

Starvation and the size structure of zooplankton communities*

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Summary

The survival time of zooplankton under conditions of total starvation is expressed as a function of weight-specific respiration rate and the fraction of initial (pre-starvation) body weight which may be lost prior to death. Data from the literature on these two components of survival time are used to formulate a general expression of survivorship of zooplankton at 20°C as a function of body weight: $t = 2.95 w^{0.25}$, where t is in days and w is μg dry weight. Survival time data from the literature on 25 marine and freshwater species are compared to this prediction as are new data on *Daphnia pulex* Leydig, *D. magna* Straus and *Simocephalus serrulatus* (Koch). The effects of age-specific (non-starvation) mortality are considered; in particular, older individuals of each of these species survive for shorter periods of time than predicted and an interaction between age-specific and starvation-induced mortality is proposed. The effects of total and partial starvation on the size structure of zooplankton communities are discussed.

Introduction

The effects of food limitation on the size structure of freshwater zooplankton communities have been the subject of much discussion during the past decade

(e.g., Brooks & Dodson, 1965; Hutchinson, 1967; Sprules, 1972; Dodson, 1974; Neill, 1975). Although food limitation has been suggested as leading to competitive displacement (Brooks & Dodson, 1965) and single species' population crashes (Hutchinson, 1967; Bosselmann, 1974; Clark & Carter, 1974; Kwik & Carter, 1975; Nowak, 1975), little convincing evidence is available (Hrbackova-Esslova, 1963; Neill, 1975).

Any food regime which, by its poor quality or insufficient quantity, permits less individual growth and reproduction than what is physiologically possible may be considered as limiting. Different degrees of food limitation will affect reproduction, growth and survivorship of individual animals; these individual responses to food conditions will be reflected in similar population growth patterns. The present paper investigates the effects of an extreme form of food limitation on zooplankton community structure: starvation. Intense grazing pressure or shifts in the physical and chemical properties of a water body which direct algal succession may reduce the quantity of edible particulate matter and cause starvation. While there is no compelling evidence of starvation of natural populations of zooplankton, precipitous population crashes in predator-free systems (Clark & Carter, 1974; Kwik & Carter, 1975), as well as the favourable responses of some species to additions of food (Hrbackova-Esslova, 1963), suggest that starvation may sometimes occur. Whether starvation is a mechanism in competitive exclusion is not known. It is my hope then, that investigation of the impact of starvation on zooplankton survival according to body size may yield insight to various patterns of community composition.

My approach to this problem has been to develop a model of starvation based on survival time, and then compare its predictions with my own data and that collated from the literature. Other considerations regarding food limitation in natural communities are also discussed.

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Table 1. Weight-specific respiration rate regressions on body weight for various zooplankton species determined at or near 20°C

Zooplankton	Temperature (°C)	Respiration (R , $\mu\text{g } \mu\text{g}^{-1} \text{ day}^{-1}$; w , μg)	Reference
<i>Diatomus gracilis</i> Sars	20	$R = 0.483 w^{-0.3861}$	Kibby (1971)
<i>Daphnia pulex</i> var. <i>pulicaria</i> Forbes	20	$R = 0.207 w^{-0.124}$	Richman (1958)
<i>Simocephalus vetulus</i> (O. F. Müller)	22	$R = 0.133 w^{-0.107}$	Ivanova & Klekowski (1972)
<i>Diatomus</i> spp.	20	$R = 0.4913 w^{-0.374}$	Comita (1968)
Marine temperate zooplankton	17	$R = 0.3816 w^{-0.309}$	Ikeda (1970)
<i>Macrocyclus albidus</i> Jurine	21	$R = 0.39 w^{-0.16}$	Shushkina <i>et al.</i> (1968)
<i>Daphnia</i> , <i>Cyclops</i> , <i>Diatomus</i>	20	$R = 0.3106 w^{-0.3384}$	Scherbakoff (1935)
<i>Daphnia magna</i> Straus	18	$R = 0.2935 w^{-0.184}$	Kersting (1973)
'Average' regression		$R = 0.337 w^{-0.248}$	

The model

The survival time of a starving organism may be expressed by the following equation:

$$t = \frac{k}{g} \quad (1a)$$

where t is the survival time in days, g is the rate at which the animal loses weight ($\mu\text{g } \mu\text{g}^{-1} \text{ day}^{-1}$), and k is the fraction of initial (pre-starvation) body weight that can be lost and still permit survival (expendable body weight fraction: $0 < k < 1$).

