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Food ingestion, density-dependent feeding and growth of vendace (*Coregonus albula* (L.)) larvae

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A bioenergetic model developed for coregonid larvae was used to estimate food ingestion of vendace larvae (*Coregonus albula* (L.)) reared in *in situ* enclosures. Zooplankton density, production and food ingestion of vendace larvae at different densities in net enclosures were compared in Lake Ylä-Enonvesi, eastern Finland. The model was fitted for different fish densities using feeding time as an iterative parameter. The growth of the larvae was greatly affected by the fish density in the enclosures. At higher density the larvae could capture less food daily than at low density; this is obviously caused partly by a high scramble competition and the ensuing decrease in efficient feeding time. It is suggested that when the hatching of the larvae is synchronized close to the break-up of the ice, a shortage of prey animals alone should not cause the high mortality of vendace larvae. While death of larvae as a direct result of the low food density is suggested to be rare, scarce or variable food conditions, high intra- or interspecific competition for food or predation disturbance may result in increased energy costs, weak growth and decreased survival of the larvae.

1. Introduction

The hypothetical framework for studying the recruitment of commercial fish stocks has long been dominated by Hjort's (1914) hypotheses concerning starvation and high mortality among larval fish (e.g. May 1974, Cushing 1988). The high larval mortality and possible starvation soon after the yolk resources are depleted have invoked numerous estimates of the minimum food requirements or the optimal zooplankton density for planktivorous fish larvae (e.g. Dabrowski 1976, Werner & Blaxter 1980, Cushing 1983, Kiorboe & Munk 1986, Wroblewski & Richman 1987, Dabrowski et al. 1988).

To estimate the food ingestion or growth rate of different fish species, several bioenergetic models have been constructed (e.g. Stewart et al. 1983, Stewart & Binkowski 1986, Dabrowski et al. 1988, Cui & Wootton 1989, Helminen et al. 1990). The basic approach in these models is that the energetic parameters of feeding, metabolism, egestion and excretion are measured in the laboratory, growth of "wild" fish is estimated in the

field, and the general energy budget equation for fish is applied in order to extrapolate the laboratory measurements to field conditions.

In general, the models and values for the energetic parameters are calculated for large or adult fish. Application of these results directly to fish at different developmental stages may lead to considerable errors, because the mode of locomotion, feeding, metabolic efficiency, vision etc. change during the early life of fish (Balon 1985, Dabrowski 1986c, Dabrowski 1989). Owing to the continuous change in the basic parameters of the models, the requirements of food ingestion and growth modeling are even more elaborate for larval fish than for adult fish.

A bioenergetic model of coregonid larvae (Dabrowski et al. 1988) was applied which estimates food ingestion of vendace larvae (*Coregonus albula* (L.)) reared at different densities in *in situ* enclosures. Zooplankton density, production and food ingestion of larval vendace in net enclosures were compared in Lake Ylä-Enonvesi in eastern Finland. The primary objective was to study possible starvation of the larvae (c.f. Karjalainen 1991) and to compare the food demands of the larvae with the available food resources as part of a research project on mechanisms of population regulation in vendace.

2. Materials and methods

2.1. Model description

The starting point was the bioenergetic model developed for coregonid larvae (Dabrowski et al. 1988, Dabrowski 1989, Dabrowski et al. 1989). The general model for food ingestion (I, J/mg/d), growth (G, J/mg/d) and metabolism (R, J/mg/d) is expressed as:

$$qI = G + R.$$

The net energy intake was described as a coefficient q, which is an energy absorption coefficient ($r = 1-0.25$) multiplied by a coefficient of specific dynamic action ($SDA = 1-0.28$). Food ingestion (I) was calculated from the Holling equation (Holling 1965) with modifications by Ware (1975) and Dabrowski et al. (1988). Parameter values for this equation are given in Table 1. The equation of STM_1 (standard me-

Table 1. Parameter values used in the bioenergetic model for vendace larvae. Sources: (1) Dabrowski et al. 1988, (2) Dabrowski 1986a, b, c, Kaushik et al. 1986, (3) Dabrowski et al. 1986, (4) Dabrowski 1989 or (5) recalculated.

