waves, the height of the parent bedforms may have significantly exceeded this estimate. A porosity of 40% is plausible for the loosely packed avalanched sand[19], whence $\gamma = 1{,}600\ \mathrm{kg\,m^{-3}}$. The calculated tidal peak speeds and amplitudes[14] are plausible (Table 1, values not in parentheses), suggesting that the general tidal model is apt, but seem low by a factor of ~2, judging from the Holocene case of the overall mean tidal ranges (springs = 4.4 m, neaps = 2.9 m) predicted at Flushing[15]. Equation (2) apparently overestimates the bedload transport rate when k is based on laboratory experiments, possibly because these were performed at relatively very shallow flow depths. Although Colby's[20] data on the total sand transport of four moderate to large rivers do not equal in quality the laboratory results, they give estimates for k (Table 1, values in parentheses) significantly lower than the experimental ones, when empirically adjusted to bedload alone[13]. The peak tidal speeds and ranges are better (Table 1, values in parentheses) but still low, indicating overestimation of bedload transport. In the tidal case, the widespread deposition of mud and its persistence on the bed from one tide to another may significantly inhibit sand transport during the episodes of dominant current, by armouring the bed (U_{ce} raised) and by reducing the area from which sand can be scoured (flow undercharged with sand). Underestimation of the sand-wave height may also have affected the results.

The above simple model helps us to quantify past cross-bedded tidal sediments. It strengthens the tidal interpretation, and provides crude estimates of the ratios of spring and neap peak tidal speeds and ranges, together with very rough absolute values for range and speed. Its imperfections are attributable to (1) the simplicity of the flow and sediment transport functions used, (2) poor understanding of sediment transport, and (3) possible differences between sand transport in tidal conditions, when mud can accumulate extensively, and in rivers and flumes. The third factor may prove a permanent limitation, in which case the model would be better applied to cross-bedding sets devoid of mud drapes.

Received 24 April; accepted 13 July 1981.

1. Allen, J. R. L. & Narayan, J. *Geologie Mijnb.* **43,** 451–461 (1964).
2. Allen, J. R. L. *Sediment. Geol.* **26,** 281–328 (1980).
3. Allen, J. R. L. *Geol. Mag.* **117,** 437–446 (1980).
4. Allen, J. R. L. *Nature* **289,** 579–581 (1981).
5. Nio, S. D. *Geologie Mijnb.* **55,** 18–40 (1976).
6. Visser, M. J. *Geology* **8,** 543–546 (1981).
7. Klein, G. deV. *Bull. geol. Soc. Am.* **82,** 2585–2592 (1971).
8. Klein, G. deV. *Bull. geol. Soc. Am.* **83,** 539–546 (1972).
9. Bagnold, R. A. *The Physics of Blown Sand and Desert Dunes* (Methuen, London, 1941).
10. Gadd, P. E., Lavelle, J. W. & Swift, D. J. P. *J. sedim. Petrol.* **48,** 239–242 (1978).
11. Bagnold, R. A. *Prof. Pap. U.S. geol. Surv.* **422-I** (1966).
12. Gilbert, G. K. *Prof. Pap. U.S. geol. Surv.* **86** (1914).
13. Guy, H. P., Simons, D. B. & Richardson, E. V. *Prof. Pap. U.S. geol. Surv.* **462-I** (1966).
14. Doodson, A. T. & Warburg, H. D. *Admiralty Manual of Tides* (HMSO, London, 1941).
15. Hydrographer of the Navy *Admiralty Tide Tables,* Vol. 1 (Taunton, 1980).
16. Jopling, A. V. *J. Geol.* **75,** 287–305 (1967).
17. Allen, J. R. L. *Georgr. Annlr* **A53,** 157–187 (1972).
18. Jopling, A. V. & Forbes, D. L. *Geogr. Annlr* **A61,** 67–85 (1979).
19. Allen, J. R. L. *J. Geol.* **78,** 326–351 (1970).
20. Colby, B. R. *Prof. Pap. U.S. geol. Surv.* **462-A** (1964).

