

Limnol. Oceanogr., 47(4), 2002, 925–933
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Size-dependent visual predation risk and the timing of vertical migration: An optimization model

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Abstract

Diel vertical migration (DVM) by zooplankton to deep, poorly illuminated habitats during the day is thought to reduce the probability of attack by visual predators at the cost of decreased net energy gain. Herein, I develop a trade-off model used to predict the timing of vertical migration of zooplankton. The model is based on “Gilliam’s rule”—the notion that animals will select habitats that minimize the ratio of mortality risk/energy gain—and incorporates light- and size-dependent vulnerability to visual predators. The model predicts that smaller, less vulnerable prey should ascend into food-rich surface waters earlier and descend later than larger, more conspicuous organisms over a wide range of conditions. The model has been parameterized for a population of *Euphausia pacifica* in Saanich Inlet, British Columbia, and predicts that 7-mm (larval) animals will ascend/descend ~35 min earlier/later than more conspicuous 24-mm adults. These predictions are consistent with acoustic observations of the timing of DVM in this population. The proposed mechanism for size-dependent timing of DVM is based on the potential for increased energy gain in surface waters and diel changes in vulnerability to size-selective predators. These conditions prevail in both freshwater and marine pelagic environments, and size-dependent DVM is likely to be widespread in zooplankton.

Diel vertical migration (DVM), in which pelagic organisms migrate away from food-rich surface waters during the day, is a common behavior that occurs in a wide range of taxa and environments. The adaptive value of DVM is thought to be a trade-off concerning predator avoidance (Ohman 1990; Lampert 1993), because organisms forgo feeding opportunities in the food-rich surface waters to avoid spatio-temporal overlap with visual predators under high light intensities during the day. Visual predators (planktivorous fish) are highly selective and feed preferentially on large-bodied and pigmented zooplankton prey, which are more optically conspicuous (Brooks and Dodson 1965; Batty et al. 1990; Brodeur 1998). Although vertical migration behavior in zooplankton has been the subject of substantial study in the past, the focus of previous work has been on the amplitude and

presence/absence of migratory behavior (Lampert 1993), whereas the timing of vertical migration has received little attention (but see Enright 1977; Enright and Honegger 1977). If vertical migration behavior is a consequence of the conflicting requirements of feeding and predator avoidance, the time at which organisms migrate between a deep refuge and food-rich surface waters should reflect this trade-off.

In this paper, I present a simple life history model that predicts the timing of vertical migration on the basis of the trade-off between mortality risk and energy gain. The model predicts that, in environments dominated by visual predators, the timing of exchange between the surface and deeper waters should not be identical for all size classes within a population. Rather, smaller prey should enter surface waters earlier and leave later than the larger, more vulnerable organisms. The model is first developed in a general sense and is then parameterized to predict the timing of vertical migration of the euphausiid *Euphausia pacifica* in Saanich Inlet, British Columbia.

Materials and methods

Timing of DVM model—The trade-off model of vertical migration between two vertically separated habitats is based on the notion that animals select habitats that minimize the ratio of mortality/energy gain, (μ/g), where μ is the mortality rate (probability of death d^{-1}) and g is the rate of energy

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Acknowledgments

I am indebted to M. D. Ohman for guidance and criticism in all stages of this work. The comments of D. M. Checkley, J. S. Jaffe, J. T. Enright, M. M. Mullin, P. Ressler, and C. Greene improved the manuscript. J. Gower of the Institute of Ocean Sciences, Sydney, B.C., kindly provided the irradiance measurements. This work was supported by a National Science Foundation graduate fellowship and the Scripps Institution of Oceanography.

Table 1. Symbols, definitions, and units for model parameters.

Symbol	Parameter	Units
z	Depth	m
L	Euphausiid length	mm
μ	Mortality risk	d^{-1}
g	Energy gain	$\mu gC d^{-1}$
k	Diffuse attenuation coefficient	m^{-1}
c	Beam attenuation coefficient	m^{-1}
I_o	Surface irradiance	$\mu E m^{-2} s^{-1}$
E_{bz}	Background irradiance	$\mu E m^{-2} s^{-1}$
T_1	Prey visibility parameter	m^2
K_e	Fish vision saturation parameter	$\mu E m^{-2} s^{-1}$
m_{nv}	Nonvisual mortality risk	d^{-1}
m_v	Visual mortality risk	d^{-1}
r	Visual range	m^{-1}
C_{dm}	Energetic cost of migration	$\mu gC d^{-1}$

gain (mass d^{-1}) in a given habitat (Gilliam and Fraser 1987). Minimizing μ/g maximizes survivorship to a given body size and is an appropriate fitness measure for species able to adjust their generation time and fecundity through increased feeding (Aksnes and Giske 1990; Houston et al. 1993). The use of a ratio as a fitness measure is advantageous when one has imperfect knowledge of the environment, because it requires specification of only the relative levels of μ and g in different habitats (Gilliam and Fraser 1987; Tarling et al. 2000). This construct serves as the basis of an optimization model used to predict the timing of diel vertical migration of several size classes of *E. pacifica* in Saanich Inlet, British Columbia.

