Limnol. Oceanogr., 51(1), 2006, 109–116

Individual foraging behaviors and population distributions of a planktonic predator aggregating to phytoplankton thin layers

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Abstract

Resource distributions in the ocean are heterogeneous in time and space. Theory predicts planktonic predators may exploit these resource patches by modifying their movements in response to mechanical or chemical stimuli. In the laboratory, we used the protistan predator *Oxyrrhis marina* to simultaneously quantify changes in predator population distributions on scales of centimeters and hours and predators' individual three-dimensional swimming behaviors on scales of micrometers and seconds. Movements of *O. marina* in a 0.3-m column were monitored for several hours before and after introducing a 5-mm layer of either *Isochrysis galbana* prey cells or cell-free *I. galbana* filtrate. Within both types of layers, significant increases in turning rates and decreases in vertical velocities were observed. *O. marina* swimming speed increased significantly in response to intact *I. galbana* cells, but not in response to *I. galbana* exudates. Changes in predators' microscopic movements were concurrent with rapid (minutes) and sustained (hours) increases in relative predator abundance within layers. After 4 h, predator abundance inside the thin layers was up to 20 times higher than before introduction of prey. Estimates of realized growth rates for predator populations with aggregate behaviors were an order of magnitude faster than estimates for hypothetical, nonaggregating predators. The observed foraging behaviors of *O. marina,* and by implication other planktonic predators, increase effective prey availability to the predators. Modulation of individual-level behaviors can result in significant changes in community-level characteristics, including population distributions, growth, and ingestion rates.

The abundance and distribution of resources in the pelagic is heterogeneous over a wide range of temporal and spatial scales (e.g., Krembs et al. 1998; Folt and Burns 1999; Franks and Jaffe 2001). Vertically thin and horizontally extensive phytoplankton layers are one frequently observed type of spatial heterogeneity (Cowles et al. 1998; McManus et al. 2003). Patches represent areas of locally intensive biological activity, and the size and distribution of patches impact magnitude and variability of biological rates and processes. To consumers, resource patches contain higher concentrations of suitable prey than the surrounding waters, and consumers that are located within those patches could benefit from substantially higher effective prey availabilities. However, most analyses of trophic and demographic rates in marine microbial food webs assume that prey availability is uniform and constant at the scale of individual consumers. Assuming average prey availability when resources are patchy could result in significant errors, typically underestimates, of actual trophic and demographic rates.

The ability of consumers to navigate within such heterogeneous environments dictates how spatially heterogeneous prey distributions affect ecological dynamics. Planktonic predators must contend with biomechanical constraints on their abilities to sense and swim. To cope with these constraints, many planktonic predators alter their movements in response to local external stimuli, including the presence of prey (e.g., Levandowsky and Kaneta 1987; Buskey and Stoecker 1989; Fenchel and Blackburn 1999). Changes in individual-level swimming behaviors can alter predator population distributions, potentially increasing spatial correlations between predator and prey populations. However, how effectively specific predators can exploit specific resource distributions is determined by the temporal and spatial characteristics of the resource patches and the swimming behavior of the predators (e.g., Grünbaum 2001).

Previous field studies have demonstrated that distributions of planktonic predators can be, but are not always, highly correlated with those of their prey (Stoecker et al. 1984) and that these correlations may be augmented through the creation of artificial prey patches (Tiselius 1992; Saiz et al. 1993; Jensen et al. 2001; Bochdansky and Bollens 2004). Methodological limitations have made it difficult to observe individual predators at sufficiently high resolution (micrometers) over sufficiently large time and space scales (hours and meters) to establish in a mechanistic way why predator–prey correlations do or do not arise. Thus, the quantitative consequences of resource patchiness and foraging behaviors on trophic and demographic rates in marine microbial food webs are still poorly understood.