Symbol	Parameter description	Value or equation	Source
Metabolism (J/mg/h)			
STM_1	Standard metabolism of larvae, 1–2.3 cm	$STM = 0.1272e^{0.7344TL}$	2, 5
STM_2	Standard metabolism of larvae	$STM = 2.87e^{-0.605TL}$	3
V	Swimming speed, cm/sec	$V = 0.1926e^{1.282TL}$	4
b	Slope of activity equation	$b = 6.76e^{-1.094}$	1
ACT	Active metabolism	$ACT = e^{bV}$	1
Q_{10}	Dependence of R on temperature	2.41	1
Consumption (J/mg/h)			
s	Area of the visual field, m^{-3}	$s = 0.0001217TL-5.0306\times10^{-6}$	1
c	Probability of successful prey capture	$c = (0.8703TL-0.81603)/(TL+0.32115)$	5
p	Prey density, J/m^3	variable, see text	
h	Handling time, h/J	$h = 3.0124e^{-1.55107TL}$	1
$F(T)$	Temperature-dependent function of h	$F(T) = 3.81599e^{-0.1167T}$	4, 5
V	Swimming speed, m/h	$V = 6.932e^{1.282TL}$	4
FT	Feeding time h	8.5–20	
r	Absorption coefficient	0.75	1
SDA	Coefficient, specific dynamic action	0.28	1

tabolism vs. fish length) was recalculated from the standard metabolic rates of coregonid larvae extrapolated to zero swimming speed by Dabrowski (1986a, b) and Kaushik et al. (1986). Handling time was calculated from the equation where *TL* is total length (cm) of the larvae and *F(T)* (Table 1) is the temperature-dependent function of the handling time (recalculated from data for 0.5-g coregonids, Rösch 1986, c.f. Dabrowski 1989). Daily feeding time of the larvae was used as a variable for adjusting the predicted body mass to the observed mean body mass of the larvae. Active metabolism was assumed to be restricted to the active period of 20 hours (cf. Karjalainen & Viljanen 1992), and for the rest of the day standard metabolism was assumed (Dabrowski et al. 1988).

The observed growth rates of the larvae based on the growth in total length (*TL*), were converted to wet mass (*WM*) using the equation:

$$WM = 3.184\ TL^{3.663},\ (n = 70,\ r^2 = 0.967),$$

which was recalculated from unpublished data of M. Viljanen (Karelian Institute, Univ. Joensuu, Finland). A constant relative energy density of both the larvae and the prey animals was assumed in the calculations. The energy densities were used 4134 J/g*WM* for coregonid larvae (Kaushik et al. 1986) and 2543 J/g*WM* for zooplankters (Salonen et al. 1976, Dumont et al. 1975). The energy estimates were converted to dry mass (*DM*) or wet mass using the coefficients of 46 J/mgC, 0.5025 mgC/mg*DM* (Salonen et al. 1976) and 0.11 mg*DM*/mg*WM* (Dumont et al. 1975).

2.2. Fish rearing conditions and zooplankton conditions

Vendace larvae were reared in the small cove of Lake Ylä-Enonvesi (62°05′6″N, 28°56′14″, physical and chemical properties of water are given in Table 2) in net enclosures at three densities of fish (Low = 100, Medium = 500 and High = 2000 larvae/enclosure) without additional feeding (Karjalainen 1991). The enclosures were anchored in the littoral zone, where the depth of the water was 2.5 m. The mesh size of the enclosure net was 500 µm and the volume of each enclosure was 1.1 m^3. The experiments were started on May 17, 1988 and May 3, 1989, immediately after break-up of the ice, and lasted for 44 days. The modelling interval was from the tenth experimental day by which time the larvae had consumed their yolk and had reached the length of 9–10 mm, to the end of the experiment.

Table 2. The physical and chemical properties of water (0–2 m) of Lake Ylä-Enonvesi in 1986–88. Each seasonal average was based on bimonthly measurements. The analyses were made at the Central Fish Culture Station for Eastern Finland, Enonkoski.