In the model, the water column is represented as a two-layer depth-stratified system, with a deep habitat ($z_1 = 90$ m) that corresponds to the daytime depth of the euphausiid population (80–100 m) and a shallow habitat ($z_2 = 10$ m) that corresponds to the 0–20 m nighttime depth of the population (De Robertis 2001). The optimal time at which euphausiids of different body sizes should migrate between these two habitats is predicted on the basis of the μ/g trade-off, which takes into account the rates of energy gain and the size- and time-dependent risk of attack by visual predators in the two habitats. Symbols, definitions, and units for all model parameters are given in Table 1.

Visual range, the distance at which a predator can see a given prey, is used as a proxy for the risk of attack by visually orienting predators. Visual range (r) was derived from ambient irradiance, water clarity, and prey body size using the model of Aksnes and Utne (1997). In this model, two conditions must be met for a fish to detect a prey item: (1) the visual system must be sufficiently sensitive to detect prey at the ambient illumination, and (2) there must be sufficient visual contrast for prey to be distinguished from the background against which they are viewed. The maximum distance at which a given prey can be detected is given by

$$r^2 \exp(cr) = T_1(E_{bz}/[K_e + E_{bz}]) \quad (1)$$

where c is the beam attenuation coefficient, E_{bz} is the ambient background irradiance, K_e is a parameter that controls the irradiance at which the visual system becomes light saturated, and T_1 is a composite parameter that describes prey

visibility incorporating prey area, prey contrast, and predator visual capacity. T_1 is unknown for *E. pacifica* and was approximated under the assumption of similar optical characteristics as for *Gobiusculus flavescens* preying on *Calanus finmarchicus* for which values of $T_1 = 7.5 \times 10^{-2} m^2$ and $K_e = 5 \mu E m^{-2} s^{-1}$ have been determined experimentally (Aksnes and Utne 1997). To account for the size-dependent probability of detection, T_1 was scaled by prey area using a regression of *E. pacifica* length versus projected area (Jaffe et al. 1998), and an area of $2.55 mm^2$ for adult female *C. finmarchicus* derived from measurements of relative body dimensions (Barnes and Barnes 1953) and prosome length (Frost 1974).

The temporal dependence of r in each habitat was modeled on the basis of surface irradiance (I_o) measurements made in Saanich Inlet on 13 August 1996, one of the days of the field study. These measurements were made as 30-min averages and were interpolated with a spline fit. Irradiance prior to 0545 and after 2045 h was below instrument detection limits and was assumed to decay exponentially to $10^{-4} \mu E m^{-2} s^{-1}$, equivalent to the illumination of a half moon (Macy et al. 1998). E_{bz} , the irradiance at habitat depth z , was derived from I_o using Beers law:

$$E_{bz} = I_o e^{-kz} \quad (2)$$

where k is the diffuse extinction coefficient for light intensity perceived by fish (assumed to be $0.15 m^{-1}$ for these waters). The beam extinction coefficient c , which is used to calculate r , was approximated as $c = 4k$ (Aksnes and Giske 1993).

The risk of attack by a cruising visual predator is proportional to r^2 (Aksnes and Giske 1993), and r^2 is used here as a proxy for m_v , the risk of attack by visual predators. Nonvisual sources of mortality, including nonvisual predation by fish and invertebrate predators, as well as mortality due to pathogens and parasites, were assumed to be constant with body size, time of day, and depth. The relative importance of nonvisual sources of mortality relative to visual predators was parameterized as m_{nv} and is expressed as a fraction of the mean mortality risk imposed by visual predators on a 10-mm euphausiid at 10 m depth over a 24-h period. m_{nv} was assumed to be 0.1, which indicates that, for a 10-mm euphausiid residing in the shallow habitat, visual predators impose 10 times more mortality risk than nonvisual sources combined. The ratio of mortality risk/energy gain over 1 day divided into 1-min discrete time steps is given by

$$\mu/g = \sum (m_v[t, z] + m_{nv}) / \sum g(z) \quad (3)$$

where $g(z)$ is the rate of net energy gain at habitat depth z and t is time in min. Because the model minimizes the ratio of μ/g , only the relative levels of mortality risk ($m_v + m_{nv}$) and energy gain $g(z)$ in the two habitats must be specified. The optimal timing of vertical migration that minimizes μ/g was determined by a computer search of possible ascent/descent times. Model solutions were constrained to behaviors in which ascent/descent occurred after/before solar noon and those that resulted in positive energy gain over a 24-h period (i.e., $\sum g[z] > 0$).

Model parameterization—The model was parameterized using carbon as a currency on the basis of measurements

Table 2. Water temperature, food availability, metabolic rates, and rates of energy gain of *E. pacifica* in the shallow (0–20 m) and deep (80–100 m) habitats in Saanich Inlet during summer 1996 and 1997. Negative energy gain ratios reflect a net energy loss in the deep habitat.