Recently, we developed laboratory methods that overcome some of these limitations by enabling us to simultaneously quantify both three-dimensional (3D) swimming behaviors of large numbers of individual organisms and the resultant macroscopic changes in population distributions (Menden-Deuer and Grünbaum unpubl.). The observations are made under controlled fluid-dynamic conditions in relatively large,

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Acknowledgments

We thank the Friday Harbor Laboratories and director A. O. D. Willows, R. N. Bearon, E. J. Lessard, R. R. Strathmann, S. Summit, and D. Thoreson for valuable contributions to this research. We also thank G. Smalley, H. H. Jakobsen, and S. L. Strom for generously sharing their plankton cultures. Funding was provided by the National Science Foundation (OCE-0220284 to D.G., and CCR-9980058 to J. K. Parrish and D.G.).

spatially defined environments. Here, we describe use of these methods to quantify the ability of the heterotrophic dinoflagellate, *Oxyrrhis marina*, to exploit thin layers of the prey alga *Isochrysis galbana*. The specific goals of this investigation were (1) to quantify how quickly and effectively *O. marina* can locate remote prey patches, (2) to associate changes in individual-level behaviors with resulting changes in predator distribution, and (3) to estimate the quantitative significance of prey distribution and predator behaviors on trophic and demographic rates.

Materials and Methods

Culture of microorganisms—The heterotrophic dinoflagellate *O. marina* and the haptophyte prey alga *I. galbana* were grown in nutrient-amended filtered seawater, f/2 (Guillard 1975). Cultures were maintained on a 16 : 8 light : dark cycle, at 18°C at 50 μmol photons m^{-2} s^{-1} provided by cool and warm white lights. The cultures were not axenic. The salinity of the medium was 30 psu. Both predator and prey cultures were able to grow in media ranging in salinity from 24 to 32 psu. Cultures were transferred every 4–6 d to maintain exponential growth. Cell concentrations of both predator and prey cultures were determined with a Coulter Multisizer just prior to the experiments. Predator and prey cells for all three experiments were taken from the same source culture on three successive days. The concentrations of *O. marina* and *I. galbana* in the source cultures were approximately 10^3 and 2×10^5 cells mL^{-1}, respectively.

Water column set-up—A total of three experiments were conducted in complete darkness in a 30-cm-high, 80-mL octagonal plexiglas tank at ambient room temperature (19°C). To suppress water movement, the water column was stabilized through a weak linear salinity gradient, ranging from 28 to 30 psu.

Stereo video capture—Video images were captured with stereo infrared-sensitive cameras (Cohu 4815-3000/000), equipped with Nikon 60-mm Micro Nikkor lenses with illumination from infrared light-emitting diodes (Ramsey Electronics, 960 nm). A 3D calibration grid was used to convert video pixel dimensions to real physical units (Menden-Deuer and Grünbaum unpubl.) The stereoscopic field of view was approximately 1.8 cm wide, 1.3 cm high, and 4.0 cm deep. Thus, cells within a volume of approximately 9 mL were observed. The resolution of the cameras showed *O. marina* cells (13 μm length) but not *I. galbana* cells (5 μm diameter). Approximately 2×10^4 *O. marina* cells were introduced at the bottom of the water column at the beginning of each experiment. The cameras were positioned at a fixed horizon throughout the experiment. Prey layers were introduced within the field of view of the camera. Relative abundance and swimming behavior of *O. marina* were recorded at that fixed horizon, in the center of the water column, for 2 min, at intervals of 2–15 min for a total duration of 16–26 h. Video was captured at 15 Hz (15 frames s^{-1}).

Three to eight hours after predators were introduced, a single 5-mm layer of phytoplankton prey was introduced in the center of the water column, 15 cm above the point of introduction of *O. marina*. The layer was created by slowly siphoning 10 mL of water from the target horizon, mixing it with *I. galbana* prey stimulus, and slowly reintroducing the mixture back to the water column. In experiment 1, the thin layer contained intact *I. galbana* cells. In experiments 2 and 3, the thin layers contained cell-free *I. galbana* filtrate (i.e., exudates) obtained by gently filtering *I. galbana* culture through a 0.2-μm filter. The final concentration of prey or prey equivalent exudates in the thin layer was 10^4 *I. galbana* mL^{-1}. After introduction of thin layers, filming continued for several hours at 10 min to 1 h intervals.

Data analysis—The pixel position of organisms in the video footage was determined with ImageJ image-processing software by removing stationary background objects and thresholding. 3D swimming paths were generated from pixel positions by Tracker3D, a Matlab-based motion-analysis package to track organism movement (Grünbaum unpubl.).

