Some previous models verified the predation avoidance hypothesis (demographic simulation model, Wright *et al.*, 1980; game model, Iwasa, 1982; life history model, Fiksen, 1997). Furthermore, Gabriel and Thomas (1988a, b) examined the coexistence of two migrating behavior by an ESS model. These previous models have been constructed focusing mainly on food abundance and predation pressure, and have shown influence of such environmental factors on migrating behavior. However, in these previous studies, it was not clearly shown the influence of internal factors on migrating behavior, though internal factors such as nutritional status are drastically changed by reproduction even if environmental factors are constant. There are few studies to investigate the influence of the internal condition on DVM, although Fiksen and Giske (1995) showed that internal condition affected vertical distribution of copepods by a dynamic optimization model. In the present study, we investigate an optimum migrating schedule under visual predation within the reproductive cycle which maximizes reproductive fitness using a simple mathematical model. We further examine how such a schedule changes according to food abundance and predation pressure. Here, we define the ratio of the two migrating behaviors within each period as the migrating schedule. The present study is carried out using *Daphnia* (Cladocera: Crustacea) as a model animal because they are the dominant zooplankton species in most lakes.

Model

Since mature *Daphnia* produce eggs at each molt, each reproductive cycle corresponds to one molt cycle (Fig. 1). Within each inter-molt period, *Daphnia* accumulate energy and invest in egg production at the end of the inter-molt. The eggs are released into the brood pouch where they develop until the next maternal molt when the neonates are released (Tessier and Goulden, 1982). Since eggs in the brood pouch do not obtain any nutrition from the maternal individual, duration of egg development depends only on water temperature. As egg development time is roughly equal to inter molt duration (Tessier and
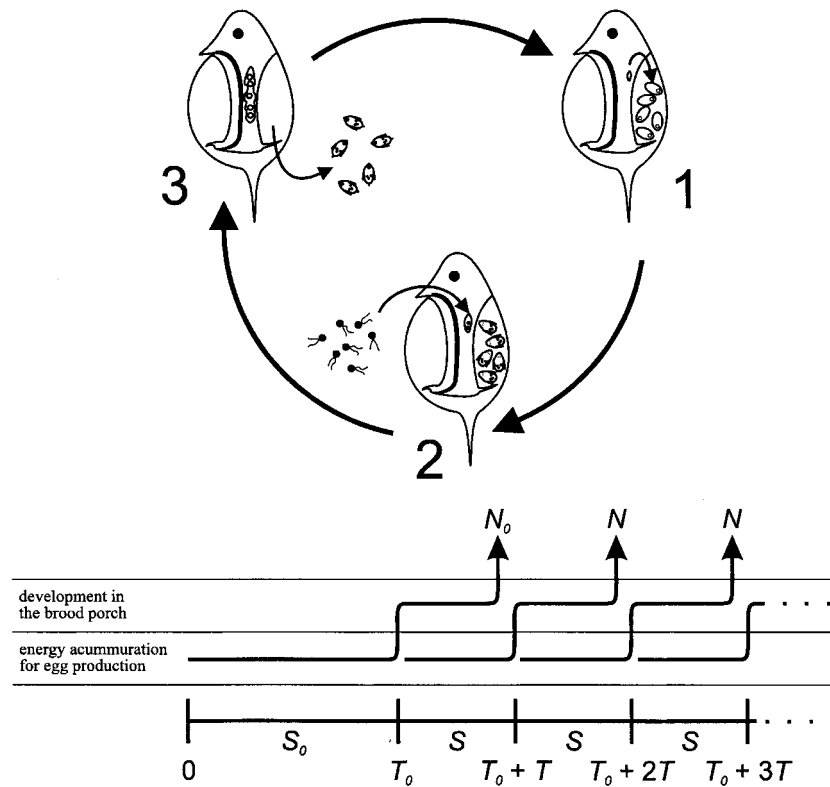

Figure 1. The upper panel is a reproductive cycle of *Daphnia*. (1) A maternal *Daphnia* produces eggs from accumulated energy, and moves the newly produced eggs into the brood pouch. (2) The *Daphnia* develops the eggs in the brood pouch, and accumulates energy for the next reproductive investment. (3) The *Daphnia* releases eggs in the brood pouch. The lower panel is a life times reproductive schedule of *Daphnia*. After the juvenile period (T_0), the *Daphnia* begins reproduction with a period (T). Using accumulated energy from the juvenile period, the first clutch N_0 is released after the first egg development period (T). The *Daphnia* repeats the reproductive cycles. In each cycle, it releases N offsprings using accumulated energy from the previous reproductive cycle. The survival probability of each period is shown in parameters S and S_0.

Goulden, 1982), our model assumes that one reproductive cycle corresponds to the egg development time.

