

Body size distribution in *Daphnia* populations as an effect of prey selectivity by planktivorous fish

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Abstract We test the hypothesis that size distribution of a *Daphnia* population reflects the vulnerability of each size category (instar) to predation by planktivorous fish. We hypothesize that due to the different reaction distances from which separate prey categories can be seen by a foraging fish, each category is preyed upon until its density is reduced and its size-specific apparent density level (number of prey within a hemisphere of radius equal to the reaction distance) or encounter rate (number of prey encountered per time within a tube with a cross section of radius equal to the reaction distance) become equal to those of other size categories. An experiment was performed with populations of *Daphnia hyalina* and *D. pulicaria* grown at two *Scenedesmus* + *Chlamydomonas* food levels (0.2 and 0.05 mg C per liter) in outdoor mesocosms (1000 l tanks) with predation by invertebrates (phantom

midge) prevented by mosquito netting. Once the populations had become established, roach were added to the tanks at dusk each day and allowed to feed for 3 h, while control tanks were kept fish-free. After 20–60 days, while *D. pulicaria* was at low density level, the densities of *D. hyalina* in fish tanks were high enough to see that the age structure and size distribution matched those from simulations with the age-structured population model based on size-specific encounter rate. This match, however, remained only up to the point of first reproduction when—in contrast to the size/age distribution predicted by the model—the percentage share of adult instars in the total population decreased rapidly with age. This deviation from the predicted densities of adult instars suggests that neither encounter rates nor apparent densities derived from instar-specific reaction distances are sufficient to explain the instar-specific impact of a visual predator on planktonic prey. This implies that a foraging fish may temporarily change its feeding mode from the typical low-speed harvesting of small but abundant prey from within its visual field volume, to high-speed hunting for more scarce but larger ovigerous females when their abundance allows higher net energy gain. Shifting from one feeding mode to the other may be responsible for damping population density oscillations in *Daphnia*.

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Introduction

Small-bodied animals are more abundant than those of large body size. This is also evident in lake zooplankton and, since the 1960s, has been attributed to size-selective predation by planktivorous fish (Hrbáček, 1962; Brooks & Dodson, 1965). These inverse size-density proportions are very apparent in different *Daphnia* species such as the smaller *Daphnia cucullata* and larger *Daphnia hyalina*, which are often found in density proportions of 10:1 (Pijanowska, 1980) that remain remarkably similar throughout the seasons and from one lake to another, even when lakes differ greatly in their productivity potential (Gliwicz, 2001).

Such fixed proportions have been explained by an individual-based age-structured population model (Gliwicz & Wrzosek, 2008) which predicts that (1) a *Daphnia* population is held at low density by fish predation irrespective of food level, with greater recruitment at higher food being instantly compensated by raised mortality reflecting increased predation, and (2) *Daphnia* density levels are species-specific and inversely related to body size at first reproduction, and hence the reaction distance, RD : the maximal distance from which a foraging fish can see its *Daphnia* prey. These two predictions were confirmed experimentally in mesocosm studies on different *Daphnia* species released from invertebrate predation but controlled by fish allowed to feed on them each evening for 2 or 3 h (Gliwicz & Wrzosek, 2008). In the absence of fish, each *Daphnia* quickly reached high density with reproduction halted by food limitation, while in the presence of fish the populations were detained at much lower species-specific densities that were similar at low and high food levels. This suggests that fish will feed on a given prey species until its density falls below a threshold level, at which point it becomes ignored by the fish. This also implies that this level should be equal to an apparent density of one individual per visual field volume, VFV : a hemisphere of diameter equal to a given prey-specific RD in which this prey category can be seen by a foraging fish (Fig. 1).

Inverse size-density proportions are also observed for different instars within a population of the same *Daphnia* species, with juveniles being much more abundant than adults. Body size distributions of different *Daphnia* species are often skewed toward the youngest instars of smallest body sizes when they originate from lakes (e.g., Threlkeld, 1979, Langeland & Nost, 1995) or mesocosms with *Daphnia* or *Diaphanosoma* exposed to fish predation (e.g., Vanni, 1987). Could inversed size-density proportions of different size or age categories of individuals within a population of a single *Daphnia* species be accounted for by the same reasoning used to explain proportions among co-existing species?

In this study, we have used *Daphnia* samples collected during a previous study (Gliwicz & Wrzosek, 2008) to look at size distributions and age structures, and check whether the model's outcome would be similar for different instars from a single species population (*D. hyalina*). In other words, we examined whether the density of each instar is set at a specific level that is inversely related to the body size and RD . We also checked whether the proportions of different instars reflect the inversed proportions of the instar-specific RD (or their squares, or cubes), implying that fish predation would lead either (a) to identical apparent densities of different instars in the fish's VFV ($\sim RD^3$, Fig. 1C), or (b) to identical encounter rates that could be either within a circular cross section of the fish's visual field ($\sim RD^2$, Fig. 1D), or within an ellipsoidal cross section of the fish's visual field, when only the horizontal component of the fish's search volume reflects the instar-specific RD (Fig. 1E). Intuitively, the uniformity of a weighted distribution of prey classes, with weights calculated as a function of RD , would be expected to reflect the foraging pattern of size-selective predation by planktivorous fish.

The cornerstone of the model proposed in our earlier paper (Gliwicz & Wrzosek, 2008) was the concept of a prey density threshold level at which a given prey species is included or excluded from the diet of a size-selective visual predator, this level being inversely related to the prey body size and reaction distance at first reproduction.

The initial aim of this study was to see whether the same can also be applied to different age classes of a single species prey population by examining whether the application of our model would lead to

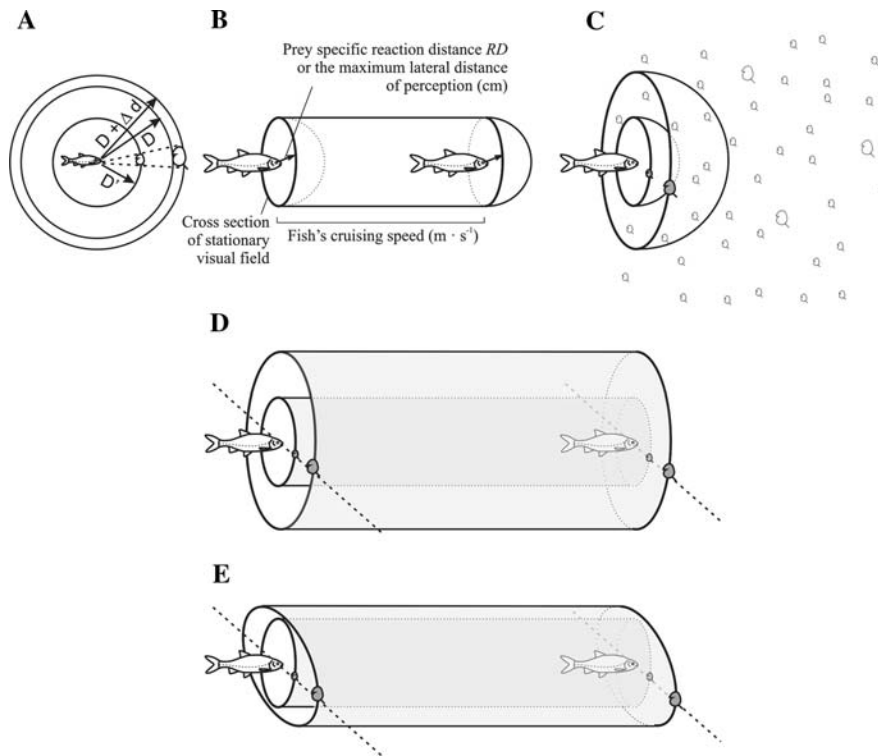


Fig. 1 Different aspects of the *VfV* of a foraging fish. **A** The apparent size as a determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*); the size of each of the two prey categories appears the same when they are sighted from distance D : the maximum distance from which the prey can be recognized (redrawn from O'Brien et al. 1976). **B** The volume visually penetrated by a fish in the time needed to swim from the beginning to the end of the tube (Eggers, 1977, redrawn), where the prey-specific reaction distance or the maximum lateral distance of perception of a prey, RD (D in O'Brien's figure), is the radius of the circular cross section of a stationary visual field, and where the fish's cruising speed is a distance covered in a time unit that is dependent on the time engaged in search of each item of a single prey category. **C** Reaction distances, RD , and visual field volumes, *VfV*, for two prey categories of different body size. The probability of encounter or assessment of prey density by a foraging fish is different for the two prey categories; a foraging fish will perceive the