In the three experiments, a total of 121 two-minute video segments were collected over a period of 67 h. High-frequency (15 Hz) noise was removed from paths with a cubic smoothing spline, with knot spacing every 5 frames. These analysis parameters were selected after a systematic study to optimize discrimination of actual movements from noise and resulted in nearly half a million 3D swimming paths. Only cells tracked for a minimum duration of 1 s or longer were included in the analysis, totalling over 250,000 swimming trajectories. Swimming statistics were calculated from 3D paths, subsampled at 0.25-s intervals. Relative abundance of *O. marina* was estimated from the number of 3D trajectories observed in each video frame. Due to the nonnormal distribution of the frequency data, nonparametric Kruskal–Wallis tests were used to determine statistical significance of differences in swimming behavior.

Results

Predator population distribution—In all experiments, introduction of a thin layer of *I. galbana* prey (cells in Exp. 1; cell-free filtrate in experiments 2 and 3) resulted in a rapid and persistent increase in relative predator abundance within the thin layer (Fig. 1). Maximum abundance occurred approximately 4 h after the introduction of the thin layer, and abundance of *O. marina* remained elevated for several hours after peak abundance had been reached (Table 1). In experiments 2 and 3, an initial peak in predator abundance, lasting approximately 25 min, was observed before the prey thin layer was introduced. This transient peak was a result of *O. marina* cells rapidly swimming upward, from the point of introduction at the bottom of the water column. In experiment 1, no increase in relative abundance in the prelayer treatment was observed. This may be because the transient occurred between observations. Maximum increases of *O. marina* cells over prelayer, background concentrations was 20-fold in experiment 1, and 9- and 3-fold, respectively, in experiments 2 and 3.

Individual swimming behaviors—The geometry of swimming trajectories recorded in the absence of prey appeared generally less convoluted than trajectories recorded in the

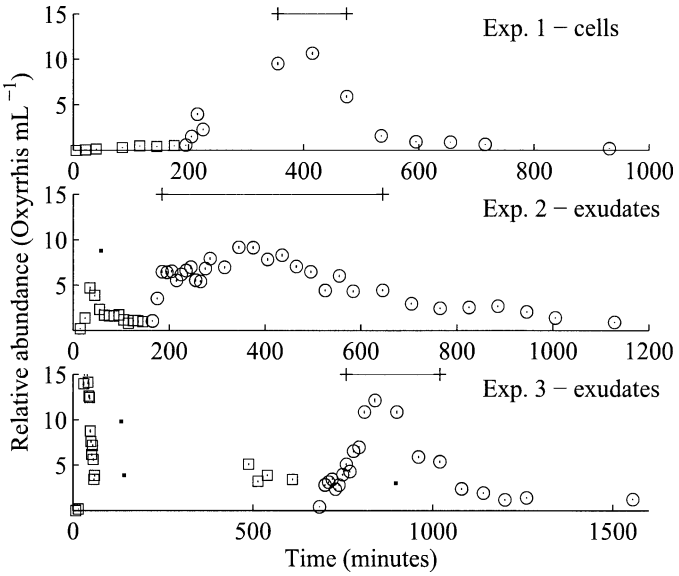

Fig. 1. Relative abundance of *Oxyrrhis marina* before (squares) and after (circles) the introduction of a thin layer of either *Isochrysis galbana* prey (experiment 1) or cell-free filtrate (experiments 2 and 3). Each value shown represents mean predator abundance in 2 min of video footage recorded at 15 frames per second. Error bars (within symbols) are 95% confidence intervals of the mean. Horizontal lines mark peak aggregation phase, defined here as samples within 40% of the peak abundance observed. Note differences in experiment durations. Due to a programming error, footage was collected continuously for the first hour of experiment 3 and resumed only after 7 h.

presence of prey (Fig. 2), suggesting differences in swimming behaviors and consequently differences in rates of population dispersal. We quantified these apparent differences through comparison of movement statistics across several phases of the aggregation response. First, to characterize overall behavioral responses to the presence of prey and identify the behavioral mechanisms of aggregation, we compared all observations made for predators swimming before and after the introduction of prey. Second, to identify differences between aggregative and dispersive phases, we classified all observations according to the time of observation, relative to the peak aggregation observed. We defined the peak-aggregation phase arbitrarily as all samples within 40% of the peak abundance observed within one experiment (Fig. 1). We then classified observations made after introduction of the thin layer but before the peak period as prepeak and observations made after the peak phase as postpeak and compared movement statistics among these different phases of aggregation.

