

Estimates of the nonconsumptive mortality of mesozooplankton by measurement of sedimentation losses

Abstract—Nonconsumptive mortality of mesozooplankton in Lake Constance was directly estimated by collecting dead zooplankton with sediment traps. Patterns of zooplankton sedimentation observed in the sediment trap reflected the population dynamics in the pelagic zone. The migration of *Cyclops vicinus* toward the sediment (where they spend their diapause) at the end of May resulted in a pronounced occurrence in the traps (migration rate $>10^6$ individuals (ind.) $m^{-2} d^{-1}$). Other copepods and *Daphnia hyalina* had only sedimentation losses of 0.5 and 0.2% of the standing stock per day, respectively, demonstrating the minor role of nonconsumptive mortality for these species. In contrast, nonconsumptive mortality had a high significance on the population dynamics of nonmigrating epilimnetic *Daphnia galeata*. High sedimentation rates (up to 3×10^3 ind. $m^{-2} d^{-1}$; in total, 38% of the total population decline from 16×10^4 to 1×10^4 ind. m^{-2} within 21 d) in June 1993 were attributed to an unidentified infection. From April to November, losses of *D. galeata* as a result of nonconsumptive mortality (average of 2.3% of standing stock per day) accounted on average for 23% of the estimated production (10% of the standing stock per day).

Zooplankton are important members of aquatic food webs. Numerous articles deal with standing stock, production, grazing impact on lower trophic levels, and nutrient regeneration by zooplankton. The control of zooplankton by invertebrate predators and fish has also been the subject of many studies (Gliwicz and Pijanowska 1989). While most studies have focused on the production of different groups of zooplankton and their interactions within the food web, comparatively little is known about the impact of nonconsumptive mortality on zooplankton population dynamics (Andersen 1997). Few articles address zooplankton mortality per se (Clarke and Carter 1974; Prepas and Rigler 1978; Ghilarov 1985; Gabriel et al. 1987; Brett et al. 1992). There is general agreement that consumptive mortality is the most important factor determining zooplankton population dynamics (Gliwicz and Pijanowska 1989). However, there are several potential reasons for nonconsumptive mortality: e.g., senescence, starvation (due to shortage of food quantity and quality), unsuccessful predator attack, and illness. The importance of these factors relative to mortality rates has yet not been examined in detail in nature (Green 1974; Schwartz and Cameron 1993).

In culture experiments, mortality rates can be measured relatively easily (Brett et al. 1992). Under natural conditions, mortality is usually estimated as the difference between a calculated estimate of birth rate (b) and estimated population growth rate (r) (Clarke and Carter 1974; Prepas and Rigler 1978; Rigler and Downing 1984; Ghilarov 1985). Like all field-estimated parameters, both r and b are subject to methodological errors (see Prepas and Rigler 1978). In particular, heterogeneous population distributions (horizontal and ver-

tical) (Patalas 1969; Patalas and Salki 1993) and egg mortality (Green 1974; Threlkeld 1979; Boersma and Vijverberg 1995) may cause over- or underestimates of r and b . Estimates of death rate (d), calculated as $d = b - r$, are confounded by errors in r and b and are therefore less precise than either (Taylor and Slatkin 1981). Consequently, it is difficult to obtain reliable estimates of mortality under natural conditions (Prepas and Rigler 1978; Brett et al. 1992). In addition to problems associated with the estimation of d , these estimates do not address the mechanistic causes of mortality. In this paper we describe a direct in situ estimate of nonconsumptive mortality, one that is based on sediment trap collection of dead or morbid zooplankton.

There are few articles dealing with the sedimentation of zooplankton. Rigler and MacCallum (1974), for example, found a nearly perfect fit, over the course of 2 yr, between the calculated production rates and production estimates based on cast exuviae that were collected from sediment traps. Frequently, however, sediment trap data are thought to overestimate sedimentation rates because of the use of poisons (Coale 1990; Michaels et al. 1990; Bathmann et al. 1991). A swimming zooplanktoner that randomly enters such a trap can be poisoned, immobilized, and added to the settled zooplankton. As a consequence, trap-collected mesozooplankton are often removed prior to analysis to avoid an overestimation of the sedimentation rate (Coale 1990; Michaels et al. 1990; Lee et al. 1992; von Bodungen et al. 1995). Therefore, we used unpoisoned traps and kept the exposure time short (3 to 4 d) to minimize the degradation of the settled material (Bloesch and Burns 1980).

Our study area was Lake Constance, a large, deep, warm-monomictic, mesotrophic, prealpine lake (area, 500 km²; $Z_{\max} = 253$ m; $Z_{\text{mean}} = 95$ m; Braun and Schärpf 1994). The sampling station was located at the center of Überlinger See, a fjordlike northwestern sidearm with a maximum depth of 147 m.

Zooplankton were collected twice per week from the end of March to November 1993 using a net and a sediment trap. Swimming zooplankton were collected within the upper 50 m with a Clarke–Bumpus sampler (30-cm diameter, 140- μ m mesh). The samples were stored in lake water at 4°C and were transported within 4 h to the laboratory, where they were filtered again (140 μ m), transferred into preweighed scintillation vials, and frozen at –25°C (Shapiro and Wright 1989). After lyophilization (Berberovic and Pinto-Coelho 1989), an aliquot of each sample (200–1,000 ind.) was counted under a dissecting microscope ($\times 16$ magnification). To avoid a counting bias, samples were counted in arbitrary order, beginning with pelagic samples and ending with trap samples (see below). Three different taxa were distinguished: copepods, of which only *Cyclops vicinus* was identified to the species level, *Daphnia galeata*, and *Daphnia*

hyalina. Other taxa or groups were only rarely found in the trap (0 to 5 ind./trap, *see* below) and thus are not reported here.