equal apparent densities (Fig. 1C) or equal encounter rates (Fig. 1B) for different size categories in such a population. We anticipated that fish predation would lead to an equilibrium between the process of recruitment into a given instar or size category (from the preceding instar or size category) and the sum of the process of recruitment to the subsequent size category and the process of mortality due to fish

densities of both prey categories as equal, even though their real densities differ by 10-fold, because the individuals depicted as dotted silhouettes are beyond the field of fish vision (redrawn from Gliwicz, 2001). **D** The volume visually penetrated by a fish in the time needed to swim from the beginning to the end of the tube for each of the two prey categories of different body size (as in Confer & Blades, 1975). Note the volumes of the two tubes differ by the power 2, reflecting the difference in the encounter rate between the two prey categories. **E** The volume visually penetrated by a fish in the time needed to swim from the beginning to the end of the tube for each of the two prey categories of different body size when only the horizontal component of the fish's search volume reflects the prey-size-specific reaction distance; the vertical component being reduced for the larger prey category as suggested by Evans & O'Brien (O'Brien, 1987), its *VfV* changing from a hemisphere to a hemispheroid

predation. We also expected that such size-selective predation would lead to size/age distributions different from those produced by nonselective mortality in all size or age categories, as in the mechanistic approach to resource competition of Tilman (1982), with mortality restricted to the rate of loss of the same proportions from each size or age category.

Methods

Mesocosm experiments

Daphnia samples used to test our hypotheses were collected in July–September 2004 in the course of one of two outdoor mesocosm experiments that have been described previously (Gliwicz & Wrzosek, 2008). Data on the size distribution of *D. hyalina* populations were pooled from all samples collected within two periods, days 8–24 and days 52–58, during the 60 days when the *Daphnia* density in all tanks was held within the range of 2–8 ind. l⁻¹ by fish predation.

The experiments were carried out in 8 circular 1000-l steel tanks (1.2 m in height, and 1.3 m and 1.1 m in diameter at the rim and at the bottom, respectively) filled with 1 µm mesh-filtered water (100 mm diameter Millipore filters) pumped from the epilimnion of Lake Ros (Mazurian Lakes, NE, Poland). Each tank received a mixed inoculum of green algae from mass cultures of *Scenedesmus obliquus* and *Chlamydomonas reinhardtii* as the food source for the *Daphnia*. The same algae were added every evening to increase the food concentration by 0.2 and by 0.05 mg C per liter, respectively, in 4 ‘high-food’ and 4 ‘low-food’ tanks, one of each set of four being left as a fish-free reference and the other three being used as replicates with fish. Food levels were monitored daily by measuring light extinction in the tanks using a photometer (LI-COR LI-189; light intensity readings in integrated PAR units at 0.1 and 0.9 m depth), and by assaying chlorophyll in water samples using a fluorometer (Turner model III; calibrated with standard conversion tables for mg chlorophyll *a* per liter). The temperature of the water in the tanks was 18–23°C, but gradually declined to reach 10°C in the final week, reflecting September cooling.

Each *Daphnia* population was started from 2- to 6-day-old juveniles of the smaller *D. hyalina* (*D. hyalina* × *galeata* clone HG011 from Lake Swiecayty, Great Mazurian Lakes, previously described as *D. hyalina*; Gliwicz, 2001, 2003) and the larger-bodied *D. pulicaria* (a clone from Plön, Germany) using inocula of 850 *Dh* and 150 *Dp*. The *Daphnia* were allowed to grow, first in the absence of predation, and later in the presence of eight fish: 1 + (1–2-year-old) roach (*Rutilus rutilus*) of 50–75 mm in length, for 3 h starting at the time of sunset. Each evening different groups of roach were

added to the tanks with high and low food levels. *Daphnia* densities, body size and clutch sizes (number of eggs per clutch) were enumerated every second day in 10-l samples taken immediately before each dusk fish feeding session and after the tank water had been mixed by five gentle bottom-to-surface movements of a perforated Secchi disc. The *Daphnia* were collected using a quantitative plankton net, fixed with formalin-sugar solution and examined under a dissecting microscope. All individuals in the sample were counted, but only the more abundant *D. hyalina* were assessed for body length (upper edge of the eye to the base of the tail spine), and the number of eggs per clutch in each egg-carrying female was recorded.

To imitate a natural field situation, fish predation was constrained by the number of fish and the time that the fish were allowed to feed on the *Daphnia*. The light level was reduced below 9 µmol m⁻² s⁻¹ (integrated PAR) by shading the experimental system using greenhouse netting, thus imitating light conditions in natural lake habitats where feeding by planktivorous fish is usually restricted to anti-predation windows at dusk and dawn (Clark & Levy, 1988). To exclude the predation of *Daphnia* by invertebrate predators, the experimental setup was covered with mosquito netting to prevent egg deposition by phantom midge (*Chaoborus*) and other insects. Fish were transferred to each tank in a 1-l steel bowl constituting the central part of the bottom of a cage made of nylon netting (5 mm mesh), and shaped to match the inside of the tank by upper and lower steel rings of diameters corresponding to the tank’s rim and bottom. Following each feeding session, the fish (trapped in the bottom bowl of their cage) were transferred back to one of 6 ‘refuge’ tanks. Cages without fish were placed in the control tanks at the feeding time (details in Gliwicz & Wrzosek, 2008).

Converting body size categories into age classes

D. hyalina body size distribution in each treatment was used to calculate the age structure in the separate populations following the procedure of Geller (1987), by applying Bertalanffy’s (1938) equation:

$$L_t = L_\infty \left(1 - e^{-k(t-t_0)} \right), \quad (1)$$

where $L(t)$ is the body length of an animal of age t , L_∞ is the maximum length attained by very old animals, k is

the individual rate of growth at the reference temperature of 25°C, commonly accepted for all daphnids, t_0 is the intercept $L(t_0) = 0$, and β is a scaling parameter taking into account the effect of temperature on the rate of individual growth. Bertalanffy's (1938) body growth model can be expressed mathematically as a linear differential equation determining the average body size of an animal at a given age. It is based on the simplistic assumption that the body growth rate decreases linearly (with a rate constant, k/β) when its size increases up to a species-specific maximum (*Daphnia* body length in this case, L_∞). The formula (1) is the solution of this differential equation. The rate constant is assumed to depend linearly on the temperature, and can be expressed as a multiple of a reference value k corresponding to an ambient temperature of 25°C. Even though this growth model should be treated as a rough approximation of real body growth, it still fits a wide range of various experimental data on invertebrates if the temperature variability is not too high, and when the oldest animals are not accounted for, as in Geller's (1987) study. A simple transformation of (1) gives the inverse relationship:

$$t(L) = \frac{\beta}{k} \ln \frac{L_\infty - L_0}{L_\infty - L}, \quad (2)$$

where L_0 is a new parameter replacing t_0 , which depicts the minimum length of a newborn *Daphnia* released from the brood cavity.

Computing encounter rates

D. hyalina body-size-specific apparent density was identified as the number of individuals of a given size category k within the VFV, this being a hemisphere of radius δ_k , with δ_k representing the prey-size-specific reaction distance for each body size category. Thus, the size-specific apparent density of the k th class is equal to $(2/3)\pi\delta_k^3 N_k$, where N_k is the density of individuals from the k th class. When the stationary visual field of a foraging fish is assumed to have a circular cross section (as in Fig. 1A–D), the encounter rate for the k th class can be calculated as $\pi\delta_k^2\alpha N_k$, where α is the cruising speed of a foraging fish. When the stationary visual field is assumed to have an elliptical cross section (as in Fig. 1E), the encounter rate for the k th class can be calculated as $\pi\delta_H\delta_l N_k$, where the horizontal, semi-major axis of the ellipse for a given prey size category is equal to $\delta_H = \delta_k$,

and the vertical, semi-minor axis is assumed to be the same for all size categories and equal to the reaction distance for the smallest prey category δ_1 .

