SURVIVAL IN A VARYING ENVIRONMENT PHENOTYPIC AND GENOTYPIC RESPONSES IN DAPHNIA POPULATIONS

W. Lampert

Max Planck Institute of Limnology, Postfach 165, D-24302 Plon, Germany

ABSTRACT

Environmental conditions in a lake vary on different time scales, from years to minutes. Organisms faced with environmental changes, which are ecosystem properties, must evolve survival strategies in order to persist in cuch a syctem. Predictability and velocity of environmental changec determine the most profitable (in terms of fitness) ctrategies. In response to predictable environmental varriations, organisms can evolve fixed life-history traits; unpredictable changes should favor the evolution of phenotypic plasticity. However, recurrent moderately predictable conditions can also lead to shifts in genotypic frequencies in a population. Different strategies can co-exist if the environment fluctuates at varying time scales simultaneously. *Daphnia* is used as a model organicm to explain various adaptations to changec in bottom-up and top-down forces. They live in a nutritionally dilute environment, thus reactions to cudden changes in food resources are essential. Phenotypic placticity of the filter screens is used to optimize energy input. On the other hand, daphniids are subject to strong, size selective predation pressure by fish and invertebrate predators, which require different defenses. The relative importance of these predators and, thus, the optimum defense ctrategies vary during the season. Daphniids react to changes in predator pressure with life-history changes, e. g. variable size at first reproduction (SFR). Clonal replacement, phenotypic recponses to specific predator signals, and maternal effects determine the seasonal shift of SFR in the lake. Experiments in large indoor mesocosms are reported to demonstrate the interaction of phenotypic and genotypic responses in the exprecsion of diel vertical migration (DVM), a behavioral strategy of avoidance of fish predation. Daphniids can gain the same fitness from either migrating deeper during the day or maturing at a smaller size. It is concluded that natural selection, although it must act on individuals, creates ecosystem properties through shaping the characteristics and interactions of populations.

Keywords: Ecological time scalec, Adaptation, Phenotypic placticity, Genotypic shifts, Predator defense

RESUMEN

Las condiciones ambientales de un lago varían u lo largo de varias escalas temporales, de años a minutos. Los organismos se enfrentan a estos cambios, o propiedades de un ecosistemu, y desarrollan, en su evolución, estrategias de supervivencia para mantener sus poblaciones en el sistema. Las estrategias más provechosas (en términos de eficiencia) vienen determinadas por la rapidez y capacidad de anticipación a los cambios ambientales. Los organismos pueden llegar a desarrollar caracteres fijos en sus ciclos vitales en ambientes con cambios predecibles. Por el contrario, los cambios impredecibles deberán favorecer la evolución de la plasticidud fenotípica. Sin embargo, los cambios no tan fácilmente predecibles, pero recurrentes también pueden llevar a desplazamientos en las frecuencias genotípicas de una población. Pueden incluso coexistir varias estrategias si las condiciones ambientales fluctúan simultáneamente pero u diferentes escalas de tiempo. Daphnia *es un organismo modelo utilizado para explicar diversas adaptaciones frente a cambios en las fuerzas "top-down" y "bottom-up". Viven en un ambiente en el que el alimento se halla diluido, por lo que la capacidad de respuesta u los cambios repentinos en el alimento disponible es esencial. La plasticidad fenotípica de los peines de sedas de los apéndices es utilizada para optimizar la entrada de energía. Por otra parte, los dafnidos se hallan sometidos a fuertes presiones selectivas en función de su tamaño ya que son acosados por predadores como peces o invertebrados para los que necesitan defensas diferentes. La importancia relativa de estos depredadores varía y, así, la estrategia defensiva ópiima cambia estacionalmente. Los dafnidos reaccionan a los cambios en las presión del depredador con cambios en sus ciclos vitales, por ejemplo, con la variación del tamaño en el momento de su primera reproducción (TPR). Los cambios estacionales de TPR en un lago dado vienen deierminados por la división clónica, por respuestas fenotípicas a señales específicas de depredadores, y por efecto de la mndre. En experimentos en mesocosmos de gran tamaño en el laboratorio se ha encontrado que hay una interacción de respuestas fenotípicas y genotípicas en la migrución vertical diaria (MVD), una estrategia comportamental de evitación del riesgo de predación. Los dafnidos pueden alcanzar la misma eficiencia migrando a capas más profundas durante el día o alcanzado la madurez a un tamaño menor. Se concluye que la selección natural, si bien actua sobre individuos, puede crear propiedades ecosistémicas mediante el moldeado de características e interaciones de las poblaciones.*

Palabras clave: Escalas de tiempo ecológico, Adaptación, plasticidad fenotípica, Deriva genotípica, Defensa

