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Detecting food search in *Daphnia* in the field

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Abstract

From laboratory experiments, it has been suggested that visually guided feeding, chemical and mechanical perception of increased ingestion rate (including perception of hunger and satiation), and odors associated with algae help *Daphnia* in tracking food gradients. To test the ability of *Daphnia* to find food in the field, suspended yeast, suspended clay, or control water was pumped into a localized point in the littoral zone of Lake Myravann (Bergen, Norway). *Daphnia longispina* and *Daphnia pulex,* the most numerous zooplankton species in the experimental area, aggregated in areas of yeast input but not when adding suspended clay or control water. Thus, *Daphnia* is able to evaluate the patches both quantitatively and qualitatively, possibly through perception of increased ingestion rate and odor, while light scattering is indicated to be unimportant. This is the first experiment to demonstrate that *Daphnia* is able to find patches of food under natural conditions.

In the laboratory, zooplankton express a capacity to track gradients in food availability (e.g., Jakobsen and Johnsen 1987; Cuddington and McCauley 1994; Neary et al. 1994; Larsson and Kleiven 1996; Larsson 1997; Jensen and Larsson in press). Despite the numerous, nonexperimental studies testing for an association between zooplankton and algae in the field (reviewed in Pinel-Alloul 1995), a clear-cut analog to the laboratory results has never been demonstrated (Folt and Burns 1999). The discrepancy between laboratory and field results may partly come from the methods used in many field studies; a common methodological inaccuracy is the measure of food availability for herbivorous zooplankton as amount of chlorophyll *a* (Chl *a*) or carbon per volume unit. Since both are highly influenced by the abundance of nonpreferred, inedible, or even toxic algae and bacteria, these units are imprecise measures of food availability. Factors such as water currents, predation, and competition may also make it difficult for zooplankton to precisely track gradients of food. Thus, the combined effects of inaccurate measures of food availability and factors confusing foraging zooplankton may explain the discrepancy between field and laboratory results.

In general, a spatial association between zooplankton and Chl *a* or carbon becomes more evident on larger scales (Pinel-Alloul 1995). Since wind is known to greatly influence algal distribution (e.g., Small 1963; George and Edwards 1976; George and Heaney 1978; Webster and Hutchinson 1994), such large-scale associations could be expected from the accumulation of algae caused by wind-driven currents. A problem with citing these large-scale associations as evidence for selective aggregation, however, is that zooplankton may also have been driven by these currents to the same site by passive drift. Further, since stability must be expected to be relatively high on larger scales, an association between zooplankton and their food may come from a high reproduction in areas of high food and not due to food-searching behavior. Thus, to demonstrate the behavioral responses of zooplankton to food concentrations in the field, it is necessary to measure behavior on a relatively small scale and within a short time period. It is also necessary to have measures of food availability in relation to food preference of different zooplankton species. By contrast, small-scale measurements in which the environment shifts rapidly may not reveal any association, due to the above-mentioned factors. Therefore, the best way to demonstrate food search in the field is to manipulate food experimentally on a relatively small scale. Finally, it is crucial to perform control tests in which the zooplankton are offered nonfood particles. We did this in a small, wind-protected lake in Norway by creating local increases in the abundance of yeast or suspended clay and monitoring the response of daphniids to these local perturbations in particle abundance.

From laboratory experiments, it has been suggested that (1) visually guided feeding (Young and Getty 1987), (2) chemical and mechanical perception of increased ingestion rate (including perception of hunger and satiation) (Young and Getty 1987; Cuddington and McCauley 1994; Larsson and Kleiven 1996), and (3) odors associated with algae (van Gool and Ringelberg 1996; Laurén-Määttä et al. 1997) help *Daphnia* in tracking food gradients. If daphniids respond to both edible and inedible particles by aggregating in particle-rich areas, this indicates that they use only factors (1) and (2) to quantitatively find particles, while odor is unimportant. By contrast, if there is no response to clay particles but a positive response to yeast, they are able to evaluate the patches both quantitatively and qualitatively, possibly through perception of increased ingestion rate and odor, while light scattering is indicated to be unimportant.