Season	Temp. °C	O_2 mg/l	O_2 %	Cond. mS/m	pH	Color Pt mg/l	COD_{Mn} mg/l	Total N µg/l	NH_4-N µg/l	Total P µg/l	Chl-a µg/l
1986											
Dec–Feb	0.1	14.0	96.3	8.3	6.7	40	7.1	488.0	39.7	12.3	–
Mar–May	2.7	12.2	89.3	8.0	6.6	42	6.6	370.7	59.0	13.7	–
Jun–Aug	16.9	9.6	98.8	7.7	6.9	43	8.4	301.3	173.0	23.3	3.5
Sep–Nov	8.0	11.3	95.2	6.5	7.0	36	8.4	301.0	10.7	15.7	3.0
1987											
Dec–Feb	0.5	14.5	100.0	9.0	7.0	35	7.4	401.0	44.5	16	–
Mar–May	3.2	13.0	96.7	8.9	6.8	35	7.2	382.0	19.0	12.7	2.9
Jun–Aug	14.8	10.0	98.7	8.2	6.9	35	6.7	398.7	16.3	11.3	4.0
Sep–Nov	9.0	10.2	88.0	7.6	6.8	37	6.9	396.7	10.7	10	2.8
1988											
Dec–Feb	0.8	10.9	75.7	8.4	6.7	50	9.9	415.0	38.3	11.3	–
Mar–May	1.9	9.2	66.0	7.2	6.2	53	9.7	591.3	77.3	15.7	–
Jun–Aug	18.6	8.6	91.2	7.4	6.6	66	10.3	588.8	12.3	16.3	6.7
Sep–Nov	11.9	9.7	89.3	8.2	7.1	60	9.0	495.0	17.0	17	–

During the experiments, zooplankton was sampled with a tube sampler every 4th day both inside and outside the enclosures (Karjalainen 1991). Outside the enclosures, three replicates were sampled (0–2 m). The maximum depth of the water in the experimental area was 4 m. In 1989, in order to follow the population dynamics of the prey populations, sampling was extended both before and after the experimental period. The zooplankters were counted with an inverted microscope and the counts were converted to carbon mass (μgC) by using average carbon values for the size classes of each taxon. The length-carbon mass conversions were based on the measurements of the carbon mass of crustaceans collected in 1990 from Lakes Paasivesi and Pyhäselkä, both in Lake Saimaa, (own unpublished data) and the equations of Vasama & Kankaala (1991). For calculation of food ingestion, the biomass of zooplankters was converted to energy (J/m^3). According to zooplankton samples the food available for vendace larvae were estimated. Adults of *Eudiaptomus gracilis* and *Cyclops* spp. were excluded from the estimation of available food resources. Thus, the length of the copepods included in the food available ranged between 100 and 900 μm and the length of the cladocerans were mainly under 800 μm.

The production of the dominant crustacean species was calculated by the "growth increment summation" method (Rigler & Downing 1984). Cladoceran production was estimated by summing the production of eggs and 4–5 size classes of juveniles and adults. Copepod production was calculated by summing the production of eggs, three developmental stages of both nauplii (N1–2, N3–4, N5–6) and copepodids (C1–2, C3–4, C5) and adults. The mass increments were estimated from the analyses of individual carbon content. The developmental durations of eggs and the different developmental stages of the species for the mean water temperature were based on the laboratory experiments of several authors: *Eudiaptomus gracilis*, eggs (Herzig 1983), nauplii and copepodids (Bosselman 1975); *Mesocyclops leuckarti* and *Thermocyclops oithonoides*, eggs, nauplii and copepodids (Vijverberg 1980); *Bosmina coregoni*, eggs (Kankaala & Wulff 1981), adults (Vijverberg 1980); *Daphnia cristata*, *Chydorus sphaericus* and *Diaphanosoma brachyurum* eggs, adults (Vijverberg 1980). Duration of the egg development of *Ceriodaphnia quadrangula* and *Holopedium gibberum* was calculated from the general equation of Bottrell et al. (1976), and duration of the adult stage was the same as for *Daphnia*. For nauplii and copepodids of copepods, development was assumed to be isochronal.