The duration of a reproductive cycle is influenced by migrating behavior, because migrating zooplankton which stay in the cool deep layer during daytime have a longer reproductive cycle than zooplankton which stay in the upper water layer throughout the day (Orcutt and Porter, 1983; Ringelberg *et al.* 1991). When the duration of the reproductive cycle for a migrating individual is expanded at a rate of g_m, the number of days for an individual which performs DVM during a whole reproductive cycle (T_m) is expressed as

$$T_m = g_m \cdot T_s \tag{1}$$

where T_s is the number of days for an individual which stays in the upper water layer during a whole reproductive cycle. If an individual which stays in the upper water layer for i days and migrates during the remaining days of the reproductive cycle, number of days of a reproductive cycle (T) for can be expressed as

$$T = i + g_m(T_s - i) \tag{2}$$

since duration for not staying in the upper water layer (i.e. migrating) is expanded at the rate of g_m. Therefore, the number of eggs produced within one reproductive cycle (N) can be expressed as

$$N = k(ia_s + g_m(T_s - i)a_m) \tag{3}$$

where a_s and a_m are the daily amounts of accumulated energy ($J \cdot day^{-1}$) for the staying and migrating individuals, respectively, and k is the number of eggs produced par unit energy (eggs $\cdot J^{-1}$). To simplify the model, it is assumed that N does not change due to size of *Daphnia*, though this may change in real *Daphnia*. Here, we assume $a_s > a_m$, because the migrating individuals stay in the food-poor deeper layer during daytime. The number of eggs in the first clutch (N_0) is different from that in the subsequent clutches (N), because these eggs are produced from energy accumulated during juvenile development (Fig. 1). Survival probability during a reproductive cycle (S) can be expressed as

$$S = s_s^i s_m^{g_m(T_s - i)} \tag{4}$$

where s_s and s_m are the daily survival probabilities (day^{-1}) for the staying and migrating individuals, respectively. Here, we assume $s_s < s_m$, because the death rate due to predation is lower for migrating individuals relative to staying individuals.

When survival probability during juvenile development is S_0, the survival probability between birth of the individual and releasing of neonates at the xth clutch is

$$S_0 S^x.$$

A growth rate of the population (r) satisfies Euler's equation (Stearns, 1976):

$$\sum 1(y)m(y)\mathrm{e}^{-ry} = 1, \tag{5}$$

where y is an age, $1(y)$ is the survival provability to age y, and $m(y)$ is the fertility at age y. In the present case (see Fig. 1), the equation is described as

$$S_0 SN_0 \mathrm{e}^{-r(T_0+T)} + S_0 S^2 N\mathrm{e}^{-r(T_0+2T)} + S_0 S^3 N\mathrm{e}^{-r(T_0+3T)} + \cdots = 1, \tag{6}$$

where T_0 is the number of days before maturation. Summing up the geometric series in the above equation, we have

$$S_0 \mathrm{e}^{-rT_0}\left(N_0 S\mathrm{e}^{-rT} + N\frac{(S\mathrm{e}^{-rT})^2}{1 - S\mathrm{e}^{-rT}}\right) = 1. \tag{7}$$

Following standard evolutionary models of life history, we assume that the migrating schedule evolves so that the population growth rate (r) is maximized. If the growth rate (r) is maximum when $i = T_\mathrm{s}$, staying in the upper water layer during a whole reproductive cycle (non-DVM) is the optimum migrating schedule. If the growth rate (r) is maximum when i is 0, DVM during the whole reproductive cycle (continuous-DVM) is the optimum migrating schedule. If the growth rate (r) is maximum when i is between 1 to $T_\mathrm{s} - 1$, the optimum migrating schedule is to stay in the upper water layer for i days, and then perform DVM for $g_\mathrm{m}(T_\mathrm{s} - i)$ days (occasional-DVM). The i values which maximize r were calculated by a computer under given parameters, and then conditions for these optimum migrating schedules were represented as regions in the space of the ratios of $s_\mathrm{m}/s_\mathrm{s}$ and $r_\mathrm{m}/r_\mathrm{s}$.

To examine relationship between optimum migrating schedule and environmental conditions, we used literature values on *Daphnia* species to obtaion standard values for parameters. We also examined the effect of deviations from these standard values. We set T_s at 5 days and g_m at 2 according to Bottrell *et al.* (1976), assuming that water temperatures in the epi- and hypolimnion are 14 and 8 °C, respectively. Since duration of maturation for *Daphnia* species is about 8 days at 14 °C (Hovenkamp, 1991), we set T_0 at 8, assuming that juveniles always stay in the upper water layer. If mature individuals continue to stay in the upper water layer during all T_s days of a reproductive cycle, the number of produced eggs within the reproductive cycle (i.e. the clutch size) is expressed as $ka_\mathrm{s}T_\mathrm{s}$. Assuming this egg number is the clutch size for the next reproductive cycle ($ka_\mathrm{s}T_\mathrm{s}$), it was set to 15 which falls within the usual clutch size range for *Daphnia* species (Hall, 1964). Therefore, ka_s was set equal 3.0. Daily survival probability of adults s_m was tentatively assumed to be 0.9. Survival probability during T_0 days of the juvenile period S_0 was set at 0.4, assuming that daily survival probability of juveniles was roughly equal to that of adults ($0.9^8 \cong 0.4$). Number of eggs in the first clutch N_0 was also assumed to be 5 eggs.