Methods

Suspended food or nonfood particles were introduced into the littoral zone of Lake Myravann to determine if herbivorous zooplankton are able to locate patches of food particles

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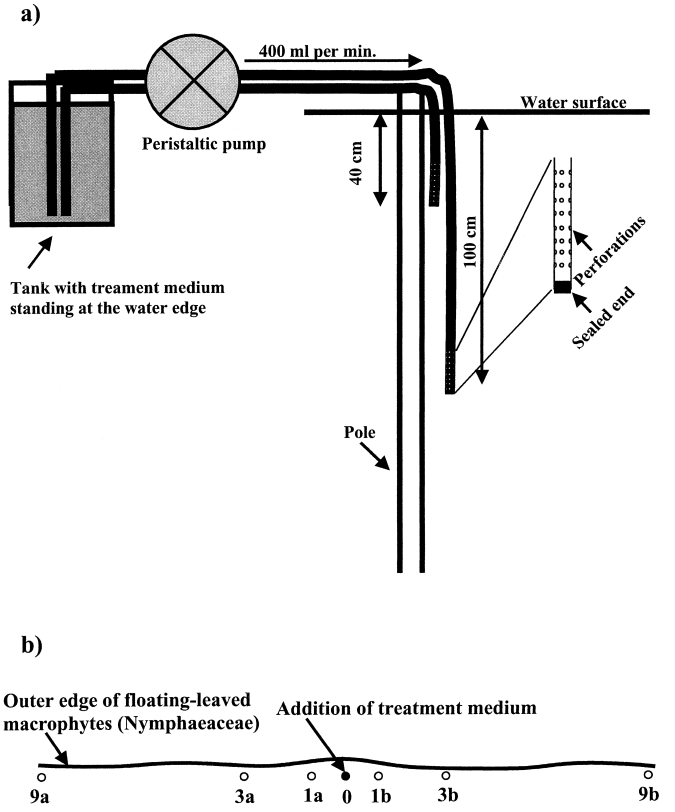

Fig. 1. Schematic view of the experimental design. Panel (a) shows how the input media was pumped into the lake through two tubes ending at different depth. The tubes were attached to a wooden pole to ensure a stable location of the input point. The tank standing at the water edge contained 25 liters. Therefore, medium had to be refilled approximately every hour. Panel (b) shows the horizontal distribution of sampling stations alongshore where the numbers represent meters from the input point.

and to distinguish these from the inedible ones. Lake Myravann (60°20′N, 5°20′E) is a small (area = 61,500 m^2, volume = 465,000 m^3), relatively wind-protected, mesotrophic lake, with pike (*Esox lucius*) and eel (*Anguilla anguilla*) as the only fish species (Giske 1986). The experiment was carried out 9 July 1999–17 July 1999. The Secchi depth at this time was 3.64 m, and *Daphnia longispina* and *Daphnia pulex* were the most numerous species of zooplankton. The experiment was designed to measure patterns of plankton distribution at distances of 0, 1, 3, and 9 m from an input point (Fig. 1).

Dry yeast (''Idun tørrgjær'') and blue clay (A/S Hana and Holmens Potterier, ''blåleir'') were used as food and nonfood particles, respectively. Clay was chosen because these particles are close to the size of yeast and are within a size range that is readily ingested by *Daphnia* (Burns 1968; Gliwicz 1980). The particles were suspended in filtered lake water taken from the same location as the experiment on the day of each replicate. This was done to ensure that the water quality was as similar as possible to that of the lake before adding the suspensions. The filtering of lake water was performed through a 60-μm plankton net so that zooplankton larger than rotifers were removed, and algae could pass the filter without reducing its natural concentration. Trials were performed on nine different days at the same time each day (1000–1400 h): Three days were assigned to each treatment; with addition of suspended yeast; with suspended clay; and with control water (filtered lake water only). The treatments were performed, starting with control (lake water), followed by suspended yeast and suspended clay, and then again control, etc., for 9 d. Treatment medium was added by a peristaltic pump standing on the shore, connected to two tubes leading into the water at the same point but ending at different depths, 40 and 100 cm beneath the surface. This point was located at the outer edge of floating-leaved macrophytes, ≈10 m from land (Fig. 1). To ensure a better mix between input medium and water at the input point, the last 20 cm of the tubes was perforated with small holes in all directions, while the end was sealed (Fig. 1a). Water and particles were pumped during the entire duration of each experiment lasting for 4 h. We added yeast suspension at 400 ml min^{-1} with 0.2 g C L^{-1}, based on results from an earlier experiment (Jensen and Larsson in press). The particle concentration in this suspension was ≈400 times higher than the average natural concentration of particles measured in the lake at the time of the experiment. The concentration of clay was determined by measuring the absorption of the yeast suspension at 750 nm in a photo spectrometer (Shimadzu UV-160) and then adding the amount necessary to give the same absorption at 750 nm. This concentration was determined to ≈0.2 g clay per liter.