TIME SCALES OF ENVIRONMENTAL CHANGE IN TEMPERATE LAKES

Organisms in a lake are faced with environmental changes on different ecological time scales, from years to minutes. Some processes are slow and require many years, e.g. eutrophication and re-oligotrophication. They are accompanied by species shifts, but many species remain in the community despite a considerable change in conditions, i.e. they must have a broad niche or a way of buffering environmental variation. Another slow change is associated with global climate change and there is first evidence that lakes react to changing climate conditions (Gerten & Adrian, 2000). Within a single year, conditions in a lake change in a regular pattern and communities undergo a seasonal succession (Sommer *et al.,* 1986). In particular, abiotic conditions are rather predictable (Lampert, 1987a). For example, unlike in terrestrial systems, there is never a shortage of water, temperature rises and falls slowly and constantly and the chemical conditions (e.g., oxygen stratification) do not vary much between years. Even some biotic conditions show similar patterns year for year. Figure 1 depicts an example taken from a long-term mo-
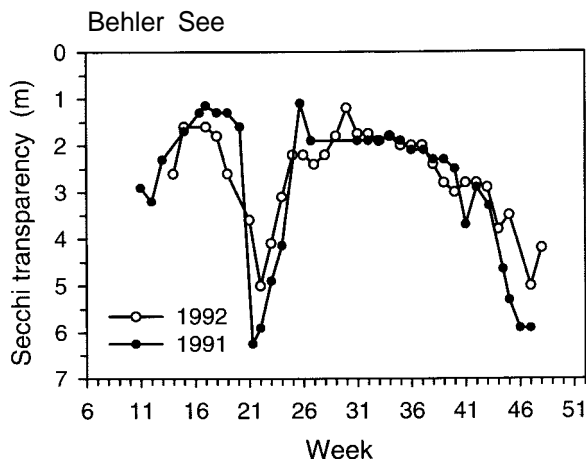
nitoring study. Secchi transparency (i. e. algal abundance) in stratified lakes in Northern Germany shows little interannual variation. Only two year cycles are superimposed in the graph for clarity, but it would be possible to add many more years without disturbing the pattern.

Long-lived organisms can adapt their life cycles to such predictable patterns. For example, some cyclopoid copepods perform a summer diapause in order to avoid the deteriorating food conditions for their nauplii after the clear-water phase (Santer & Lampert, 1995). They can adjust their life cycle and rest all summer, because the probability of the clear-water phase occurring at the end of May is very high (Fig. 1). On the other hand, short-lived organisms with many generations per year experience the pattern shown in figure 1 as a dramatic and unpredictable shift in environmental conditions. Daphniids living in the lake grow so well during the spring algal bloom as to overshoot the carrying capacity and cause the clear-water phase. Within one week, their food is in very low abundance and they may starve to death. Predation pressure can vary quickly, too, if fish fry grow to the right size to prey on the daphniids, but later become too large. They may be replaced by a cohort of invertebrate predators, with very different prey selection. Depending on their generation time, populations surviving rapid changes in their environment can either adapt by phenotypic plasticity of the individuals or by reversible shifts in genotypic frequencies.

Finally, very rapid changes on time scales of hours or minutes, require fast reactions of metabolism and behavior. Such rapid changes may be caused by a patchy distribution of food and predators or diel rhythms of activity.

Rapid, unpredictable changes should, according to life-history theory, favor the selection of phenotypic flexibility rather than of constitutive traits (Bradshaw, 1965). Recent years have, in fact, seen the discovery of many phenotypic reactions, hence phenotypic plasticity has again become a central topic in aquatic ecology (Tollrian & Harvell, 1999).

Phenotypic and genotypic reactions to environmental change on varying time scales have

Figure 1. Seasonal change of transparency in a eutrophic **lake** (Behler See) in northern Germany. *Cambio estacional en la transparencia de un lago eutrófico (Behler See) en el Norte de Alemania.*

been studied particularly well in *Daphnia* for several reasons. (1) Being effective filter feeders, which can monopolize algal resources (cf. Fig. 1), daphniids have a considerable ecological relevante. (2) They are located in the center of pelagic food webs, being controlled by abundance of edible particles (bottom up) as well as predation (top down). *(3)* Due to their clonal population structure, shifts in genotype frequencies can be monitored easily by molecular methods. (4) They are easy to cultivate and, thus, accessible for experimental work. Hence there is a wealth of literature reporting morphological, behavioral and life-history reactions of *Duphnia* to environmental change on the individual and population level. 1 will use *Daphnia* as a model organism to explain some of the strategies of adaptation.

SURVIVAL IN A NUTRITIONALLY DILUTE ENVIRONMENT

Plankton live in a nutritionally dilute environment (Conover, 1968), although this is not always evident if we look at a green lake. To explain this statement, let us look at a *Daphnia*'s environment from a human perspective. The size relationship between a human of 1.80 m height and a 2-mm *Duphnia* is 900:1. Consider the mean particle diameter of *Daphnia*'s food to be 5 μm; this would be 4.5 mm, which is about the size of a pea, from the human point of view. Assuming a density of 10^4 particles per cm^3, the mean distance between two particles is approximately 460 μm, i.e. 42 cm from the human perspective. Hence *Daphnia's* food environment would look for a human like a space filled equally with peas at 42 cm distance. Visibility in this "pea soup" would be about 10 m. However, a 2-mm *Daphnia* has a maximum filtering rate of about 2 mL h^{-1} (Lampert, 1987b), which equals more than 5 cells eaten per second. In order to appreciate the performance of a *Duphnia* imagine catching and eating five peas per second from the surroundings.