Predator evasion as an explanation of diurnal vertical migration by zooplankton

Hans-Bernd Stich & Winfried Lampert

Max-Planck-Institut für Limnologie, Postfach 165, D-2320 Plön, FRG

Diurnal vertical migrations of planktonic crustaceans are widespread phenomena both in freshwater lakes and in the sea. The adaptive significance of this behaviour is unclear. This movement from the warm surface layers, which provide abundant food, to colder, deeper water with its poor food supply must place the migrating animals at a disadvantage compared with individuals remaining near the surface. The reduced availability of food and the energy consumed in migration result in reduced growth and reproductive capacity of migrating individuals. Moreover, the development time of the eggs carried in the brood pouch or in egg sacs is prolonged in cold water and the birth rate is reduced. We have studied vertical migration in a deep lake and report here that two very similar *Daphnia* species have different strategies. *Daphnia hyalina* shows a pronounced diurnal migration whereas *Daphnia galeata* remains near the surface. Although the non-migrating *D. galeata* has a much higher birth rate than *D. hyalina*, the latter is numerically dominant, as *D. galeata* suffers a high mortality near the surface. These results support the hypothesis that predator avoidance is one of the most important factors in vertical migration.

As migration behaviour has evolved in different taxonomic groups in spite of a probable reduction in fitness, there must be some selective pressure favouring it and providing a higher overall fitness to migratory populations. Many hypotheses have been put forward to explain this selective pressure, including the avoidance of optically orientating predators[1] and metabolic advantages of alterations in temperature[2] or food[3]. To determine the distribution patterns of zooplankton and the changes in food levels and temperature to which these animals are exposed, we carried out an intensive study of diurnal migration and environmental parameters in Lake Constance (southern FRG). This lake is mesotrophic with an area of 476 km², a maximum depth of 252 m and a mean depth of 100 m.

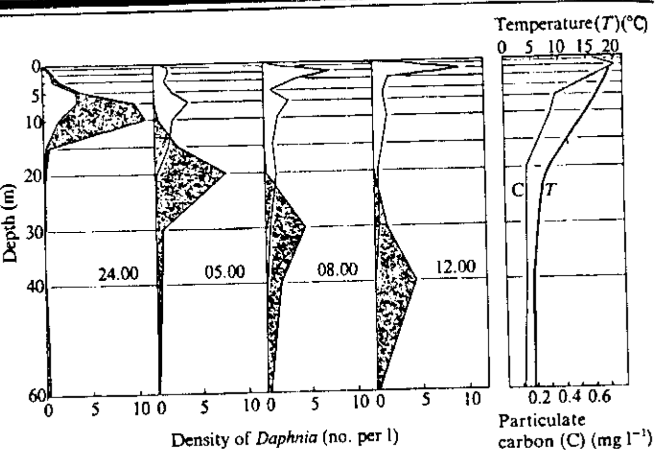

Fig. 1 Typical examples of the different diurnal vertical migrations of *D. galeata* (open area) and *D. hyalina* (shaded area) in Lake Constance, July 1977. The left panel shows four of seven measured depth distributions of the populations at different times of day. The right panel illustrates the temperature and food gradients in the water column. Only that fraction of particulate carbon <30 μm is considered as filterable food. Such distributions were recorded monthly from February 1977 to April 1978. Zooplankton samples were taken at 11 different depths (vertical lines) using a 30-l zooplankton trap every 4 h for 28 h. Temperature and particulate carbon were measured 4 times a day; as there were only minor diurnal variations the values were averaged.

When following the migratory pattern during an annual cycle, we discovered interesting differences between the populations of *D. galeata* and *D. hyalina*, which are of a similar maximum size (1.7–2.0 mm) and general morphology. A typical example of the difference in behaviour is shown in Fig. 1. During the night both populations are in the upper layers of water, whereas in the morning *D. hyalina* moves downwards so that the two populations are clearly separated during the day. In the late afternoon *D. hyalina* migrates back to the upper layers so that the two populations again overlap during the night. As there are substantial vertical gradients of temperature and food the populations are exposed to different environmental conditions. Most of the *D. galeata* population stays in warm water in conditions of abundant food, whereas *D. hyalina* lives at 5 °C for a considerable part of the day. The concentration of food in

0028-0836/81/400396—03$01.00

Table 1 Seasonal changes in the population dynamics and mean environmental conditions to which migrating *Daphnia hyalina* and non-migrating *Daphnia galeata* are exposed