Results

Using the values mentioned above, we calculated the number of days necessary to stay in the upper water layer (i) so that the growth rate (r) is maximized in space ($a_{\mathrm{m}}/a_{\mathrm{s}}$, $s_{\mathrm{m}}/s_{\mathrm{s}}$) which is depicted in Fig. 2. It is shown that when the value of $s_{\mathrm{m}}/s_{\mathrm{s}}$ is low, the fitness is maximum at $i = T_{\mathrm{s}}$. This means that the optimum migrating schedule is staying in the upper water layer during the whole reproductive cycle (non-DVM). As $s_{\mathrm{m}}/s_{\mathrm{s}}$ increases, the optimum value of i, the number of days for staying in the upper water layer, decreases. This implies that the increase in $s_{\mathrm{m}}/s_{\mathrm{s}}$ enhances DVM. When the optimum value of i is 0, the individual performs DVM everyday during the whole reproductive cycle (continuous-DVM). Whereas, when the optimum value of i is between 1 and 4 (i.e. $T_{\mathrm{s}} - 1$), the individual continues to stay in the upper water layer for i days, and then performs DVM for $T_{\mathrm{s}} - i$ days (occasional-DVM). However, occasional-DVM never becomes the optimum strategy for any $s_{\mathrm{m}}/s_{\mathrm{s}}$ when $a_{\mathrm{m}}/a_{\mathrm{s}}$ takes the special value of 0.5. Non-DVM is optimal for any $a_{\mathrm{m}}/a_{\mathrm{s}}$ at a low value of $s_{\mathrm{m}}/s_{\mathrm{s}}$. At higher values of $s_{\mathrm{m}}/s_{\mathrm{s}}$, the optimum value of i gradually decreases as $a_{\mathrm{m}}/a_{\mathrm{s}}$ increases. This means that with decreasing daily energy
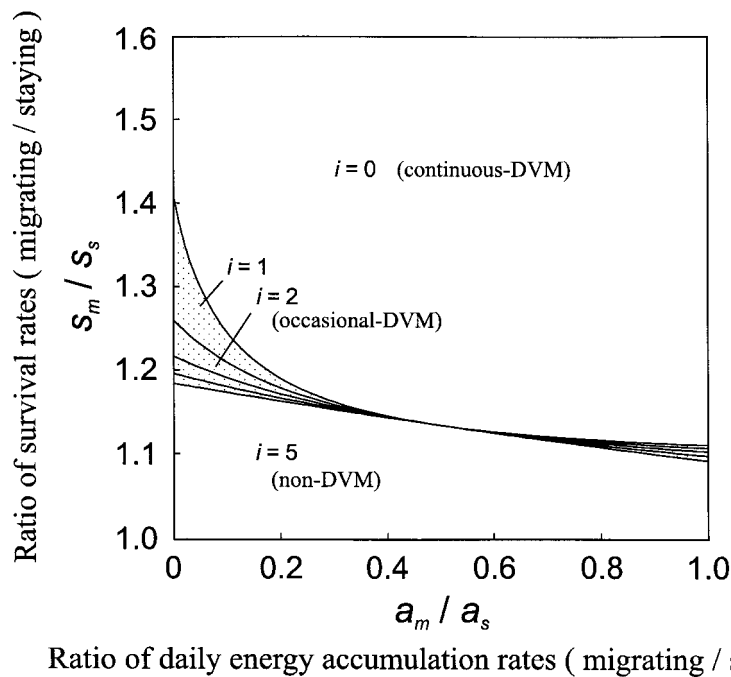

Figure 2. The number of days for staying at the upper water layer (i) to maximize the growth rate (r), illustrated as regions in the space of the ratio of survival probabilities ($s_{\mathrm{m}}/s_{\mathrm{s}}$) and the ratio of daily energy accumulation ($a_{\mathrm{m}}/a_{\mathrm{s}}$). $T_{\mathrm{s}} = 5$; $T_0 = 8$; $g_{\mathrm{m}} = 2$; $ka_{\mathrm{s}} = 3.0$; $s_{\mathrm{m}} = 0.9$; $S_0 = 0.4$; $N_0 = 5$.

accumulation in the upper water layer, the optimum migrating schedule changes from non-DVM to continuous-DVM through occasional-DVM. However, when s_m/s_s takes a still higher value, non-DVM never becomes the optimum migrating schedule for any a_m/a_s. As s_m/s_s increases further, the only optimum migrating behavior is continuous-DVM for the optimal behavior for any a_m/a_s. In this sense, we can say that the ratio of survival probabilities s_m/s_s affects more strongly than the ratio of energy accumulating rates a_m/a_s.

Since the duration of a reproductive cycle (T_s) and the duration of maturation (T_0) are affected by water temperature (Hall, 1964; Bottrell et $al.$, 1976; Hovenkamp, 1991), we examined the effect of water temperature on the optimum migrating schedule. The optimum migrating schedules in space (s_m/s_s, a_m/a_s) were calculated for 18 °C (high temperature) and 10 °C (low temperature) in the upper water layer, where reproductive cycles of $Daphnia$ (T_s) are 3 and 8 days, respectively, and maturation of $Daphnia$ (T_0) is 6 and 14 days, respectively (Fig. 3). In the calculations, the other parameters were fixed to those given for 14 °C where $T_s = 5$ and $T_0 = 8$ in Fig. 2. The regions of occasional-DVM for the higher temperature occupy higher positions so that the region of non-DVM decreases and that of non-DVM increases, implying that high water temperature makes DVM disadvantageous. Specifically, we can say that non-DVM is restricted only to low values of s_m/s_s when temperature is low.