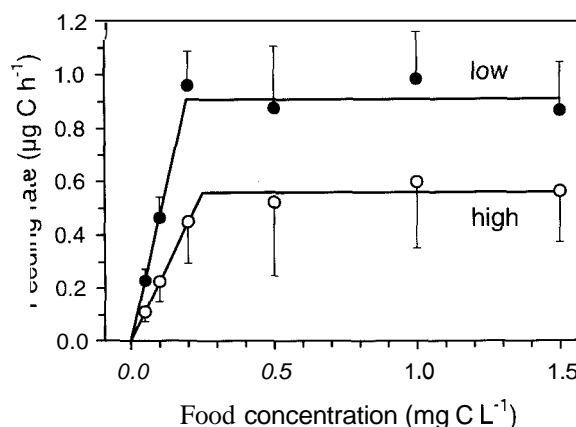This simple anecdote demonstrates the importance of efficiency in extracting food from the

Figure 2. Functional responses of the feeding rate of *Daphnia pulicaria* raised at high (1.5 mg C L^{-1}) and low (0.06 mg C L^{-1}) food concentrations. Symbols represent means and 1 SD of 10 to 12 individuals of 1.9 mm size. [from Lampert (1994a)]. *Respuestas funcionales a la tasa de alimentación de* Daphnia pulicaria *cultivada u alta (1.5 mg C L^{-1}) y baja (0.06 mg C L^{-1}) concentración de alimento. Los símbolos* indican *la media y 1 SD de 10 a 12 individuos de 1.9 mm de tamaño* [según Lampert (1994a)].

environment for filter feeders competing for similar resources. Small differences in efficiency may affect the food threshold for growth (Gliwicz, 1990) and thus the outcome of competition (Kreutzer & Lampert, 1999). Maintaining a high filtering rate involves costs for pumping and processing the water. Flexibility will be advantageous if food concentration changes, as during the clear-water phase (Fig. 1). When food drops to very low levels near the threshold concentration, increasing the filtering rate can be essential for the survival of a daphniid.

It has, indeed, been reported that *Daphnia* at very low food concentration show considerably higher filtering and feeding rates compared to their equally sized sisters raised at high food levels (Fig. 2). Increased filtering rates are especially important below the incipient limiting concentration where the ingestion rate is linearly related to particle concentration. There are two possibilities of increasing the filtering rate, (1) to increase the beat rate of the filtering limbs or (2) to increase the size of the filter screens at the filtering limbs (at the third and fourth pair of legs in
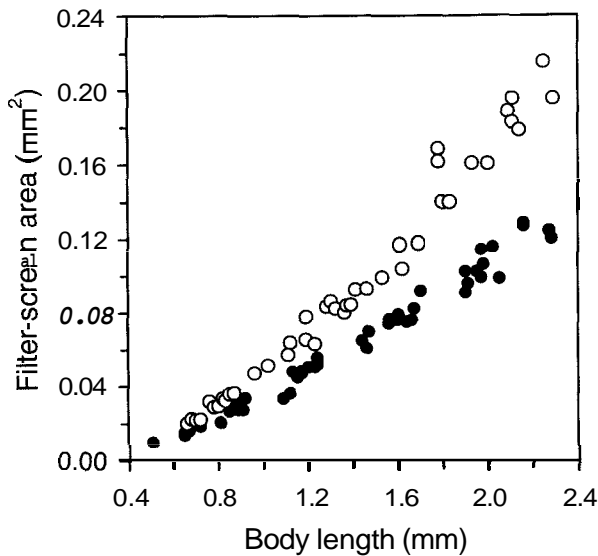
Figure 3. Body-size dependence of the filter-screen area of a third limb of *Daphnia pulex* cultured **at** high and low food concentration. Each dot represents an individual *Daphnia* grown at *0.06* mg C L^{-1} (open circles) or 1.5 mg C L^{-1} (closed circles) of *Scenedesmus*. [from (Lampert (1994a)]. *Dependencia del tamaño en el área de filtrado* **de** *la tercera pata* **de** Daphnia pulex *cultivado a alta y baja concentración de alimento. Cada punto representa un individuo de* Daphnia *cultivado a* 0.06 *mg* C L^{-1} *(círculos claros) o a* 1.5 mg C L^{-1} *(círculos oscuros)de* Scenedesmus *[según Lampert (1994a)].*

Daphnia). Both strategies do not only increase the filtering success, they also increase the costs of the filtering process. Predictions about the best strategy can be made from theoretical considerations of the energy spent for filtering. The energy *(R)* needed to pump water through a *Daphnia* filter is $R = c_2 \cdot U^2 \cdot A / w$ (Equ. 1), where c_2 is a constant, U is the average flow rate across the filter, A is the area of the filter screen, and w is the mesh width of the filter (Lampert & Brendelberger, 1996). The flow rate across the filter is proportional to the beat rate of the limbs, thus the energy costs for increasing the filtering rate by higher appendage beat rates grows with the square of the beat rate, while the area enters the formula linearly. Therefore, theory predicts that it is more profitable to enlarge the filter screens than to beat faster.

In fact, Koza & Korinek (1985) already cultured *Daphnia* at varying food concentrations and measured their filter screens after dissection. They found enlarged filters for daphniids grown at low food, and Korinek *et al.* (1986) reported considerable changes in filter-screen size for field populations sampled at times with differing food availability. In the succeeding years, the phenomenon has been observed for various *Daphnia* species (e. g., Pop, 1991; Stuchlik, 1991). Lampert (1994a) showed that some *Daphnia* species grown at very low concentrations of food can have filter-screen areas twice as large as those grown at high levels of food (Fig. *3)*. However, under low-food conditions, *Daphnia* not only get larger filters, the filters also get finer meshes (Lampert, 1994b), i. e. the daphniids expand the size range of edible particles towards smaller bacteria (Brendelberger, 1991). Increased filter-screen areas and finer meshes translate into higher energy uptake (e.g., Stuchlik, 1991), thus they result in lower threshold food concentrations for growth (Lampert, 1994b). It is not yet known what triggers the morphological response to low food levels. Eventually, the allometric growth of the filters is coupled to the growth rate (intermolt time) as it has been found that other factors inhibiting growth, like flocs of ferric sulphate and clay, resulted in large filter screens, too (Randall *et al.,* 1999).