Month	Species	Abundance (no. per m^2)	Mean concentration of food (mg C l^{-1})	Mean temperature (°C)	No. of eggs per adult	Egg development time (days)	Instantaneous birth rate
May	*D. galeata*	41,514	0.705	9.3	6.2	8.9	0.101
	D. hyalina	9,887	0.633	8.9	4.2	9.6	0.079
June	*D. galeata*	342,006	0.080	9.5	0.05	9.1	0.002
	D. hyalina	600,133	0.075	7.4	0.2	13.3	0.003
July	*D. galeata*	639,906	0.143	14.6	3.5	6.8	0.122
	D. hyalina	220,610	0.096	7.4	0.64	13.1	0.024
August	*D. galeata*	38,207	0.336	14.2	7.1	8.8	0.147
	D. hyalina	91,500	0.155	7.1	3.68	14.5	0.055
September	*D. galeata*	154,789	0.184	12.4	2.20	9.1	0.056
	D. hyalina	272,212	0.107	6.7	1.01	15.4	0.029
October	*D. galeata*	14,155	0.161	10.5	1.90	7.1	0.105
	D. hyalina	30,580	0.122	8.3	0.88	8.9	0.039
November	*D. galeata*	18,634	0.144	9.9	2.60	7.9	0.057
	D. hyalina	123,044	0.116	8.3	2.60	9.9	0.056

Population size was estimated by integrating the depth distribution of numbers from 0 to 60 m and taking the average of six estimates per day. Particulate carbon smaller than 30 μm was considered as food. A weighted average of the food concentration was calculated for each sampling time using the concentrations at the different depths and the corresponding numbers of animals. The mean concentration of food to which the animals were exposed during the whole day was calculated for the 24-h series; the same procedure was followed for the mean temperature. Animals 1.3 mm long were considered to be adults. This was the minimum size at which the first eggs appeared in the brood pouch. Egg development time was calculated from the mean temperature[5]. It was assumed that temperature fluctuations do not significantly affect the speed of development. Instantaneous birth rates were calculated from the number of eggs and the egg development times[7].

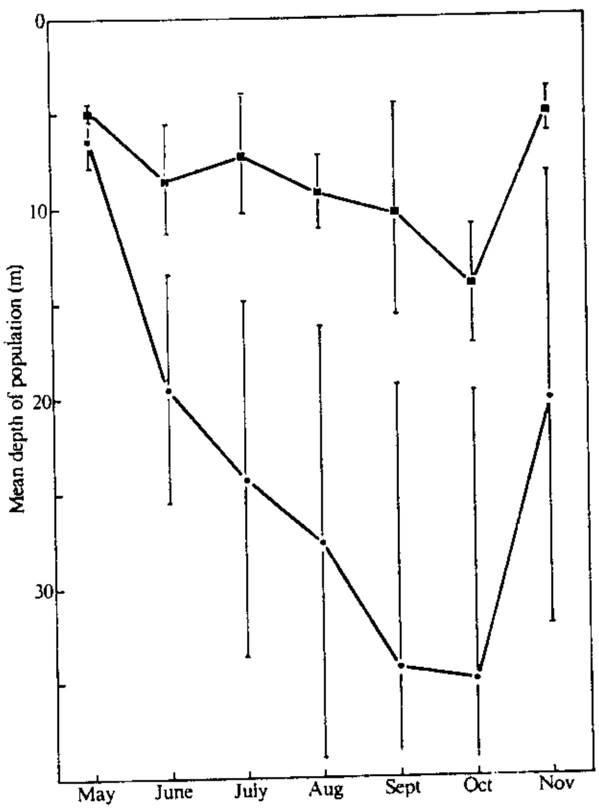

Fig. 2 Seasonal variations in the vertical migrations of the two daphnid species. The mean depth of the whole population was calculated from the distributions at different times of the day as illustrated in Fig. 1. Points represent the average of six mean vertical positions per day, with standard deviations calculated from these six positions, which give a measure of the daily amplitude of migration. From May to October, depth and amplitude of the vertical migration of *D. hyalina* (●) increase continuously, whereas there is only a slight seasonal effect in *D. galeata* (■).

deep water can hardly meet the minimum energy demands of the daphnids although at the lower temperatures that prevail there, the metabolic rate is also reduced. However, the feeding rate is lower in these conditions. Food particles (smaller than 30 μm) must provide a minimum concentration of 0.1 mg carbon per l for the animals to reproduce[4].

Differences between the two populations change during the annual cycle (Fig. 2); during early spring and winter there is no migration at all. Differential behaviour starts in June, after which the mean depth of the *D. hyalina* population is much greater than that of *D. galeata*, as is the daily amplitude of migration. In October, the *Daphnia* reach their maximum depth and amplitude of migration, and then the population returns to the initial state in winter. This behaviour cannot be explained by a simple avoidance reaction to the warm water, as in laboratory experiments both species grow and reproduce very well at a constant temperature of 20 °C. In these conditions *D. galeata* has only a slightly higher reproductive capacity than *D. hyalina*. We also studied both species simultaneously in simulated migratory conditions. In a flow-through system they were exposed to 20 °C with food during the night, and to 8 °C without food during the day. In this case *D. hyalina* produced more young than did *D. galeata*.