Table 1 shows eight weight-specific respiration rate regressions against body weight for zooplankton determined at or near 20°C. I have included only those regressions that were verified against figured or tabular data in the original papers cited. Respiration values were converted to weight loss rates assuming protein metabolism (5.65 kcal/g) and an oxycaloric equivalent of 4.63 cal/ml O_2 (Winberg, 1971; Elliott & Davison, 1975). Two coefficients from the regressions in Table 1 (the weight exponent and level of metabolism) are necessary to estimate g in equation (1a). The mean value (\pm SE) of the weight exponent was -0.248 ± 0.041 , while the mean value of the level of metabolism was 0.337 ± 0.047 . Because respiration rate usually falls by about 50%

under starvation conditions (Comita, 1968; Ikeda, 1971, 1974; Omori, 1970; Shadowsky, 1936; Jorgensen, 1966), the equation constant was halved, to 0.17. This reduction in respiration rate is probably due to a combination of several factors, including reduced feeding activity (Thompson & Bayne, 1972), lowered metabolism of food processing (specific dynamic action) (Hubbell, 1971), and net loss of respiring body tissue (Richman, 1958; Hubbell, 1971). The exponent used was -0.25 , the value also used by Kleiber (1961) and Schmidt-Nielsen (1972).

The second component in equation (1a) is k (expendable body weight fraction). Chossat's rule (1843, in Kleiber, 1961) states that animals which are starving catabolize about half of their body weight and then die. Comparative data are scarce for planktonic animals, and do not seem to follow any consistent pattern with body size (Table 2). These data points on expendable body weight are of several types (taken at 50% survivorship, experiment termination, etc.) and are not amenable to rigorous statistical analysis or discrimination. As data are scarce, it is necessary to assume that Chossat's rule is appropriate for use in equation (1a).

When the average weight specific respiration rate regression (from Table 1) is combined with Chossat's rule as in equation (1a), the final form of a predictive

Table 2. Expendable body weight fraction for various zooplankton species

Species	Dry weight (μg)	Expendable body weight fraction	Data type	Reference
<i>Daphnia pulex</i> var. <i>pulicaria</i> Forbes	23	0.52	Experiment termination	Richman (1958)
<i>Daphnia magna</i> Straus	101	0.32	Median	Smith (1963)
<i>Calanus helgolandicus</i> (Claus)	109	0.19	50% survivorship	Cowey & Corner (1963)
<i>Daphnia pulex</i> Leydig	127	0.69	Experiment termination	Kerb (1910)
<i>Calanus helgolandicus</i> (Claus)	200	0.34	50% survivorship	Cowey & Corner (1963)
<i>Calanus cristatus</i> Kröyer	1800	0.47	50% survivorship	Ikeda (1971)
<i>Calanus cristatus</i> Kröyer	1800	0.67	Inferred from weight variations in field samples	Omori (1970)
<i>Calanus cristatus</i> Kröyer	1800	0.75	Inferred from weight variations in field samples	Omori & Tanaka (1967)

equation for survival time as a function of body weight results:

$$t = \frac{k}{g} = 0.5 / (0.17w^{-0.25})$$

$$= 2.95w^{0.25} \quad (1b)$$

where w is the initial (pre-starvation) dry weight of the animal in μg . This survival time relationship is proposed for zooplankton starving at or near 20°C and assumes catabolism of proteins only; if variations in body composition and catabolism of lipid compounds (or other metabolic reserves) during starvation are considered (Giese, 1966; Ikeda, 1971, 1974; Lee *et al.*, 1970, 1971; Mayzaud, 1973, 1975), the predicted survival times could be as much as 70% greater.