Sedimentation rates (ind. m⁻² d⁻¹) were determined twice per week from March to November 1993 in four unpoisoned, transparent, cylindrical tubes (1-m length, 10-cm diameter) attached to a common frame suspended at 50-m depth. The trapping efficiency of this type of trap is assumed to be 100% (Bloesch and Burns 1980; Gardner 1980a, 1980b). After recovery of the traps, the overlying water and any swimming zooplankton were gently removed by siphon. The material on the bottoms of the four tubes was combined and filtered through 140- μ m gauze to separate the mesozooplankton from other settled material. Mesozooplankton were filtered (HT-450 0.45- μ m Tuffryn membrane filter; Gelman Sciences), frozen at -25°C, lyophilized, and counted like the water samples. In order to avoid overestimation of non-consumptive mortality, only whole organisms or partial organisms with eye spots were counted, whereas exuviae from regular molting or individuals sucked out by carnivorous crustacean were disregarded. Degradation of zooplankton, which occurs very quickly within the first 3–4 d after death (Krause 1959, 1960, 1961), might result in an underestimation of sedimentation rate. Not all zooplankton entered the trap dead, but some were unable to maintain their position in the water column (e.g., because of partial loss of the second antennae or because of their weak condition). At the recovery of the trap, some of these animals were lying on the bottom of the trap. Since it is very unlikely that a zooplankton in such a weak condition will recover in the hypolimnion and migrate back to the upper water layers to continue life, animals lying on the bottom of the trap were counted as settled zooplankton. A more serious problem was the fact that some individuals were covered by exuviae. After lyophilization, it was not possible to uncover these organisms, and consequently, they were not counted. We estimate that omitting exuviae-covered individuals led to sedimentation rate underestimation that reached 30 to 50% at the maximum. As a result, our rate of nonconsumptive mortality may have been underestimated, since only “complete” individuals were counted.

Daily losses [% d⁻¹] from March to November as a result of sedimentation were calculated as follows:

$$\text{daily loss } (t) = 100 \times \left(\frac{\text{sedimentation rate}}{\text{standing stock}} \right)_t$$

with t = date of sediment trap recovery and zooplankton sampling. Incorporation of a time lag did not change the principle pattern, and it was therefore omitted. Average daily losses [% d⁻¹] over the whole investigation period were calculated as follows:

$$\text{average losses} = 100 \times \frac{\text{average sedimentation rate}}{\text{average standing stock}}$$

To compensate for the bias of uneven sampling intervals on the average, the sample interval was used as a weight variable. The average daily loss of the copepods was calculated from 1 July to the end of the investigation period in order

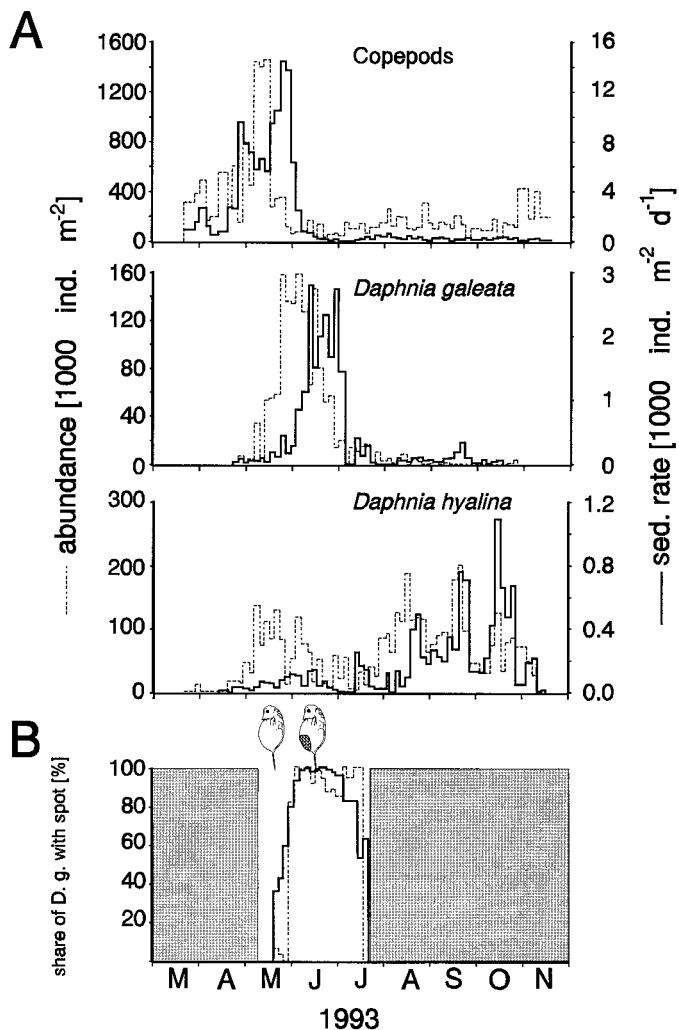


Fig. 1. (A) Abundance and sedimentation rate of copepods and daphnids. Note the different axis scales. (B) Share of *D. galeata* with spot. Broken line: abundance; solid line: sedimentation rate.

to exclude the migration toward the sediment that precedes diapause (*see* below).