Estimating reaction distance

The reaction distance for each prey size category, RD_k , was defined as the distance covered by a foraging fish (1 + roach of 5–8 cm length) from where it sights a prey object (a given instar of *Daphnia hyalina*) and turns to view it with both eyes, to the point at which the prey is successfully captured. The reaction distance, RD_k , was measured in the laboratory by studying video recordings of the trajectories of individual foraging fish visualized against a grid of black lines marked on the side of an aquarium (Fig. 2). At least 15 assessments were made for each of 5 roach, at each of 4 prey densities, and with each of the three *D. hyalina* juvenile instars (first, second, third) and one adult (fourth) instar (all individuals with eggs in their brood cavities). Low prey densities were used in these assessments to prevent RD underestimations due to the presence of more than one prey item (on average) in the visual field of a foraging roach (O'Brien et al. 1976).

Results

In the presence of fish, *Daphnia* populations were held at much lower density levels, i.e. two orders of magnitude lower than those in control populations, which rapidly (in 20 days) reached densities exceeding 50 individuals per liter (Fig. 3). The size distribution (Fig. 3A, B) and age structure (Fig. 3C, D) of *D. hyalina* in the presence of fish were markedly different from those of the control populations. This is more apparent when these parameters were compared as percentage distributions (Fig. 4). In the control populations, further density increase was prevented by a halt in reproduction due to severe food limitation. Only a small fraction of adults had eggs in their brood cavities (Table 1), and the reproductive effort (the mean number of eggs per adult) was an order of magnitude lower than in the presence of fish (two orders lower at the end of the experiment) (Table 2). One obvious sign of increased per-offspring investment was that many large-bodied adults carried single-egg clutches in brood cavities

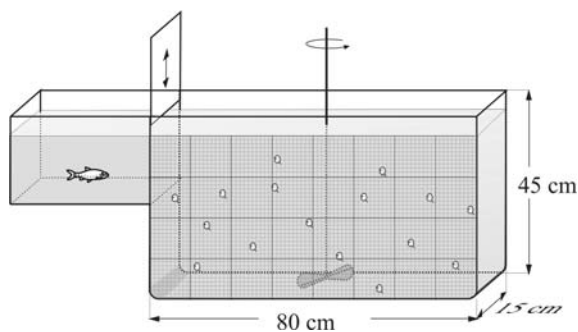


Fig. 2 Experimental setup for video recording the trajectory of a foraging fish (1 + roach, of 6–8 cm body length), from where it stops and turns to stereoscopically sight the prey (one of the different instars of *Daphnia hyalina*), to the point at which the prey is captured (the distance in between is taken as the reaction distance *RD*). The system was illuminated from above by a pair of halogen lamps (20 W, 12 V) shining through a frosted glass diffuser to produce a light intensity of $9 \mu\text{mol m}^{-2} \text{s}^{-1}$, which is equivalent to that at 1 m depth 2 h before sunset on a sunny day in a mesotrophic lake when cyprinid fish such as roach feed on zooplankton. The aquarium annex on the left permitted the gentle introduction of the fish into the main aquarium via a sliding plastic door once a given density of prey had been attained and its distribution homogenized by an upwelling current produced by a centrally positioned electric stirrer. Each subsequent capture was followed by manual addition of one *Daphnia* from an automatic pipette. The observation period for each individual roach was terminated after 15 successful captures. The front of the main aquarium faced into a dark room in which a video camera was supported on a cart that could be moved horizontally on metal rails to follow the trajectory of a foraging fish. All sides of the aquarium apart from the front were painted black to preclude penetration of light other than from the top. The bottom edges of the aquarium were rounded to improve mixing, thus preventing *Daphnia* aggregations in the corners. The width of the main aquarium was restricted to 15 cm to ensure that captures predominantly occurred in the plane perpendicular to a line projecting along the center of the camera's field of view. Fine black lines marked on the front of the aquarium in the form of a grid (squares of 1 and 10 cm) assisted the viewer of the video in making accurate assessments of *RD*

large enough to accommodate 15 eggs (the maximum number seen in our tank populations). The reduction in the proportion of ovigerous females was most severe in the smallest adult size categories (Fig. 5), due to postponed reproduction in the absence of size-selective predation. Due to the lack of reproduction, the numbers of the smallest (earliest) instars were very low, particularly at the lower food level at the end of the experiment (Fig. 4C). Severe food limitation did not permit fast individual growth. This is shown by the difference in the mean body length of

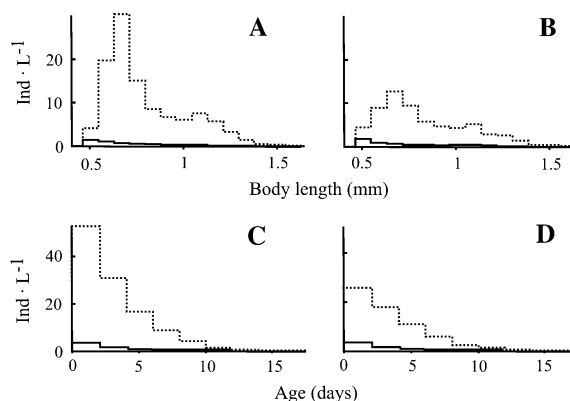


Fig. 3 Densities of different body size categories (A and B) and age classes (C and D) in experimental *D. hyalina* populations at low (left) and high (right) rates of reproduction permitted by different food levels in control tanks free of fish (dotted lines), and in tanks with fish predation applied at dusk (solid lines) on days 8–24

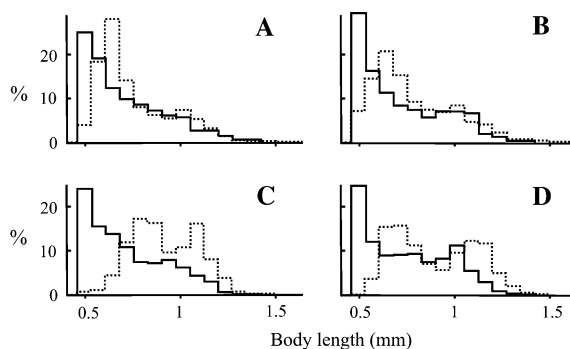


Fig. 4 Size distribution (%) in the experimental *D. hyalina* populations at low (A and C) and high (B and D) rates of reproduction (solid lines), compared with size distribution in *D. hyalina* grown in control tanks free of fish (dotted lines) on days 8–24 (A and B) and days 52–58 (C and D). The *P* values (Kolmogorov–Smirnov's Chi-Square Approximations) for data in panels A, B, C, and D were <0.015 , <0.004 , <0.001 , and <0.001 , respectively, showing a significant difference between experimental and control distributions

the juvenile cohort at the middle (Fig. 4A, B) and at the end (Fig. 4C, D) of the experiment, with nearly 30 days required for increases in body length of 0.21 mm (0.67–0.88 mm) and 0.08 mm (0.67–0.75 mm) in the lower and higher food levels, respectively (Fig. 4A, C and Fig. 4B, D).

As the absence of reproduction meant that the *Daphnia* populations in tanks free of fish did not represent a proper control for the populations in tanks with fish predation (they were free from predation and also food limited), virtual *Daphnia* populations

Table 1 Proportions (%) of ovigerous females among adult *Daphnia hyalina* in experimental populations at low and high rates of reproduction permitted by different food levels in control tanks free of fish (Control, without replicates) and in three tanks with fish predation (Fish), in the middle (days 8–24) and at the end (days 52–58) of the experiment

	Middle		End	
	Low food	High food	Low food	High food
Control	5.2	4.2	1.7	2.5
Fish	59.0 ± 12.6	53.5 ± 12.0	54.1 ± 5.8	65.2 ± 2.9

The proportion of ovigerous females is significantly lower in the control tanks than in fish tanks. Only data for the three replicates in fish tanks were homogenous, with the mean for the two control tanks being significantly different from the mean for the six fish tanks at $P < 0.001$, $df = 1$, $F = 116.36$; not different ($P = 0.792$) for low and high food level ($df = 1$, $F = 0.07$), and the food \times fish interaction is not significant ($P = 0.781$, $df = 1$, $F = 0.08$; general ANOVA)

Table 2 Reproductive effort (average number of eggs per adult) in experimental *Daphnia hyalina* populations (mean \pm 1 SD) at low and high rates of reproduction permitted by different food levels in control tanks free of fish (control, without replicates) and in three tanks with fish predation (fish), in the middle (days 8–24) and at the end (days 52–58) of the experiment

	Middle		End	
	Low food	High food	Low food	High food
Control	0.49	0.44	0.02	0.03
Fish	2.98 ± 0.82	2.80 ± 0.82	1.82 ± 0.67	2.94 ± 0.36

For the entire data set, the reproductive effort is significantly lower in control tanks than in fish tanks, but only at $P < 0.001$ ($df = 1$, $F = 33.76$), not different ($P = 0.596$) for low and high food level ($df = 1$, $F = 0.30$), and the food \times fish interaction is not significant ($P = 0.559$, $df = 1$, $F = 0.36$; general ANOVA)

exploited by a nonselective predator were used as a substitute. These populations exhibited age structures (dashed lines in Fig. 6A and B) distinctly different from those predicted as an effect of body size-selective predation typical of planktivorous fish (dotted lines in Fig. 6A and B).