Migration also delays egg development due to the thermal structure in the water column. Hence we examined the effect of changes in g_m, according to the thermal structure, on the optimum migrating schedule. The optimum migrating
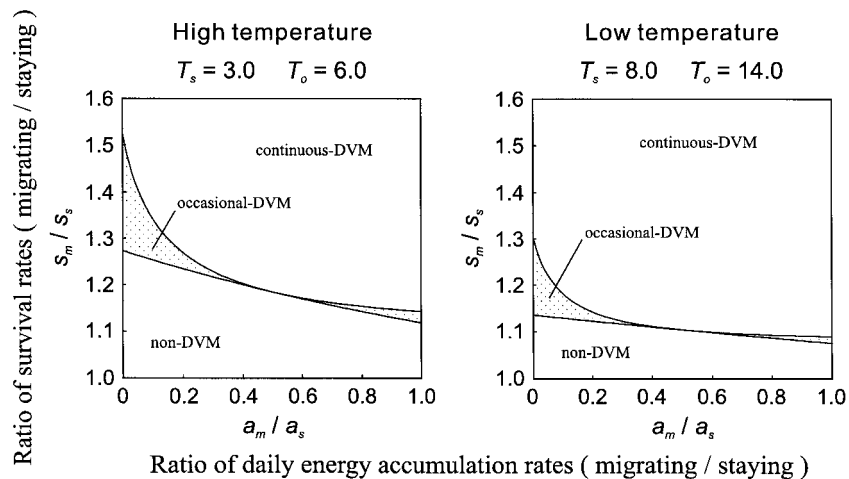

Figure 3. Influence of egg developmental times due to different temperature on the optimum migrating schedule. Left panel (a), $T_s = 3$ and $T_0 = 6$ (high temperature); right panel (b), $T_s = 8$ and $T_0 = 14$ (low temperature). The other parameters are the same in Fig. 2.
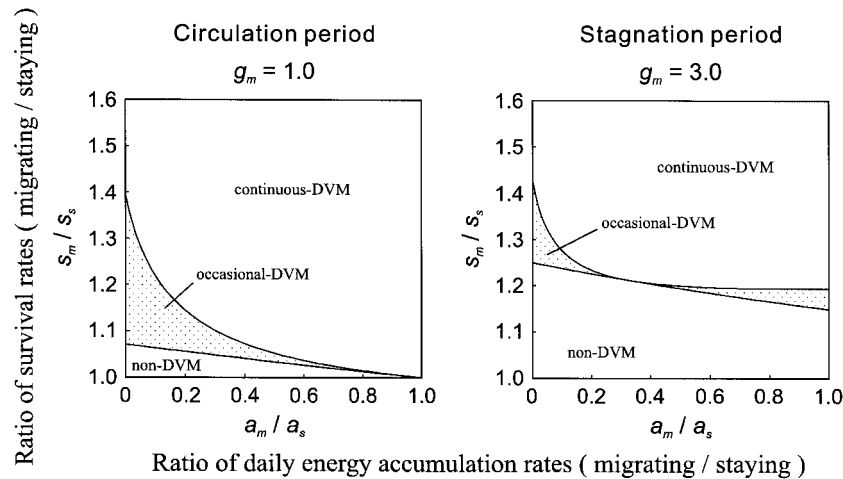
Figure 4. Influence of thermal structure in water column on the optimum migrating schedule. Left panel (a), $g_m = 1.0$ (circulation period); right panel (b), $g_m = 3.0$ (stagnation period). The other parameters are the same in Fig. 2.

schedules in space (s_m/s_s, a_m/a_s) were calculated when the values of g_m are 1 (circulation period: water temperature in whole water column is $14\,°C$) and 3 (stagnation period: water temperature in the epilimnion is $14\,°C$ and that in the hypolimnion is $6\,°C$) (Fig. 4). In the calculations, the other parameters were fixed to those when $g_m = 2$ as in Fig. 2. As g_m value decreases, the region of occasional-DVM becomes large, and s_m/s_s values to optimize occasional-DVM become low. Furthermore, the a_m/a_s value where occasional-DVM never become optimal for any s_m/s_s changes according to g_m. This result indicates that thermal structure in water column greatly affects the conditions in which occasional-DVM is optimal.

Survival probabilities are influenced by predation pressure. Decreasing the survival probability of adults s_m or that of juveniles S_0, the optimum migrating schedules under higher predation pressure were calculated (Fig. 5). In the calculation, the other parameters were fixed to those when $s_m = 0.9$ and $S_0 = 0.4$ as in Fig. 2. When s_m is decreased to 0.5, the region of occasional-DVM is extremely small. However, when S_0 is decreased to 0.1, the region of occasional-DVM is scarcely different from Fig. 2. These results indicate that occasional-DVM is not often optimal under high predation pressure for adults, while predation pressure for juveniles does not have great influence on migrating behavior.