Copepods numerically dominated the water column mesozooplankton assemblage in early spring, with an abundance of about 1.5×10^6 ind. m⁻² in early May (Fig. 1A). At this time, the copepods consisted mainly of individuals in the fourth copepodite stage of *Cyclops vicinus*. The population of *C. vicinus* declined sharply within 2.5 weeks to 7×10^4 ind. m⁻² after mid-May, and abundances of 10^5 ind. m⁻² were maintained throughout the summer. Copepod numbers in the traps showed two distinct peaks at the ends of April and May, with 1.0×10^4 and 1.4×10^4 ind. m⁻² d⁻¹, respectively (Fig. 1A). From 17 May to 31 May, copepod abundance declined from 1.4×10^6 to 10^5 ind. m⁻². The total sum of copepods found in the trap during that period was 1.9×10^5 ind. m⁻² (13.4% of the decline of the standing stock in the water column). Most of the copepods were lying motionless on the bottom of the trap but looked healthy. The daily sedimentation losses at the end of May were >10% of the standing stock per day (Fig. 2). From 1 July to Novem-

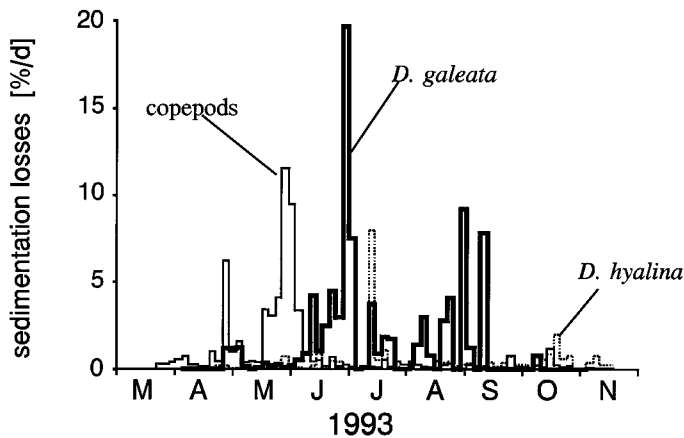


Fig. 2. Seasonal course of daily zooplankton losses due to sedimentation.

ber, few ($<500 \text{ ind. m}^{-2} \text{ d}^{-1}$) copepods were found in the traps, resulting in an average daily loss of 0.2% of the standing stock per day (Fig. 2). The abundance and population dynamics of the copepods are well known for Lake Constance (Einsle 1967; Wöfl 1991). The springtime decline in abundance results from migration of the fourth copepodite stage of *C. vicinus* (toward the sediments where they spend their diapause; Einsle 1967). This explains the healthy appearance of trap-collected organisms. Therefore, the term "migration" should be used rather than "sedimentation," since sedimentation should only describe passive sinking forms. It is possible that the copepods could detect that the trap does not have a good substrate in which they might spend their diapause, and thus they may have actively avoided the trap (Schröder 1960). This active avoidance could explain the relatively low estimate of trapping efficiency (13.4%) for migrating copepods (assumptions: the total decrease in the abundance is the result of migration [i.e., the predator-induced mortality can be neglected during these 2.5 weeks] and lack of reproduction). The migrating copepods generally laid motionless on the bottom of the trap, and few were actively swimming in the overlying trap water, indicating that the copepods had already begun their diapause in the trap. A high occurrence of copepods in traps during migration toward the sediment has also been found in the ocean (Haake et al. 1993).

D. hyalina exhibited five more or less distinct peaks between April and November, with a seasonal maximum in August/September of about $2.0 \times 10^5 \text{ ind. m}^{-2}$ (Fig. 1A). Similarly, *D. hyalina* had five sedimentation peaks, with a maximum rate of $1.1 \times 10^3 \text{ ind. m}^{-2} \text{ d}^{-1}$ in October. However, the correlation between abundance and sedimentation was not as clear as it was for *D. galeata* (see below), and the daily losses relative to the standing stock never reached rates as high as they were in the copepods and *D. galeata* (Fig. 2).

In mid-May, *D. galeata* abundance reached $1.6 \times 10^5 \text{ ind. m}^{-2}$, an abundance that remained relatively constant for the next 2 weeks. A dramatic population decline occurred in June, with abundances dropping below $2 \times 10^4 \text{ ind. m}^{-2}$ by July (Fig. 1A). During this population decline, *D. galeata*