	1996		1997	
	0–20 m	80–100 m	0–20 m	80–100 m
Temperature (°C)	14.26	9.37	12.6	8.89
Chl <i>a</i> ($\mu\text{g L}^{-1}$)	10.61	0.20	2.73	0.18
Food availability ($\mu\text{g C L}^{-1}$)	530.5	0.20	136.5	0.18
Energy gain ($\mu\text{g C d}^{-1}$)	413.42	17.25	278.56	13.67
Metabolic demand ($\mu\text{g C d}^{-1}$)	107.89	82.57	98.80	80.49
Net energy gain ($\mu\text{g C d}^{-1}$)	+305.53	−65.32	+179.76	−66.82
Energy gain ratio (shallow/deep)		−4.7		−2.7

made in Saanich Inlet in midsummer of 1996 and 1997. The rate of energy gain in the 10- and 90-m habitats was estimated from measurements of temperature and chlorophyll *a* (Table 2). Food availability in the shallow stratum was estimated from the average Chl *a* concentration in the 0–20 m stratum, under the assumption of a carbon:Chl *a* ratio of 50 (Welschmeyer and Lorenzen 1984). In Saanich Inlet, there is a conspicuous layer of suspended particulate material at ~90 m (Mackie and Mills 1983; De Robertis et al. 2001), which is a potential food source for euphausiids (Dilling et al. 1998). To parameterize the increased availability of detrital material, which has a higher carbon:Chl *a* ratio than phytoplankton (Alldredge 1998), a carbon:Chl *a* ratio of 100 was used in the deep habitat. Chl *a* concentrations at 0–20 m are based on five vertical profiles of extracted chlorophyll made in 1996 and six profiles in 1997, whereas 80–100 m concentrations are based on single profiles. Ingestion rates were estimated on the basis of the functional response of Ohman (1984) and were temperature compensated using a Q_{10} of 2 (Ohman 1984). Gross energy gain was computed from ingestion assuming an assimilation efficiency of 81.3% (Ross 1982). Metabolic loss in carbon units was computed from measurements of oxygen consumption (Torres and Childress 1983) under routine activity assuming a respiratory quotient of 0.9 (Ross 1982). Metabolic demand was computed for an 18-mm (6.31 mg dry weight) euphausiid and was adjusted to environmental temperatures from experimental temperatures of 8°C and 12°C using a Q_{10} of 1.7 (Torres and Childress 1983). In both years, net energy gain (i.e., assimilation–metabolism) was positive in surface waters and negative in deep waters (Table 2).

Initial model runs were conducted with composite “base case” parameters that represented conditions averaged over both years (Table 2). An energy gain ratio of −3.7 between habitats (i.e., shallow/deep habitat) was used in the “base case” scenario. The negative ratio reflects an average energy gain of 242.7 $\mu\text{g C d}^{-1}$ at 10 m and a net energy loss of −66.1 $\mu\text{g C d}^{-1}$ at 90 m.

Sensitivity analyses—The effects of departures from the “base case” parameters were explored in a series of model runs. In these model runs, the time at which 10- and 20-mm euphausiids were predicted to migrate between the deep and shallow habitats was computed for a wide range of nonvisual mortality risks (m_{nv} , 10 to 0.01) and net energy gain ratios

between the shallow and deep habitats. Simulations were conducted for environments in which negative net energy gain ratios reflect a net energy loss in the deep habitat (−1.1 to −40) and those in which energy gain is positive in the deep habitat (1.1–40). In addition, the impact of the energetic cost of vertical migration on optimal migration time was explored by assessing an additional energetic cost for migratory animals. The energetic cost associated with vertical migration was defined as C_{dvm} and was expressed as a fraction of the daily routine metabolic rate of an animal that is resident in the deep layer. C_{dvm} was 0 for nonmigratory euphausiids. In these model runs, μ/g was computed as follows:

$$\mu/g = \Sigma (m_v[t, z] + m_{nv}) / (\Sigma g[z] - C_{dvm}) \quad (4)$$

Model runs were conducted with C_{dvm} ranging between 0% and 30% of the average metabolic rate in the 90-m habitat (81.5 $\mu\text{g C d}^{-1}$).

The fish in Saanich Inlet are different species (primarily juvenile walleye pollock *Theragra chalcogramma* and Pacific herring *Clupea harengus pallasii*; De Robertis et al. 2000) than the species used to parameterize the model. To assess the sensitivity of the model predictions to the visual sensitivity of the visual predators, a series of simulations in which K_e , the parameter that controls the irradiance at which vision becomes saturated, was varied between 10^{-3} and $10^2 \mu\text{E m}^{-2} \text{ s}^{-1}$. In addition, the effect of water clarity on the optimal timing of vertical migration was investigated by varying k , the diffuse extinction coefficient over the range of 0.04 to 0.4 m^{-1} .

Results

Predator visual range (r) increases with prey body length (L), but is asymptotic at high irradiance (Fig. 1A). Maximum visual range increases approximately linearly with prey size, and, because the mortality risk inflicted by visual predators (m_v) is proportional to r^2 , m_v is approximately proportional to L^2 at saturating light intensities (Fig. 1B). The ability of visual predators to detect prey is light-dependent. It is low throughout the day in the deep habitat and varies greatly over the course of a day in the 10-m habitat, changing rapidly at twilight (Fig. 2A,B). The relative mortality risk among habitats varies with time of day and is greatly elevated in the 10-m habitat during daylight hours (Fig. 2C).