Although food abundance for each migrating behavior was expressed as relative value (a_s/a_m) in Fig. 2, absolute food abundance may affect migrating behavior. Furthermore, number of eggs in the first clutch (N_0) is also affected by food abundance. To examine the effect of changes in absolute food
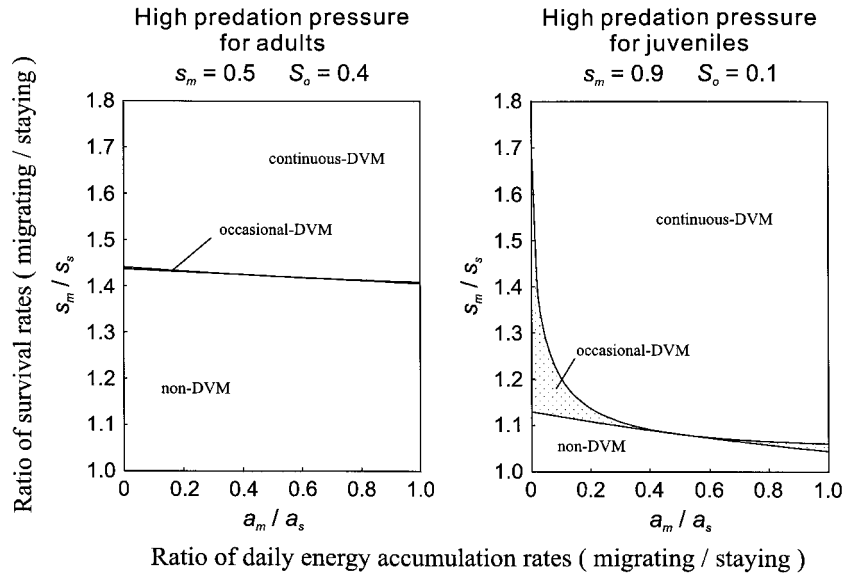
276

Figure 5. Influence of predation pressure on the optimum migrating schedule. Left panel (a), $s_m = 0.5$ and $S_0 = 0.4$ (high predation pressure for adults); right panel (b), $s_m = 0.9$ and $S_0 = 0.1$ (high predation pressure for juveniles). The other parameters are the same in Fig. 2.

abundance, the optimum migrating schedules when $ka_s = 1.0$ and $N_0 = 2$ (poor food) and $ka_s = 5.0$ and $N_0 = 8$ (rich food) were calculated (Fig. 6). In the calculations, the other parameters were fixed to those when $ka_s = 3.0$ and $N_0 = 5$ as in Fig. 2. Occasional-DVM is optimal at larger s_m/s_s values for larger ka_s and N_0 values, and hence the region of non-DVM is larger and that of continuous-DVM is smaller. This result indicates that increase in absolute food abundance restricts the conditions for performing DVM.

Discussion

The present study suggests that *Daphnia* may change its migrating behavior during a reproductive cycle depending on the amount of accumulated energy. Since the reproductive cycle of *Daphnia* is not generally synchronized among individuals (Hall, 1964), we may observe two groups with different migrating behaviors within a population: one group stays in the upper water layer throughout the day and the other group performs DVM. In previous studies, coexistence of different migrating behaviors has been explained by genetic differences (Guisande *et al.*, 1991; De Meester *et al.*, 1995). In support of this explanation, some genotypes are known to coexist simultaneously in a lake (Weider, 1984; Müller and Seitz, 1993; Spaak and Hoekstra, 1993). However,
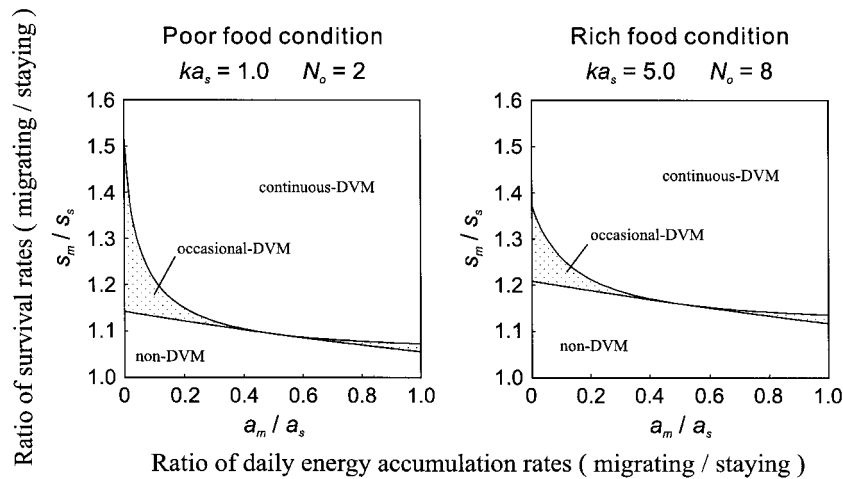
Figure 6. Influence of absolute food abandance on the optimum migrating schedule. Left panel (a), $ka_s = 1.0$ and $N_0 = 2$ (low food abandance); right panel (b), $ka_s = 5.0$ and $N_0 = 8$ (high food abandance). The other parameters are the same in Fig. 2.

our result suggests that difference in migrating behavior can also be explained simply by a difference in the amount of accumulated energy among individuals within the same population. If migrating behavior is changed only by difference in genotype, an individual *Daphnia* cannot change its migrating behavior by changes in the amount of accumulated energy. Nevertheless, some previous studies showed that changes in migrating behavior of zooplankton can be explained by phenotypical polymorphism because the changes were induced by the presence of predators (Ringelberg, 1991; De Meester, 1993), suggesting that phenotypical changes in migrating behavior may also be induced by changes in the amount of accumulated energy.