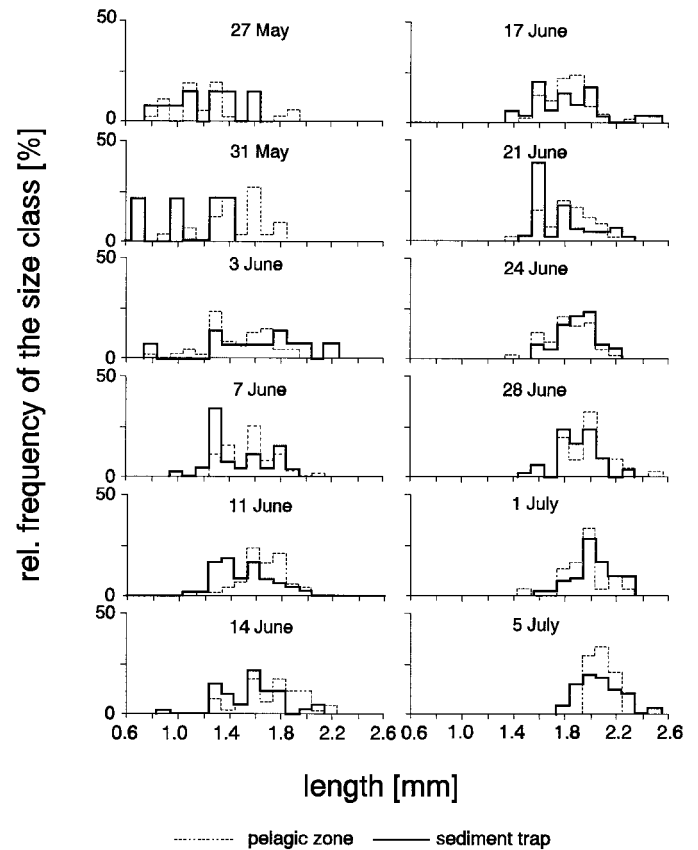


Fig. 3. Size spectra of *D. galeata* in the pelagic zone and the sediment traps at their sedimentation peak, 1993.

contained many lipid droplets along the gut and at the base of the filter appendages. From July to November, the abundance of *D. galeata* was low ($<2 \times 10^4 \text{ ind. m}^{-2}$). *D. galeata* showed a sedimentation maximum of $3.0 \times 10^3 \text{ ind. m}^{-2} \text{ d}^{-1}$ in June at the time of the population decline. The total amount of $5.3 \times 10^5 \text{ D. galeata m}^{-2}$ found in the trap in June corresponds to 38% of the decline from 1.6×10^5 to $2.0 \times 10^4 \text{ ind. m}^{-2}$ (average population decline of $10\% \text{ d}^{-1}$), which occurred at the same time in the pelagic zone. Relative daily losses were highest (18% of the standing stock per day) at the end of June (Fig. 2). Size spectra indicate negligible birth rates in June (Fig. 3), supporting the significance of nonconsumptive mortality during this period. From mid-July to November, the sedimentation rate of *D. galeata* was low ($<2 \times 10^2 \text{ ind. m}^{-2} \text{ d}^{-1}$). On average, the daily loss attributable to sedimentation was 2.3% of the standing stock per day, while the production was 10% per day (Straile pers. comm.).

Like the copepods, *D. galeata* exhibited a clear correlation between the decline of water column abundance and occurrence in the traps. *D. galeata* lived within the upper 15 m of the water column (Stich and Lampert 1981; Geller 1986) and, in contrast to *D. hyalina*, did not show a diel vertical migration. The only possible mechanism for getting into the trap was settling due to immobilization by death or morbidity. Einsle (pers. comm.) found morbid *D. galeata* deeper than 50 m in Lake Constance for many years during times

of population declines, indicating that the phenomenon of nonconsumptive mortality was not limited to our investigation.

There are several potential causes that might lead to nonconsumptive mortality: senescence, starvation (due to shortage of food quantity and quality), unsuccessful predator attack, and illness. In order to gain a better understanding of the causes of death, we compared size spectra of *D. galeata*, measured from the top of the head without the helmet to the base of the spina, in the water column and in the sediment trap. The size spectra of the daphnids from the water column indicated that very few offspring were produced in June; thus, one distinct cohort could be followed from 27 May to 5 July (Fig. 3). There was no significant difference between the size spectra of *D. galeata* from the water column and those found in the traps (GSK-test; Grizzle et al. 1969; PROC CATMOD, SAS version 6.03; $P = 0.07$; $N = 942$) (Fig. 3).

Data on the life spans of cladocerans is meager (Bottrell 1975). Culture experiments indicate maximum life spans of 20 to more than 60 d, depending on temperature, food quality and quantity, and species (McArthur and Baillie 1929; Wood et al. 1939; Lynch 1980). The life span is negatively correlated with the temperature and positively correlated with the size of the species (Bottrell 1975). In addition to temperature (Geller 1987), assumptions about food availability are necessary to predict the maximum life span of daphnids. Little is known about the contribution of senescence to population dynamics in lakes. Lampert and Sommer (1993) suggested that daphnids rarely attain their maximum possible age, noting that most mortality is the result of predation. Low rates of sedimentation relative to production rates suggest that senescence was trivial for *D. hyalina* and for copepods. However, sedimentation losses were as high as 0.2 d^{-1} for *D. galeata*, and nonconsumptive mortality may be very important to the dynamics of this population. Wood et al. (1939) reported a mean life span of about 30 d for *Daphnia longispina*. *D. galeata* is about the same size as *D. longispina*. A *D. longispina* life span of 30 d was determined at 20–25°C, and it is likely that the maximum life span of *D. galeata* is longer than 30 d under cooler in situ conditions. Geller (1986) calculated the average generation time of 18 d for *D. galeata* in June. The age of *D. galeata* at the time of the population crash in mid-June was, on average, about 20 d (duration of the June maximum; Fig. 1A). The similar size distribution of *D. galeata* in the pelagic zone and in the sediment traps indicates no size bias for mortality factors. Therefore, it is very unlikely that senescence of older individuals is the reason for the drastic population crash of *D. galeata*.

