

## Selectivity by planktivorous fish at different prey densities, heterogeneities, and spatial scales

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### Abstract

Studies in artificially confined, small-scale experimental systems with a homogeneous prey distribution suggest that selectivity in planktivorous fish for more conspicuous and rewarding prey (such as adult *Daphnia* with eggs in the brood cavities) is stronger at high than at low prey population density. We examined whether prey selectivity is altered when fish are allowed to feed in larger scale systems and on more heterogeneously distributed prey. The experimental system was comprised of 1000 liter tanks (one, four, or eight), interconnected to allow free movement of roach (*Rutilus rutilus*, eight per tank), with different densities of *Daphnia* prey, distributed with varying levels of homogeneity. As reported previously, the selectivity of roach increased at higher *Daphnia* densities, but only in small-scale systems where prey distribution was homogeneous. However, the opposite was found in large-scale systems with heterogeneous prey distribution, i.e., greater selectivity at lower prey densities. The reversed slope of the selectivity-on-prey-density regression was linked to increased swimming speed at low prey density, where the fish, less constrained by the limited size of the experimental system, accelerate, possibly in an effort to compensate for low encounter rate and to more rapidly locate patches of prey. More selective feeding on scarce and patchy prey may result from the decreased relative visibility of smaller prey and from the increased capture costs due to the need to expend more energy for postcapture accelerations to regain a higher speed.

Size-selective feeding by planktivorous fish is believed to be the key factor in structuring zooplankton communities of lakes (Hrbacek 1962; Brooks and Dodson 1965) and oceans (Hassel et al. 1991), and its effects on zooplankton prey have been the subject of much research (reviewed by Hunter and Thomas 1974; Lazzaro 1987; Gerking 1994). Despite this, the true nature of this pattern of feeding is not fully appreciated because data have been acquired in the confinement of experimental systems, often small aquaria, with zooplankton prey in homogenous distribution. Moreover, selectivity can be observed at each of the subsequent events in the predation process, i.e., prey encounter, pursuit, attack, and retention (Holling 1966; O'Brien 1979). However, in the case of prey such as *Daphnia*, selectivity is restricted to the encounter and pursuit phases, being entirely the function of detection and predator choice, with—in contrast to the situation with copepods—little chance of evasion or escape from the mouth of the predator (Gerking 1994). When a foraging fish actively chooses one prey item from among multiple prey after detecting it within its visual field volume, this selectivity may be an effect of either the different mechanistic accessibility of separate prey categories (O'Brien et al. 1976; Mills et al. 1986; Fiksen and MacKenzie 2002) or the different accessibility of each category combined with the predator's preference (Werner and Hall 1974). The first scenario has been readily adapted in theoretical works, since it offers a simple way to explain the effect of selectivity as a function of reaction distance alone (O'Brien et al. 1976; Wright and O'Brien 1984) or in combination with the speed of a foraging fish (Eggers 1977; Luo et al. 1996). The second scenario has primarily been used in experimental tests of the concept of optimal foraging (Emlen 1966; MacArthur and Pianka 1966; Schoener 1971)

by assuming that a foraging fish chooses a single prey, among the many encountered, to maximize energetic benefits (Werner and Hall 1974). Although both of these scenarios predict stronger selectivity toward larger or more conspicuous prey items (e.g., *Daphnia* females with eggs in their brood cavities), the majority of studies demonstrate that selectivity is greater than would be expected from differences in prey accessibility alone (Gardner 1981; Bence and Murdoch 1986; Manatunge and Asaeda 1999).

The two scenarios, each based on size-selective models of prey selectivity in fish, predict stronger selectivity at higher prey densities due to the enhanced probability of encountering a prey that is either easier to detect (O'Brien et al. 1976) or more profitable (Werner and Hall 1974). However, neither scenario takes into account the possibility that the selectivity could be affected by the swimming speed of a foraging fish, the greater speed resulting from the need to compensate for the reduced encounter rate at low prey densities, as suggested by Hunter and Thomas (1974), Munk and Kiørboe (1985), and Ruzicka and Gallager (2006). The acceleration may either cause a decline in the relative visibility of smaller or more transparent prey (Gendron and Staddon 1983) or make the cost of obtaining prey greater in the “fast mode” as a result of the energy expended for deceleration during the capture (Ware 1978) and for the postcapture acceleration (Domenici and Blake 1997), hence making slowing down for a small-bodied prey unprofitable (Kramer and McLaughlin 2001). Separately, each of these two effects may result in greater than expected selectivity of foraging fish at low prey density. Moreover, the underestimation of selectivity at low prey density can be even greater when prey is randomly distributed, as is often assumed in theoretical studies on prey-density-dependent selectivity (e.g., optimal foraging model, Werner and Hall 1974; apparent size model, O'Brien et al. 1976; reactive field

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volume model, Eggers 1977; spatial foraging model, Luo et al. 1996). Such an underestimation may stem from the even greater swimming speed of fish in sites with a low density of heterogeneously distributed prey, not only to compensate for the reduced number of prey encountered, but also to more rapidly locate a more prey-profitable site.

The hypothesis that selectivity becomes stronger and diet breadth narrower at higher prey densities has been confirmed by landmark experimental studies (Werner and Hall 1974; Croy and Hughes 1991; Munk 1995) and limnological textbooks (Lampert and Sommer 2007). This notion is often considered the key to understanding the nature of foraging behavior in planktivorous fish such as predator-harvesters (Munk 1995), as well as the effects of selective foraging by fish on the structure of a typical prey population (Gliwicz et al. 2010). However, there are two reasons why this notion—despite its multiple experimental verifications—does not necessarily apply to genuine field situations. The prey-density-dependent selectivity models and their experimental testing have all been based on spatially small experimental systems in which the mobility of foraging fish is restricted, thus preventing them from achieving a sufficient speed to effectively search for a site with more abundant prey (e.g., 30 or 45 liters in experiments of MacKenzie and Kiørboe 1995 and Gliwicz et al. 2010, respectively). Even when performed in relatively large 450 liter tanks (Werner and Hall 1974) or 172 liter aquaria (Munk 1995), the experimental fish were offered homogeneously distributed prey (Werner and Hall 1974; Gibson 1980; Munk 1995). Moreover, in the few experiments performed with patchily distributed prey, the focus was on other aspects of feeding (competition or predation risk), rather than selectivity itself (Milinski and Heller 1978; Milinski 1979; Croy and Hughes 1991). The only exception, so far, is a recent study by Gliwicz et al. (2013) performed in a large-scale (8000 liter) experimental system with heterogeneously distributed prey, but its focus was on the adaptive value of aggregating behavior in *Daphnia* prey rather than on selectivity of roach (*Rutilus rutilus*) as its predator.