Evaluation of the model

(a) Methods and materials

Data on the survivorship of twenty-five marine and freshwater species of zooplankton under starvation were collected from twenty literature sources (Table 3); the survival time data were converted to conditions at 20°C , when necessary, using a Q_{10} value of 2.0. My own starvation experiments included approximately 500 individuals of *Daphnia pulex* Leydig, *D. magna* Straus, and *Simocephalus serrulatus* (Koch), identified according to Edmondson (1959). The animals were obtained from laboratory cultures, maintained at 20°C on an *Ankistrodesmus-Chlorella* algal mixture. Animals were starved in groups of ten in 175 ml glasses of Millipore filtered ($0.45 \mu\text{m}$) lake water (from Gull Lake, Michigan) at 20°C under a 12-h light:12-h dark photoperiod. Animals were transferred daily by pipette to freshly Millipore filtered water. No ovigerous females were used in any of the experiments. Initial (pre-starvation) dry weights of the animals to be starved were determined using the length-weight regressions of Dumont, DeVelde & Dumont (1975) and Ivanova & Klekowski (1972).

(b) Results and discussion

The results of my experiments with *Daphnia pulex*, *D. magna* and *Simocephalus serrulatus* only partially corroborate the survival time model. In all three cases the survival times of the smaller size classes of each species agreed with the model, but mean survival times for older, larger-bodied size classes

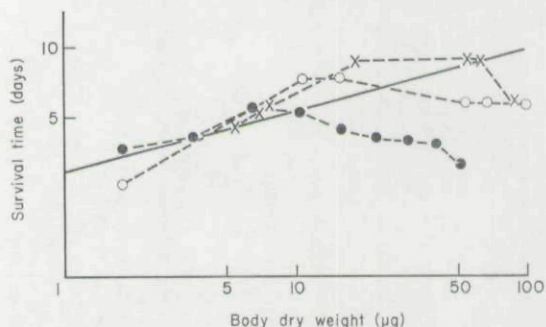


Fig. 1. Mean survival times of *Daphnia pulex* (●), *Daphnia magna* (○) and *Simocephalus serrulatus* (×) at 20°C as a function of body weight. The solid line is the prediction of the survival time model (equation 1b).

were consistently lower than predicted. This 'humped curve' pattern (Fig. 1), although not expected from equation (1b), is not surprising. Since age-specific (non-starvation) mortality rates are higher in older (larger) stages than in younger (smaller) stages (e.g., MacArthur & Baillie, 1929; Frank, Boll & Kelly, 1957; Lei & Clifford, 1974), it should be expected that as individuals age under conditions of starvation their survival times will be progressively shorter than expected from a model based on respiratory processes alone.

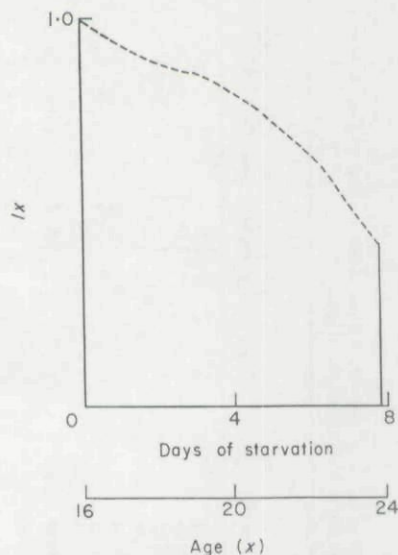


Fig. 2. Hypothetical survivorship curve for a cohort of *Daphnia pulex* (pre-starvation individual weight, $53 \mu\text{g}$; age, 16 days) affected by age-specific (-----) and starvation-induced (——) mortality. Although expected survival time under conditions of starvation is 7.96 days (equation 1b), age-specific mortality reduces mean survival time for the cohort to 5.8 days.