Data from all six experimental *D. hyalina* populations subjected to fish predation showed that the age structure was very close to that obtained from simulations (Fig. 6) with our age-structured population model (Gliwicz & Wrzosek, 2008), parameterized for roach as the predator and the prey size/instar-specific reaction distance (*RD*) of

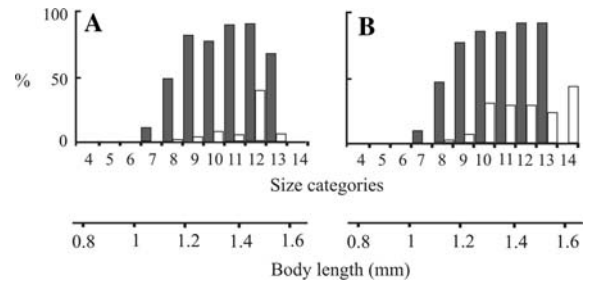


Fig. 5 Proportions of adults with eggs in their brood cavities within different adult size categories in experimental *D. hyalina* populations at low (A) and high (B) food levels in tanks with fish predation and reproduction reduced by low densities of adult females (shaded), and in control tanks free of fish with reproduction reduced by food shortages due to high population density level (unshaded) on days 8–24

D. hyalina (Fig. 7). This model takes into account predator-induced mortality in different prey size categories, as well as age-dependent fecundity for each age category of respective body length. The age-/size-specific mortality is expressed as a multi-prey functional response that links the density-dependent attack rate (encounter rate multiplied by attack probability) with the prey-specific *RD*. The probability with which a prey of a given size category is captured by a foraging fish depends on its specific apparent density, i.e., the number of individuals per size-specific visual field volume, *VFV*. Thus, the prey category that appears to be most abundant is more likely to be captured, and there is no other determinant of prey choice except that resulting from the size-specific *RD*.

Even though the age structure produced by the model did not differ significantly from that in experimental populations (dotted lines and solid lines, respectively, in Fig. 6A and B), the distributions did not match completely, suggesting that not every assumption used in the model's parameterization was correct. The most apparent deviation of age structure in the experimental *Daphnia* populations from that produced by the simulation with the model was detected in age classes representing first reproduction (dotted vertical lines in Fig. 6). These observations encouraged us to use the experimental data on size distribution for testing other hypotheses that could connect the observed size distributions of prey with foraging patterns different from that used in our theoretical model (Gliwicz & Wrzosek, 2008).

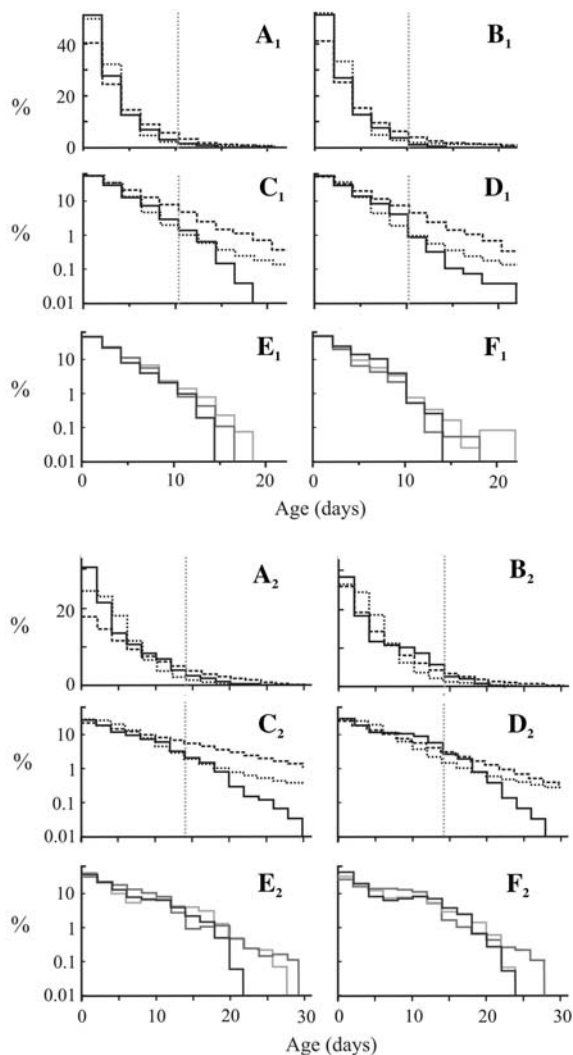


Fig. 6 Age distribution (%) in the experimental *D. hyalina* populations at low (**A**, **C**, **E**) and high (**B**, **D**, **F**) rates of reproduction permitted by two different food levels in tanks with fish predation applied at dusk on days 8–24 (**A**₁ to **F**₁) and days 52–58 (**A**₂ to **F**₂) of the experiment. **A** and **B** – means from the three experimental replicates (*solid lines*) compared with the theoretical age distribution from simulations with the model of Gliwicz & Wrzosek (2008), with prey-size-dependent mortality increasing with *Daphnia* body size and its specific reaction distance (*dotted lines*), and nonselective mortality (*dashed lines*) expressed in our population model as a fixed instantaneous per capita mortality rate with the same value in each age class prescribed in such a way that after 20 days it attains an equilibrium (the instantaneous per capita birth rate equaled by the per capita mortality rate). Vertical *dotted lines* indicate the age at first reproduction where ovigerous females constitute $\geq 90\%$ of *Daphnia* in a given adult age class. Our model was parameterized for roach as the predator and *D. hyalina* as the prey: the predator density was $0.008 \text{ ind. l}^{-1}$, the daily feeding time 2 h, and data on daily egg production were taken from experimental populations. The age-specific reaction distance was calculated with formula (1) using the best-fit emerging from the experimental data presented in Fig. 7. The *P* values for data in panels A and B (derived from the Kolmogorov–Smirnov test) were <0.81 , <0.08 , <0.52 , and <0.37 for **A**₁, **A**₂, **B**₁, and **B**₂, respectively, showing no significant difference between the experimental distribution and theoretical distributions derived for size-selective predation. A significant difference ($P < 0.0001$) was found between experimental age distribution and theoretical distributions derived for nonselective predation. **C** and **D** – the same data as in **A** and **B** shown on a logarithmic scale to reveal the age at which age distributions in the experimental *Daphnia* populations deviate from those in theoretical populations exploited by a size-selective predator. **E** and **F** – data for each of the three experimental replicate tanks (marked by different lines) revealing the inter-sample variability in the age distributions. The Kolmogorov–Smirnov test values were 1.00 for all three comparisons for **E**₁, 0.94, 1.00, and 0.37 for **F**₁, 0.62, 0.57, and 1.00 for **E**₂, and 1.00, 0.55, and 0.03 for **F**₂, with even the last difference ($P = 0.03$) becoming insignificant after Bonferroni adjustment

As mentioned in the “Introduction” section, our working hypothesis was that predation leads to the uniformity of a weighted distribution of prey classes (the density level of each class multiplied by a class-specific factor), which might reflect the foraging pattern of the predator. Initially, we anticipated that the age structure and thus the resulting prey size distribution would reflect the size proportions fixed in the prey population by fish according to the cube of the size-category-specific reaction distance, as was found in the case of separate *Daphnia* prey species of different body sizes at first reproduction (Gliwicz & Wrzosek, 2008). In other words, we anticipated that densities of different size categories (such as those in Fig. 8A) would be such that the corresponding apparent densities form a homogeneous distribution.