Prey-density-dependent selectivity has also been examined in the field by comparing the relative abundance of various zooplankton species or different size categories of a single species in the intestines of freshly netted fish, with zooplankton samples collected at the same time in the seining area. Such comparisons have shown that selectivity for larger, more visible, and more rewarding prey is stronger when the zooplankton prey are more abundant (Mittelbach 1981; Eggers 1982; Magnhagen 1985), thus confirming the results of theoretical and laboratory studies. However, such temporal changes in prey-density-dependent selectivity by planktivorous fish do not necessarily prove that the same should be expected for spatial changes in prey abundance across a lake or a sea bay, the study of which would be rather difficult because the intestinal contents of a freshly netted fish give no information on where or at what prey density the examined fish has been feeding. The situation is further complicated by the high unpredictability and instability of zooplankton prey distribution as well as the high mobility of fish, and this could be the reason why interest in optimal foraging and the mechanisms of prey

selection by fish declined after its peak between the 1970s and 1990s.

The ability to verify spatial prey-density-dependent selectivity in the field requires an experimental system that fulfills two conditions: first, it should be closer to the typical field situation in terms of both its spatial dimensions and the heterogeneity of prey distribution, and second, it must allow free movement of foraging fish among persistent patchily distributed prey. Such a system, using different densities of prey in various combinations of tanks that are interconnected to allow free movement of foraging fish between them, has been employed in this study.

Our aim was to test whether specific predictions that stem from the existing theory on optimal foraging (Emlen 1966; MacArthur and Pianka 1966; Schoener 1971), as well as earlier observations on feeding behavior in planktivorous fish (Croy and Hughes 1991; Munk 1995; Gliwicz et al. 2013), could be confirmed by experimental studies on fish allowed to feed in systems of different sizes and different levels of heterogeneity of zooplankton prey distribution.

The first prediction is that in a spatially small system with homogenous prey distribution, the selectivity of a foraging fish should increase (its optimal diet breadth being reduced) with the density of the prey population, when the encounter rate of the larger, more visible, and more rewarding prey category is high enough to ignore smaller prey. In this scenario, the subsequent large-bodied prey appears within the fish's visual field volume even before the previous prey has been handled and ingested. At lower densities of prey, the interval between the moment of successful ingestion and the appearance of the next large-bodied prey in the visual field volume might be too long to keep ignoring smaller prey that are usually more abundant and hence more frequently encountered.

The second prediction is that the tendency of the selectivity of a foraging fish for the larger prey category to increase with the density of the prey population should become weaker as the spatial scale of the system increases, i.e., the stronger selectivity for large-bodied prey at high than at low density of prey becomes offset by the stronger selectivity for large-bodied prey at low than at high prey density. The lack of confinement would allow fish to swim faster, with their swimming speed in the sites with scarce prey becoming high enough to make stopping for smaller prey maladaptive due to the costs of postcapture accelerations, as suggested by Gliwicz et al. (2013). For example, when feeding on a mixture of 2-d-old juveniles and 6-d-old adults of *Daphnia hyalina* with individual body carbon of 3.7 and 9.0  $\mu\text{g}$ , respectively, and the cost of a postcapture acceleration assumed to be 5  $\mu\text{g}$  carbon per capture regardless of prey body size, the juveniles should be ignored. This would make the selectivity for large-bodied prey equally high in areas of high and low prey population density.

The third prediction is that the tendency for the selectivity of a foraging fish for larger prey to increase with the density of the prey population should become reversed when a homogenous prey distribution in a spatially small system is replaced by a heterogeneous prey distribution in a spatially large system. Thus, the mechanism of prey-size selectivity based on optimal choice of prey

size in sites with abundant prey becomes overcome by a mechanism based on optimal decisions on whether or not to stop for a prey of different value when patrolling vast areas with scarce prey at great speed, where the gain from ingesting smaller prey is less than the investment necessary for postcapture acceleration. Rapidly regaining speed is essential to locate rare sites with more abundant prey before it has been annihilated by smarter and quicker fish (Gliwicz et al. 2013).

Each of these three predictions was tested using experimental data collected for a typical planktivorous fish (*R. rutilus*) as the predator with *Daphnia* as its typical prey, whose vulnerability is usually entirely a function of detection and predator choice. The effect of confinement was studied in experimental systems of different scale (a single tank, and in four or eight interconnected 1000 liter tanks with homogeneously distributed *Daphnia* prey), and the effect of prey patchiness was examined in the systems with interconnected tanks with different levels of heterogeneity in the distribution of the *Daphnia* prey.

## Methods

*The approach*—A large experimental data set was collected in the years 2007–2009 in an effort to test whether aggregating may be used as an antipredation defense in *Daphnia* in spite of the strong numerical response of fish in space (Gliwicz et al. 2013). This study was performed in experimental systems composed of four or eight 1000 liter tanks, interconnected into a loop to allow free movement of fish (1-yr-old roach, *R. rutilus*) to forage on known densities of *D. hyalina* prey for periods of between 2 and 12 h. These data have been supplemented by two unpublished sets of data, the first with the same roach feeding on the same clone of *D. hyalina* in the same tanks, but used as single, independent 1000 liter experimental compartments (2009), the second with the same roach feeding in the multitank systems on different *Daphnia* prey, namely, *Daphnia magna*, and *Daphnia cucullata*, of larger and smaller body size at first reproduction, respectively (2007), with data collected at the beginning of the experiments to identify the most convenient prey for a study on optimal foraging and food selectivity in a typical planktivorous fish.