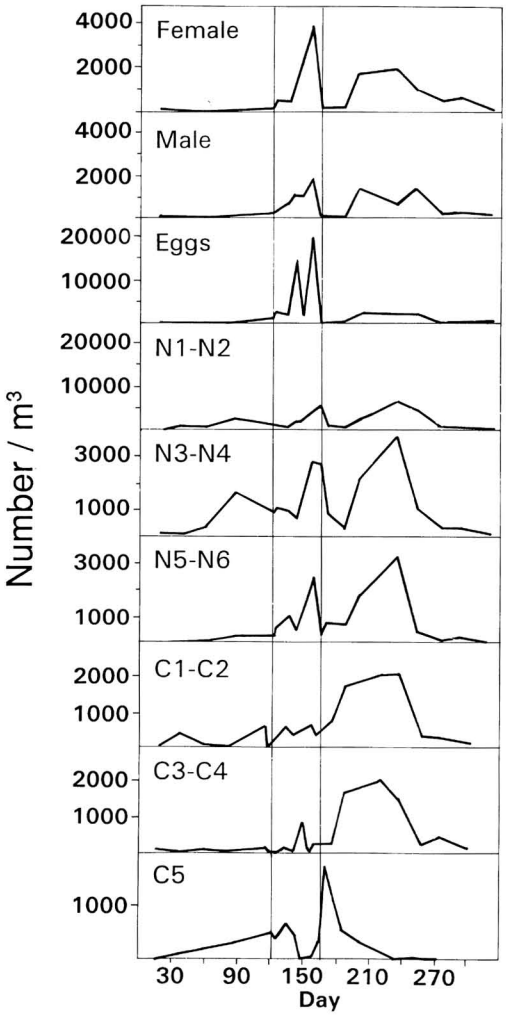

Fig. 1. Density (ind./m^3) of *Eudiaptomus qracilis* in Lake Ylä-Enonvesi in 1989. The developmental stages included N1–2, N3–4 and N5–6 nauplii and C1–2, C3–4 and C5 copepodids of *Eudiaptomus*. The horizontal axis indicates days since the beginning of the year. The experimental period (May 3–June 15, 1989) is marked with two vertical lines.

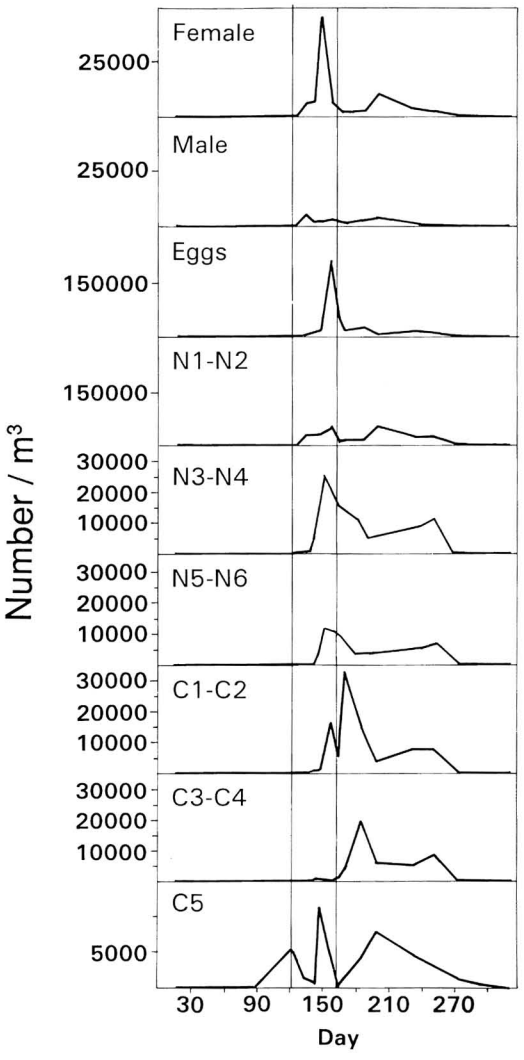

Fig. 2. Density (ind./m^3) of *Mesocyclops* and *Thermocyclops* (combined) in Lake Ylä-Enonvesi in 1989. The developmental stages included N1–2, N3–4 and N5–6 nauplii and C1–2, C3–4 and C5 copepodids of *Mesocyclops* and *Thermocyclops*. The horizontal axis indicates days since the beginning of the year.