However, Fig. 8B shows that these proportions differed greatly from those expected. The proportions of different size categories became slightly closer to those expected (more homogenous size distribution) when examined as size-specific encounter rate, with the cross section of the stationary visual field of a foraging fish assumed to be either circular (Fig. 8C) or elliptical.

The proportions only became very close to homogenous when calculated as the size-specific encounter rates, assuming an elliptical cross section of the stationary visual field, but with its vertical parameter (semi-minor axis of the ellipse) reduced to that representing the smallest prey size category (earliest instar of *D. hyalina*, Fig. 8D), hence with the reaction distance in a horizontal plane appearing to be the only

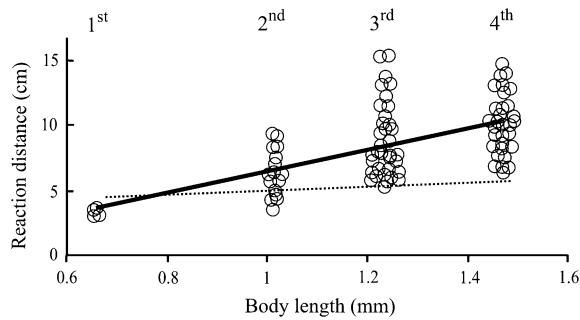


Fig. 7 Reaction distance on body length regression using experimental data for *D. hyalina* from 4 different instars: three juvenile (first, second, and third) and one adult (fourth, all individuals with eggs in their brood cavities) at the lowest prey density of 0.01 *Daphnia* l⁻¹ (points and solid thick regression line: $y = 8.2989x - 1.8862$, $R^2 = 0.3395$), and at the highest prey density of 10 *Daphnia* l⁻¹ (dotted line). Note that a real density of 0.01 *Daphnia* l⁻¹ corresponds to 0.0097, 0.0589, 0.1227, and 0.2297 *Daphnia* per instar-specific VFV, for the first, second, third, and fourth instar, respectively. Also note that the regression is significant at each of the four lower density levels of 0.10, 0.33, 1, and 3.3 *Daphnia* l⁻¹, but not significant for the highest density of 10 *Daphnia* l⁻¹

meaningful factor. This suggests that size selection by planktivorous fish leads to size proportions in a *Daphnia* prey population that result in a similar encounter rate for each *Daphnia* size category with a foraging fish, assuming that the size-specific reaction distance is responsible for the width (horizontal parameter) but not the height (vertical parameter) of the elliptical cross section of a fish's stationary visual field. In reality, this cross section might be even more flattened (Fig. 8D₂), thus resembling that found in terrestrial predators with their field of vision restricted to the horizontal plane (Fig. 8D₃) and depicted by the reaction distance to the power 1 rather than the power 2 (RD rather than RD^2).

This observation, however, is evidently restricted to juvenile *Daphnia* size categories, i.e. below the size of first reproduction, which is assumed to be between 1.04–1.13 mm body length (in this category at least 75% of our experimental *D. hyalina* carried eggs in their brood chambers). The level of representation in the total population, so similar in all juvenile size categories, was quickly reduced with each consecutive adult size category (Fig. 8D). This indicates an abrupt increase in *Daphnia* vulnerability to predation that cannot be explained by encounter rate, suggesting a different basis for prey choice when a foraging fish is faced with egg-carrying *Daphnia*.

This increase in *Daphnia* vulnerability to predation by a foraging fish that harvests all prey from its VFV, does not seem to be related to the presence or absence of eggs in the brood cavity. From the linear regression of the reaction distance on *Daphnia* body size (Fig. 7), no difference in the distance at which a foraging fish sees its prey would be anticipated for an adult *Daphnia* with or without eggs in its brood cavity. The sharp increase in *Daphnia* vulnerability was also evident as a steep decline in size-specific encounter rate for adult females at both the middle (days 8–24, Fig. 8D and Fig. 9A, B) and the end (days 52–58, Fig. 9C, D) of the experiment, and also in the age structure (Fig. 9E–H). This implies that fish feeding behavior may change abruptly when the number of *Daphnia* females with eggs becomes higher than that observed in our experimental populations. It is important to note that the proportion of egg-carrying females in our experimental populations is overestimated in Fig. 5 since the *Daphnia* were sampled just before the start of the daily 3 h fish feeding session at dusk, i.e., after 22 or 21 h free of predation, during which many females could lay eggs into their brood chambers, thus increasing the number of the smallest ovigerous females in the experimental *Daphnia* populations. The unimpeded growth in the preceding 21 h may be the reason why the proportion of individuals in the first, smallest adult size category (1.04–1.13 mm body length) was nearly as high as the proportion in juvenile categories (Fig. 8D).

The strong selection for *Daphnia* with eggs in their brood cavities is clearly reflected in panel E of Fig. 8 as a drastic increase in the factor by which the size-specific encounter rate C_k must be multiplied (x_k) to yield identical values (0.07 ind. s⁻¹) for all size categories across the entire size spectrum of the *Daphnia* prey population, egg-carrying adult females included (dotted lines in Fig. 8D). The encounter rate

$$C_k = N_k(\pi\delta_H\delta_V)\alpha, \quad (3)$$

where N_k is the density of *Daphnia* prey of a given size category k , $\pi\delta_H\delta_V$ is the area of the elliptical cross section of the stationary visual field of a foraging fish (with δ_H the prey-specific reaction distance in the horizontal plane, and δ_V the prey-specific reaction distance in the vertical plane) and α is the cruising speed of the foraging fish.

The value of the factor x_k (Fig. 8E) indicates how much the cruising speed would have to increase to ensure that the encounter rates for adults were as high

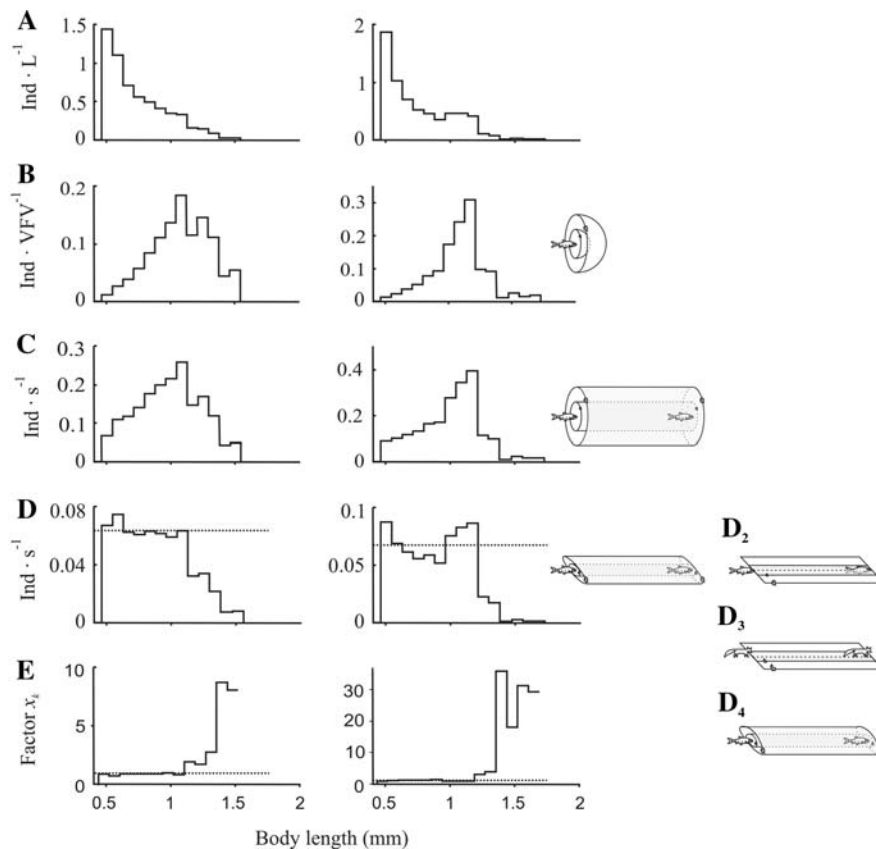


Fig. 8 A search for a best-fit explanation of size-selective predation of a *Daphnia* prey population by a foraging fish in an effort to identify a factor that would show equal values for each prey size category across the entire range of body sizes. All values are shown for size distributions (%) in the same experimental *D. hyalina* populations as those in Fig. 4 at low (left) and high (right) rates of reproduction in tanks with fish predation applied at dusk on days 8–24. **A** Real densities (ind. L⁻¹). **B** Apparent densities or the numbers of *Daphnia* of a given size category *k* in each size-specific visual field volume VFV_{*k*} (ind. VFV_{*k*}⁻¹). **C** Size-specific encounter rate (ind. s⁻¹) assuming that the cross section of the stationary visual field of a foraging fish is circular (as in the sketch at the side). **D** Size-specific encounter rate (ind. s⁻¹) assuming that the cross section of the stationary visual field of a foraging fish is elliptical, but the vertical semi-minor axis of the ellipse is the same in each size category and equal to that of the smallest prey category (as in the sketch at the side), with the VFV changed from a hemisphere to a hemi-ellipsoid. The dotted line shows each population's homogenous distribution of encounter rate for juveniles of different size categories when it is assumed that fish selectively remove the size category most frequently