From a total number of 211 feeding sessions completed in the years 2007–2009, the 118 sessions selected for the present study were those that fulfilled two conditions: that the fish were allowed to forage overnight for 12 h, and that quantitative data were available on the densities of juvenile and adult *Daphnia* prey before and after the feeding session. This number comprised three series of sessions: those carried out in eight tanks separated one from another (32 sessions in 2009), and those carried out in the system of tanks interconnected in groups of four (37 sessions in 2008–2009), or in groups of eight (24 sessions with *D. hyalina*, 13 with *D. cucullata*, and 12 with *D. magna* in 2007). Detailed information on the sessions performed with *D. hyalina*, including each session's number in the previous paper (Gliwicz et al. 2013), initial prey densities, mortalities, and recovery rates (each for two different initial density levels), is presented in the Web Appendix, Table A2 ([www.aslo.org/lo/toc/vol\\_59/issue\\_1/0068a.html](http://www.aslo.org/lo/toc/vol_59/issue_1/0068a.html)).

Detailed information on the sessions with *D. magna* and *D. cucullata* is presented in the Web Appendix, Table A1 (also for two different initial density levels).

All feeding sessions took place in a greenhouse with mosquito-netting walls and a semitransparent roof at the Hydrobiological Station in Pilchy, Poland (Gliwicz et al. 2013). For each session, eight fish were introduced into each of the tanks. Their number remained constant in the single-tank feeding sessions (2009), but fluctuated greatly in each tank of the multitank (four or eight) systems due to the high mobility of fish between tanks. Fish movement between tanks was via round windows of 18 cm in diameter (upper edge positioned 20 cm below the water surface), which allowed unconstrained cruising but prevented water currents that might homogenize the distribution of *Daphnia* prey during the feeding session (the windows were closed in the daytime when the fish were returned to their daytime refuges). All tanks were filled with filtered (Millipore 1  $\mu$ m mesh) water from the epilimnion of Lake Roś (Great Mazurian Lakes, Poland).

Each of the 2009 feeding sessions was from one of four 1-d experiments with different numbers of *Daphnia* prey introduced into each of the eight tanks, each treated as a separate system (Web Appendix, Table A2). The 2007–2009 multitank sessions were performed as a part of multiday experiments, each commencing with the mass introduction of *Daphnia* to the single “high-density” tank, with the remaining three (2008–2009) or seven (2007) “low-density” tanks in each system receiving small numbers of *Daphnia* prey. The initial densities of *Daphnia* prey resulted from dividing the maximum number of animals taken from the mass-culture tanks into one large portion of 88.1–92.2% for the high-density tank in the four- and the eight-tank systems, and into three or seven smaller portions of at least 4.0% or 1.1% each for the remaining three or seven low-density tanks, respectively. The density of *Daphnia* prey at the start of each experiment depended on the total number of *Daphnia* available. However, the initial densities for each of the subsequent feeding sessions in multiday experiments were dependent on the outcome of the preceding session, being the result of recruitment combined with mortality in each individual tank of either the single- or the multiple-tank systems. In the subsequent overnight feeding sessions, the differences in prey density between the high- and the low-density tanks were slightly reduced due to the persistently greater effect of fish in the high-density tanks resulting from the strong numerical response of fish in space (Gliwicz et al. 2013).

Although the data were collected in different seasons of separate years, efforts were made to ensure that for each spatial scale and each prey heterogeneity level examined, the experimental parameters remained constant, i.e., the number and size of the fish and their *Daphnia* prey (*D. hyalina*), the light conditions during each feeding session, and the dimensions of the experimental tanks. In addition, the mean water temperature range in each experimental variant was similar, remarkably so for the three different prey heterogeneity levels (18.6°C, 18.8°C, and 18.6°C), and only slightly different for the three spatial scales (19.2°C,

17.7°C, and 19.3°C; see Table 1). This was necessary to eliminate the possibility that any differences between the three scales and the three heterogeneity variants were caused by any interyear variation.

The effect of confinement was examined by comparing the results of feeding sessions carried out in three different tank systems representing three different spatial scales: one, four, or eight tanks with homogeneously distributed *Daphnia* prey among tanks, i.e., the difference in initial *Daphnia* density between tanks not exceeding three individuals (ind.) per liter. The analyzed data were obtained from 32, 13, and 5 feeding sessions performed in the single-, four-, and eight-tank systems, respectively (Table 1, Web Appendix, Table A2).

The effect of prey heterogeneity level was examined in 61 sessions performed in the four-tank (37) and the eight-tank (24) systems. The level of *Daphnia* prey spatial heterogeneity was assumed to be high when the difference between the tank with the highest density and the remaining three or seven tanks (mean values for these remaining tanks) was  $> 15$  *Daphnia* L<sup>-1</sup>, medium when the difference was 3–15 *Daphnia* L<sup>-1</sup>, and low when the difference was  $< 3$  *Daphnia* L<sup>-1</sup>. These ranges for the three heterogeneity categories gave a similar number of data points, the maximum and minimum densities in the high- and low-density tanks being 48 and 0.04 *Daphnia* L<sup>-1</sup>, respectively.

*Experimental animals*—At least 2 months before the start of the first feeding session of every year, 1+ yr-old roach (length 50–75 mm) were collected from Lake Roś (Mazurian Lakes, Poland), using a standard trawl net. The fish were acclimated in 500 liter holding tanks, and then groups of eight were maintained in separate daytime refuges: 60 liter containers filled with aerated lake water that was changed twice a week. The roach in these refuges were fed daily by the addition of 100–150 frozen *Chironomidae* larvae. The prey animals, represented by three different *Daphnia* species (*D. hyalina* clone HG011 from Lake Świącajtę, Mazurian Lakes; *D. cucullata* clone C014 from Lake Roś; and *D. magna* clone DM001 from an artificial temporary pond at Pole Mokotowskie, Warsaw, Poland) were cultured to densities below half the carrying capacity level in additional 1000 liter tanks and fed daily with the green alga *Scenedesmus obliquus* at a concentration above the incipient food level of 1 mg C L<sup>-1</sup> (Gliwicz and Maszczyk 2007). The fish and *Daphnia* cultures were maintained in water from the epilimnion of Lake Roś that had been filtered through a 1 µm Millipore membrane filter.

*Experimental design*—Each feeding session of every series was started 2 h before sunset, in similar light conditions. The initial illumination inside the tanks 0.1 m beneath the surface was between 1 and 10 µmol m<sup>-2</sup> s<sup>-1</sup>. Before each feeding session, the fish were gently transferred from their daytime refuges to the 1000 liter tanks—each group of eight fish from one refuge added to one tank. Next, a submersible infrared video camera was placed into either every second tank in each single-tank feeding session (2009) or into each of the two most widely separated tanks in each multitank feeding session (2007–2009), one with the

high initial density and another with the low initial density of *Daphnia* prey. In each feeding session analyzed in this study, foraging by the roach was terminated after 12 h (2–3 h after sunrise) by transferring them back to their daytime refuges. Following the removal of fish from the multitank systems, the number of roach was adjusted to eight per daytime refuge tank by random manual transfer.