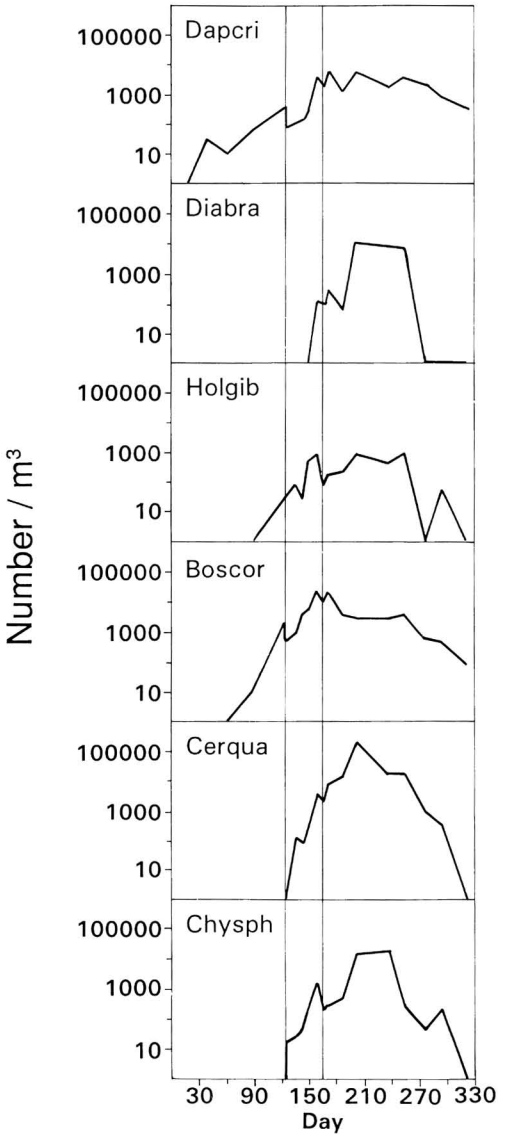

Fig. 3. Density (ind./m^3) of cladocerans in Lake Ylä-Enonvesi in 1989. Cladoceran species are: *Bosmina coregoni* (Boscor), *Ceriodaphnia quadranqula* (Cerqua), *Chydorus sphaericus* (Chysph), *Daphnia cristata* (Dapcri), *Diaphanosoma brachyurum* (Diabra), *Holopedium qibberum* (Holgib). The horizontal axis indicates days since the beginning of the year.

3. Results

In the experimental area, three copepod (Figs. 1, 2) and six cladoceran species (Fig. 3) comprised about 80% of the total biomass of zooplankton and over 95% of the crustacean biomass in both 1988 and 1989. In 1988, the total crustacean biomass outside the enclosures increased from 16 to 70 mgC/m^3 (17 May–11 June) and in 1989, from 10 to 90 mgC/m^3 (3 May–15 June). The

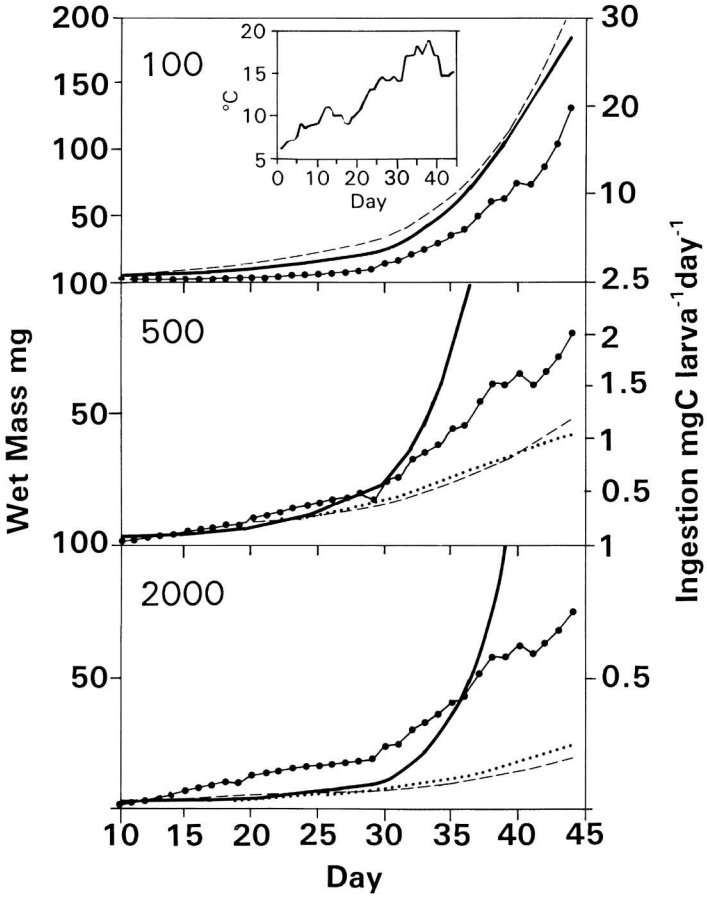

Fig. 4. Observed (dashed lines) and modelled (constant 20 h feeding time, solid lines and iterated feeding time, dotted lines) wet mass as well as ingestion rate (circles) of vendace larvae in enclosures at the different densities (100, 500 and 2000 larvae per enclosure) in 1989. Water temperature inside the enclosure is shown in the upper section.