Zooplankton samples were taken by boat by lowering a 4-liter water sampler (length = 0.84 cm; 7.9 cm in diameter) to a depth between the two input points. In each trial, seven points were sampled at 0, 1, 3, and 9 m from the input point and parallel to the shore (Fig. 1b). We chose these distances because they fall into two categories: central (0–1 m) and peripheral (3–9 m) stations, respectively. We expected the response to food input to be observed in the immediate neighborhood of the input point and to be negligible beyond 1 m (Jensen and Larsson in press). Water depth in the input area was ≈2 m. For each station and trial, five samples were taken at hourly intervals and repeated for 4 h, starting with a control sample just before the onset of the trial. Sampled zooplankton were identified to species, and the number of each was counted. Whenever the total number of zooplankton was >400, the sample was subsampled before counting.

Water was collected from the zooplankton samples to determine the particle concentration at the different sampling sites. These samples were analyzed by using a Casy particle counter (Schärfe System GmbH). This counter also made it possible to get the typical size distribution of small particles (1.4–15 μm) and the change in distributions as an effect of particle input. Measure of particle size by the Casy counter requires that the insulating cell membrane be present in living cells (Schärfe System GmbH 1995). Therefore, to get the real size of particles in the clay suspension, particles from pure suspension were also measured visually by light microscope. We also sampled phytoplankton on 14 July to identify the natural composition of larger algae in the experimental area. This sample was performed by hauling a Ruttner net (20-μm mesh size and 20-cm opening) from a boat for 8 min at a depth of 0.1–2 m.

In each trial, the size distribution of *Daphnia* from the third hour of particle input was measured (from subsamples of each sample). This was done to look for differences in mean size in relation to density in aggregates and thus, to elucidate possible competitive interactions among *Daphnia.*

To get information on how weather conditions varied during the experimental period, wind speed and light intensity were measured everyday at 1000, 1200, and 1400 h. As the *Daphnia* populations in Lake Myravann are known to exhibit diurnal horizontal migration (Kvam and Kleiven 1995), the total *Daphnia* abundance in the experimental area was tested for an association with light intensity. To minimize treatment effects, only the peripheral stations were included in this analysis.

Statistical analysis—To evaluate the effects of particle input on *Daphnia* aggregation, a centering index (CI) was calculated for each sampling hour. The CI is a measure of mean concentrations at central sampling stations (0–1 m from the input point) divided by mean concentrations at peripheral ones (3–9 m). As explained above, this division of central and peripheral stations is based on results from an earlier experiment (Jensen and Larsson in press) where no effects of food input were found at 3–9 m from input. The measures of CI minimize the influence of day-by-day variation in abundance of zooplankton. Thus, data from all days were pooled in one test to compare regression lines of CI for the different treatments depending on time. Comparisons were performed separately for ''yeast-sized particles'' (2.25–7.5 μm), for *D. longispina* and *D. pulex,* respectively. This was done by using an analysis of covariance model where time was set as covariate. Such a model is often used to evaluate differences in slope or elevation between regression lines (Goldberg and Scheiner 1993). In these models, a significant interaction between time and treatment reveals a difference in slope of treatments depending on time. If there is no difference in slope, the interaction term is removed from the model to analyze for differences in elevation. To determine which of the three treatment groups that are different in slope or elevation, contrast analyses involving the interaction term or treatment factor are performed, respectively.

To get an overview of the magnitude of particle input and *Daphnia* responses, the concentrations of particles and *Daphnia* per liter at each sampling station were averaged for each treatment. When calculating particles, both calculations for measured particles in total (1.4–15 μm) and measured particles within yeast size (2.25–7.5 μm) were performed. The first 2 h of sampling were excluded from these calculations because *Daphnia* takes ≈2 h to respond to input of particles (Jensen and Larsson in press). Thus, any confounding factors of time delay between onset of a treatment and its effects are avoided in the analysis.