*Daphnia* samples were collected from each tank just before and after each feeding session. The water in each tank was mixed with a perforated Secchi disk and a sample taken immediately using a quantitative plankton net (six vertical hauls to sample *Daphnia* from 30 liters) and preserved in formalin–sugar solution. The *Daphnia* were enumerated, measured under a dissecting microscope, and assigned to three categories: juveniles, adults without eggs, or adults with eggs. In an attempt to amplify the data bank for selectivity-index computation, the samples from the low-density tanks in the eight-tank system (seven tanks) and the four-tank system (three tanks) were pooled into one sample comprising those from both the eight- and four-tank systems. Juveniles included all individuals of body size below, and adults, all those above, the size of the smallest gravid female for each of the three species (Fig. 1). The rate of *Daphnia* recovery was assessed as the expected percentage population density increase due to the recruitment of juveniles in the course of the 12 h feeding session in relation to the initial population density (*Daphnia* per liter). The recruitment was calculated as the number of eggs per liter (the sum of the eggs in brood cavities of all ovigerous females per liter in the sample taken before the start of the feeding session), divided by the temperature-dependent egg developmental time taken from Bottrell et al. (1976).

In an effort to compare the strength of roach selectivity for more rewarding adults when feeding on *Daphnia* of different body sizes, the mean selectivity index was derived from all feeding sessions with *D. cucullata* (13) and *D. magna* (12), and from 13 feeding sessions for *D. hyalina* (with data from the low-density tanks and the high-density tank) randomly selected from the 24 sessions available for this species from the same period of August to October 2007. The number of *D. hyalina* sessions was restricted in order to examine equal numbers of sessions for each of the three species in each heterogeneity-level category for the interspecies comparisons. Mean body length values were obtained from measurements of 338, 712, and 659 *Daphnia* used in the first three sequential feeding sessions performed with *D. cucullata*, *D. magna*, and *D. hyalina*, respectively.

Selectivity was assessed using Ivlev's (1961) selectivity index modified by Jacobs (1974) according to the equation  $D_i = (r - p)/(r + p - 2rp)$ , where  $r$  stands for the proportion of a given category ( $i$ ) among consumed *Daphnia* (estimated from the difference between samples taken before and after each feeding session) and  $p$  is the proportion of each category in samples taken from the tank before each feeding session. The Jacobs' index was used in the subsequent feeding sessions, since it is less sensitive than that of Ivlev to the relative proportion of the prey categories in the medium (Lampert and Sommer 2007). The selectivity was estimated either from the single samples taken before and after the feeding session in the one-tank

Table 1. Summary of the results of the 93 overnight feeding sessions of roach on *Daphnia hyalina* in three spatially different experimental systems (single tanks, or four or eight interconnected tanks) and at three different prey heterogeneity levels (< 3, 3–15, and > 15 *Daphnia* L<sup>-1</sup> in multitank systems), the data collected in 2009, 2008–2009, and 2007, respectively. The range of heterogeneity in *Daphnia* distribution is shown as the difference in *Daphnia* density between the high- and the low-density tanks. Other data presented are the water temperature, the number of sessions used in assessments of the effects of spatial scale and heterogeneity on selectivity by fish, the fish selectivity index (Jacobs 1974) for adults without eggs and those with eggs in their brood cavities when feeding at low and at high density of *Daphnia* prey, the recovery of the *Daphnia* population (as expected percentage of population density increase due to the recruitment of juveniles in the course of the 12 h feeding session in relation to the initial population density), and the speed of fish foraging in the high- and low-*Daphnia*-density tanks.

Parameters	One tank		Four tanks			Eight tanks		
	Jul 2009		Jul 2008–Jul 2009			Aug 2007–Sep 2007		
	<3 ind. L <sup>-1</sup>	19.3±1.67	<3 ind. L <sup>-1</sup>	3–15 ind. L <sup>-1</sup>	>15 ind. L <sup>-1</sup>	<3 ind. L <sup>-1</sup>	3–15 ind. L <sup>-1</sup>	>15 ind. L <sup>-1</sup>
Temp. mean ±1 standard deviation (°C)	19.2±0.56	19.3±1.67	19.9±1.19	19.8±1.31	16.9±4.29	18.1±2.97	15.4±3.13	
No. of feeding sessions in assessments								
Spatial scale effect	32	13	0	0	5	0	0	0
Heterogeneity effect	0	13	8	16	5	13	6	6
Mean selectivity index for adults								
Without eggs								
Low prey density	0.02*	0.14	0.37	0.29	0.25	0.29	0.37	
High prey density	0.05*	0.08	0.23	0.03	0.11	0.07	-0.11	
With eggs								
Low prey density	-0.01*	0.14	0.46	0.26	0.29	0.24	0.53	
High prey density	0.10*	0.17	0.07	0.08	0.16	0.00	-0.06	
Mean <i>Daphnia</i> recovery (% population density per 12 h)	6.4	6.9	5.0	9.9	6.0	9.4	4.6	
Mean speed of fish (cm s <sup>-1</sup> )								
Low prey density	18.9*	22.2	28.3	22.4	28.9	27.2	26.5	
High prey density	16.5*	29.6	12.9	15.0	23.0	26.8	10.4	

\* Exceptionally, < 3 ind. L<sup>-1</sup> at low-density tank and > 3 ind. L<sup>-1</sup> at high-density tank.