energy density of available prey animals inside the empty enclosure (without larvae) was 1318–3008 J/m^3 in 1988 and 552–1710 J/m^3 in 1989. In both years, during the experiments 70–80% of the crustacean biomass consisted of copepods.

Total annual production (0–2 m) of those nine crustacean species was 1404.7 mgC/m^3 (2668.9 mg*DM*) in 1989. During the experimental period, the production of *Eudiaptomus gracilis* was 32–13% (start–end of period) of the copepod production. *Mesocyclops* and *Thermocyclops* species were responsible for 35–97% and *Cyclops* spp. 30–0% of the copepod production. *Bosmina coregoni* and *Daphnia cristata* produced 87–98% of the cladoceran production during the 6-week period after break-up of the ice.

Larval growth rate was inversely related to their density (Fig. 4). The daily ingestion rate per larva (mg/mg/d) estimated by the bioenergetic model was highest at the lowest fish density and lowest at the highest density (Fig. 4). During the 44-day modelling period in 1989, the larvae ingested 129.6 mgC/larva at the low density, 23.0 mgC/larva at the medium density and 7.5 mgC/larva at the high density. This cumulative estimate is greatly affected by difference in growth; i.e. the fast growing larvae increased their food ingestion rapidly.

The model fitted for larvae reared at the low density overestimated the growth of the larvae at the medium and high fish density (solid line, Fig. 4). At the low density, the efficient daily feeding time was set as 20 hours. The model was fitted for the medium and high fish density using the feeding time as an iterative parameter. The daily feeding time was adjusted so that the predicted wet mass of the larvae at the last modeling day agreed (±0.1%) with the final mass of the

larvae. Thus, feeding time changed according to the metabolic costs and the feeding efficiency of the larvae reared at the different densities. The mean daily efficient feeding time was 15.5 hours at the medium density and 14 hours at the high density.

Comparision of the change in total biomass of vendace larvae in the enclosure with their total food ingestion and the total crustacean production outside the enclosure (Table 3) during the 10-day intervals showed that the food ingestion of the larvae was nearly 3–7 times greater than their net production and that ingestion was 2–100 times greater than their food production in a cubic metre. In 1988, during the first 25 days of the experiment, the total production of the larvae at the low fish density was 289 mg *DM* and at the medium density 1029.3 mg *DM*. The total ingestion rate of the larvae during the 10 days (from day 15 to day 25) was 800.3 mg *DM* at the lower density and 4217.5 mg *DM* at the higher density.

The model fitted for the larvae reared at the highest density as used to estimate the minimum prey density (mgC/m^3) which would support the daily growth rate of $1 \pm 0.1\%$, $0 \pm 0.1\%$ and $-1 \pm 0.1\%$ at the different temperature (Fig. 5). The efficient daily feeding times for a 10 mm long larva and a 20 mm long larva were 20 hours and 8.5 hours, respectively.

4. Discussion

The bioenergetic model of coregonid larvae simulates food ingestion according to the Holling disk equation (Ware 1975, Dabrowski et al. 1988), which estimates the feeding capacity of the larvae in given conditions. Swimming speed, volume of visual field, handling time of prey and catch success determine the feeding capacity. Those components are influenced by water temperature, size and developmental stage of the fish, prey density and quality (e.g. Ware 1976,

Table 3. Total number (N), average biomass (mg dry mass), total production (mg dry mass) and ingestion (mg dry mass) of vendace larvae in the net enclosures (Karjalainen 1991), and the crustacean production (mg dry mass / m^3) outside the enclosures in Lake Ylä-Enonvesi. The food ingestion was estimated by the bioenergetic model. The experiment was started on 3 May 1989 (Day 0).