Results

There is an increase in particle density of both the yeast and clay treatments, and the elevation of their CI lines is significantly higher than for the control treatment. There is no statistical difference between the CI lines of yeast and clay treatments (Fig. 2; Table 1). To compare the degree of

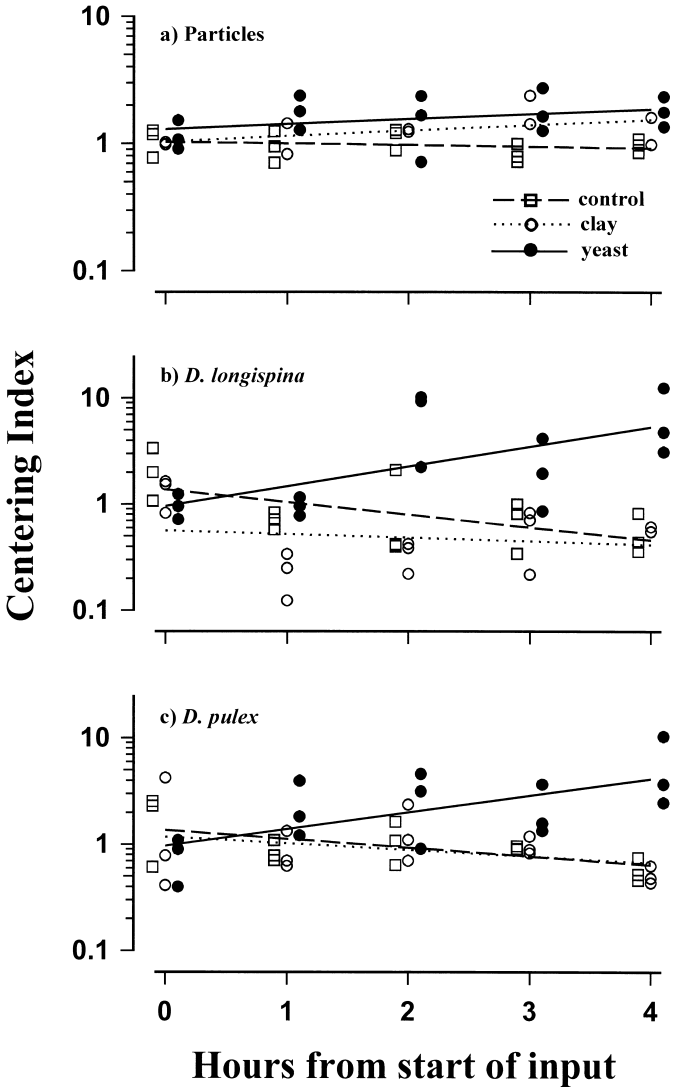

Fig. 2. Regression of CIs for yeast-sized particles (2.25–7.5 μm) and the associated responses in *D. longispina* and *D. pulex,* depending on time from onset of input treatments. The open squares represent controls, while the open and solid circles represent clay and yeast treatments, respectively. The associated lines are dashed, dotted, and solid, respectively. Statistical tests for these data are given in Table 1. The reason why $n = 8$ within clay treatment instead of 12 is that the water samples from the last day of clay input were lost during transport.

Daphnia aggregation to the relative increase in the concentration of particles in the yeast size range, the same analyses were performed for *D. longispina* and *D. pulex* separately. The results show that both *Daphnia* species respond to yeast input by increasing their tendency to aggregate at the input area relative to input of clay or control (Fig. 2; Table 1). The magnitude of particle input is difficult to detect when calculated for measured particles in total (Fig. 3a). However, when only particles within yeast size are included, a clear effect of input is revealed (Fig. 3b). When comparing the degree of *Daphnia* aggregation to the relative increase in the concentration of particles in the yeast size range, the *Daphnia* responses (Fig. 3c,d) are of greater magnitude than the

Table 1. ANCOVA tests for differences in slope or elevation in CI regression lines among treatments depending on time from onset of input. The test for particles did not reveal differences in slope among treatments (Time × Treatment MS = 0.0266, $F = 1.59$, $P = 0.22$). Therefore, the interaction term was removed from the model to test for differences in elevation. As in Fig. 2, the response variable in all tests are log transformed to ensure a linear association between dependent and independent variables.

Test object	Source	df	Mean square	*F* value	*P*
Particles	Model	3	0.1154	6.69	0.0011
	Error	36	0.0173		
	Time	1	0.0370	2.15	0.15
	Treatment (elevation)	2	0.1546	8.96	0.0007
	Contrast analysis				
	Control vs. yeast	1	0.3081	17.86	0.0002
	Control vs. clay	1	0.0767	4.44	0.042
	Clay vs. yeast	1	0.0482	2.79	0.10
D. longispina	Model	5	0.9996	10.31	0.0001
	Error	39	0.0970		
	Time	1	0.0112	0.12	0.74
	Treatment	2	0.1889	1.95	0.16
	Time × treatment (slope)	2	0.7449	7.68	0.0015
	Contrast analysis				
	Control vs. yeast	1	1.4002	14.44	0.0005
	Control vs. clay	1	0.1104	1.14	0.29
	Clay vs. yeast	1	0.7241	7.47	0.0094
D. pulex	Model	5	0.4470	7.13	0.0001
	Error	39	0.0627		
	Time	1	0.0015	0.02	0.88
	Treatment	2	0.0272	0.43	0.65
	Time × treatment (slope)	2	0.5281	8.42	0.0009
	Contrast analysis				
	Control vs. yeast	1	0.8598	13.72	0.0007
	Control vs. clay	1	0.0064	0.10	0.75
	Clay vs. yeast	1	0.7180	11.45	0.0016