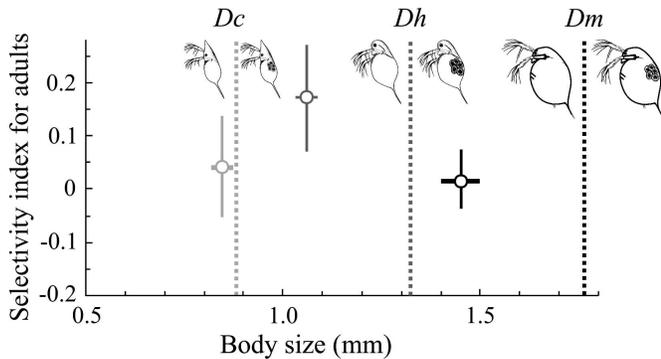


Fig. 1. Roach selectivity (Jacobs' index) for adult *Daphnia* with eggs (means shown by circles, with lines indicating standard error), of three species of different body size: *D. cucullata* (*Dc*, light gray), *D. hyalina* (*Dh*, dark gray), and *D. magna* (*Dm*, black). Dotted lines show species-specific size at first reproduction, assumed to be equal to the body size of the smallest female with eggs in the brood chamber in samples taken directly before the start of a feeding session.

system or separately for the tank with the highest *Daphnia* density and for the three or seven remaining tanks in the four- and eight-tank systems, respectively (pooled data on *Daphnia* densities from samples taken from each of the remaining tanks). Three assumptions were necessary in order to calculate the selectivity index: (1) predation was the exclusive cause of state-dependent mortality in each *Daphnia* age category, (2) the number of juveniles recruited to the population was equal to the number of juveniles attaining maturity in a given low- or high-density tank, and (3) the change in *Daphnia* abundance was due to mortality and not movement between the tanks.

The speed of fish movement was estimated in 16 (out of 37) single-tank feeding sessions (8+ measurements during the first 60 min of the feeding session), 18 (out of 38) in the four-tank, and 13 (out of 24) in the eight-tank feeding sessions (eight to ten measurements in the tank with the lowest and with the highest prey density in each multitank system) from video recordings stored on digital video disk. This was achieved by examining two freeze frames of a moving fish and measuring the distance traveled against a centimeter scale on the tank's bottom, then dividing this by the time elapsed between the two images.

## Results

The data accumulated from all fish feeding sessions with *D. cucullata* and *D. magna* as the prey, as well as from the 13 sessions with *D. hyalina* (performed in the same period; details in Web Appendix, Table A1), revealed greater selectivity (Jacobs' selectivity index) for adults without or with eggs ( $F_{1,50-52} \geq 6.61$ ,  $p \leq 0.0133$ , one-way ANOVA with Bonferroni's adjustment for three comparisons) in *D. hyalina* than in either *D. cucullata* and *D. magna*, but no such difference was found in either *D. cucullata* or *D. magna* (Fig. 1). This indicated that the middle-sized *D. hyalina* was the most convenient experimental prey, with fish showing the greatest selectivity difference between juveniles and adults of this species.

Although no controls were run to examine *Daphnia* density changes in the absence of fish, an earlier study based on the first data set obtained with the four- and eight-tank systems (fig. 2 in Gliwicz et al. 2013) showed that the effect of selective feeding on *Daphnia* ovigerous females was strongest at the beginning of each feeding session. Therefore, the 12 h recovery of the *Daphnia* population was likely to be lower than that calculated from the initial number of eggs in *Daphnia* brood cavities (Table 1) and well below 10% of the population density, hence well within the sampling error range (10–15%) for the density estimates.

Comparison of slopes of regressions for the relationship between selectivity and log-transformed prey density in each of the three spatial scales (i.e., one-, four-, and eight-tank feeding sessions; Fig. 2A,B) revealed a significant difference only between eight-tank and single-tank sessions for adult *D. hyalina* with eggs (analysis of covariance [ANCOVA], Table 2). Moreover, the elevations (intercepts) of the regression lines were different for the comparison between eight-tank and single-tank sessions for adults without eggs, as well as between four-tank and single-tank sessions, but only for adults with eggs (Table 2). The lack of a difference between four- and eight-tank sessions in both the slopes and the elevations indicated that data from these trials could be combined to examine the effects of heterogeneity of prey distribution on fish selectivity.

Regression analysis of the data combined from all four- and eight-tank feeding sessions (those from the high- and low-density tanks) for the selectivity at different log-transformed densities of *Daphnia* prey for the data plotted from all three heterogeneity levels showed greater selectivity at lower prey density for both the adults without and those with eggs ( $F_{1,122} = 13.4$ ,  $p < 0.0004$  and  $F_{1,122} = 20.6$ ,  $p < 0.0001$ , respectively; Fig. 2C,D). The same regression analysis for each heterogeneity level showed greater selectivity at lower prey density, but only for medium and high heterogeneity levels for both adults without and those with eggs ( $F_{1,42} > 7.6$ ,  $p < 0.0089$  and  $F_{1,42} > 11.9$ ,  $p < 0.0013$ , respectively). Such a difference in selectivity according to the prey density level could not be detected in the data from single-tank sessions ( $n = 32$ , not shown in Fig. 2C,D).

Comparison of regressions for selectivity on log-transformed prey density for the three different prey heterogeneity ranges (small,  $< 3$ ; medium, 3–15; and large,  $> 15$  ind.  $L^{-1}$ ) revealed a significant difference between the sessions with small and large heterogeneity and between those with small and medium heterogeneity for both adults without and those with eggs, when the identity of their slopes was tested. However, there was no significant difference between sessions with medium and large heterogeneity, in either their slopes or elevations (Table 2; Fig. 2C,D).

The mean fish speed for the first 60 min of each feeding session was found to be much lower in the one-tank system ( $17.0 \pm 4.9$  cm  $s^{-1}$ ,  $n = 16$ ) than in the four- or eight-tank systems, where it was  $27.7 \pm 8.9$  ( $n = 8$ ; four for each high- and low-density tank) and  $26.9 \pm 8.1$  cm  $s^{-1}$  ( $n = 6$ ; three for the high-density tank and the other tanks), respectively. This was a possible effect of eliminating heterogeneity by restricting estimates to the sessions where the between-tank difference in density did not exceed three *Daphnia* per liter.