The survival probability for each migrating behavior (s_m and s_s) depends on predation pressure at different depths. When predators are absent, s_m/s_s is 1. As predation pressure in the upper water layer increases, s_m/s_s increases due to decreasing s_s. A survival probability of less than 0.5 per day for *Daphnia* is not usually observed in a natural population (Hall, 1964; Byron *et al.*, 1986; Lueck *et al.*, 1990; Walters *et al.* 1990; Lampert, 1991), so the maximum s_m/s_s is not larger than 2. Thus, most s_m/s_s values for a natural population are likely to be in the range of between 1 and 2. Therefore, the range of s_m/s_s observed in the present study is realistic in natural populations. In addition, Lampert (1987) reported that daily death rates of migrating individuals and of staying individuals were 0.019 and 0.100, respectively in a natural population of *Daphnia* in Lake Constance. In this case, since $s_m = 0.981$ and $s_s = 0.900$, s_m/s_s is 1.090.

The daily amount of energy accumulation (a_m and a_s) depends on food abundance in the upper and the deeper water layers. The vertical difference in

food abundance changes between seasons (Huntley and Brooks, 1982). When the vertical difference in food abundance is small, a_m/a_s approaches 1. On the other hand, when food abundance in the deeper layer is smaller than that in the upper water layer, a_m/a_s is less than 1. If the vertical difference in food abundance is great, a_m/a_s is roughly equal to the ratio of length of night to length of day because length of night determines the period that migrating individuals can gain food in the food-rich upper water layer. Thus, a_m/a_s can be much less than 0.5 in summer except for low latitudes. In addition, since migrating individuals require time for migration between the deeper and the upper water layer, the period that migrating individuals gain food at the upper water layer is shorter than the length of nighttime. Therefore, a_m/a_s may often approach 0. Consequently, it is supposed that the value of a_m/a_s in a natural population may take on various values in the range between 0 and 1 for which we examined the optimal migrating behavior.

As shown in Fig. 2, occasional-DVM appears generally in a region where $s_m/s_s \cong 1.2$ and $a_m/a_s < 0.5$ when other parameters take standard values for *Daphnia* species. The above discussion implies that these values are not unrealistic in natural populations, and therefore, the occasional-DVM may be realistic as an optimum migrating schedule.

Occasional-DVM was defined as the migrating schedule in which zooplankton perform DVM after staying in the upper water layer within a reproductive cycle. In our model, however, the growth rate does not change between individuals performing DVM before and after staying in the upper water layer, if the number of days they stay in the upper water layer is the same (see equations (2)–(4)). Nevertheless, in natural populations, it is supposed that *Daphnia* perform DVM after staying in the upper water layer in occasional-DVM, for the following reason which was not included in the model assumption. *Daphnia* accumulate lipid as energy for reproductive investment (Tessier and Goulden, 1982). These lipids are combined with carotenoids, and therefore are colored (Green, 1957). Colored eyes appear in eggs in the brood pouch as the eggs develop (Threlkeld, 1979). Therefore, individuals with colored lipid and developed eggs during the latter period of a reproductive cycle are more visible than individuals during the earlier period of the reproductive cycle. Generally, size, transparency and color of zooplankton body affect visibility to a predator (Zaret and Kerfoot, 1975; Kerfoot, 1985), and cause difference in migrating behavior (Bollens and Frost, 1991; Hays *et al.*, 1994). Thus, predation pressure is higher during the later period than the earlier period of a reproductive cycle. This difference in predation pressure between the periods implies that individuals should stay at the upper water layer during the earlier period of the reproductive cycle in occasional-DVM. This is consistent with an observation by Sekino and Yoshioka (1995) that *Daphnia* with early stage eggs stayed in the upper water layer throughout a day, while *Daphnia* with late stage eggs

performed DVM. It is also easily expected that if the model is modified so that the survival probability decreases more strongly in s_s than s_m as reproductive cycle proceeds, the above order of migrating behavior becomes optimal.

Decrease in water temperature causes an increase in the period of a reproductive cycle. Therefore, migrating zooplankton which stay in the cool deep layer during daytime have a longer period of the reproductive cycle than zooplankton which stay in the warm upper water layer throughout the day (Orcutt and Porter, 1983; Ringelberg et $al.$ 1991). In our model, the effect of low temperature in the deeper layer for a reproductive cycle was expressed as a parameter g_m, (Figs. 2 and 4). The a_m/a_s value where occasional-DVM is not optimum for any s_m/s_s changed according to g_m, and was $1/g_m$. When $a_m/a_s = 1/g_m$, number of eggs produced by a reproductive cycle (N) is constant for any i from equation 2. This may be the reason why migrating behavior changes directly between non-DVM and continuous-DVM at a certain value of s_m/s_s. However, the condition where occasional-DVM is not optimal is confined to a special value of a_m/a_s for each g_m. This result implies that the conditions for occasional-DVM to be optimal are widely satisfied, even if the reproductive cycle is changed by the difference of water temperature between the upper and deeper layers. McLaren (1963, 1974) suggested that when thermal stratification is developed, migrating behavior of copepods in later developmental stage is advantageous to increase fecundity. This implies that migrating behavior may change once in their life. However, our results suggests that migrating behavior of $Daphnia$ changes many time according to reproduction cycle, and the change (i.e. occasional-DVM) occurs at a certain condition regardless of thermal structure in a water column.