The adjustment of the filter screens is a clear example of an adaptive phenotypic response to bottom-up factors. Even at the beginning of the clear-water phase, food conditions will not deteriorate immediately but during several days or weeks, time enough for the present *Daphnia* to adapt through two to three molts. Filters will be large if needed. On the other hand, larger and finer filters require more energy (cf. Equ. 1),thus it is advantageous to reduce them if plenty of food is available. Although it would be energetically even more profitable to maintain large filters but reduce the beat rate, the latter is not possible as the water current created by the filtering limbs is also used for gas exchange (Pirow *et al.,* 1999). *Daphnia* seems to have found the optimum solution to handle varying food conditions.

COPING WITH CHANGING PREDATOR PRESSURE

Top-down factors can be even more powerful selection forces than bottom-up factors (Brooks & Dodson, 1965).However, as for food availability, the threat by predators varies through time and is not always predictable. Predator abundance and activity changes during season. For example, fish hatching in spring are first too small to attack large zooplankton, but a few weeks later they are large enough and still present in large numbers to have a serious impact. Later in the season, mortality has reduced numbers of young-of-the-year fish and the remaining individuals of most species may be already large enough to switch to benthic food. This pattern is rather predictable, but there is still a large amount of variation. Fish recruitment shows remarkable fluctuations between years and short-term variability in predation activity can result from weather conditions (delayed spawning of fish). Moreover, different types of predators are present at different times of the year, for example, fish predation may be replaced by invertebrate predation, which requires different defense strategies. No wonder that the majority of inducible phenotypic responses has been found to be defenses against predators (Tollrian & Harvell, 1999). Both, shifts in clonal composition of the population and phenotypic reactions have been reported as responses of *Daphnia* to predator pressure. Clones in a single lake can differ in fixed life-history characteristics (Tessier & Consolatti, 1989), but can also differ in their phenotypic response to predators (Spitze, 1992; Walls *et al.,* 1997). In the latter case, selection does not act on a specific trait but on the reaction norm (i.e., the way a phenotype is expsessed under environmental variation). An important point for the optimum response is the question if the prey can detect the presence of the predator (Taylor & Gabriel, 1993). If they can not detect the predator, the optimum strategy would be adapted to the long-term average of the season; if they can, a phenotypic response would be more profitable.

Numerous traits in morphology, life-history and behavior of Daphnia have been described to be phenotypically flexible and identified as inducible defenses [summary in Tollrian & Dodson (1999)]. A lake, however, is a multipredator environment and different predators require different defense strategies to either reduce the capture efficiency of the predator or enhance the escape ability of the prey. Most planktivorous fish are visual hunters and they select large, conspicuous prey. In contrast, most invertebrate predators locate their prey with mechanoreceptors, but have problems handling the prey, thus they prefer small prey. If both predator types are present or succeed each other quickly, a mixed strategy may be optimal, for example life-history adaptations may be a reaction to fish while morphological defenses may protect against invertebrate predators. Life-history theory (Stearns, 1992) can make predictions about optimum strategies. Taylor & Gabriel (1992) developed a model predicting the opti-
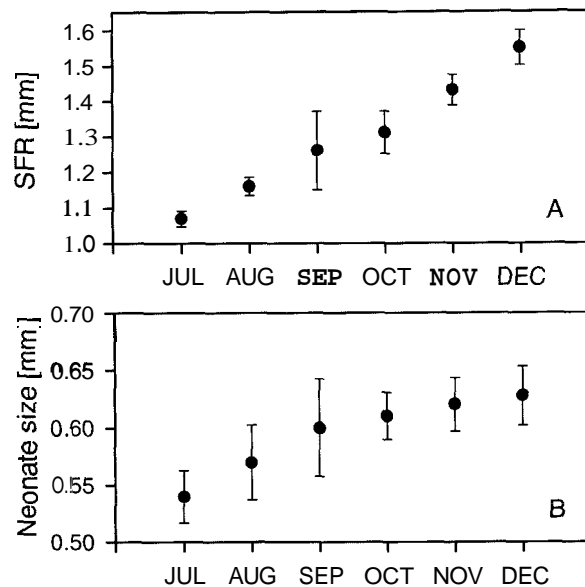

Figure 4. Seasonal change in neonate size and size at first reproduction (**SFR**) of *Daphnia hyalina* from a mesotrophic lake (Schohsee) in northem Germany under *in situ* conditions. [from Stibor & Lampert (2000)]. *Cambio estacional en el tamaño de los neonatos y tamaño u la primera reproducción (SRF) de* Daphnia hyalina *en un lago mesotrófico (Schöhsee) en el Norte de Alemania en condiciones* in situ. *[según Stibor & Lampert (2000)].*

mum life-history of *Daphnia* under predation by fish or invertebrates. The basic assumption is a trade-off between energy allocation to growth and reproduction. As expected, the optimum strategy against fish predation is for daphniids to start allocating energy to reproduction as early as possible in their life, i.e. to reproduce at a small size and not to grow much larger. On the contrary, under invertebrate predation, daphniids must use the available energy to grow fast and allocate energy to reproduction late in order to be invulnerable when they reproduce the first time.