effect of yeast input. When the peak in yeast-sized particle concentration at yeast input is divided by the mean values of control, the concentration of yeast-sized particles increased by a factor of 2.40 (Fig. 3b). The equivalent responses in *D. longispina* and *D. pulex* were factors of 13.07 and 4.40, respectively (Fig. 3c,d). All animal species that were present in the samples are shown in Table 2.

The two most numerous species of large, naturally occurring phytoplankton found in the phytoplankton haul were *Sphaerocystis schroeteri* (cell diameter = 6–12 μm, colony

Table 2. Numbers of all species in the samples (excluding Rotatoria). Total is the total number in all samples summarized, mean is the mean among samples, and min and max are minimum and maximum for these, respectively.

Order, family, or species	Total	Mean	Min	Max
D. longispina	295,185	937.1	0	13,968
D. pulex	81,541	258.9	5	4,104
Polyphemus pediculus	7,301	23.2	0	432
Calanoid copepodites and nauplia	3,329	10.6	0	72
Eudiaptomus gracilis	369	1.2	0	18
Cyclopoid copepodites and nauplia	486	1.5	0	48
Eucyclops cerrulatus	1,263	4.0	0	264
Macrocyclops albidus	535	1.7	0	60
Diacyclops bicuspidatus	27	0.1	0	6
Scapholebris mucronata	424	1.3	0	36
Chaoborus flavicans (I–IV instar + pupae)	495	1.6	0	72
Ostracoda	366	1.2	0	72
Chironomidae	133	0.4	0	20
Acellus aquaticus	115	0.4	0	35
Corixidae	61	0.2	0	9
Eylaidae	8	0.0	0	1
Ephemeroptera	1	0.0	0	1