Table 3. Survival time data for starving zooplankton plotted in Fig. 4. Where body weights were not recorded in the original paper, the source used for body weight estimates is listed as the second paper per datum

Species	Initial (pre-starvation) dry weight (μg)	Temperature ($^{\circ}\text{C}$)	Survival time (days)	Survival time data type	References
<i>Daphnia magna</i> Straus	101	20	6	Median	Smith (1963), Burns (1969)
<i>Daphnia magna</i> Straus	150	18-20	4	Mean	Gulati (pers. comm.)
<i>Daphnia pulex</i> Leydig	127	15	11	Experiment termination	Kerb (1910)
<i>Daphnia pulex</i> var. <i>pulicaria</i> Forbes	230	20	5	Experiment termination	Richman (1958)
<i>Moina macrochaeta</i> Straus	12-7	20?	4	Text	Stuart <i>et al.</i> (1931), Dumont <i>et al.</i> (1975)
<i>Penilia avirostris</i> Dana	2-7	25-26	1	Maximum	Pavlova (1959), Raymont (1963), Dumont <i>et al.</i> (1975)
<i>Penilia avirostris</i> Dana	0-5	25-26	0-41	Maximum	Pavlova (1959), Raymont (1963), Dumont <i>et al.</i> (1975)
<i>Artemia salina</i> (L.)	1-5	23	6-5	Midrange	Baylor & Sutcliffe (1963), Anraku (1964)
<i>Palaemonetes vulgaris</i> (Say)	250	25-27	5	Maximum	Broad (1957), Ikeda (1970)
<i>Palaemonetes pugio</i> Holthius	250	25-27	10	Maximum	Broad (1957), Ikeda (1970)
<i>Ostrea edulis</i>	1	20	8	Experiment termination	Miller & Scott (1967), Holland & Spencer (1973)
<i>Acartia clausi</i> Giesbrecht	13-2	13	2-3	Minimum	Mayzaud (1973)
<i>Acartia longiremis</i> (Lillj.)	10-4	6-8-11-0	22	Median	Ikeda (1974)
<i>Acartia longiremis</i> (Lillj.)	8-9	9-11	13	Median	Ikeda (1974)
<i>Calanus cristatus</i> Kröyer	1800	6-9-11-9	29-59	50% survivorship	Ikeda (1971)
<i>Calanus cristatus</i> Kröyer	892	9-0-12-8	38	Median	Ikeda (1974)
<i>Calanus finmarchicus</i> Gunner	209	5	32-5	Midrange of mode	Marshall & Orr (1952), Marshall (1973)
<i>Calanus helgolandicus</i> (Claus)	109	7	11-6	50% survivorship	Cowey & Corner (1963)
<i>Calanus helgolandicus</i> (Claus)	200	12	8-89	50% survivorship	Cowey & Corner (1963)
<i>Calanus hyperboreus</i> Kröyer	1800	5?	28	Experiment termination	Conover (1962)
<i>Calanus hyperboreus</i> Kröyer	1800	5?	80	Experiment termination	Conover (1964)
<i>Calanus planichirus</i>	556	5-0-11-0	29-5	Median	Ikeda (1974)
<i>Epischura lacustris</i> Forbes	5	20	6	Mean	Main (1961)
<i>Epischura lacustris</i> Forbes	25	20	8	Mean	Main (1961)
<i>Eucalanus bungii</i> bungii	1011	5-0-12-8	64	Median	Ikeda (1974)
<i>Labidocera jollae</i>	160	18	2-5	Midrange	Lillelund & Lasker (1971)
<i>Metridia pacifica</i>	188	9-0-12-8	27	Median	Ikeda (1974)
<i>Oithona similis</i> Claus	1-35	10	10-5	Midrange	Marshall & Orr (1966)
<i>Paracalanus parvus</i> Claus	5-1	13-15	5-5	Median	Ikeda (1974)
<i>Pseudocalanus elongatus</i> (Boeck)	20-7	10	29	Mean	Urry (1965), Marshall & Orr (1966)
<i>Pseudocalanus elongatus</i> (Boeck)	11-6	10	17-5	Mean	Urry (1965), Marshall & Orr (1966)
<i>Sagittia hispida</i> Conant	121	23	7	Text	Reeve <i>et al.</i> (1970)