Daphnia control energy allocation according to this model (Stibor & Lüning, 1994). They are able to recognize the predator type by a chemical signal (kairomone). Confronted with a fish kairomone, they start allocating energy to reproduction significantly earlier then when experiencing the kairomone of *Chaoborus* larvae. They show a pronounced phenotypic change of the size at first reproduction (SFR) if the predator type changes.

Field studies have revealed pronounced seasonal changes in SFR (Stibor & Lampert, 1993), but it is not possible with such observations to decide if the variability in SFR is due to seasonal replacement of clones differing in constitutive life-history traits or to phenotypic responses to changing predator pressure. The analysis of the different components of variance requires common-garden experiments as performed by (Stibor & Lampert, 2000). They collected samples of *Daphnia hyalina* from a mesotrophic lake at monthly intervals from July to December. A shift in predator activity occurs during this period as juvenile fish are most active in summer while fourth-instar *Chaoborus flavicans* larvae appear in the lake in September. Daphniids were transferred to the laboratory alive. They were measured and each month 20 females that were close to maturation were isolated and kept individually in 200-ml glass jars at 20°C with 1 mg carbon L^{-1} *Scenedesmus obliquus* as food. These animals had experienced true lake conditions (temperature, food, kairomones) dunng their juvenile phase when they are most sensitive to predator signals (Stibor, 1995). When they matured short-

ly after isolation, they were assumed to reflect the status of lake daphniids at this particular time. After they had deposited their first clutch of eggs, SFR was measured and energy allocation to reproduction calculated. Descendants of the 20 daphniids were used to establish clones that were kept in the laboratory for at least 6 generations to make sure they were no longer influenced by the lake conditions. Finally, standardized, third-brood neonates from all 20 clones per month were isolated and again raised individually. They were split in three groups: untreated (controls) or treated either with fish kairomone or *Chaoborus* kairomone. SFR and energy allocation were measured after the daphniids had deposited their first clutch of eggs. A comparison of life-history characteristics expressed in the lake and under stan-
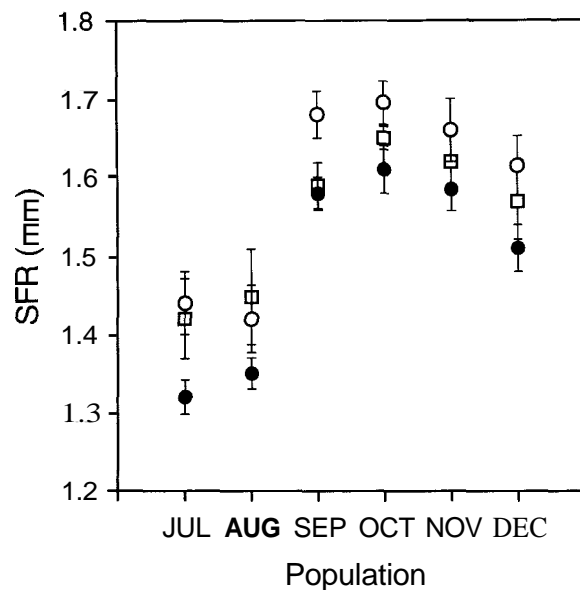

Figure 5. Size at first reproduction (means ± 95 % conf. lim., n = 20) of clones of *D. hyalina* that had been isolated at different times of the year and cultured for at least **6** generations in the laboratory. Squares: controls; open circles: daphniids exposed to *Chaoborus* kairomone; closed circles: daphniids exposed to fish kairomone. [from Stibor & Lampert (2000)]. *Talla a la primera reproducción (medias ± 95 % lim. conf., n = 20) de clones* de D. hydiina *que han sido aisladas en diferentes épocas del año y cultivadas en el laboratorio durante, al menos,* **6** *generaciones. Cuadrados: controles; círculos claros: daphnidos expuestos a cairomona de* Chaoborus; *círculos oscuros: daphnidos expuestos a cairomona de peces. [según Stibor & Lampert (2000)].*

dardized laboratory conditions would allow separating phenotypic and genotypic components of the variation.