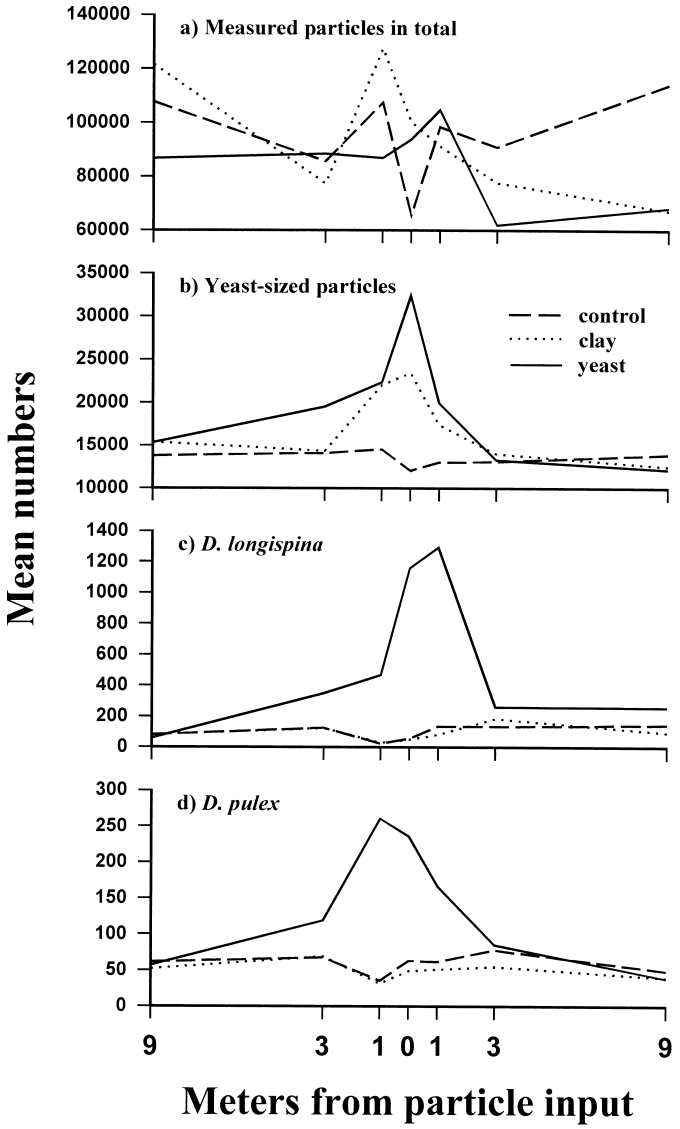

Fig. 3. The magnitude of particle input and *Daphnia* responses. The y-axes represent mean number of particles per milliliter (a and b) or *Daphnia* per liter (c and d). Each data point is the mean value for a sampling station within a treatment. To avoid the time delay between the onset of a treatment and its effect, the first 2 h after onset of a trial are excluded from the calculations. Dashed, dotted, and solid lines represent days of control, clay treatments, and yeast treatments, respectively. Figure (a) shows the distribution of all measured particles (1.425–15 μm), while (b) shows the distribution for yeast-sized particles (2.25–7.5 μm). Figures (c) and (d) show the magnitude of responses in *D. longispina* and *D. pulex*, respectively.

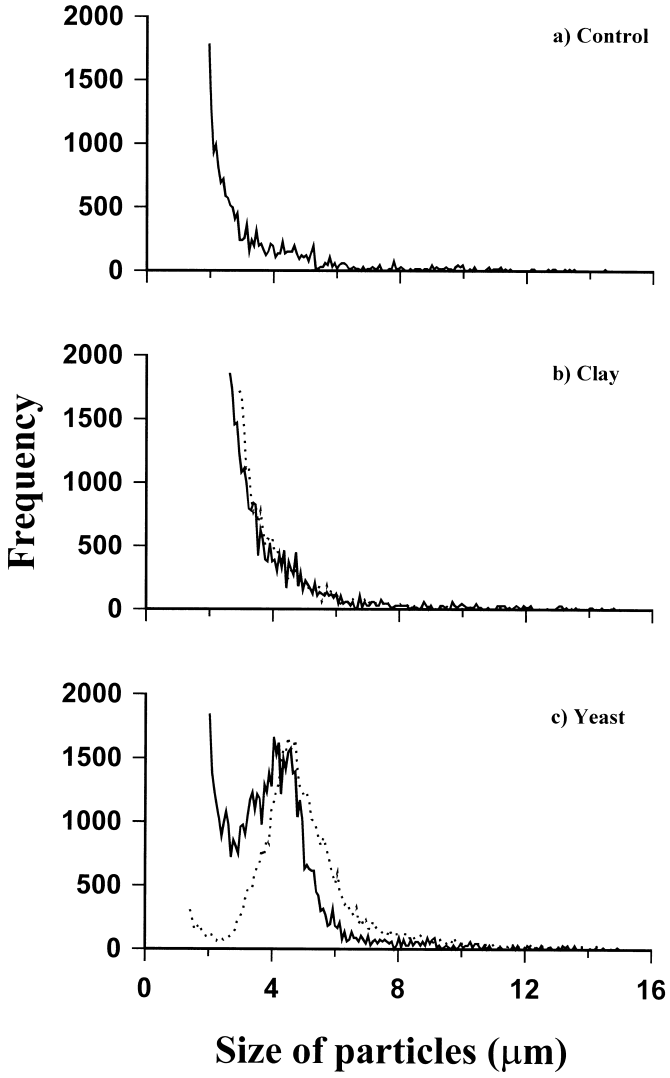

Fig. 4. Typical size distributions of particles taken from samples at the input station at different treatments. Figure (a) shows the size distribution from a single sample taken on a control day, while (b) and (c) are from a day of clay and yeast treatment, respectively. The dotted lines in (b) and (c) represent the size distributions of pure clay and yeast suspensions, respectively.

size = 50–1,500 μm) and *Mallomonas* sp. (cell length = 40–100 μm). Other species present were *Pediastrum duplex* (colony diameter = 20–208 μm) and *Monoraphidium griffithii* (length = 50–72 μm; breadth = 1.5–4 μm). The typical size distribution of measured particles (1.4–15 μm) in the experimental area shows that there is a change in particle size distribution when adding yeast and that this change is in accordance with the distribution of pure yeast suspension (Fig. 4).

Clay input seems to follow the same distribution as the control but with a higher number of particles within each size class. This distribution is in accordance with the one for pure clay suspension (Fig. 4). However, when measuring the size of clay particles visually by light microscope, the mean size was 10.50 μm (SD = 7.10 μm, n = 100). This demonstrates the described requirement of an insulating cell membrane on particles that are to be measured using the Casy counter (Schärfe System GmbH 1995).