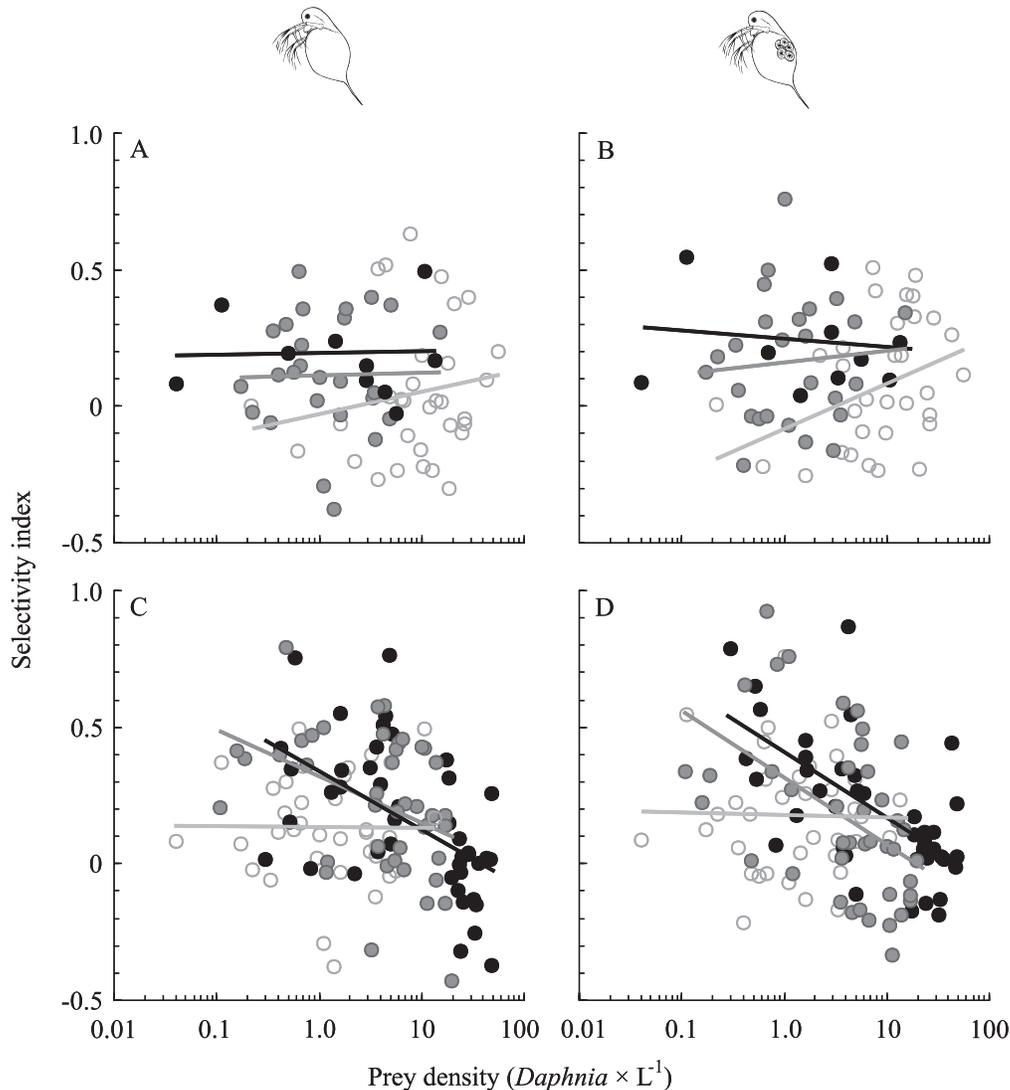


Fig. 2. Fish selectivity (Jacobs' index) for adult *D. hyalina*, (A, C) without and (B, D) with eggs in feeding sessions starting at different initial prey densities, performed (A, B) at three spatial scales (single tank, or four or eight interconnected tanks: light gray, dark gray, and black circles and regression lines, respectively), or (C, D) at different prey heterogeneity levels in the four- or eight-tank systems (shown as the difference in prey density between the tanks with the highest and lowest *Daphnia* densities: < 3, 3–15, and > 15 ind.  $L^{-1}$ ; light gray, dark gray, and black triangles and regression lines, respectively). The effect of spatial scale was examined in 32 one-tank overnight feeding sessions performed in 2009 and in 5 and 13 sessions with eight and four interconnected tanks performed in 2007 and 2008–2009, respectively. The selectivity was estimated for one prey density in each of the single-tank sessions, and for two densities in each of the four- or eight-tank sessions: that from the tank with the highest *Daphnia* density and that from the three or seven remaining tanks (with samples pooled to produce a single value), with the difference between the tank with the highest density and the other tanks never exceeding three *Daphnia* per liter. The same procedure was used to examine the effect of heterogeneity level in 61 feeding sessions performed in the four-tank (37 sessions) and the eight-tank (24 sessions) systems in 2007–2009, to produce selectivity data from 122 points ( $n = 61 \times 2$ ).

In spite of the wide variability of the data, the fish speed was found to decline with an increase in log-transformed density of *Daphnia* prey, when the data for both high- and low-density tanks were plotted for all 31 multitank sessions (out of 61) in which speed was assessed (ANCOVA,  $p < 0.0001$ ,  $F_{1,62} = 24.8$ ).

Regression analysis of the fish speed on log-transformed prey density revealed a negative correlation in each of the one-, four-, and eight-tank sessions (16, 4, and 3, respectively, each from the high-density tank and the mean of the remaining three or seven tanks in each of the

multitank sessions,  $n = 16, 8, \text{ and } 6$ , respectively;  $F_{1,6} = 8.49$ ,  $p = 0.0435$ ; Fig. 3A). However, no significant differences were found in any comparison of one-, four-, and eight-tank sessions when the identity of their slopes was tested (Fig. 3A; the difference in density between the tank with the lowest and that with the highest prey density not exceeding 3 ind.  $L^{-1}$  in each of the second- and third-series sessions). Comparison of the regressions revealed significant differences between the one- and four-, as well as the one- and eight-tank sessions, when the identity of their elevations was tested ( $F > 7.25$ ,  $p < 0.0136$ ; Fig. 3A).

Table 2. Influence of the spatial scale of the experimental system and the heterogeneity of prey distribution on selectivity-on-prey-density regressions for roach tested (in each of the two combinations) by ANCOVA ( $F$ ,  $p$ , degrees of freedom [df]). The number of tanks in the experimental system was one tank (2009), or four or eight interconnected tanks (2008–2009 and 2007, respectively). The heterogeneity of prey distribution in the four- and eight-tank sessions is expressed as the difference in prey density between the tank with the highest and the tank with the lowest density of *Daphnia* prey in the system ( $N^{\text{Highest}} - N^{\text{Lowest}}$ ). Regressions are evaluated for *Daphnia* adults without eggs and adults with eggs, with no difference in slopes or elevations (intercepts) detected in juveniles. Statistical significance (in bold) accepted after Bonferroni’s adjustment for three comparisons at  $p < 0.0167^*$ ,  $p < 0.0017^{**}$ . ns indicates nonsignificance.