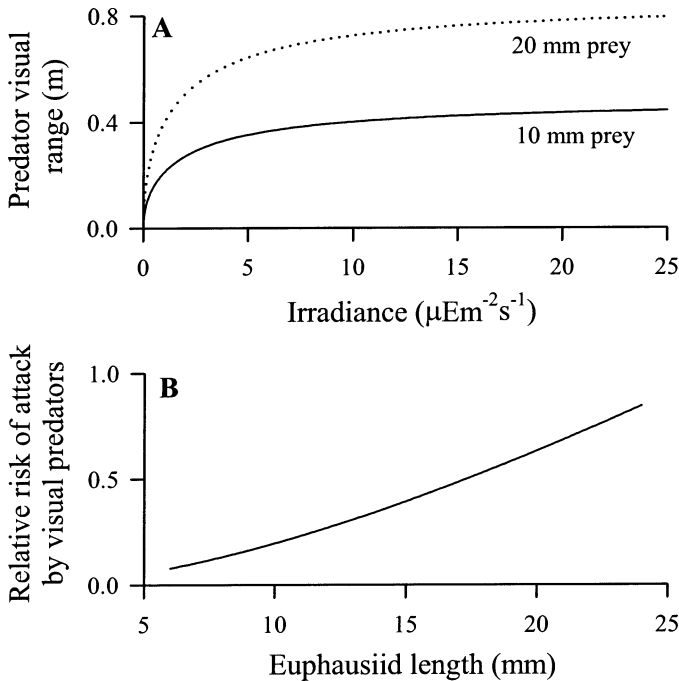


Fig. 1. Vulnerability to visual predators depends on light intensity and prey size. (A) Modeled dependence of the visual range at which a fish can detect two sizes of euphausiid prey (10 and 20 mm) on irradiance level. Visual range increases with prey size and is asymptotic at high irradiance (i.e., $E_{bc} \gg K_e$). (B) Risk of attack by visual predators (m_v) as a function of euphausiid prey size at saturating light intensity ($E_{bc} = 5 K_e$).

Large-bodied euphausiids are disproportionately vulnerable to predatory attack in surface waters relative to deep waters during the daytime (Fig. 2C) because they are more optically conspicuous.

Minimization of the mortality/energy gain trade-off predicts that the timing of DVM should vary with body size. Smaller-bodied prey should ascend earlier (Fig. 3A) and descend later (Fig. 3B) than larger, more conspicuous organisms. Under the “base case” parameters, euphausiids in the 7–24 mm size classes are predicted to ascend into surface waters between 2006 and 2043 h (–10 to +27 min relative to sunset) and descend into the deep habitat between 0606 and 0532 h (+14 to –20 min relative to sunrise). The predicted difference in timing between 7 mm (larval) and 24 mm (large adult) euphausiids is 34 min on ascent and 37 min on descent. Size-dependent differences in the timing of migration are similar for ascent and descent in all model runs, and, in the interest of brevity, only ascent time will be presented for the sensitivity analyses.

Although the predicted times of migration depend on the specific parameter values used (Fig. 4A,B), the prediction of size-dependent DVM is robust under a wide range of environmental conditions. Euphausiids spend more time in the food-rich surface waters when visual predation is less intense (i.e., m_v/m_m is low). Size-dependent vertical migration with smaller-bodied animals ascending earlier and descending later than adults is predicted to occur over a wide range of energy gain ratios and relative intensities of visual pre-

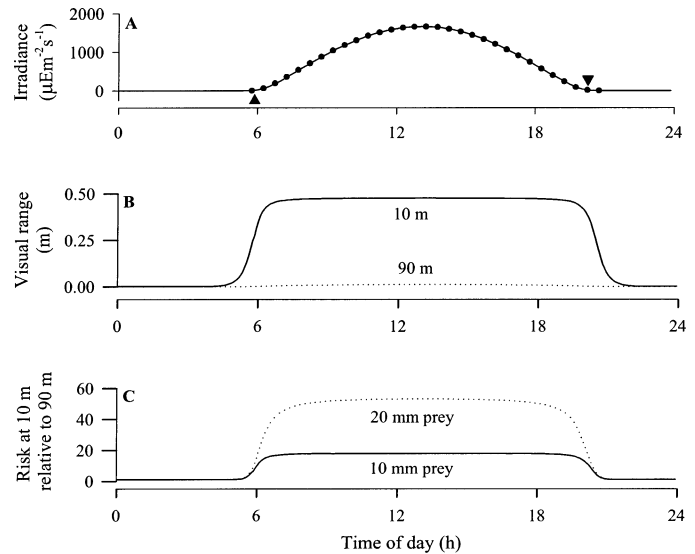


Fig. 2. Ambient irradiance and euphausiid mortality risk in Saanich Inlet. (A) Surface irradiance on 13 August 1996, a cloud-free day. The black circles indicate the measurements. Triangles indicate sunrise and sunset (0552 and 1816 h). (B) Visual range of a visual predator preying on 10-mm euphausiids in the 10- and 90-m habitats as a function of time of day. (C) Temporal dependence of the mortality risk at 10 m relative to that at 90 m for 10- and 20-mm euphausiids.

dation in the two habitats (Fig. 5A,B). Migration patterns in environments where net energy gain is negative (i.e., respiration > assimilation) in the deep habitat (Fig. 5A) are predicted to differ from those in environments with positive net energy gain in the deep habitat (i.e., respiration < assimilation; Fig. 5B). Euphausiids that lose energy while at depth are constrained to spend a fraction of their time (equivalent to deep loss/shallow gain) in the shallow habitat, to compensate for the energetic losses sustained in the deep habitat. As a result, when net energy gain ratios are negative and low, euphausiids that experience energy losses in the deep habitat are more likely to remain in surface waters throughout the day (Fig. 5A). In both types of environments, size-dependent migration is predicted when visual predation is