The summer decline of *Daphnia* populations has often been ascribed to starvation of the daphnids (Ghilarov 1985; Threlkeld 1985; Sommer et al. 1986), but to our knowledge, there are no direct measurements in support of the notion that the daphnids died of starvation. In Lake Constance, reduced egg numbers and increased ash content indicate starvation of the daphnids during the time of the clear-water phase in June (Geller and Müller 1985; Berberovic 1990). However, this does not necessarily imply that daphnids starved to death. The appearance of lipid droplets in *D. gal-*

eata suggests that a limited supply of energy (i.e., carbon) was not the principal reason for the high mortality rate (Gliwicz 1991). The occurrence of lipid droplets is not only an indication for both feeding success and energy investment into future offspring (Tessier and Goulden 1982), but it can be also a hint that poor food quality exists (Groeger et al. 1991; Sterner 1993), defined as a shortcoming of certain essential organic compounds, which results in a lower fecundity and/or higher mortality. Examples are highly unsaturated fatty acids like eicosapentaenoic acid (20:5 ω 3) (Ahlgren et al. 1990; Müller-Navarra 1995) or minerals (Elenndt 1990; Sterner 1993; Rothhaupt 1995). Food with a deficit of one or more essential components and an excess of carbon (e.g., nitrogen-limited algae) results in an accumulation of lipids in *Daphnia* (Groeger et al. 1991). We conclude that the presence of lipid droplets does not exclude starvation (as a result of low food quality) as a reason for the high nonconsumptive mortality of *D. galeata* during clear-water phase.

An attack of invertebrate predators, like copepods and carnivorous cladocera (in Lake Constance, *Leptodora kindii*, *Bythotrephes longimanus*), or vertebrate predators, like fish, does not necessarily result in a consumption of the prey. Unsuccessful attacks may damage a prey item in such a manner that it dies or cannot maintain its position in the water column (Hambright pers. comm.). We have no data about the impact of fish, and especially of fish larvae, on the mortality of zooplankton in Lake Constance, and thus, the impact of these factors on nonconsumptive mortality cannot be excluded. On the other hand, there are also no data demonstrating that a great deal of importance is associated with fish larvae in terms of nonconsumptive mortality. Since the population crash of *D. galeata* occurred at a time when the abundance of carnivorous crustaceans was low, it is unlikely that an unsuccessful attack from carnivorous crustaceans is the reason for the higher sedimentation rate for *D. galeata* at the end of June.

The period of high mortality of *D. galeata* coincided with a high incidence of a black spot on the daphnids, a spot that was possibly symptomatic of an infection. From June to mid-July, nearly all *D. galeata* exhibited a black-colored spot in the carapace, and sometimes also on the abdomen (Fig. 4). The spot was almost exclusively observed in *D. galeata*; only 12 of 1,447 daphnids with the spot were *D. hyalina*. The spot was first observed in mid-May. The portion of spot-bearing individuals increased from zero to nearly 100% within 2.5 weeks, both in the pelagic zone and in the sediment trap (Fig. 1B). After the population crash, the portion of spot-bearing daphnids decreased. The in situ black spot on *D. galeata* was visible enough that it was possible to distinguish between spot-bearing and "normal" daphnids while scuba diving. After lyophilization, the color of the spot changed from black to red. Individuals preserved with formaldehyde lost the spot completely within 1 week. The coloring was located inside the carapace and abdomen and did not result from epibionts. 4',6-diamidino-2-phenylindole (DAPI) did not stain any bacteria or fungi on the surface of the carapax. Thus, the reason for the occurrence of the spot has not yet been discerned. The spot was found every year and was most common during or at the end of the clear-

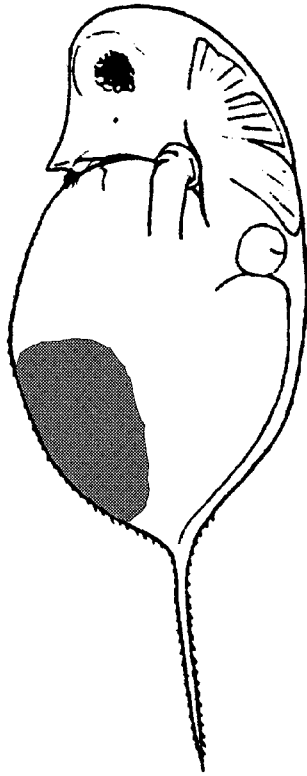


Fig. 4. Location of the spot in *D. galeata*. Length of the individual, 1.5 mm.

water phase (June to mid-July), from the beginning of our investigation in 1992 until 1997 (unpubl. data). Thus, the spot was not just a chance event during the summer of 1993.

With some exceptions (Green 1974; Burns 1989; Schwartz and Cameron 1993; Ebert 1995), there has been little study of the epidemiology of zooplankton. Therefore, the potentially dramatic impact of epidemiology on the physiology and longevity of zooplankton under natural conditions is uncertain (Green 1974; Schwartz and Cameron 1993).

Several hints support the hypothesis that the high mortality of *D. galeata* in June was caused by a species-specific infection. The reasons are as follows: (1) Within a very short period of time, nearly the entire population displayed the spot (Fig. 1B); (2) Only *D. galeata* showed the spot, while *D. hyalina* rarely showed symptoms; (3) The sedimentation rate of *D. galeata* increased dramatically after the occurrence of the spot; and (4) Green (1974) reported an infection of cladocerans by the carotenoid-producing bacterium *Spirobacillus cienkowskii* Metchnikoff, which resulted in the scarlet appearance of the infected individuals. Although we are not able to ascribe the pigmentation of *D. galeata* to a bacterial infection, it has at least been demonstrated that a bacterial infection may change the color of daphnids.