The condition for occasional-DVM to be optimal is very strict for small survival probabilities of migrating adults s_m (Fig. 5a). This result implies that the occasional-DVM is rarely an optimal migrating schedule under high predation pressure for adults. When $s_m = 0.5$ in Fig. 5, death rates for the staying individuals is more than 0.5 since $s_m/s_s > 1$. Such high death rates do not seem to be realized in natural populations (Hall, 1964; Byron et $al.$, 1986; Lueck et $al.$, 1990; Walters et $al.$ 1990; Lampert, 1991). Thus, the conditions for occasional-DVM to be optimal usually have a wide range in natural $Daphnia$ populations, though intensity of predation pressure affects the conditions.

In previous studies, migrating behavior of zooplankton has often been explained by the trade-off between avoidance of visually searching predators and food gain (Johnsen and Jakobsen, 1987; Lampert, 1989). Our model explains this mechanism via changes in s_m/s_s and a_m/a_s which relate to vertical difference in predation pressure and food abundance, respectively. Furthermore, our model demonstrates that not only relative food abundance in the upper water layer but also an increase in absolute food abundance restricts DVM (Fig. 6). However, some previous studies demonstrate contrarily that a

decrease in absolute food abundance restricts DVM (Huntley and Brooks, 1982; Johnsen and Jakobsen, 1987). According to these studies, zooplankton decrease DVM at low food abundance to avoid starvation even under a high predation pressure. However, our model assumed that *Daphnia* are not starved, and invest net energy gain for reproductive investment. Therefore, for high food abundance, energy gain by staying in the upper water layer exceeds the mortality loss. The difference in the present and previous studies suggests that the influence of absolute food abundance on migrating behavior differs between starved and unstarved conditions.

In conclusion, difference in migrating behavior of *Daphnia* can be explained by behavioral changes depending on the amount of accumulated energy. This conclusion implies that the nutritional status of zooplankton individuals is important in determining their migrating behavior. In previous studies, nutritional status as a result of the migrating behavior has been studied (Guisande *et al.*, 1991; Duncan *et al.*, 1993). However, nutritional status has scarcely been studied as the factor influencing migrating behavior, though Fiksen and Giske (1995) examined how the internal state of copepods affect DVM. By connecting the nutritional status directly to the migrating behavior, our model provides a theoretical base which explains various types of DVM of *Daphnia* and other Cladocera without the need to involve genetic difference or fluctuating environmental conditions. Since our model is concentrated on the internal nutritional state, other important factors may not be involved. However, by modifing our model, more comprehensive models would be made with other factors such as the effect of fish kiromones on DVM.

Acknowledgements

References

Bollens, S.M. and Frost, B.W. (1991) Ovigerity, selective predation, and variable diel vertical migration in *Euchaeta elongata* (Copepoda: Clanoida). *Oecologia* **87**, 155–161.

Bottrell, H.H., Duncan, A., Gliwicz, Z.M., Grygierek, E., Herzig, A., Hillbricht-Ilkowska, A., Kurasawa, H., Larsson, P. and Weglenska, T. (1976) A review of some problems in zooplankton production studies. *Norw. J. Zool.* **24**, 419–456.

Brooks, J.L. and Dodson, S.I. (1965) Predation, body size, and composition of plankton. *Science* **150**, 28–35.

Byron, E.R., Sawyer, P.E. and Goldman, C.R. (1986) The recurrence of *Daphnia rosea* in Lake Tahoe: analysis of a population pulse. *J. Plankton Res.* **8**, 771–783.

Cushing, D.H. (1951) The vertical migration of planktonic crustacea. *Biol. Rev.* **26**, 158–192.

De Meester, L. (1993) Genotype, fish-mediated chemicals, and phototactic behavior in *Daphnia magna. Ecology* **74**, 1467–1474.

De Meester, L., Weider, L.J. and Tollrian, R. (1995) Alternative antipredator defenses and genetic polymorphism in a pelagic predator-prey system. *Nature* **378**, 483–485.

Duncan, A., Guisande, C. and Lampert, W. (1993) Further trade-offs in *Daphnia* vertical migration strategies. *Arch. Hydrobiol. Beih.* **39**, 99–108.

Fiksen, Ø. (1997) Allocation patterns and diel vertical migration: modeling the optimal *Daphnia. Ecology* **78**, 1446–1456.

Fiksen, Ø. and Giske, J. (1995) Vertical distribution and population dynamics of copepods by dynamic optimization. *ICES J. Mar. Sci.* **52**, 483–503.

Gabriel, W. and Thomas, B. (1988a) Vertical migration of zooplankton as an evolutioarily stable strategy. *Am. Nat.* **132**, 199–216.

Gabriel, W. and Thomas, B. (1988b) The influence of food availability, predation risk, and metabolic costs on the evolutionary stability of diel vertical migration in zooplankton. *Verh. Internat. Verein. Limnol.* **23**, 807–811.

Green, J. (1957) Carotenoids in *Daphnia. Proc. R. Soc. Lond. Ser. B* **147**, 392–401.

Guisande, C., Duncan, A. and Lampert, W. (1991) Trade-offs in *Daphnia* vertical migration strategies. *Oecologia* **87**, 357–359.

Hall, D.J. (1964) An experimental approach to the dynamics of a natural population of *Daphnia galeata mendotae. Ecology* **45**, 94–112.

Hays, G.C., Proctor, C.A., John, W.G. and Warner, A.J. (1994) Interspecific difference in the diel vertical migration of marine copepods: The implications of size, color, and morphology. *Limnol. Oceanogr.* **39**, 1621–1629.