	Vendace larvae				Crustacean production	
Day	N	Biomass	Production	Ingestion	Copepoda	Cladocera
Enclosure 100						
0	100	25	–	–	–	–
1–10	89	51	25	–	11	2
11–20	71	142	100	271	25	5
21–30	53	270	160	845	40	9
Total			285		76	16
Enclosure 500						
0	500 ± 0	125 ± 9	–	–	–	–
1–10	485 ± 7	238 ± 15	113 ± 8	–	11	2
11–20	482 ± 9	528 ± 58	298 ± 34	1108	25	5
21–30	466 ± 10	824 ± 103	613 ± 88	3099	40	9
Total			1024 ± 154		76	16
Enclosure 2000						
0	2000	500	–	–	–	–
1–10	1942	738	238	–	11	2
11–20	1850	1276	545	1996	25	5
21–30	1669	1485	765	5074	40	9
Total			1548		76	16

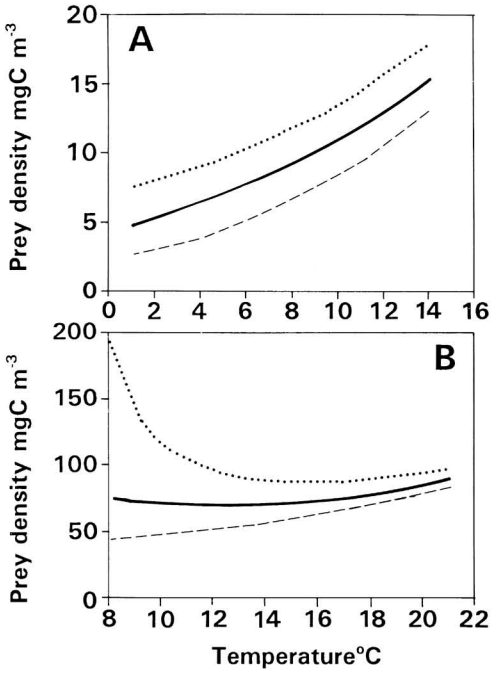

Fig. 5. The minimum prey density (mgC/m^3) that supports a 1% (dotted line), 0% (solid) and –1% (dashed) daily growth rate of vendace larvae at a size of 10 mm (A) and 20 mm (B). The estimates are based on the bioenergetic model fitted at a density of 2000 larvae per enclosure.

Dabrowski 1989) and movement of the prey animals (Gerritsen 1984, Evans 1989). The movement of prey may be active (swimming) or passive (currents) and the movement in relation to the fish location may increase or decrease the number of available food objects in the different environmental conditions. The model considered neither the active nor the passive movements of the prey animals in relation to the larvae.

Modelling of both the food ingestion and the crustacean production immediately after the break-up of the ice involves several uncertainties. The continuous change in the water temperature induces continuous changes in the development of organisms, and the assumption of steady-state conditions (e.g. Dabrowski 1989, Kimmerer 1987) is hardly ever fulfilled. Furthermore, the model assumed that the prey animals are randomly distributed and that all prey species are captured equally successful. Both assumptions greatly simplify the conditions in any lake. Dabrowski et al. (1988) and Dabrowski (1989) modelled the optimum foraging swimming speed, field of vision, handling time and catch success for coregonid larvae as a function of body length. Actively feeding 12–25 mm long coregonid larvae have been observed to swim 1.5–2.5 cm/sec (Hoagman 1973, 1975, Braum 1978). The validity of the rest of functions could not be assessed due to lack of experimental works. The effects of temperature on the feeding capacity have not been included in the model developed by Dabrowski et al. (1989). However, higher temperature obviously improves feeding capacity (cf. Dabrowski 1989). Swimming speed is governed by temperature (Stewart & Binkowski, 1986), and handling time and *SDA* are likely to be influenced by temperature. Thus, the temperature-dependent function of the handling time applied from the calculation of Dabrowski (1989) was added to the food ingestion model for vendace larvae.

Copepod nauplii and copepodids as well as rotifers are the most important food for newly hatched vendace larvae (e.g. Karjalainen et al. 1991, Karjalainen 1991). When the larvae grew to be over 10 mm long, the cladocerans, especially *Bosmina*, *Holopedium*, *Chydorus* and *Polyphemus*, in the diet of the larvae began to increase. Due to the large variation of the diet between the larvae at different rearing densities, only large adult copepods (cf. Karjalainen 1991) and rotifers were excluded from the estimates of the potential prey animals. Thus, all copepod nauplii, copepodids and cladocerans inside the enclosures were assumed to be possible food for the larvae during the modelling interval. The different developmental stages of *Eudiaptomus*, *Thermocyclops*, *Mesocyclops*, *Bosmina*, *Daphnia* and *Chydorus* composed over 90% of the potential prey biomass and the diet of the larvae.