Size of *Daphnia* was positively correlated with density in the samples (Fig. 5). The average size of *D. longispina* was 1.45 mm (SD = 0.37, n = 2,945) and 1.18 mm (SD = 0.32, n = 2,922) for *D. pulex*, respectively. These two size distributions are significantly different (t = 29.04, df = 5,865, $P < 0.0001$).

Winds were weak while light intensity varied during the

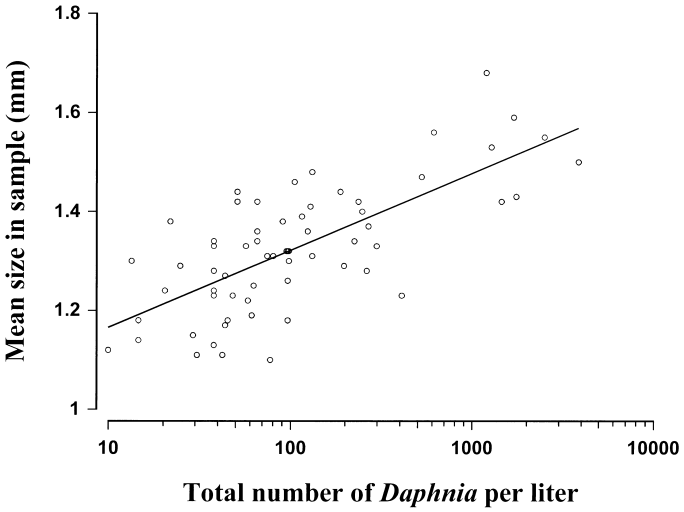

Fig. 5. Mean size of animals in a sample versus number of animals in the sample. The association between these two variables is highly significant (Pearson linear regression, $R^2 = 0.51$, $P < 0.001$, $n = 63$).

experiment (Table 3). Light intensity was negatively correlated with total zooplankton abundance in the experimental area (Pearson linear regression, $R^2 = 0.20$, $P = 0.020$, $n = 27$).

Discussion

This experiment demonstrates active food search in *Daphnia* in the field. Food search has previously been demonstrated only in laboratory studies (e.g., Jakobsen and Johnsen 1987; Cuddington and McCauley 1994; Neary et al. 1994; Larsson and Kleiven 1996; Larsson 1997; Jensen and Larsson in press). Thus, a link between laboratory and field results is established. Since *Daphnia* showed aggregation behavior to yeast and not to clay particles, *Daphnia* is able to differentiate between patches of high and low particle quality. The mechanism is most likely to be perception of hunger and satiation where the daphniids reduce swimming speed in areas where foraging is successful (Cuddington and McCauley 1994; Larsson and Kleiven 1996) and/or change turning behavior (Young and Getty 1987). This allows the daphniids to remain within a patch that could be discovered by random movement. Under this circumstance, high- and low-quality particles are perceived differently. Further, the results indicate that light scattering is a relatively unimportant factor, while mechanical and/or chemical perception are the most important factors for *Daphnia* to find patches of food under natural conditions. When forced to forage in a homogeneous mixture of both edible and inedible particles, *Daphnia* seems to be incapable of discriminating chemically between them (DeMott 1986). This is in contrast to many other zooplankton species both within Cladocera and Copopoda (DeMott 1986, 1988). In such particle selection ex-

Table 3. The wind speed (m s^{-1}) and illumination (μE m^{-2} s^{-1}) during the experiment. For the given wind directions, southeast wind is perpendicular to the line of sampling stations in Fig. 1b.

Date	Time	Treatment	Wind speed	Wind direction	Illumination
9 Jul 99	1000 h	Control	0.28	NNW	900
	1200 h		0.70	SSE	1,380
	1400 h		1.17	SSW	1,715
12 Jul 99	1000 h		0.97	SSE	1,007
	1200 h		1.77	NNW	1,724
	1400 h		1.08	WSW	1,907
15 Jul 99	1000 h		0.83	SSE	1,356
	1200 h		0.25	SSE	658
	1400 h		1.05	SSE	564
10 Jul 99	1000 h	Yeast	0.67	SSE	1,466
	1200 h		1.02	SSE	1,853
	1400 h		1.72	SSE	225
13 Jul 99	1000 h		1.03	WSW	368
	1200 h		0.67	SSW	820
	1400 h		2.22	SSE	1,988
16 Jul 99	1000 h		0.67	SSW	1,583
	1200 h		0.55	Variable	768
	1400 h		1.83	SSW	2,471
11 Jul 99	1000 h	Clay	1.22	SSE	456
	1200 h		0.97	SSE	1,856
	1400 h		0.52	SSE	1,892
14 Jul 99	1000 h		0.33	SSW	683
	1200 h		0.67	SSW	488
	1400 h		0.92	SSE	734
17 Jul 99	1000 h		2.22	SSE	1,414
	1200 h		1.10	SSE	1,614
	1400 h		1.23	SSE	871