Parameters compared	Combinations	Adults without eggs						Adults with eggs					
		Slopes			Elevations			Slopes			Elevations		
		$F$	$p$	df	$F$	$p$	df	$F$	$p$	df	$F$	$p$	df
Scale (number of tanks)	1 and 4	0.38	ns	1.55	2.07	ns	1.56	0.66	ns	1.55	<b>7.03</b>	*	<b>1.56</b>
	1 and 8	0.31	ns	1.38	<b>6.94</b>	*	<b>1.39</b>	<b>5.53</b>	*	<b>1.38</b>	7.89	*	1.39
	4 and 8	0.01	ns	1.29	0.97	ns	1.30	0.20	ns	1.29	0.68	ns	1.30
Heterogeneity (ind. L <sup>-1</sup> )	<3 and 3–15	<b>6.78</b>	*	<b>1.74</b>	6.14	*	1.75	<b>6.98</b>	*	<b>1.74</b>	1.02	ns	1.75
	<3 and >15	<b>7.71</b>	*	<b>1.76</b>	5.68	*	1.77	<b>10.96</b>	**	<b>1.76</b>	6.47	*	1.77
	3–15 and >15	0.31	ns	1.82	0.05	ns	1.83	0.31	ns	1.82	0.05	ns	1.83

Regression analysis of the selectivity of adult *D. hyalina* (those without and with eggs) at different log-transformed fish speeds in the tank with the lowest and the tank with the highest prey density in each of the 31 feeding sessions performed in the four- or eight-interconnected tank systems revealed a positive correlation between speed and selectivity of fish ( $F_{1,62} = 8.95$ ,  $p = 0.0040$ ; Fig. 3B). However, ANCOVA testing for differences in the selectivity on fish speed regressions between each of three combinations of the three ranges of heterogeneity in prey distribution did not show any significant difference in their slopes or elevations for adults without or with eggs.

### Discussion

The results of this study support each of the three predictions on size selectivity of planktivorous fish at different zooplankton prey densities. First, they reveal that the selectivity of a foraging fish, confined to a small volume of water with homogenous prey distribution, increases with the density of the prey population due to selection of the most conspicuous and most valuable prey class where prey is more abundant. This finding is exactly as predicted by classical theory on optimal foraging and as anticipated from the results of numerous earlier experiments in which fish confined to a small water volume were allowed to feed on zooplankton prey that was mixed well to reduce the scatter of data. Second, the results show that the tendency of the selectivity of a foraging fish for larger prey to increase with the density of the prey disappears in larger volume experimental systems when the stronger selectivity for large-bodied prey at high prey density is offset by the stronger selectivity for large-bodied prey at low prey density. This occurs when the greater space allows foraging fish to swim faster until their swimming speed becomes sufficiently high to make stopping for smaller prey maladaptive due to the high costs of postcapture accelerations. Thus, the effects of the two mechanisms of prey-size selection make the selectivity for large-bodied prey equally strong in habitats with high and low prey population

densities. Third, the results of this study also reveal that the tendency of the selectivity of a foraging fish for larger prey to increase with the density of the prey population becomes reversed when a homogenous prey distribution in a spatially small system is replaced by a heterogeneous prey distribution in a spatially large system. In this case, the mechanism of prey-size selectivity based on optimal choice of prey size becomes overcome by another mechanism based on the decision of whether or not to stop for prey of different value. Smaller prey may represent a gain that is less than the investment required to support the postcapture acceleration needed to regain a higher speed that, in habitats of large spatial scale with a patchy prey distribution, is necessary to continue seeking sites with more abundant prey.

Each of the three predictions was confirmed by the analysis of data from experiments with young European roach, a typical size-selective predator–harvester, and a medium-sized cladoceran, *Daphnia hyalina*, that has been used as a prey in many earlier studies with roach (Gliwicz and Wrzosek 2008; Maszczyk and Bartosiewicz 2012), including experiments on prey-size selectivity (Gliwicz et al. 2010, 2012, 2013). The choice of this prey species was based on the findings of preliminary experiments that demonstrated strong positive size selectivity in young roach for egg-carrying females of *D. hyalina*, as compared with weak selectivity for smaller adults of *D. cucullata* (possibly too small a difference in net gain between juveniles and adults) and negligible selectivity for large-bodied adults of *D. magna*, which could stem from the gape limitation of young roach. While the relative difference in visibility between juveniles and adults seems to be similar for each of the three *Daphnia* species, the stronger selectivity for adults of *D. hyalina* (Fig. 1) implies that the active selection of energetically more rewarding prey individuals should be most profitable when a predator is feeding on medium-sized prey. This hypothesis has yet to be supported by any data, but it seems expedient to match the body size of experimental prey to the size of the predator and its judgment that the net reward from consuming juveniles and adults is significantly different.