Of these four potential causes of death (senescence, starvation, unsuccessful predator attack, and infection), only senescence can be excluded as a single cause for the population crash. It is likely that starving daphnids are more susceptible to an infection than are well-fed ones. Thus, a combination of several factors might enhance the suscepti-

bility of an animal to an infection, resulting in the high mortality noted in June.

Taking into account that the predation pressure by vertebrate and invertebrate predators with visual orientation on spotted *D. galeata* should be much higher than on daphnids without pigmentation (Willey et al. 1990), the nonconsumptive mortality in June of at least 38% of the total mortality of 10% d^{-1} (assumption zero birth rate, see above) is of greater importance for the population dynamics than previously assumed. Daily losses of *D. galeata* were 2.3% of the standing crop per day. Average estimated birth rate from April to November was 10% d^{-1} (Straile pers. comm.), indicating that the nonconsumptive mortality contributed to 23% of the total mortality. For *D. hyalina* and copepods with estimated birth rates of about 5 and 2% d^{-1} , respectively, the nonconsumptive mortality of 0.5 and 0.2% d^{-1} , respectively, was only of minor importance.

A bias of the sedimentation rate might be seen in the diel vertical migration of zooplankton, resulting in an overestimation of the sedimentation related to the migration of the zooplankton into the traps during daytime. This bias can be minimized by positioning the trap well under the depth at which diel vertical migration occurs or by sampling the traps during the night. The impact of diel vertical migration on the appearance of zooplankton in the trap can be estimated by comparing the losses of migrating with nonmigrating zooplankton. The nonmigrating epilimnetic *D. galeata* (Geller 1986) had the highest rates of daily loss, whereas the migrating zooplankton, *D. hyalina* and copepods, had much lower rates of loss. This suggests that the bias of the sedimentation rate, in 50-m depth, attributable to vertical migration is low in our study. However, even if there should be a bias of the sedimentation rate due to diel vertical migration, the principle results, which indicate that copepods and *D. hyalina* had low nonconsumptive mortality (= high predator-induced mortality) and that *D. galeata* suffered high nonconsumptive mortality (= low predator-induced mortality), remain unaffected.

Nonconsumptive mortality might also be an important consideration for other lakes and seasons (Green 1974; Threlkeld 1985; Luecke et al. 1990). In predator-free lakes, all mortality must be the result of nonconsumptive mortality. For example, for this type of lake, Kwik and Carter (1975) found strong fluctuations of crustacean abundance in the predator-free Hangdog Pond. The calculated death rate of approximately 0.2 deaths per day for *Daphnia ambigua* was ascribed to food shortage. After removing fish from Lake Haugatjern, the sedimentation of zooplankton contributed to a significant phosphorus loss from the euphotic layer (Reinertsen et al. 1990). In Lake Mendota, a lake with predators, the calculated mortality for *D. galeata* (as a result of fish predation) was about 2% of production (Luecke et al. 1990), and the crash of the spring population was attributed to nonconsumptive mortality (starvation due to lack of edible algae) during the clear-water phase. Invertebrate predators were only important after the decline of the *Daphnia* spring maximum (Lunte and Luecke 1990). Taking into account that fish larvae were not considered in this estimation and thus that fish predation might be higher by an order of magnitude (Luecke et al. 1990), a very high proportion of mor-

tality is unexplained and might be the result of nonconsumptive mortality.

In summary, the example from Lake Constance has shown that it is possible to directly estimate the nonconsumptive mortality of zooplankton with the use of sediment traps. Nonconsumptive mortality and parasitism appears to be at least seasonally significant for crustacean zooplankton population dynamics, especially if predators are rare (Burns 1989). We believe that the application of this simple method for the estimation of nonconsumptive mortality will give new and important insights into the regulation of the population dynamics of mesozooplankton and therefore of aquatic food webs.