SFR as well as neonate size increased considerably from July to December in the lake (Fig. 4). This change reflects the integrated influences of all lake conditions as well as a possible shift in clonal composition of the *Daphnia* population. The long-term adapted laboratory clones showed an increase in SFR between August and September (Fig. 5). Controls of summer clones were significantly smaller than those isolated in autumn and winter, i.e., there was a shift in the genetic composition of the population reflected in SFR. The shift is consistent with the model predictions (Taylor & Gabriel, 1992) that fish predation (in summer) selects for small SFR. In addition, clones differed in their response to kairomones. Summer clones reacted to fish kairomone
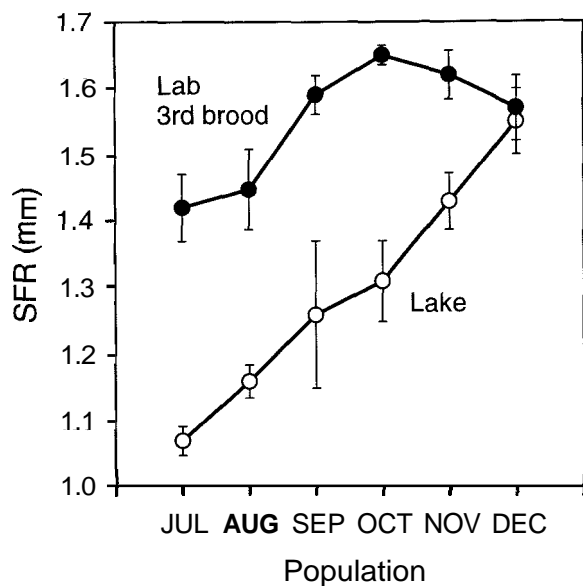
with a significant increase in energy allocation to reproduction and a reduction in SFR, but they did not react to *Chaoborus* kairomone. In September, fish kairomone had no effect, but *Chaoborus* kairomone induced a significant increase in SFR. There was a continuing trend of larger SFR with *Chanborus* kairomone and smaller SFR with fish kairomone compared to the controls from October to December, but these differences were not significant. Consequently, a seasonal shift in clonal composition takes place in the lake. when the importance of predators changes. Not only does the SFR change as predicted but also the sensitivity of the clones to predator kairomones.

However, the factors studied in the laboratory explain only part of the change in SFR in the lake (Fig. 6). The range of SFR obtained in the laboratory is much smaller than in the lake. Particularly in summer, field daphniids mature at a much smaller size than the laboratory controls, and the addition of fish kairomones to laboratory daphniids does not have a large enough effect to match the field results (cf. Fig. 5). SFR in the lake increases much more during the season than SFR in the laboratory so that **lake** values and laboratory values match in December.

There are evidently other factors controlling SFR in the field that were not considered in the laboratory. One of them may be temperature (Lampert, 1994b), but the explanation for the discrepancy between the field and laboratory studies is more likely a maternal effect that can be considered adaptive to changing predator pressure (Lampert, 1993a). The size of neonates hatching from parthenogenetic eggs of *Daphnia* increases with successive broods of a female. First-brood neonates are small; neonate size increases to the third brood and approaches a maximum thereafter (Ebert, 1993). Therefore, neonate size is positively related to the body size of the mother. Another strong positive correlation exists between neonate size and SFR, thus SFR is positively related to the size of the mother (Fig. 7). Offspring of large females mature at large sizes and vice versa. The size distribution of *Daphnin* in the field is controlled by predator pressure. Fish will first remove larger, older females.

Figure 6. Comparison of the SFR of *D. hyalina* freshly isolated from the lake at different seasons (unknown mothers) and after at least 6 generations in the laboratory (untreated 3rd-brood offspring). [from Stibor & Lampert (2000)]. *Comparación de la SRF de* D. hyalinü *recién aislada de un lago en diferentes estaciones (de madres desconocidas)* y *después de cultivada en el laboratorio durante, al menos,* **6** *generaciones (3" puesta sin tratamiento).* [según Stibor & Lampert (2000)].

Consequently, the size distribution of daphniids is shifted towards smaller sizes, i. e., the proportion of first-brood females in the population will be large if fish predation pressure is high. As the offspring of these small females are even smaller than their mothers (cf. Fig. 7), the mean SFR must decrease dramatically. Large females, however, have more eggs than small ones and contribute more offspring to the population when they are present. They will become important when the population is relaxed from fish predation and, as a consequence, the mean SFR will increase rapidly.

When juvenile daphniids were isolated from the field, the size of their mothers was unknown. They reflected a random sample of the population. The common-garden experiments in the laboratory, however, were always performed with third-brood neonates in order to avoid the confounding maternal effects (Fig. 4). Although fish predation in the lake has not been measured it is reasonable to assume that it declined in autumn
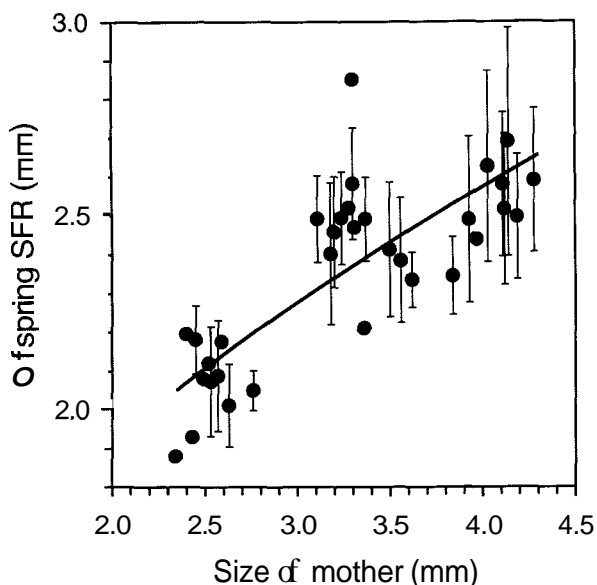
and was very low in December (Mehner *et al.,* 1998), resulting in a large share of older *Daphnia* in the population. Probably SFR in the lake and in the laboratory matched in December as the proportion of large females in the lake was high. This maternal effect is a powerful mechanism of phenotypic adaptation to changing predator pressure that does not require the prey to recognize the predator. Although the response needs more than one generation and is slower than the chemical induction of defenses, it may be effective on the time scale of seasonal succession. The control of life-history patterns in the lake is complex. Contributions of genotypic variance and phenotypic plasticity vary during seasons, but there are enough mechanisms to react to changing predator pressure on different time scales.