as those for juveniles. The higher cruising speed required to achieve equal encounter rates would allow each foraging fish to maximize its feeding rate by ignoring juveniles and temporarily excluding them

encountered. Such distribution is also attained when it is assumed that either the field of vision of a foraging fish is as two-dimensional (D₂) as that of a visually oriented terrestrial predator (D₃), or has the upper border of its elliptical cross section of the stationary visual field expanded by elongation of the vertical semi-axis above the fish's eyeline (D₄) to better reflect prey background contrast when viewing items against the lake surface. This expansion seems to be greater in the case of a larger prey category (of greater value) making the ascent worth the increased risk of piscivore predation in the more illuminated upper strata. **E** Factor *x_k* by which the size-specific encounter rate from Fig. 8D has to be multiplied to yield identical values for all size categories across the entire size spectrum of the *Daphnia* prey population, adults included. *x_k* equals 1 (dotted line in F) when the size-specific encounter rate equals 0.07 ind. s⁻¹ (dotted line in D). This factor indicates how much the cruising speed would have to be increased to ensure encounter rates for adults (>1.1 mm body length) that are as high as those for juveniles (<1.1 mm). Equal encounter rates for adult *Daphnia* (due to an increase in the fish's cruising speed) would allow each foraging fish to maximize its feeding rate by ignoring juveniles and concentrating on adults alone

from its diet, even though they are constantly encountered at a very high rate. An increased cruising speed seems to be more likely than active selectivity for females with eggs in their brood cavities.

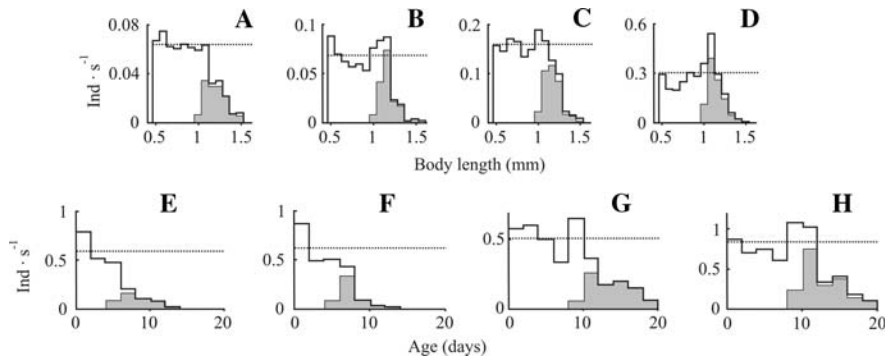


Fig. 9 Size-specific encounter rate (ind. s^{-1}) for different size categories (**A, B, C, D**) and for different age classes (**E, F, G, H**) in experimental *D. hyalina* populations at low (**A, C, E, G**) and high (**B, D, F, H**) rates of reproduction in tanks, with fish predation applied at dusk on days 8–24 (**A, B, E, F**), and days 52–58 (**C, D, G, H**). It is assumed that the cross section of the stationary visual field of a foraging fish is elliptical, and that the vertical diameter is the same in each size and age category and equals that of the smallest or the youngest prey category (as in Fig. 8D), with its *VFV* changed from a hemisphere to a hemi-ellipsoid. The *shaded area* shows the contribution of ovigerous females in each size category. The *dotted line* indicates each population's homogenous distribution of

encounter rates for juveniles of different size categories when it is assumed that fish selectively remove the size category most frequently encountered. Three of the four size distributions are not different from this homogenous distribution; only at high reproduction (high food level) in days 52–58 (**D**), is the slope different from 0 (at $P < 0.05$, $R^2 = 0.57$, linear regression analysis), reflecting an exceptionally high proportion of juveniles in the largest size categories (see Fig. 8A, right panel). This was probably caused by the decreased temperature at the end of the experiment (from 23 to 10°C). Note that the shape of each curve is determined both by selective mortality due to fish predation and by continuous recruitment to each consecutive size class

Notably, at the end of each experiment, the shape of the size distribution in each *Daphnia* population (Fig. 4), as well as the shape of the “apparent distribution” (Fig. 8B) and encounter rate for different prey size categories (Fig. 8C), reflected the state of an equilibrium in each population: the instar-to-instar (size-to-size category) recruitment and the size-selective mortality are balanced for each instar or size category, with greater recruitment at the higher food level being instantly compensated by raised mortality due to increased predation.

Discussion

Prey choice as a function of apparent density and encounter rate

Although the concept of apparent density and *VFV* was commonly employed in experimental and theoretical studies of the 1970s (Werner & Hall, 1974; Confer & Blades, 1975; Eggers, 1977) and 1980s (Eggers, 1982; Butler & Bence, 1984; Wetterer & Bishop, 1985), it was focused on fish behavior rather than the effect of fish predation on cladoceran prey populations. This may be why it had not been used in

efforts to understand density proportions among different cladoceran species until recently (Gliwicz, 2001; Gliwicz & Wrzosek, 2008) and has never been used to elucidate the selective effects of fish predation on size distribution or age structure of a cladoceran population. However, for a time, it remained the cornerstone of the notion of prey apparent body size that determines prey choice by planktivorous fishes (O'Brien et al., 1976, Fig. 1A), and of Egger's foraging model, which was the first to incorporate the effects of prey body size distribution, encounter rate, handling time, and selection among encountered prey items (Eggers, 1977, Fig. 1B).

Although its generality in the context of the optimal foraging theory was later called into question by Eggers (1982) and Butler & Bence (1984), the concept of apparent body size has further enhanced our understanding of prey choice. The prey selected by an optimally foraging fish is that which appears largest of all prey items within its specific visual field volume (*VFV*, Fig. 1C). This is a more or less forward-directed hemisphere of radius equal to the prey's specific reaction distance: the maximum distance from which the prey object can be seen and recognized by a fish (Confer & Blades, 1975; Eggers, 1977; Confer et al., 1978; Luecke & O'Brien,

1981; Wright & O'Brien, 1982; Dunbrack & Dill, 1984; O'Brien et al., 1984; O'Brien, 1987).

We had no notion whether the selective effect of fish predation on size distribution and age structure of our *Daphnia* populations would be a function of apparent density, hence the cube of its *RD* (used in setting interspecific density proportions as in Fig. 1C), or a function of encounter rate, hence the square of its *RD* (as in Fig. 1D). The encounter rate appeared identical for all *D. hyalina* juvenile instars when the cross section of the stationary visual field of a foraging fish is assumed to be elliptical (as in Fig. 1E), with its vertical semi-minor axis either the same (Fig. 8D), or only slightly larger (Fig. 8D₄) compared with smaller prey size categories. An elliptical rather than a circular cross section of the stationary visual field (as in Fig. 8D rather than Fig. 8C) seems to be the correct assumption since both the light intensity and the background contrast of the prey change with the angle of fish vision in the vertical but not in the horizontal plane. Moreover, a reduced vertical dimension of the search volume was reported many years ago following observations of white crappie (*Pomoxis annularis*) by Evans and O'Brien (cited in O'Brien, 1987). Furthermore, the reduction in the vertical dimension of the search volume was found to be greater when these fish fed on smaller rather than larger prey, with the search volume becoming 'more constricted resembling a pie shape in the horizontal plane' (O'Brien, 1987).