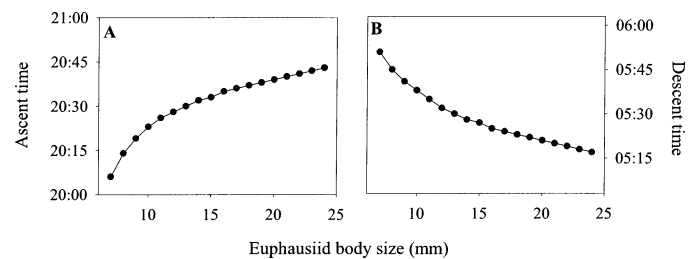


Fig. 3. Results of the “base case” mortality/energy gain (μ/g) trade-off model, which predicts the timing of euphausiid DVM on the basis of size- and light-dependent vulnerability to visual predators. Euphausiids are considered to migrate between two habitat depths (10 and 90 m). Timing of (A) dusk ascent and (B) dawn descent for a series of body sizes predicted by the minimization of μ/g over a 24-h period. Smaller individuals are predicted to ascend earlier and descend later than larger ones.

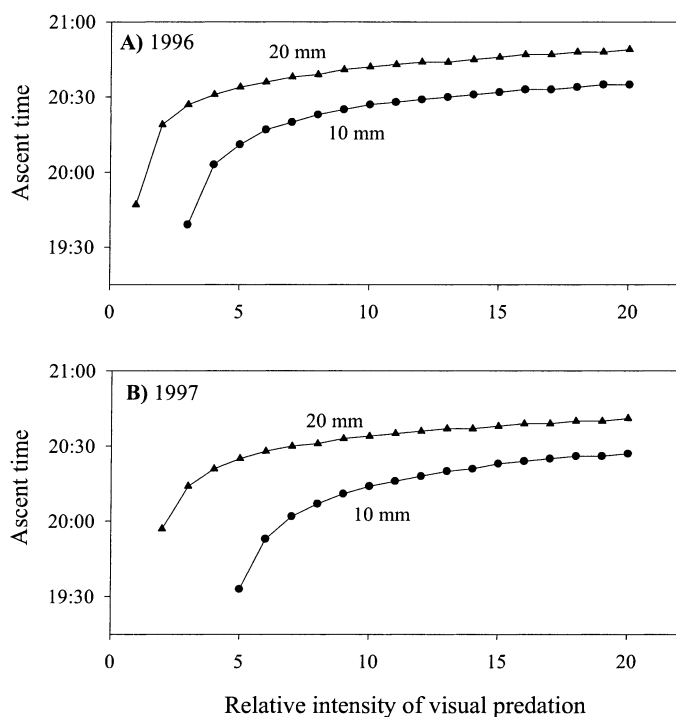


Fig. 4. The time at which 10- and 20-mm euphausiids are predicted to ascend as a function of the relative intensity of visual to nonvisual predation (m_v/m_{nv}). The model was parameterized with (A) an energy gain ratio of -4.7 in the 10- and 90-m habitats, which corresponds to conditions in 1996, and (B) an energy gain ratio of -2.7 , which corresponds to conditions in 1997. Negative energy gain ratios indicate that the euphausiids incur a metabolic loss in the 90-m habitat. Cases at low intensities of visual predation in which euphausiids are predicted to be nonmigratory have been excluded. In all cases, smaller individuals are predicted to ascend earlier than larger ones.

an important source of mortality and energy gain at 10 m is high relative to that at 90 m. The model predicts that, as the relative importance of visual predation decreases, first the smaller-bodied euphausiids and then the more vulnerable larger-bodied euphausiids will discontinue DVM and will remain in the more energetically profitable surface waters throughout the day.

Imposing an energetic cost to vertical migration does not change the prediction of size-dependent DVM (Fig. 6). As the cost of vertical migration increases, euphausiids expose themselves to higher predation risk by ascending earlier and descending later. In addition, the difference in predicted migration times among size classes increases as vertical migration becomes more energetically costly.

Size-dependent timing of vertical migration is predicted under a wide range of predator visual sensitivities (Fig. 7). Size-dependent timing of DVM is also predicted to occur over a range of diffuse attenuation coefficients (Fig. 8). The difference in timing between size classes increases as water clarity decreases. When high water clarity (i.e., low k) or high visual sensitivity (i.e., low K_v) enables visual predators to feed effectively in the deep habitat, the euphausiids will remain at the surface throughout the day because the deep