Hovenkamp, W. (1991) How useful are laboratory-determined growth curves for the estimation of size-specific mortalities in *Daphnia* populations? *J. Plankton Res.* **13**, 353–361.

Huntley, M. and Brooks, E.R. (1982) Effects of age and food availability on diel vertical migration of *Calanus pacificus. Mar. Biol.* **71**, 23–31.

Hutchinson, G.E. (1967) *A treatise on limnology*, vol. II. Wiley, New York, USA.

Iwasa, Y. (1982) Vertical migration of zooplankton: A game between predator and prey. *Am. Nat.* **120**, 171–180.

Johnsen, G.H. and Jakobsen, P.J. (1987) The effect of food limitation on vertical migration in *Daphnia longispina. Limnol. Oceanogr.* **32**, 873–880.

Kerfoot, W.C. (1985) Adaptive value of vertical migration: Comments on the predation hypothesis and some alternatives. *Contr. Mar. Sci.* **27**, 91–113.

Lampert, W. (1987) Vertical migration of freshwater zooplankton: Indirect effects of vertebrate predators on algal communities. In W.C. Kerfoot and A. Sih (eds.) *Predation.* University Press of New England, Hanover, N.H, USA, pp. 291–229.

Lampert, W. (1989) The adaptive significance of diel vertical migration of zooplankton. *Funct. Ecol.* **3**, 21–27.

Lampert, W. (1991) The dynamics of *Daphnia magna* in shallow lake. *Verh. Internat. Verein. Limnol.* **24**, 795–798.

Lampert, W. (1993) Ultimate causes of diel vertical migration of zooplankton: New evidence for the predator-avoidance hypothesis. *Arch. Hydrobiol. Beih.* **39**, 79–88.

Lueck, C., Vanni, M.J., Magnuson, J.J., Kitchell, J.F. and Jacobson, P.T. (1990) Seasonal regulation of *Daphnia* populations by planktivorous fish: Implications for the spring clear-water phase. *Limnol. Oceanogr.* **35**, 1718–1733.

McLaren I.A. (1963) Effects of temperature on growth of zooplankton and adaptive value of vertical migration. *J. Fish. Res. Bd. Canada* **20**, 685–727.

McLaren, I.A. (1974) Demographic strategy of vertical migration by a marine copepod. *Am. Nat.* **108**, 91–102.

Müller, J. and Seitz, A. (1993) Habitat partitioning and differential vertical migration of some *Daphnia* genotypes in a lake. *Arch. Hydrobiol. Beih.* **39**, 167–174.

Orcutt, J.D., Jr. and Porter, K.G. (1983) Diel vertical migration by zooplankton: Constant and fluctuating temperature effects on life history parameters of *Daphnia*. *Limnol. Oceanogr.* **28**, 720–730.

Ringelberg, J. (1991) A mechanism of predator-mediated induction of diel vertical migration in *Daphnia hyalina*. *J. Plankton Res.* **13**, 83–89.

Ringelberg, J., Flik, B.J.G., Lindenaar, D. and Royackers, K. (1991) Diel vertical migration of *Daphnia hyalina* (sensu latiori) in Lake Maarsseveen: Part 2. Aspects of population dynamics. *Arch. Hydrobiol.* **122**, 385–401.

Sekino, T. and Yoshioka, T. (1995) The relationship between nutritional condition and diel vertical migration of *Daphnia galeata*. *Jpn. J. Limnol.* **56**, 145–150.

Stich, H.-B. and Lampert, W. (1981) Predator evasion as an explanation of diurnal vertical migration by zooplankton. *Nature* **293**, 396–398.

Spaak, P. and Hoekstra, J.R. (1993) Clonal structure of the *Daphnia* population in Lake Maarsseveen: Its implications for diel vertical migration. *Arch. Hydrobiol. Beih.* **39**, 157–165.

Stearns, S.C. (1976) Life-history statics: a review of ideas. *Q. Rev. Biol.* **51**, 2–47.

Tessier, A.J. and Goulden, C.E. (1982) Estimating food limitation in cladoceran populations. *Limnol. Oceanogr.* **27**, 707–717.

Threlkeld, S.T. (1979) Estimating cladoceran birth rates: The importance of egg mortality and the egg age distribution. *Limnol. Oceanogr.* **24**, 601–612.

Walters, C.J., Robinson, D.C.E. and Northcote, T.G. (1990) Comparative population dynamics of *Daphnia rosea* and *Holopedium gibberum* in four oligotrophic lakes. *Can. J. Fish. Aquat. Sci.* **47**, 401–409.

Weider, L.J. (1984) Spatial heterogeneity of *Daphnia* genotypes: Vertical migration and habitat partitioning. *Limnol. Oceanogr.* **29**, 225–235.

Wright, D., O'Brien, W.J. and Vinyard, G.L. (1980) Adaptive value of vertical migration: a simulation model argument for the predation hypothesis. In: W.C. Kerfoot (ed.) *Evolution and Ecology of Zooplankton Communities*. University Press of New England, Hanover, N.H., USA, pp. 138–147.

Zaret, T.M. and Kerfoot, W.C. (1975) Fish predation on *Bosmina longirostris*: Body-size selection versus visibility selection. *Ecology* **56**, 232–237.

Zaret, T.M. and Suffern, J.S. (1976) Vertical migration in zooplankton as a predator avoidance mechanism. *Limnol. Oceanogr.* **21**, 804–813.