The different migratory pattern has severe consequences for the population dynamics of the two species (Table 1). Because of the better food conditions, the number of eggs per adult in *D. galeata* is higher than in *D. hyalina*. Moreover, the eggs of *D. galeata* develop much faster due to the higher temperature to which they are exposed[5]. As a result the instantaneous birth rate of *D. galeata* is considerably higher than that of *D. hyalina* during the period of different diurnal vertical migration. From these data, the *D. galeata* population would be expected to grow much faster than that of *D. hyalina*; the former should theoretically reach such large numbers that it eventually outcompetes the latter. Surprisingly this is not the case. Numbers of the migrating *D. hyalina* are higher almost all summer, with the exception of July. Thus, there must be severe mortality of *D. galeata*, due to predators or some other factor near the surface. In the case of optically orientating predators such as fish, this predation pressure must be reduced during the night when *D. hyalina* feeds in the upper layers. In fact, analyses of the gut contents of certain whitefish (*Coregonus wartmanni*) and perch (*Perca fluviatilis*) showed that the fish ate nine times as many *D. galeata* as *D. hyalina*.

Thus we conclude that by remaining in optimal conditions, *D. galeata* is able to compensate for high mortality by high propagation; by migrating into deeper waters during the day, *D. hyalina* reduces its mortality but must tolerate low birth rates. The results of the laboratory experiments with fluctuating temperature and food conditions indicate that the latter strategy would be less effective for *D. galeata*.

As daphnids reproduce parthenogenetically during the summer a population can be considered as an assembly of many clones[6]. Therefore the increase in depth during the day and amplitude of migration (Fig. 2) might be generated by differential response of individuals to changing environmental conditions or by selection pressures eliminating non-migrating animals from the population, as long as the predators are active. When the pressure of predators ceases in autumn, the remaining non-migrating animals would be favoured so that the variation of the population would become re-established. These hypotheses remain to be tested by genetic studies.

We thank I. Krause for help with the carbon analyses and R. N. Bohrer for critical reading of the manuscript. This work was supported by Deutsche Forschungsgemeinschaft.

Received 26 June; accepted 11 August 1981.

1. Zaret, T. M. & Suffern, J. S. *Limnol. Oceanogr.* **21**, 804–813 (1976).
2. McLaren, I. A. *J. Fish. Res. Bd Can.* **20**, 685–727 (1963).
3. Enright, J. T. *Limnol. Oceanogr.* **22**, 856–872 (1977).
4. Lampert, W. *Oecologia* **36**, 363–369 (1978).
5. Elster, H.-J. & Schwoerbel, I. *Arch. Hydrobiol.* Suppl. **38**, 18–72 (1970).
6. Hebert, P. D. N. & Crease, T. J. *Science* **207**, 1363–1365 (1980).
7. Paloheimo, J. E. *Limnol. Oceanogr.* **19**, 692–694 (1974).

Visual orientation behaviour of flies after selective laser beam ablation of interneurones

Gad Geiger & Dick R. Nässel

European Molecular Biology Laboratory, Postfach 10.2209, 6900 Heidelberg, FRG

The use of a laser microbeam has allowed us to ablate specific small groups of cells deep in the larval brain of the housefly *Musca domestica*, without damage to overlying tissues. The ablation results in various specific alterations in brain structure and behaviour of adult flies. In the experiments described here, a set of large horizontal and vertical neurones on one side of the adult optic lobes was ablated. These neurones are known to be directionally motion sensitive and are thought to play an essential part in visual orientation of the fly[1–8]. However, visually guided orientation behaviour towards single objects by flies lacking the large horizontal and vertical neurones on one side was not significantly different from the behaviour of normal flies, although the response to moving gratings was reduced on the ablated side. Therefore we suggest that other sets of nerve cells are involved in the information processing of single moving objects, whereas the horizontal and vertical cells seem to be implicated in ordinary optomotor flight stabilization.

At least 12 different classes of directionally motion-sensitive large cell have been identified anatomically and electrophysiologically in the posterior lobula plate of the optic lobes[3,9]. In the flies *Calliphora* and *Phaenicia*, some of these cells respond to horizontal motion[2–4], others to vertical motion[2–6]. Among these are two sets of larger ipsilateral neurones: the H-cells (three neurones), which respond mainly to horizontal motion and are believed to be involved in optomotor turning responses as well as in visual orientation towards single objects, for example, fixation and tracking[1,4,7,8,10]; and V-cells (8–11 neurones), which respond mainly to vertical motion, and are considered important in thrust, lift and landing responses[4–6,10] (for review, see refs 10–12). Here we investigated the role of these cells in visual orientation by examining the behaviour of the fly after their ablation.