periments, particle charges also play a role in the selection (Gerritsen and Porter 1982). By contrast, when testing for particle location instead of particle selection, chemical perceptions do play a role in *Daphnia* (e.g., van Gool and Ringelberg 1996; Laurén-Määttä et al. 1997). In van Gool and Ringelberg's experiment, the *Daphnia* was attracted to odors associated with edible algae, whereas nonedible algae did not elicit attraction. Thus, instead of being selective in the direct feeding, *Daphnia* has the ability to search areas where the concentrations of palatable particles are profitable.

When comparing the average effect of yeast input with the associated responses of *Daphnia,* the magnitude of the increase in particle concentration is much less than the response in *Daphnia* (Fig. 3). However, the experimental aggregates of *Daphnia* are about as dense as natural aggregates in Lake Myravann (Kvam and Kleiven 1995). Since the effect of particle input nearly disappears when all the measured size classes of particles are included (Fig. 3a), it is demonstrated that Chl *a* or carbon per liter as a measure of food availability would be imprecise. In addition, the larger algae probably create even more noise for the *Daphnia,* as indicated by the presence of the gelatinous green alga *S. schroeteri,* which is relatively indigestible for *Daphnia* (Porter 1975, 1976). This situation of apparently many nonpreferred particles is, of course, the situation the *Daphnia* spp. tackle when they find the patches of yeast. Thus, it is not surprising that nonexperimental field studies never have been able to measure a clear association between zooplankton and their food. Unfortunately, there is no instant method of measuring the amount of food available for herbivorous zooplankton. At the very least, one must know which algae are preferred by different zooplankton as well as the spatial and temporal distribution of algae at different scales.

Although yeast and clay treatments did not differ with respect to the regression lines for CIs, the increase in particle concentration from clay input seems to be lower than for yeast (Fig. 3). However, it is plausible that the increase in concentration from clay input is underestimated; when measuring particle concentration using the Casy counter, a weak electrolyte is added to the samples and taken through a capillary of predefined geometry at a constant stream velocity. During measurement, electricity is supplied to the capillary across two platinum electrodes. The capillary filled with electrolytes has a defined electrical resistance level. While passing through the capillary, the cells in the sample displace an amount of electrolyte solution equal to the individual cell's volume. Because complete, living cells have an insulating cell membrane, resistance along the capillary rises. This change in resistance level gives an indication of cell volume. Clay particles, of course, do not have such an insulating cell membrane, and many clay particles may therefore have been measured to lie below the lower end of the interval of yeast-sized particles and have consequently not been included in the estimates. The size of clay particles measured by the light microscope demonstrates that the particle counter underestimates clay particle size.

The average size of *Daphnia* increased within the high-density aggregates (Fig. 5), indicating that larger animals have a higher probability of locating patches of high food concentration. This may simply be caused by the larger daphniids swimming faster than the smaller ones. Since *D. pulex* on average was smaller than *D. longispina,* different swimming speed may also explain why the magnitude of *D. pulex* responses to yeast input was weaker (Fig. 3b,c).

The inverse association between light intensity and *Daphnia* abundance in the experimental area indicates that *Daphnia* spp. exhibit not only diurnal horizontal migration (Kvam and Kleiven 1995) but also migration during daytime as a response to light intensity. This daytime migration may of course be vertical. If so, they have avoided capture by the sampler, which remained ≈0.8 m from the bottom. Although this has not specifically been tested, we did not observe such strong aggregation at the bottom when doing some occasional samples at the bottom on days of high light intensity.

The option to create patches of food, as in this experiment, opens the possibility to do field experiments testing the food-searching ability among different groups of zooplankton. For instance, if daphniids have a lower ability to find patches of food compared to copepods, this may explain why *Daphnia* is less successful in oligotrophic lakes (DeMott 1989). Beside developing better methods for measuring food patchiness in nature, such experiments form a natural next step in this line of field research.

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