CO-EXISTING STRATEGIES:
BEHAVIORAL RESPONSES

The same environmental factor can vary on different time scales. For example, a slow change in fish predation can occur during eutrophication of a lake when fish species composition changes (Persson *et al.,* 1991). Zooplankton species composition will change in response to this shift, but there will also be intraspecific changes, e. g., clonal replacement in *Daphnia.* The slow change may be superimposed by rapid fluctuations of predator pressure during the season. Such conditions should favor the coexistence of different strategies in the population.

The fastest way to react to rapid changes are behavioral responses. Diel vertical migration (DVM) is a particularly well studied behavioral response in lakes and in the sea. Many taxa of zooplankton perform diel vertical migrations; they spend the day in deep, dark waters and come to the surface at night. DVM is very costly as the zooplankton spend large parts of the day in cold water, where development is slow, under poor food conditions, which results in low numbers of offspring. It has for long been a challenge to identify the ultimate causes of such behavior. Many hypotheses have been proposed and have been

Figure 7. Relationship between the size of female *Daphnia magna* and the SFR of their offspring. Each point represents the clutch of one female (mean ± 1 **SD).** [from (Lampert (1993a)]. *Relación entre el tamaño de una hembra* de Daphnia magna y *el SFR de su puestu. Cada punto representa la puesta de una hembra (media ± 1 SD). [según (Lampert (1993a)].*

falsified until evidence for the predator avoidance hypothesis accumulated (Lampert, 1993b). Zooplankton migrate into deep water to reduce vulnerability to visually hunting predators, mainly planktivorous fish, near the surface during day. Very strong evidence came from the observation that DVM is induced by a chemical signal (kairomone) emitted by fish. *Daphnia* played again a key role in these investigations.

The first large-scale evidence for the existence of a kairomone came from experiments by (Loose, 1993) in the Plon Plankton Towers, large indoor mesocosms (12 m high), that allow complete control over the vertical conditions in the water column (Lampert & Loose, 1992). Loose (1993) introduced *Daphnia* into the stratified towers, but contrary to the expectations, they would not migrate. Only when he circulated the water from the epilimnion through an aquarium with small fishes outside of the towers, was DVM induced (Fig. 8). As daphniids in the mesocosm could not visually or mechanically detect the fishes in the aquarium, the change in behavior could only have been induced by a chemical clue. DVM was triggered by the light, but daphniids needed a "motivation" in order to react to the change in light. Thus, daphniids are phenotypically plastic with respect to migration behavior. They display the costly DVM only if they receive signals concerning the presence of fish, but they save the costs if the predation risk is low. DVM is a very rapid and effective response to changing fish predation pressure.

The predator avoidance hypothesis generates testable predictions for DVM. One prediction is that large individuals should migrate for larger amplitudes than small ones as they are more conspicuous and, thus, more threatened by fish. This has, in fact, been observed frequently (Lampert, 1993b). Hence. there are two possible avoidance strategies, DVM or smaller body size. The latter is a slow strategy and would be expected under continuing or slowly changing predator pressure. If long-term and short-term fluctuations occur simultaneously in the environment, both strategies may co-exist.

Another experiment in the Plankton Towers provided evidence for such mixed strategies. De
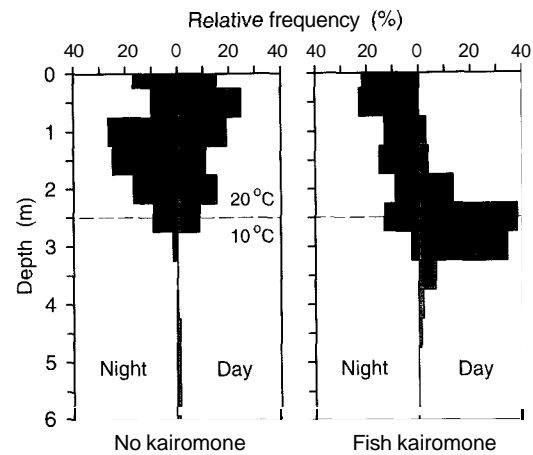

Figure 8. Day and night distributions of *Daphnia hyalina* x *galeata* in the Plankton Towers in controls (left panel) and under the influence of a fish kairomone (right panel). The thermocline is indicated by a dashed line. *[after Lampert & Loose (1992)]. Distribuciones durante el día y la noche de* Daphnia hyalina x galeata *en la torres del plancton como* **control** *(figura izquierda) y bajo la influencia de la cairomona de un pez (figura derecha). La termoclina esta indicad con una línea de puntos. (según Lumpert & Loose (1992)].*
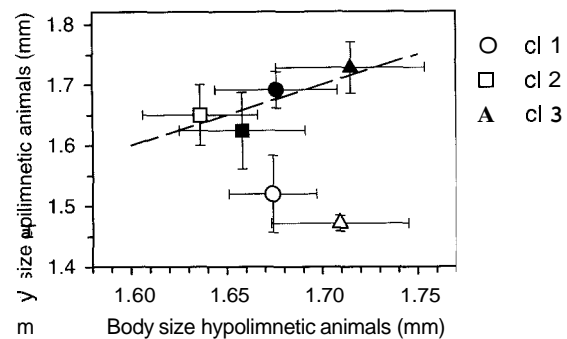