Elimination of the cells in adult flies proved to be technically difficult; therefore we decided to ablate their precursors in the larval brain. The development of the optic lobe neuropile starts halfway through the third larval instar[13], but lobula-plate neuropile differentiation starts later, probably in pupal stages[13,14]. We therefore decided to perform the ablations in larvae before the third instar.

The primary aim of the experiment was to determine and progressively tune the parameters required selectively to affect the cells of the lobula plate. Fly larvae were anaesthetized briefly with ether and brought into the light path of a microscope incorporated in a pulse dye-laser microbeam curgery unit (G.D., D.R.N. and H. S. Seyan, in preparation). The laser pulse duration was 1.3 μs and the dye used was coumarin 2, operating at ~450 nm. Then restricted ablations were made deep in one brain hemisphere without damaging overlying cells. A large variety of anatomical defects and their behaviour correlates were obtained during progressive refinement of the ablation parameters. By using this fate-correlation we were able reproducibly to eliminate the H- and V-cells in the lobula plate. The lesions were made in a postero-lateral area of the larval brain at a depth of 30–60 μm from the brain surface, and with a diameter of ~20 μm (corresponding to two to three cell diameters), 24–32 h after hatching. The larvae were reared individually and the eclosed adult flies were then tested for changes in behaviour as described below. After completion of the tests, the fly brains were examined histologically (Fig. 1).

In the 16 flies used here, all the large horizontally and vertically arranged profiles in the lobula plate were missing on the ablated side (except in three flies where residues of one to two vertical cells were detected), with the control side normal. The large H- and V-cells could easily be identified on the control side; therefore we conclude that these cells were missing on the ablated side. The lobula plate on the treated side was slightly

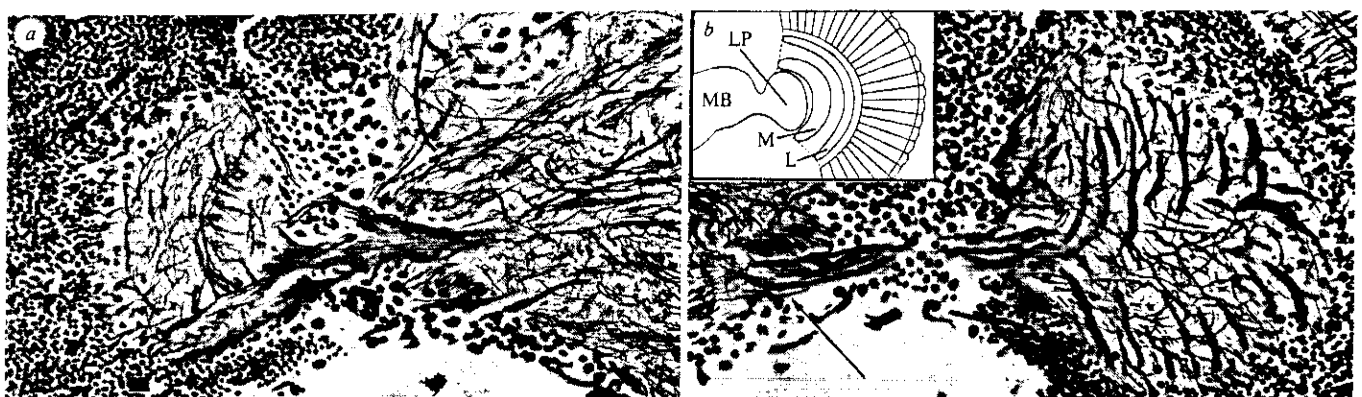

Fig. 1 Frontal (transverse) posterior-most section of lobula plates from the ablated (*a*) and normal (*b*) side of the same fly (reduced silver stain). Inset: half the brain is shown, with the optic lobes, lobula plate (LP), the medulla (M), the lamina (L), as well as part of the mid-brain (MB). The retina is peripheral to the lamina. In the micrograph only the large V-cells are shown and these are clearly distinguishable in the normal lobula plate, whereas only thin fibres remain on the treated side. The H-cells appear in deeper sections. Further evidence for the absence of the H- and V-cells is the lack of their large ipsilateral terminals in the posterior part of the mid-brain (compare with terminals on the normal side, marked by an arrow). The size of the lobula plate is slightly reduced on the treated side, although in the micrograph this difference is exaggerated, while the lobula plate on the treated side is obliquely oriented.

0028-0836/81/400398—02$01.00