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References

- AHLGREN, G., L. LUNDSTEDT, M. BRETT, AND C. FORSBERG. 1990. Lipid composition and food quality of some freshwater phytoplankton for cladoceran zooplankters. *J. Plankton Res.* **12**: 809–818.
- ANDERSEN, T. 1997. Pelagic nutrient cycles: Herbivores as source and sinks. Springer, Ecological Studies Vol. 129.
- BATHMANN, U. V., T. T. NOJI, AND B. VON BODUNGEN. 1991. Sedimentation of pteropods in the Norwegian Sea in autumn. *Deep-Sea Res.* **38**: 1341–1360.
- BERBEROVIC, R. 1990. Biomass composition of two sympatric *Daphnia* species: Impact of environmental factors and life history strategies. Ph.D. thesis, University of Konstanz.
- , AND R. PINTO-COELHO. 1989. Dry first measure later: A new procedure to preserve and measure zooplankton for ecophysiological studies. *J. Plankton Res.* **11**: 1109–1116.
- BLOESCH, J., AND N. M. BURNS. 1980. A critical review of sedimentation trap technique. *Schweiz. Z. Hydrol.* **42**: 15–55.
- BOERSMA, M., AND J. VIJVERBERG. 1995. The significance of nonviable eggs for *Daphnia*. *Limnol. Oceanogr.* **40**: 1215–1224.
- BOTTRELL, H. H. 1975. Generation time, length of life, instar duration and frequency of moulting, and their relationship to temperature in eight species of Cladocera from the River Thames, Reading. *Oecologia* **19**: 129–140.
- BRAUN, E., AND K. SCHÄRPF. 1994. Internationale Bodensee-Tiefenvermessung 1990. Landesvermessungsamt Baden-Württemberg, Stuttgart.
- BRETT, M., L. MARTIN, AND T. J. KAWECKI. 1992. An experimental test of the egg-ratio method: Estimated versus observed death rates. *Freshw. Biol.* **28**: 237–248.
- BURNS, C. W. 1989. Parasitic regulation in a population of *Boeckella hamata* Brehm (Copepoda: Calanoida). *Freshw. Biol.* **21**: 421–426.
- CLARKE, A. S., AND J. C. H. CARTER. 1974. Population dynamics of cladocerans in Sunfish Lake, Ontario. *Can. J. Zool.* **52**: 1235–1242.
- COALE, K. H. 1990. Labyrinth of doom: A device to minimize the “swimmer” component in sediment trap collections. *Limnol. Oceanogr.* **35**: 1376–1381.
- EBERT, D. 1995. The ecological interactions between a microsporidian parasite and its host *Daphnia magna*. *J. Anim. Ecol.* **64**: 361–369.
- EINSLER, U. 1967. Die äußeren Bedingungen der diapause planktisch lebender Cyclops-Arten. *Arch. Hydrobiol.* **63**: 387–408.
- ELENDT, B.-P. 1990. Selenium deficiency in Crustacea: An ultrastructural approach to antennal damage in *Daphnia magna* Straus. *Protoplasma* **154**: 25–33.
- GABRIEL, W., B. E. TAYLOR, AND S. KIRSCH-PROKOSCH. 1987. Cladoceran birth and death rates estimates: Experimental comparisons of egg-ratio methods. *Freshw. Biol.* **18**: 361–372.
- GARDNER, W. D. 1980a. Sediment trap dynamics and calibration: A laboratory evaluation. *J. Mar. Res.* **38**: 17–39.
- . 1980b. Field assessment of sediment traps. *J. Mar. Res.* **38**: 41–52.
- GELLER, W. 1986. Diurnal vertical migration of zooplankton in a temperate great lake (L. Constance): A starvation avoidance mechanism? *Arch. Hydrobiol. (suppl.)* **74**: 1–60.
- . 1987. On estimating the age and development time of *Daphnia* as a function of body size and temperature. *J. Plankton Res.* **9**: 1225–1230.
- , AND H. MÜLLER. 1985. Seasonal variability in the relationship between body length and individual dry weight as related to food abundance and clutch size in two coexisting *Daphnia* species. *J. Plankton Res.* **7**: 1–18.
- GHILAROV, A. M. 1985. Dynamics and structure of cladoceran populations under conditions of food limitation. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* **21**: 323–332.
- GLIWICZ, Z. M. 1991. Food thresholds, resistance to starvation, and cladoceran body size. *Verh. Int. Verein. Limnol.* **24**: 2795–2798.
- , AND J. PIJANOWSKA. 1989. The role of predation in zooplankton succession, p. 253–296. *In* U. Sommer [ed.] *Plankton ecology: Succession in plankton communities*. Springer Verlag.
- GREEN, J. 1974. Parasites and epibionts of Cladocera. *Trans. Zool. Soc. Lond.* **32**: 417–515.
- GRIZZLE, J. E., C. F. STARMER, AND G. G. KOCH. 1969. Analysis of categorical data by linear models. *Biometrics* **25**: 489–504.
- GROEGER, A. W., M. D. SCHRAM, AND G. RICHARD. 1991. Influence of food quality on growth and reproduction in *Daphnia*. *Freshw. Biol.* **26**: 11–19.
- HAAKE, B., V. ITTEKOT, S. HONJO, AND S. MANGANINI. 1993. Amino acid, hexosamine and carbohydrate fluxes of the deep subarctic Pacific (Station P). *Deep-Sea Res.* **40**: 547–560.
- KRAUSE, H. R. 1959. Biochemische Untersuchungen über den postmortalen Abbau von totem plankton unter aeroben und anaeroben Bedingungen. *Arch. Hydrobiol. (suppl.)* **24**: 297–337.
- . 1960. Abbau organischer Phosphorverbindungen aus totem Süßwasser-Zooplankton. *Naturwissenschaften* **17**: 401.
- . 1961. Einige Bemerkungen über den postmortalen Abbau von Süßwasser-zooplankton unter laboratoriums- und Freilandbedingungen. *Arch. Hydrobiol.* **57**: 539–543.
- KWIK, J. K., AND J. C. H. CARTER. 1975. Population dynamics of