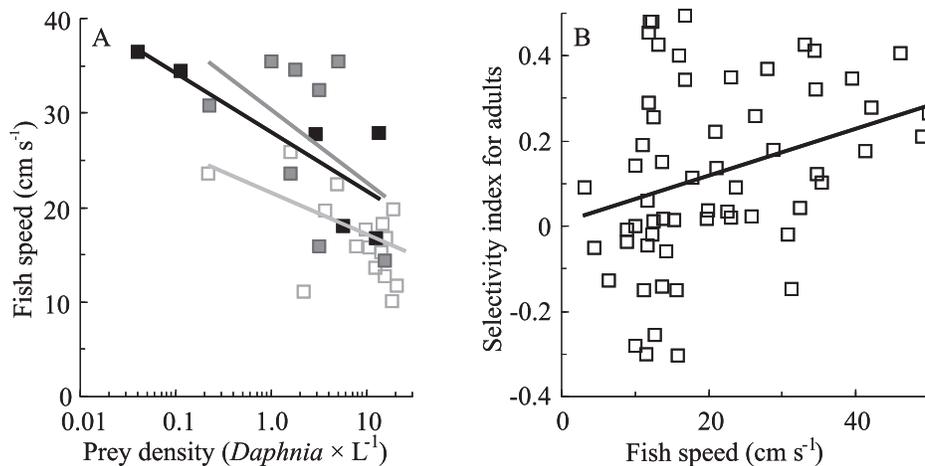


Fig. 3. Relationships between prey density or fish selectivity and fish speed obtained from video recordings. (A) Speed of fish movement on prey density regressions for feeding sessions in one-, four-, and eight-tank systems (light gray, dark gray, and black squares and regression lines;  $n = 16, 8,$  and  $6,$  respectively) performed in 2009, 2008–2009, and 2007, respectively, with the difference between densities in the high-density tank and the mean from the remaining tanks in multitank sessions never exceeding three *Daphnia* per liter. (B) Fish selectivity (Jacobs' index) for *D. hyalina* adults (those without and with eggs) on fish speed ( $\text{cm s}^{-1}$ ) regressions for data collected during the first 60 min of each feeding session from the tanks with the highest and lowest prey densities; sessions performed in eight- and four-tank systems in 2007 and 2008–2009, respectively (31 out of 61 sessions), shown as the means (squares for  $n = 62$ ) with a regression line.

Although the data collected during the single-tank feeding sessions support the notion of stronger selectivity at high than low prey density, this phenomenon was not observed when fish were allowed to move freely between interconnected tanks (four or eight) containing homogeneously distributed prey. The difference in selectivity between the single- and multitank experimental systems declined with prey density level. This was the result of increased selectivity at low rather than reduced selectivity at high prey density and was associated with fish swimming speed being higher in the more spacious and complex systems of interconnected tanks than in the single-tank system. A higher speed of foraging in a larger enclosure has also been observed in other planktivorous fishes, e.g., the brook trout *Salvelinus fontinalis* (Tang and Boisclair 1993). This higher speed could be the reason for greater prey selectivity due to either reduced visual acuity (Gendron and Staddon 1983) or the increased energetic costs of decelerations and postcapture accelerations, or both, each being more significant at increased velocity (Kramer and McLaughlin 2001; Gliwicz et al. 2013). The former could stem from the relatively lower visibility of juveniles, while the latter might call for a decision based on the relative profitability of capturing a juvenile vs. an adult. The speed of foraging roach in the single-tank experiments was comparable with that measured in small experimental systems in earlier studies, such as that carried out in 100 liter mesocosms by Linlokken et al. (2010). Moreover, in the interconnected tanks, the speeds were much greater than those recorded previously. This corroborates our hypothesis that the apparent density-dependent selectivity observed in earlier studies was due to the effects of confinement, which were stronger in smaller than in larger volume experimental

systems. The apparent increase in the swimming speed of the fish as the spatial scale of the experimental system expanded was probably due to the accessibility of more space in which to forage. The fish, released from the confinement of a small and simple experimental system, increased their cruising speed in the quest for more proficient feeding sites, an observation which could be considered a typical “wall effect”: one of the six categories of scale-dependent behavioral constraints listed by Englund and Cooper (2003).

With the increase in spatial scale (from a single tank to the systems of four and eight interconnected tanks) and with greater heterogeneity in prey distribution, the selectivity for adult *Daphnia*, particularly those with eggs, was apparently greater in sites with a low rather than a high density of prey. Therefore, it could be argued that the heterogeneity of prey distribution does affect selectivity, but only in a site where the prey density is low and when the prospects of finding patches at other sites are good (as can be observed in Fig. 2C,D). Such a scenario may result from the higher speed of a foraging fish in sites with a low density of prey. This would not only compensate for the low encounter rate resulting from the low prey density, but it would also make locating a patch quicker.

The increased speed of foraging fish when the prey density is low is consistent with the notion that fish adjust their feeding behavior, particularly their swimming speed, to the availability of prey (Munk and Kiørboe 1985; Munk 1995; Ruzicka and Gallagher 2006). This might be expected to be common in predator–harvesters, such as planktivorous fish, that move fast and have to pay a high cost for the capture of each prey item that is not much lower than the gain. However, the results of the present study are clearly contradictory to those of previous theoretical and experi-

mental studies in terms of the direction of density-dependent selectivity. Werner and Hall (1974) ignored the importance of wall effects in limiting the freedom of a foraging fish to swim faster when prey is less abundant, particularly when its distribution is heterogeneous. Therefore, this contradiction might stem from the presence or absence of this effect in experimental systems of different spatial scale. Furthermore, it may be speculated that the evident acceleration in sites with a low prey density, when the zooplankton prey distribution is heterogeneous, may result from the memorized presence of a patch at another site. Such learning may possibly be of greater importance for the direction of change in prey-density-dependent selectivity than the lower probability of encountering a more conspicuous and rewarding prey.

The results of the present study are in accordance with the claim that the majority of planktivorous fishes exhibit a saltatory foraging strategy (i.e., intermittent locomotion, Kramer and McLaughlin 2001), with acceleration when relocating without foraging. In this case “swimming bursts” are interrupted by short pauses when the fish is scanning for prey or its own predator (O’Brien et al. 1990; Bartoń and Hovestadt 2013). This behavior has been observed in both juveniles and adults (Kleerekoper et al. 1970; MacKenzie and Kiørboe 1995). In spite of the high costs of a precapture deceleration and postcapture acceleration, saltatory foraging seems to be the most efficient strategy in terms of energetic advantage (Videler and Weihs 1982; Kramer and McLaughlin 2001). A foraging fish should expend less energy when alternating between rest and movement than when moving continuously at an intermediate speed (Anderson et al. 1997). Whereas deceleration at high prey densities improves visual acuity (Gendron and Staddon 1983) and increases the chance of remaining longer in a site of high prey density (Hunter and Thomas 1974), acceleration at low prey densities allows patches to be located more rapidly (Gliwicz et al. 2013).

In conclusion, the greater selectivity of a foraging fish in the presence of a high density of prey observed in earlier studies (Werner and Hall 1974; Croy and Hughes 1991) could be at least partially attributed to the effects of its confinement and the homogeneity of its prey. In such experimental systems, the walls do not allow a foraging fish to swim with appropriate speed through the artificial habitat, and the fish has no motivation to search for an alternate site with more abundant prey. The results of the present study suggest that the gradual change from the typical laboratory world of homogeneity and confinement to the open and diverse reality of a lake or an ocean is accompanied by an increase in the complexity of fish foraging behavior, with different patterns of optimal foraging applied in locations with abundant and scarce zooplankton prey.

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