To our great surprise, neither the apparent density distribution (based on the cube of the reaction distance, Fig. 8B) nor the distribution of the encounter rate, assuming a *VFV* of circular cross section (based on the square of the reaction distance, Fig. 8C), appeared to yield the expected homogeneity of distribution. Instead, we found that the distribution of the encounter rate, assuming a *VFV* of elliptical cross section with the vertical semi-minor axis common for all prey size categories (Fig. 8D), seemed to best reflect the mode of prey selection and the homogenizing impact of the predator on the size distribution and age structure of a *Daphnia* prey population. We note that in contrast to the modes of prey selection related to the cube or the square of the reaction distance, this mode depends on the size/age-specific reaction distance taken to the power one: the same as that used to describe feeding activity of a terrestrial predator with a horizontal field of vision

(Fig. 8D₂, D₃; Case, 2000). Although these observations correspond well with our data on juvenile instars, they do not match our experimental data for all size categories of *D. hyalina* (Fig. 8D), suggesting that prey choice might be dependent on a mechanism different to that suggested for the juveniles.

Prey choice with regard to ovigerous females

The lack of match of our predictions with our experimental data for adult *Daphnia*, suggest that the presence of eggs in the brood cavities may cause a foraging fish to modify or completely change its feeding behavior. A similar conclusion might be drawn from the clear deviations of our experimental age distributions from the predictions of our model with *Daphnia* controlled by size-selective predation. These deviations started at the time of first reproduction when 90% of females carry clutches of eggs in their brood cavities (vertical dotted lines in Fig. 6A and B).

Such a modification of fish feeding mode may merely be the widening of the vertical angle of search, thus changing the cross section of the stationary visual field of a foraging fish from an oblate ellipse to a circle (from that in Fig. 8D to that in Fig. 8C). This may be due to sharper background contrast permitting *Daphnia* with eggs to be seen more clearly against the darkness of the deeper strata (thus expanding the visual field downward), or by the foraging fish taking an increased risk of piscivore predation by coming closer to the lake surface when more rewarding prey such as ovigerous *Daphnia* become more abundant (thus expanding the visual field upwards). The latter scenario seems more likely than the former because less translucent prey such as *Daphnia* with eggs in their brood cavities are easier to detect due to their greater contrast with the illuminated background above (Vinyard & O'Brien, 1975). The upward expansion of the visual field may have something to do with the apparent sinusoidal swimming pattern of roach and other cyprinid fish observed by Čech & Kubečka (2002) in their hydro-acoustic study using an echo sounder on the bottom of Rimov Reservoir facing the water surface some 30 m above.

Widening the vertical angle of search for energetically more profitable ovigerous *Daphnia* may be why the factor x_k from Fig. 8E is considerably greater for an adult *Daphnia* with eggs in its brood cavity than for *Daphnia* juveniles of a similar body size, and thus a

similar reaction distance at which they can be sighted by a foraging fish (Fig. 7). Alternatively, the fish will be able to widen the horizontal angle as well. Foraging fish would then be trading a possible energy gain against the cost of sharp turns needed to stop and aim directly at the prey to sight it stereoscopically with both eyes before attacking (Confer & Blades, 1975).

However, neither of these two reasons appear to sufficiently explain the great difference in the value of C_k for adults with eggs and juveniles of *D. hyalina* (Fig. 8D). The only reasonable explanation for the 5- to 20-fold increase in the factor x_k (Fig. 8E) required to make the size-specific encounter rate C_k equal for adult size categories and juveniles is an increase in cruising speed α (Eq. 3). However, such a dramatic increase in cruising speed would mean that less valuable and less visible small-bodied prey would be completely ignored and excluded from the diet, in spite of the greater encounter rate. Such a trade-off, involving an increased number of encounters with larger prey, may be quite rewarding if such prey are abundant enough to make the net energy gain greater than that from low-speed feeding on all size classes of the *Daphnia* population.

Switching between harvesting and hunting

Such an increase in speed represents a complete change in predation behavior, with the fish switching from slowly foraging for less valuable but more abundant prey, with more than one prey item within the *VFV*, to rapid cruising, where small-bodied prey are largely ignored but encounters with large and proficient prey, such as *Daphnia* with large clutches of eggs, increase due to the greater speed and possibly the expanded range of depths penetrated by the fish, as suggested by Čech & Kubečka (2002).

When a larger, thus more apparent, easier to capture, and more profitable prey category becomes abundant enough to fill the gut faster or with less effort, a foraging fish would be expected to switch its feeding behavior from harvesting to hunting, i.e., from meticulously selecting prey encountered within its *VFV* at low swimming speeds to foraging for more valuable prey at greatly increased swimming speeds to amplify the encounter rate. Such a possibility appears to be in line with the foraging model of Eggers (1977) and his observations on the diets of juvenile sockeye salmon suggesting an active

preference for large and nonvasive prey that became more pronounced when this prey was more abundant (Eggers, 1978, 1982).

Such a shift in feeding behavior may lay behind the phenomenon of sinusoidal cycling: a swimming pattern of roach in Rimov Reservoir that was assumed by Čech & Kubečka (2002) to be an efficient way of inspecting a larger volume of epilimnion in search of cladocerans and their aggregations. The preference for prey objects above the horizontal plane of fish movement, where a foraging fish can exploit the sharper contrast with the lighter background at the top of its visual field (Eggers, 1977; Zaret, 1980; O'Brien, 1987), causes the foraging fish to come closer to the surface with each attack, until it enters illuminated strata and is forced to descend before it can initiate further attacks, resulting in sinusoidal swimming. Such behavior would imply that the real shape of the visual field may have its top limits more expanded than its bottom limits, as depicted in Fig. 8D₄.

The shift from harvesting to hunting behavior may also lay behind diel horizontal migrations in littoral cyprinid fish, such as the long-distance excursions of roach and bleak at dusk to feed on large-bodied *Daphnia* that are more abundant far from their daytime littoral refuge (Gliwicz et al., 2006). This happens if the number of *Daphnia* females with eggs becomes very high, as occurs during the spring clear-water phase and after a local temporary release of fish predation allowing the *Daphnia* population to build up. These population increases are always followed by midsummer declines and the eradication of *Daphnia* aggregations (examples in Threlkeld, 1979; Lampert, 1988; Sommer, 1989; Gliwicz, 2003).

Consecutive switching by planktivorous fish from one feeding mode to another may be responsible for the presence of similar *Daphnia* population densities throughout the seasons, across a lake basin, and from one lake to another (Gliwicz, 2001; Gliwicz & Wrzosek, 2008). It may also be responsible for damping density oscillations in *Daphnia* and other cladoceran species. Fish might switch to hunting mode when the number of ovigerous females is high (hence preventing further fast population increases), and then switch back to harvesting mode when the number of ovigerous females has been reduced below a critical level at which the benefit or net energy gain from hunting is the same as that from harvesting

(hence allowing more females to carry their clutches of eggs until the freshly hatched juveniles can be safely released from the brood chambers).

High selectivity for *Daphnia* carrying eggs has been known since Mellors' (1975) report on the extraordinarily strong preference of fish for ephippial females, and was confirmed by numerous studies described in textbooks and reviews (Zaret, 1980; Sommer, 1989; Gliwicz, 2003). Among the best examples is the field study of Langeland & Nost (1995) showing that neither white fish nor arctic char had *Daphnia longispina* (*D. galeata* and *D. hyalina*) smaller than those at first maturation (1.1 mm body length) in their intestines. This phenomenon was confirmed by lake-to-lake comparisons of *Daphnia* size distributions and by manipulating enclosed experimental populations. For example, a steep decline between the last juvenile instar and the first adult females was consistently recorded in a lake in the Tatra Mountains that contains a natural trout population, but such a decline was never detected in a neighboring lake that is free of fish (Gliwicz et al., 2001). The same effect was seen in the study of Vanni (1987) on size distributions in cladoceran populations (*Ceriodaphnia* and *Diaphanosoma*) grown in enclosures with and without fish (bluegill sunfish). The population density of each dominant cladoceran species was much lower in enclosures with fish, the difference being most dramatic in adult instars, particularly females with their first clutch of eggs. Compared with equivalent individuals from enclosures without fish predation, their body size was considerably reduced, suggesting that fish have a very strong preference for ovigerous females.

The high selectivity for *Daphnia* carrying eggs has been commonly attributed to the greater conspicuousness of females with eggs in their brood cavities, and hence their larger apparent size and the increased reaction distance from which these valuable prey can be sighted. This by itself does not appear to be a satisfactory explanation of this phenomenon. We believe that it results from a dramatic change in the fish feeding mode characterized by increased cruising speed combined with exclusion of smaller prey items from the fish diet even though they are frequently encountered.