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- limnetic Cladocera in a beaver pond. *J. Fish. Res. Board Can.* **32**: 341–346.
- LAMPERT, W., AND U. SOMMER. 1993. Limnoökologie. 5.4. Demographie, p. 185–189. *In* Limnoökologie/ Thieme-Verlag.
- LEE, C., J. I. HEDGES, S. G. WAKEHAM, AND N. ZHU. 1992. Effectiveness of various treatments in retarding microbial activity in sediment trap material and their effects on the collection of swimmers. *Limnol. Oceanogr.* **37**: 117–130.
- LUECKE, C., M. J. VANNI, AND J. J. MAGNUSON. 1990. Seasonal regulation of *Daphnia* populations by planktivorous fish: Implications for the spring clear-water phase. *Limnol. Oceanogr.* **35**: 1718–1733.
- LUNTE, C. C., AND C. LUECKE. 1990. Trophic interactions of *Lepidodora* in Lake Mendota. *Limnol. Oceanogr.* **35**: 1091–1100.
- LYNCH, M. 1980. The evolution of cladoceran life histories. *Q. Rev. Biol.* **55**: 23–42.
- MCCARTHUR, J. W., AND W. H. T. BAILLIE. 1929. Metabolic activity and duration of life. I. Influence of temperature on longevity in *Daphnia magna*. *J. Exp. Zool.* **53**: 221–242.
- MICHAELS, A. F., M. W. SILVER, M. M. GROWING, AND G. A. KNAUER. 1990. Cryptic zooplankton in upper ocean sediment traps. *Deep-Sea Res.* **37**: 1285–1296.
- MÜLLER-NAVARRA, D. 1995. Evidence that a highly unsaturated fatty acid limits *Daphnia* growth in nature. *Arch. Hydrobiol.* **132**: 297–307.
- PATALAS, K. 1969. Composition and horizontal distribution of Crustacean plankton in Lake Ontario. *J. Fish. Res. Board. Can.* **26**: 2135–2164.
- , AND A. SALKI. 1993. Spatial variation of crustacean plankton in lakes of different size. *Can. J. Fish. Aquat. Sci.* **50**: 2626–2640.
- PREPAS, E., AND F. H. RIGLER. 1978. The enigma of *Daphnia* death rates. *Limnol. Oceanogr.* **23**: 970–988.
- REINERTSEN, H., A. JENSEN, J. I. KOKSVIK, A. LANGELAND, AND Y. OLSEN. 1990. Effects of fish removal on the limnetic ecosystem of a eutrophic lake. *Can. J. Fish. Aquat. Sci.* **47**: 166–173.
- RIGLER, F. H., AND M. E. MACCALLUM. 1974. Production of zooplankton in Char Lake. *J. Fish. Res. Board Can.* **31**: 637–646.
- RIGLER, F. H., AND J. A. DOWNING. 1984. The calculation of secondary productivity. Chapter 2. pp. 19–58. *In*: Peters, F. H. and J. A. Downing (eds.): A manual on methods for the assessment of secondary productivity in fresh waters. 2. ed. Blackwell Scientific Publications.
- ROTHHAUPT, K.-O. 1995. Algal nutrient limitation affects rotifer growth rate but not ingestion rate. *Limnol. Oceanogr.* **40**: 1201–1208.
- SCHRÖDER, R. 1960. Echoorientierung bei *Mixodiatomus lacinatus*. *Naturwissenschaften* **23**: 548–549.
- SCHWARTZ, S. S., AND G. N. CAMERON. 1993. How do parasites cost their hosts? Preliminary answers from trematodes and *Daphnia obtrusa*. *Limnol. Oceanogr.* **38**: 602–612.
- SHAPIRO, J., AND D. WRIGHT. 1989. Successful preservation of *Daphnia* for chemical and physical analysis. *Hydrobiologia* **175**: 61–63.
- SOMMER, U., Z. M. GLIWICZ, W. LAMPERT, AND A. DUNCAN. 1986. The PEG-model of seasonal succession of planktonic events in fresh waters. *Arch. Hydrobiol.* **106**: 433–471.
- STERNER, R. W. 1993. *Daphnia* growth on varying quality of *Scenedesmus*: Mineral limitation of zooplankton. *Ecology* **74**: 2351–2360.
- STICH, H.-B., AND W. LAMPERT. 1981. Predator evasion as an explanation of diurnal vertical migration of zooplankton. *Nature* **293**: 396–398.
- TAYLOR, B. E., AND M. SLATKIN. 1981. Estimating birth and death rates of zooplankton. *Limnol. Oceanogr.* **26**: 143–158.
- TESSIER, A. J., AND C. E. GOULDEN. 1982. Estimating food limitation in cladoceran populations. *Limnol. Oceanogr.* **27**: 707–717.
- THRELKELD, S. T. 1979. Estimating cladoceran birth rates: The importance of egg mortality and the egg age distribution. *Limnol. Oceanogr.* **24**: 601–612.
- . 1985. Resource variation and the initiation of midsummer declines of cladoceran populations. *Arch. Hydrobiol. Beih. Ergebn. Limnol.* **21**: 333–340.
- VON BODUNGEN, B., AND OTHERS. 1995. Pelagic processes and vertical flux of particles: An overview of a long-term comparative study in the Norwegian Sea and Greenland Sea. *Geol. Rundsch.* **84**: 11–27.
- WILLEY, R. L., P. A. CANTRELL, AND S. T. THRELKELD. 1990. Epibiotic euglenoid flagellates increase the susceptibility of some zooplankton to fish predation. *Limnol. Oceanogr.* **35**: 952–959.
- WÖLFL, S. 1991. The pelagic copepod species in Lake Constance: Abundance, biomass, and secondary production. *Verh. Int. Verein. Limnol.* **24**: 854–857.
- WOOD, T. R., L. INGLE, AND A. M. BANTA. 1939. Growth and reproductive characteristics of *Daphnia longispina*, p. 182–200. *In* A. M. Banta [ed.]. Studies on the physiology, genetics, and evolution of some Cladocera. Paper No. 39, Department of Genetics, Carnegie Institution of Washington.

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