The growth of the larvae in the enclosure was greatly affected by fish density. Possible explanations for the stunted growth of the larvae include:

1) at the high fish density the larvae could feed only on part of the prey animals which decreased considerably, or

2) the feeding area of the larvae was restricted to the thin upper layer of the water, where the prey animals consequently decreased, or
3) the differences in the energy costs of the feeding activities caused variable growth.

A detailed analysis of zooplankton showed that no component of zooplankton was exhausted. The densities of the prey animals inside the enclosures at the high fish density were lower than at the low fish density, but no drastic change in the amount of food available was observed (Karjalainen 1991). The dispersion of the larvae within the enclosures decreased the effects of competition for food at the high fish density (Karjalainen 1991). Thus, the larvae at the higher density could capture less food per day than could larvae at the low density; this is obviously caused partly by the lower efficient daily feeding time.

Ingestion rate depends on the feeding capacity and the efficient feeding time. It is not known whether any scramble competition influenced the feeding capacity (e.g. handling time, capture success) or the feeding time, but the effect was evident in the feeding model as variation in the efficient daily feeding time. The activity costs for fish may increase due to the increased density of fish (Boisclair & Leggett 1989a) or schools (Eggers 1976), predation disturbance (Morgan & Colgan 1987) or rapid changes in feeding conditions, e.g. wind speed (A. Huusko and T. Sutela, pers. comm.). The lack of a simple relationship between the growth of "wild" fish and their food ingestion makes it difficult to model the food consumption of fish (Boisclair & Leggett 1989b). Fish activity changes markedly under different conditions and the changes are difficult or impossible to measure.

The daily food ingestion of a 10.9 mm long larva estimated by the bioenergetic model in 1989 at the low fish density was 60 µgC (at 9°C). At medium and high fish densities the daily ingestion of a 10.5 mm and a 9.3 mm long larva were 41 and 12 µgC, respectively. The food ingestion rates (mean±*SD*) estimated by the evacuation model (Elliott & Persson 1978) were 41±3, 44±4 and 35±3 µgC/larva/day at low, medium and high fish density, respectively. The evacuation rate of food was estimated according to Karjalainen et al. (1991). Compared with the evacuation model, the bioenergetic model overestimated the food ingestion of larvae at the low fish density and underestimated the ingestion of larvae at the high fish density. Koho et al. (1991) observed that in laboratory experiments the minimum daily ration of food given to a 9 mm long vendace larva was 13 µgC/larva/day. The daily food ingestion of those larvae recalculated by the evacuation model was 17±9 µgC/larva at 8°C. The amount of food in the guts of the larvae in the tanks was determined from samples taken three times a day. The daily amounts of food given to the larvae at the medium and high food densities were 65 µgC and 130 µgC/larva/day, respectively (Koho et al. 1991). Karjalainen & Viljanen (1992) estimated that the maximum rate of ingestion for the 9 mm long vendace larvae would be 142 µgC/larva/day at 9.9°C. The minimum food demand of 10 to 15-day-old vendace larvae was 11.5–35 µgC/larva/day at 8–9°C. According to earlier experiments the daily food demand of coregonid larvae at the age of 10–16 days varied from 10 to 85 zooplankter/larva at 4–12°C (Braum 1964, Hoagman 1974, Dabrowski 1976). If the carbon mass of the zooplankters (copepods) is 0.5 µgC/animal, these numbers correspond to a food demand of 5–43 µgC/larva.

Any possible disturbances during embryonic development (e.g. oxygen deficit) may interrupt the temperature-syncronized development of vendace larvae and prey animals. However, at low water temperature larvae that hatch early, even under the ice cover, may survive for more than 30 days without external food (Dabrowski 1989). The ingestion rate of the larvae decreases at low temperature, which also compensates the for the risk of early hatching. While larval death that is directly due to low food density is probably rare, the effects of variable food conditions, high intra- or interspecific competition for food or predation disturbance on the feeding of the larvae may result in increased energy costs, weak growth and decreased survival of the larvae.

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