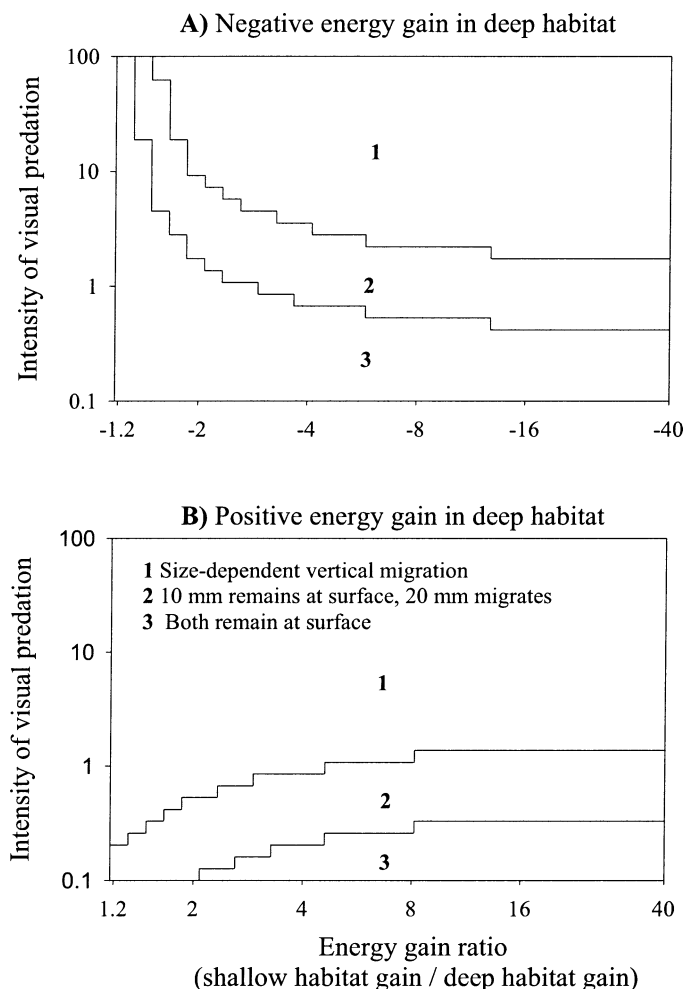


Fig. 5. General predictions of migration behavior of 10- and 20-mm euphausiids for combinations of relative intensity of visual to nonvisual predation (m_v/m_{nv}) and the energy gain ratio between habitats. Predictions of (1) size-dependent migration, (2) migration by 20-mm but not by 10-mm animals, and (3) no DVM out of surface waters by either size class are demarcated by the contour intervals. (A) Predictions for environments in which organisms incur a net energy loss in the deep habitat. (B) Predictions for environments in which organisms incur a net energy gain in the deep habitat. All other parameters are as in the "base case." In both cases, conditions in the shallow habitat are more favorable as the absolute value of the energy gain ratio increases.

habitat no longer offers a sufficient reduction in mortality to offset the lost opportunities for energy gain.

Discussion

Model predictions—The optimization model indicates that zooplankton body size alters the mortality risk versus energy gain (μ/g) trade-off and predicts that, when visual predation risk is high, smaller animals will enter the food-rich surface waters at higher light intensities than larger, more conspicuous individuals. The difference in the time at which different size classes of zooplankters are predicted to migrate depends on the interaction of the size-dependent risk of attack

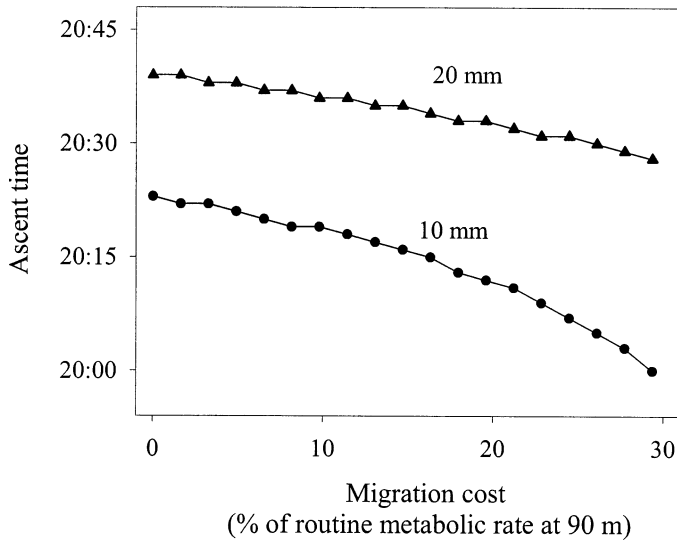


Fig. 6. Effect of the energetic cost of vertical migration on the size-dependent timing of vertical migration. The cost of migration is expressed as a percentage of daily routine metabolic cost in the 90-m habitat. In all cases, smaller individuals are predicted to ascend earlier than larger ones.

by visual predators and the rate of change of light intensity. When visual predation risk increases steeply with size, the difference in the timing of vertical migration among size classes will be larger. The difference in timing should be more pronounced at high latitudes, because the sun rises and sets more slowly at high latitudes (Seidelmann 1992).

The model indicates that vertical migrants will spend less time in surface waters when visual predation risk is large relative to nonvisual mortality. Vertical migrants that experience a net energy loss during the day at depth are predicted to spend more time in surface waters when surface food concentrations are low, because they must compensate for metabolic losses sustained at depth during the day. In contrast, migrants that gain energy in deep waters are predicted to spend less time in surface waters if energy gain in surface waters is low. Although the exact times of migration vary with the parameter values used, the model predicts size-dependent migration over a wide range of conditions.

The model predicts that in Saanich Inlet, 7-mm *E. pacifica* will ascend 37 min earlier and descend 34 min later than 24-mm adults. These predictions can be compared with previous observations of the timing of DVM in this population (De Robertis et al. 2000). In the case of descents ($n = 6$), ~22–24 mm euphausiids descended past an instrument suspended at 40 or 50 m at an average time of 4 min after sunrise, and ~6–8-mm animals descended 24 min after sunrise. In the only ascent record initiated early enough to capture the behavior of the smallest size classes, 6–8-mm euphausiids ascended 20 min after sunset, and 22–24-mm euphausiids ascended 46 min after sunset. The observed differences of 20–25 min in timing of ascent and descent are generally consistent with the model predictions.