Table 4. The probabilities (l_x) of surviving to certain ages (x) and weights (w) for *Daphnia pulex* grown at culture densities of one individual per cm^3 (data from Frank *et al.*, 1957)

l_x	x (days)	w (μg)
0.99	1	1
0.96	5	13
0.92	10	33
0.84	15	49
0.63	20	63
0.27	25	68
0.10	30	77
0.03	35	78

An example of this effect can be illustrated by using survivorship and growth data for *Daphnia pulex* (Frank *et al.*, 1957). From this information it is possible to construct a mortality rate schedule for *Daphnia* (in the absence of starvation) in terms of body size as well as age (Table 4). By using this mortality schedule for individuals of a given size, survivorship curves can be drawn for cohorts of individuals affected by natural ageing and starvation. For example, Fig. 2 shows the expected survivorship curve for a size class of *Daphnia pulex* beginning a starvation period weighing $53 \mu\text{g}$ at an age of 16 days. Even though the cohort is expected to survive for 7.96 days under conditions of starvation (from equation 1b), about 50% of its members die from age-specific mortality before that time, thereby reducing the mean survival time of the cohort to 5.8 days. When the effects of age-specific and starvation-induced mortality are combined in this way for all size classes, the relationship of survival time to body weight (Fig. 3) becomes very similar to that shown in Fig. 1.

The implication of this effect is that equal statistical

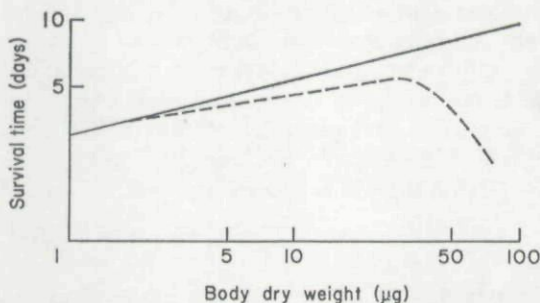


Fig. 3. Hypothetical survival times of *Daphnia pulex* according to weight calculated from starvation-induced mortality (equation 1b, —) or from a combination of age-specific and starvation-induced mortality (-----).

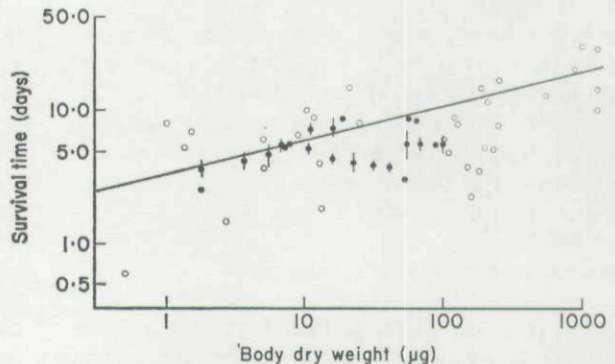


Fig. 4. Survival times of starving zooplankton at 20°C as a function of body weight. —, The prediction of the survival time model; \circ , literature data (see Table 3); \bullet the mean survival time (\pm SE) for all starved individuals of one species (of *Daphnia pulex*, *D. magna* or *Simocephalus serrulatus*) within a 0.2-mm length size class obtained in any one experiment.