If our results were from a lake, reservoir, in situ enclosure, or any other field situation, there would certainly be alternate and equally likely explanations for the strong preference for ovigerous *Daphnia* females, such as different kinds of fish and invertebrate

predation. However, the only predation impact permitted in our mesocosm experiments was by eight 1- to 2-year-old roach of the same size allowed to feed for 3 h at the time of sunset. In spite of this, the body size distributions of the *Daphnia* populations showed a sharp decline between the last juvenile instars and adult females with their first clutch of eggs, i.e. exactly the same pattern as that observed in the field where *Daphnia* are exposed to predation by separate age classes of many different species of planktivorous fish.

Conclusions

The preference of a planktivorous fish for a given prey category is determined by (1) the visual conspicuousness of individual prey (its body size and pigmentation, the opaqueness of its more visually obvious portions, and its movements) reflected in the prey-specific reaction distance, and by (2) the abundance of a given prey reflected by its apparent density (i.e., its number in the VFV) and by the encounter rate of the prey with the foraging fish. However, these two determinants are not sufficient to explain the preference of fish for *Daphnia* with eggs in their brood cavities, suggesting that there is an additional determinant related to the ratio of net energy gain to energy investment rather than to reaction distance and VFV geometry. This third determinant may depend on the ability of the foraging fish to assess the nutritional value of each prey item in the same size category, and to ignore the more abundant but less valuable ones when the encounter probability with those of greater value becomes sufficiently high. Such a mechanism would lead to a change in fish feeding behavior, switching from a predator–harvester picking up small prey objects from its VFV, to a predator–hunter that ignores smaller prey and starts to seek larger and more valuable prey objects when they become sufficiently abundant to make hunting more rewarding than harvesting.

We hypothesize that repeated switching by planktivorous fish from one feeding mode to another may cause the annihilation of *Daphnia* aggregations and the damping of cladoceran population density oscillations. Switching to hunting mode when the number of ovigerous females is high, prevents further population increase, and once the number of ovigerous females is reduced below a critical level, so that the benefit or the net energy gain from hunting is the

same as that from harvesting, the switch is made back to harvesting mode.

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References

- Bertalanffy, L., 1938. A quantitative theory of organic growth. *Human Biology* 10: 181–213.
- Brooks, J. L. & S. I. Dodson, 1965. Predation, body size and composition of plankton. *Science* 150: 28–35.
- Butler, S. M. & J. R. Bence, 1984. A diet model for planktivores that follow density-independent rules for prey selection. *Ecology* 65: 1885–1894.
- Case, T. J., 2000. *An Illustrated Guide to Theoretical Ecology*. Oxford University Press, Oxford.
- Čech, M. & J. Kubečka, 2002. Sinusoidal cycling swimming pattern of reservoir fishes. *Journal of Fish Biology* 61: 456–471.
- Clark, C. W. & D. A. Levy, 1988. Diel vertical migrations by juvenile sockeye salmon and the antipredation window. *American Naturalist* 131: 271–290.
- Confer, J. L. & P. I. Blades, 1975. Omnivorous zooplankton and planktivorous fish. *Limnology and Oceanography* 20: 571–579.
- Confer, J. L., G. L. Howick, M. H. Corzette, S. L. Kramer, S. Fitzgibbon & R. Landesberg, 1978. Visual predation by planktivores. *Oikos* 31: 27–37.
- Dunbrack, R. L. & L. M. Dill, 1984. Three dimensional prey reaction field of the juvenile coho salmon (*Oncorhynchus kisuth*). *Canadian Journal of Fisheries and Aquatic Sciences* 41: 1176–1182.
- Eggers, D. M., 1977. The nature of prey selection by planktivorous fish. *Ecology* 58: 46–59.
- Eggers, D. M., 1978. Limnetic feeding behavior of juvenile sockeye salmon in Lake Washington and predator avoidance. *Limnology and Oceanography* 23: 1114–1125.
- Eggers, D. M., 1982. Planktivore preference by prey size. *Ecology* 63: 381–390.
- Geller, W., 1987. On estimating the age and the development time of *Daphnia* as a function of body size and temperature. *Journal of Plankton Research* 9: 1225–1230.
- Gliwicz, Z. M., 2001. Species-specific population-density thresholds in cladocerans? *Hydrobiologia* 442: 291–300.
- Gliwicz, Z. M., 2003. Between Hazards of Starvation and Risk of Predation: The Ecology of Offshore Animals. International Ecology Institute, Oldendorf/Luhe.
- Gliwicz, Z. M. & D. Wrzosek, 2008. Predation-mediated coexistence of large- and small-bodied *Daphnia* at different food levels. *American Naturalist* 172: 358–374.
- Gliwicz, Z. M., M. Slusarczyk & A. Slusarczyk, 2001. Life-history synchronization in a long-lifespan single-cohort *Daphnia* population of an alpine lake free of fish. *Oecologia* 128: 368–378.
- Gliwicz, Z. M., J. Slon & I. Szykarczyk, 2006. Trading safety for food: evidence from gut contents in roach and bleak captured at different distances offshore from their daytime littoral refuge. *Freshwater Biology* 51: 823–839.
- Hrbáček, J., 1962. Species composition and the amount of zooplankton in relation to the fish stock. *Rozprawy ceskosloveske Akademie Véd. Rada Matematicko-Prirrodovedecka* 72: 1–114.
- Lampert, W., 1988. The relationship between zooplankton biomass and grazing. A review. *Limnologia* 19: 11–20.
- Langeland, A. & T. Nost, 1995. Gill raker structure and selective predation on zooplankton by particulate feeding fish. *Journal of Fish Biology* 47: 719–732.
- Luecke, C. & W. J. O'Brien, 1981. Prey location volume of a planktivorous fish: a new measure of prey vulnerability. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 1264–1270.
- Mellors, W. K., 1975. Selective predation of ephippial *Daphnia* and the resistance of ephippial eggs to digestion. *Ecology* 56: 974–980.
- O'Brien, W. J., 1987. Planktivory by freshwater fish: thrust and parry in the pelagia. In Kerfoot, W. C. & A. Sih (eds), *Predation. Direct and Indirect Impacts on Aquatic Communities*. University Press of New England, UK: 5–16.
- O'Brien, W. J., N. A. Slade & G. L. Viniard, 1976. Apparent size as the determinant of prey selection by bluegill sunfish (*Lepomis macrochirus*). *Ecology* 57: 1304–1310.
- O'Brien, W. J., B. Evans & C. Luecke, 1984. Apparent size choice of zooplankton by planktivorous fish: exceptions to the rule. *Environmental Biology of Fishes* 13: 225–233.
- Pijanowska, J., 1980. Zooplankton communities in nine Mazurian Lakes. *Ekologia Polska* 28: 451–465.
- Sommer, U. (ed.), 1989. *Plankton Ecology. Succession in Plankton Communities*. Springer, New York.
- Threlkeld, S. T., 1979. The midsummer dynamics of two *Daphnia* species in Wintergreen Lake, Michigan. *Ecology* 60: 165–179.
- Tilman, D., 1982. *Resource Competition and Community Structure*. Princeton University Press, Princeton, NJ.
- Vanni, M. J., 1987. Effects of food availability and fish predation on a zooplankton community. *Ecological Monographs* 57: 61–88.
- Vinyard, G. L. & W. J. O'Brien, 1975. Dorsal light response as an index of prey preference in bluegill sunfish (*Lepomis macrochirus*). *Canadian Journal of Fisheries and Aquatic Sciences Journal of Fisheries Research Board of Canada* 32: 1860–1863.
- Werner, E. E. & D. J. Hall, 1974. Optimal foraging and the size selection of prey by the bluegill sunfish (*Lepomis macrochirus*). *Ecology* 55: 1042–1052.
- Wetterer, J. K. & C. J. Bishop, 1985. Planktivore prey selection: the reactive field volume model vs. the apparent size model. *Ecology* 66: 457–464.
- Wright, D. I. & W. J. O'Brien, 1982. Different location of *Chaoborus* larvae and *Daphnia* by fish. *American Midland Naturalist* 108: 68–73.
- Zaret, T. M., 1980. *Predation and Freshwater Communities*. Yale University Press, New Haven.