Figure 9. Size-specific diel vertical migration of three clones of *D. haylina* x *galeata* in the Plankton Towers (means ± 1 SE). Open circles: daytime samples; closed circles: nighttime samples. The dashed line indicates equal sizes for the epi- and hypolimnion. Sizes are equally distributed at night for all clones, while in clones 1 and 3 large animals migrate into the hypolimnion during day. Overall, clone 3 is the largest and clone 2 is the smallest clone. [from De Meester *et al.* (1995)]. *Tamaño específico de la migración vertical diária de tres clones de* D. hyalina x galeata *en las Torres del Plancton (medias ± 1 SE). Círculos claros: muestras diurnas; círculos oscuros: muestras nocturnas. Las* **líneas** *de puntos indican igual tamaño para el epi- y hipolimnion. Las tallas están igualmente distribuidas por la noche para todos los clones, mientras en los clones 1 y 3 los animales grandes migran al hipolimnion durante el día. En promedio el clon 3* **es** *el mayor y el 2 el menor. [según De Meester et al. (1995)]*

Meester *et al.* (1995) isolated numerous co-exist-ing clones of *D. hyalina x galeata* from a mesotrophic lake and measured their life-history characteristics. They selected three clones differ-ing in SFR that could be discriminated elec-trophoretically by their allozyme patterns, and created genetically mixed populations by inocu-lating each tower with equal numbers of all three clones. In response to fish kairomone, and even stronger to real fish, the three clones differed in their migration behavior (Fig. 9). Clone 3 had the largest adults and showed the strongest DVM. In particular the large individuals migrated, which resulted in a large discrepancy between mean sizes in the epi- and in the hypolimnion during the day. Clone 1 had a slightly smaller body size than clone 3 and it migrated to a lesser extent. An equal vertical distribution of sizes was observed for clone 2, i. e., this clone did not migrate. All three clones coexisted during the first 25 days of the experiment before each tower was stocked with 10 juvenile fish of 3-4 cm length. The fish preyed upon the daphniids and the non-migratory clone 2 quickly became extinct (Fig. 10). The two

other clones were also reduced in numbers, but after another 25 days they both approached fre-quencies of 50 %, i. e., they had identical fitness. This was the result of mixed strategies: clone 3 was large and migrated to greater depths, while clone 1 was smaller and migrated less. Clone 2 did not migrate at all. Although it was even slightly smaller than the two other clones, it could not survive under the relatively high preda-tion pressure in the towers. However, it was pre-sent in the lake where it could probably persist over long periods of moderate predation pressure. Although the two traits under consideration (migration, size) were correlated in this example, this is not always the case as various combina-tions of traits can be expressed in response to the same selective force (Boersma *et al.,* 1998).

CONCLUSIONS

Organisms are part of communities and ecosys-tems. They are influenced by their abiotic and biotic environment, but at the same time they are "ecosystem engineers" (Jones *et al.,* 1994) that influence the environment. These are fundamen-tal properties of the ecosystem concept. Conse-quently, if organisms evolve in response to ecosystem properties (e. g., different time scales of events) this will in turn have effects on the ecosystem. For example, as daphniids evolved DVM in response to fish predation, this had seri-ous implications for the diel grazing pattern. Daphniids can now only graze at night, and algae can grow unimpeded during the day (Lampert, 1992); but without DVM daphniids would not persist in the system and there would be no *Daphnia* grazing at all.

An ecosystem cannot evolve as a unity as it does not have a common genome. We must rather understand that ecosystem properties have been created and are modified by natural selection act-ing on individuals. Elser *et al.* (2000) have recently stressed this concept with respect to ele-mental stoichiometry and biogeochemical processes. This essay has mainly been concerned with evolutionary reactions of *Daphnia*, as a
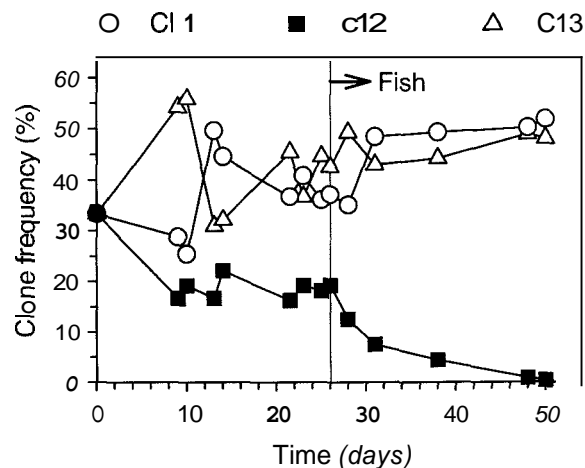

Figure 10. Frequences of three clones of *D. hyalina* x *galeata* in long-term experiments in the Plankton Towers. The vertical line indicates the introduction of fish. [combined from two graphs of De Meester *et al.* (1995)]. *Frecuencias de tres clones de* D. hyalina **x** galeata *en experimentos u largo* **plazo** *realizados en las Torres del Plancton. La* **línea** *vertical indicu la introducción* **de** *peces. [combi-nada de dos figuras de De Meesier et al. (1995)].*

model organism, to predictable and unpredictable environmental changes on different scales. Only diel and annual cycles are externally forced on the lake system; all other sources of variation involve organisms that are subject to natural selection. In order to understand why ecosystems have distinct properties, it is necessary to integrate concepts of evolutionary ecology into ecosystem theory.

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