weighting of all survival time data obtained in starvation experiments may lead to improper evaluation of survival time models based on respiratory processes alone. Data on different size classes within a single species may provide little support for the model because of the bias included due to age-specific mortality. Evaluation of the model must come from comparisons of different sized species, where the subtle effects of age-specific mortality within a species may be masked by the larger scale, body size effects. When my data are plotted with other existing survival time data (Table 3), the fit to the model's predictions is not perfect, but remains suggestive (Fig. 4). Unfortunately, a statistical analysis of the suitability of the fit of the literature data in Fig. 4 to the model is inappropriate because of their mathematical form. These survival time data are expressed as means, maxima, midranges or when starvation experiments were terminated (see Table 3); Kleiber (1961) warns against any precise comparison of such varied types of survival data. Additional survival time data of appropriate mathematical form (I suggest means, as does Kleiber) on a wide size range of species are required to fully evaluate this model.

This model of survival time under conditions of starvation is very simple. One obvious simplification is the weight loss rate term. This rate is reduced by 50% from the beginning of starvation. If this reduction is in fact related to reduced feeding activity, specific dynamic action, and the net loss of body tissue over time, then a more realistic model would incorporate this reduction in respiration rate as a

time-dependent process. Furthermore, recent information on shifts in metabolic substrates used during the course of starvation (Ikeda, 1971; Mayzaud, 1973, 1975) are subsumed by the use of an average (time-independent) weight loss rate equation based solely on protein catabolism.

Food limitation in natural communities

Analysis of the effects of food limitation on community size structure should not be restricted to aspects of total starvation. It is also necessary to assess the existence of any relationship between body size and the concentration of food at which an animal begins to starve. The importance of such a relationship cannot be denied: the impact of periods of size-related starvation on community size structure may be augmented or reversed by the timing of the onset of starvation of its members.

It is possible to define a food level at which starvation begins (or ceases) as the 'persistence' level, or where basal metabolic costs of an animal are just balanced by the energies consumed and assimilated. In its most simplistic representation, this would be equivalent to setting feeding rate (or the product of the food concentration at persistence (FC) and the filtering rate (FR)) equivalent to the metabolic rate (MR), thus:

$$(FC)(FR) = MR \quad (2)$$

Assimilation efficiency has been assumed here to be constant for all body sizes and food particles. In cladocerans, filtering rate generally increases as a power of body length somewhat greater than two (up to around four), (Burns, 1969; O'Brien, 1970; Chisholm, Stross & Nobbs, 1975), while metabolic rate usually increases at a power of body length less than two (Richman, 1958). The minimum food concentration for the maintenance ration may be expressed as a function of body length (L) in terms of these power functions:

$$FC = \frac{MR}{FR} \propto \frac{L^{-2}}{L^{>2}} \approx \frac{1}{L^{>0}} \quad (3)$$

$$FC \propto L^{-0}$$

Equation 3 states that the concentration of food necessary for the maintenance ration of a species in a community should be inversely proportional to its body length. It is thus expected that larger-bodied species should be able to persist at lower food levels

than smaller species (or smaller life stages of the same species). Data to evaluate the existence of this relationship are scarce (Hall *et al.*, 1976). Evidence on the survivorship of marked individuals of *Daphnia magna* in experimental microcosms (Neill, 1975) indicates that neonates are more vulnerable to food shortages than are adults, in accord with the relationship. If the onset of starvation generally occurs at higher food densities for smaller animals, the impact of periodic food limitation on community composition may be even greater than suggested by equation 1.

Since analyses of declining natural populations and instances of competitive exclusion have rarely been concerned with such a size-related phenomenon as starvation it would be interesting to reanalyse such samples for any trends in population or community size structure. It appears that the survival times of populations assumed to be starving can be estimated (from equation 1b) and the plausibility of severe food limitation in natural communities can be investigated by observing the rate of population decline. Ultimately, field and laboratory manipulations of the quality or quantity of natural food (e.g. Hrbackova-Esslova, 1963; Weglenska, 1971) coupled with detailed analyses of population and community size structure will be necessary to evaluate the importance of severe food limitation in natural zooplankton communities.

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