Model assumptions—The proposed mechanism for size-dependent timing of DVM is based on the potential for in-

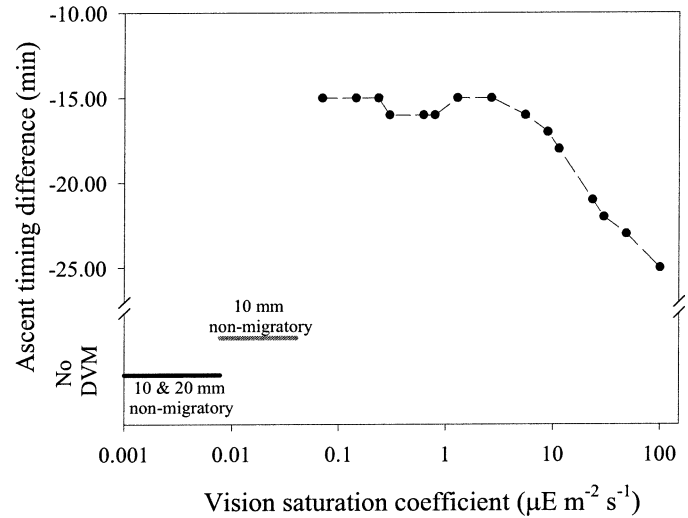


Fig. 7. Effect of fish visual sensitivity on the size-dependent timing of vertical migration. Fish visual sensitivity was changed by altering K_e , which controls the light intensity at which fish vision becomes saturated. Vertical migration out of surface waters ceases when fish are able to prey on the euphausiids at low light intensities (i.e., K_e is low).

creased energy gain in surface waters and spatiotemporal gradients in the size-dependent risk of predatory attack. Both of these conditions are fulfilled for *E. pacifica* in Saanich Inlet, because fish are abundant (De Robertis et al. 2000) and net energy gain is positive in surface waters and negative in deep waters (Table 2).

All size classes of euphausiids are assumed to migrate between the same vertical habitats. In many cases, large zooplankters migrate to deeper daytime strata than smaller-bodied individuals (e.g., Bollens et al. 1992). If there is a major difference in the daytime depth among size classes, the model could be elaborated to specify habitat depths for each size class. In addition, although the model predicts nonmigratory

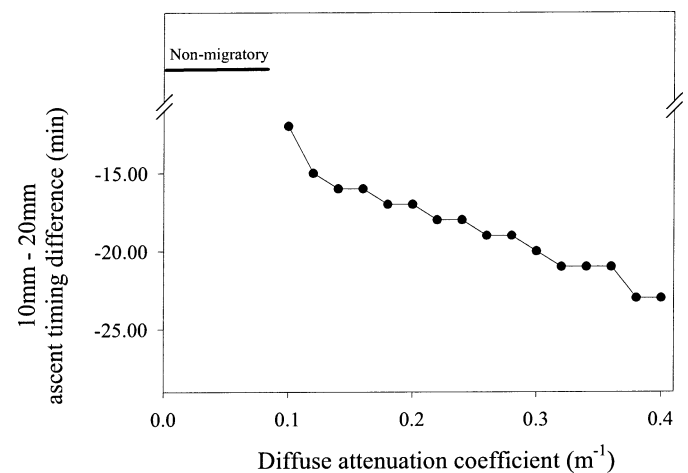


Fig. 8. Difference in predicted ascent times of 10- and 20-mm euphausiids as a function of k , the diffuse attenuation coefficient. Vertical migration out of surface waters ceases at low attenuation coefficients.

behavior when visual predators can feed effectively in the deep habitat, zooplankters in this situation are likely to increase their daytime depth (Tarling et al. 2000). The assumption of two vertical habitats is appropriate for Saanich Inlet, because poorly oxygenated deep water imposes a “false bottom” and restricts the daytime depth of all sizes of migratory zooplankton to ~100 m, which is often shallower and more brightly illuminated than observed in more oceanic habitats (Boden and Kampa 1965).

The model assumes that the ratio of net energy gain in the shallow and deep habitats is constant over the size range of euphausiids modeled. This amounts to the assumption that energy assimilation and metabolic costs scale in the same manner with body size. Ross (1982) measured the ingestion and respiration rates of *E. pacifica* as a function of body carbon and found that the 95% confidence intervals of the allometric exponents of ingestion and respiration rates overlap. This indicates that, in the case of *E. pacifica*, the assumption of no size dependence in net energy gain ratios is not severely violated.

The “base case” parameter values should only be viewed as approximations of conditions in Saanich Inlet. Food availability is likely underestimated by estimates of food concentrations based on Chl *a* values. Although *E. pacifica* exhibits comparatively high clearance rates when feeding on phytoplankton (Ohman 1984), it also consumes microzooplankton and crustacean zooplankton (Ohman 1984; Nakagawa et al. 2001). In addition, *E. pacifica* is assumed to be active and feeding while at depth rather than remaining quiescent to reduce metabolic costs. On the basis of the measurements of Torres and Childress (1983), the ratio of energy gain at 10 m relative to 90 m for nonfeeding, inactive euphausiids was -5.6 in 1996 and -3.7 in 1997. These values should be considered an upper boundary for energy gain ratios, because the euphausiids must swim to avoid sinking (Kils 1981). In Saanich Inlet, the migratory euphausiids travel ~200 m through a 4–5°C thermal gradient, which, based on the measurements of Torres and Childress (1983), is estimated to cost ~6% of the daily routine metabolic rate at depth. The sensitivity analyses indicate that deviations in the “base case” parameters of the magnitude described above do not alter the prediction of size-dependent DVM.

The visual model used here predicts that r , the distance at which zooplankton prey are located by visual predators, is approximately proportional to prey body length. This prediction is consistent with laboratory measurements of r (Confer et al. 1978; O'Brien 1979). In that model, it was assumed that visual predators search for prey as they cruise and that encounter risk is proportional to r^2 . If visual predators search for prey while stationary, encounter risk will be proportional to r^3 (MacKenzie and Kiørboe 1995), which would lead to more pronounced size-dependent DVM. The model implicitly assumes that mortality risk is proportional to encounter risk, which will overestimate the mortality risk inflicted by visual predators on larger size classes, which are likely to have more effective escape responses. In addition, in environments where planktivorous fish are small, gape limitation (Brodeur 1998) may reduce the susceptibility of larger size classes of zooplankton to visual predators. However, the contention that visual mortality risk increases with

zooplankton body size is supported by studies that have demonstrated that planktivorous fish are highly size selective and inflict disproportionate mortality on large-bodied zooplankton (e.g., Brooks and Dodson 1965; Batty et al. 1990; Brodeur 1998).

The model further assumes that nonvisual mortality is independent of body size, time of day, and depth. However, larger-bodied zooplankton are likely to be less vulnerable to nonvisual predators because of their size and increased ability to escape (Greene 1986). Size-dependent vulnerability to nonvisual predators would likely increase the differences in the size-dependent timing of DVM reported here because larger animals would become comparatively less vulnerable at depth and more vulnerable near the surface.

In addition, the model assumes that predators are evenly distributed throughout the water column. Homogeneous predator distributions are unlikely in most environments: for example, in Saanich Inlet, fish are more abundant near the surface (De Robertis et al. 2000), and contact predators such as ctenophores are more abundant in the deeper strata (Mackie and Mills 1983). However, differences in the abundance and type of predators in the shallow and deep habitats should not invalidate the conclusions of this study, because the model continues to predict size-dependent migration in the extreme case of only nonvisual mortality in surface waters and only visual predation in surface waters.

Generality of predictions—Previous field studies indicate that size-dependent DVM may be widespread in zooplankton. In addition to the acoustic observations of *E. pacifica* discussed above, size-dependent timing of DVM, with smaller-bodied organisms ascending earlier and descending later, has been directly observed in the copepod *Calanus pacificus* (Enright and Honegger 1977) and the tunicate *Pyrosoma atlanticum* (Andersen and Sardou 1994). Furthermore, analysis of the extensive continuous plankton recorder survey suggests that, on average, smaller species and life history stages of the copepod *Metridia* spend more time in surface waters (Hays 1995).

Although this is the first model to explicitly address the timing of vertical migration on the basis of the trade-off between mortality and energy gain, previous models have suggested similar behavior. A model of zooplankton and fish distributions in a two-habitat system predicted that more vulnerable prey will ascend into the surface layer at lower light intensities than less vulnerable prey (Iwasa 1982). A more detailed optimization model of copepod reproductive output (Fisken and Giske 1995) predicted that, when copepods are subject to visual predation, larger, more conspicuous stages spend less time near the surface.

The underlying premise of this model is that zooplankton use the mortality risk/energy gain (μ/g) trade-off as a mechanism for vertical habitat choice. Minimizing μ/g maximizes fitness for species able to translate increased energy gain into shortened generation times and increased fecundity (Aksnes and Giske 1990; Houston et al. 1993). In *E. pacifica*, spawning activity, larval development, and age at first reproduction is linked to food availability (e.g., Brinton 1976; Ross et al. 1982; Knight 1984; Bollens et al. 1992), and the μ/g tradeoff is a reasonable criterion to describe optimal habitat choice.

For zooplankton to adjust their behavior to minimize μ/g , they must be able to sense both energy gain and predation risk in different habitats. Although zooplankton may be unable to assess predation risk directly, most species are capable of assessing light intensity as a proxy for vulnerability to visual predators. Zooplankton vertical migrations are triggered by changes in ambient light intensity (Forward 1988; Boden and Kampa 1965). These phototactic responses are modified by chemical cues exuded by visual predators and by food availability (Ringelberg 1995; Forward and Rittshof 2000). Hence, zooplankters appear to possess the ability to estimate diel changes in μ/g by proxy.

Although the model focuses on euphausiids in a particular location, it is generally applicable to other zooplankton. Exponential light attenuation establishes steep vertical gradients of primary production and vulnerability to visual predators, and the surface waters of many marine and freshwater pelagic environments are likely to offer increased feeding opportunities at the cost of an increased risk of predatory attack. The risk of attack in food-rich surface waters is greatly reduced at night, and many pelagic organisms exploit this relative safety by migrating into surface waters at night. As suggested by this model, if the risk of attack by visual predators increases with body size, smaller, less optically conspicuous animals should ascend earlier and descend later than larger, more conspicuous individuals.

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Received: 25 September 2001

Amended: 5 February 2002

Accepted: 5 March 2002