Turning rate is a measure of the magnitude of directional change along a swimming trajectory over time. Turning rates increased significantly ($p < 0.01$) after the introduction of prey thin layers in all experiments (Fig. 3). Low turning rates were more frequent in the absence of prey. Higher turning rates, and thus more rapid changes in direction, were more frequent in the presence of prey. The increase in turning rate was more than twice as large in response to prey cells (experiment 1) than to prey exudates (experiments 2 and 3, Fig.

Table 1. Summary of changes in individual movements and population-level responses of *Oxyrrhis marina* to the introduction of a prey layer of *Isochrysis galbana.* The aggregation factor is the ratio of maximum cell concentration during peak abundance versus the average cell abundance 1 h prior to the introduction of phytoplankton layers. The two values provided to characterize individual-level movements are the mean observed for predators swimming in the absence and presence of prey, respectively.

Experiment	1	2	3
Stimulus	cells	filtrate	filtrate
Aggregation factor	20	9	3
Duration peak (hours)	≥2	7.6	4
Turning rate (degree s^{-1})	56/70	61/65	62/64
Speed (μm s^{-1})	307/339	359/360	366/365
Vertical velocity (μm s^{-1})	80/67	94/70	107/58
Run length (μm)	264/252	286/273	284/280
Curvature (degree s^{-1})	73/82	72/74	69/71

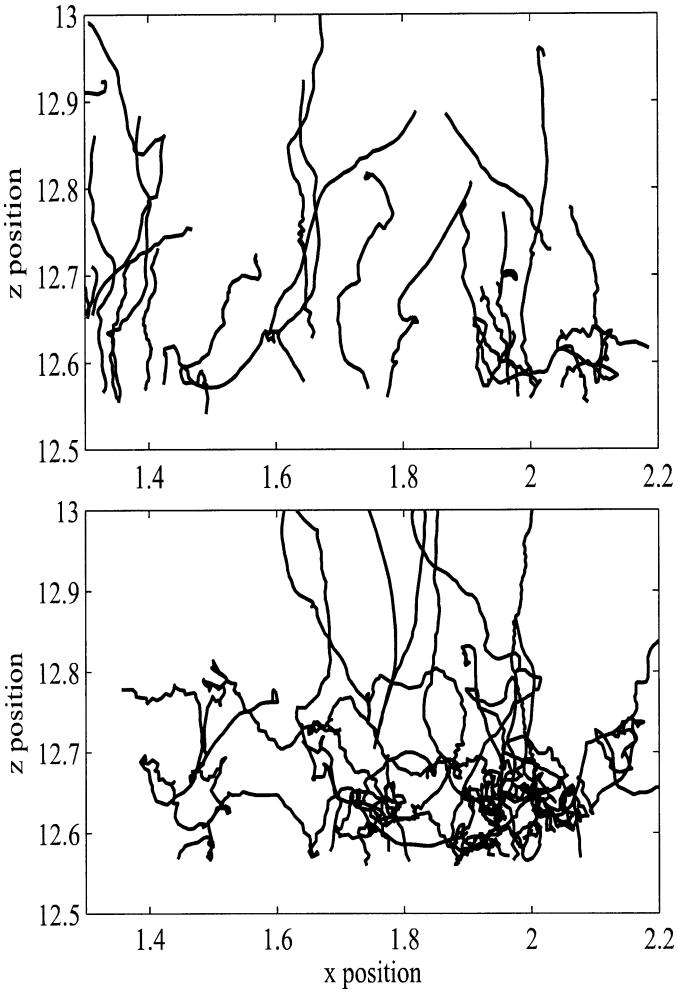

Fig. 2. Sample trajectories of *O. marina* cells swimming in the absence (top) and presence (bottom) of *I. galbana* prey cells. There are 23 and 22 paths shown in the top and bottom panels, respectively. This figure shows two-dimensional projections of 3D paths for better visibility of the horizontal versus vertical components. Dimensions are in centimeters.

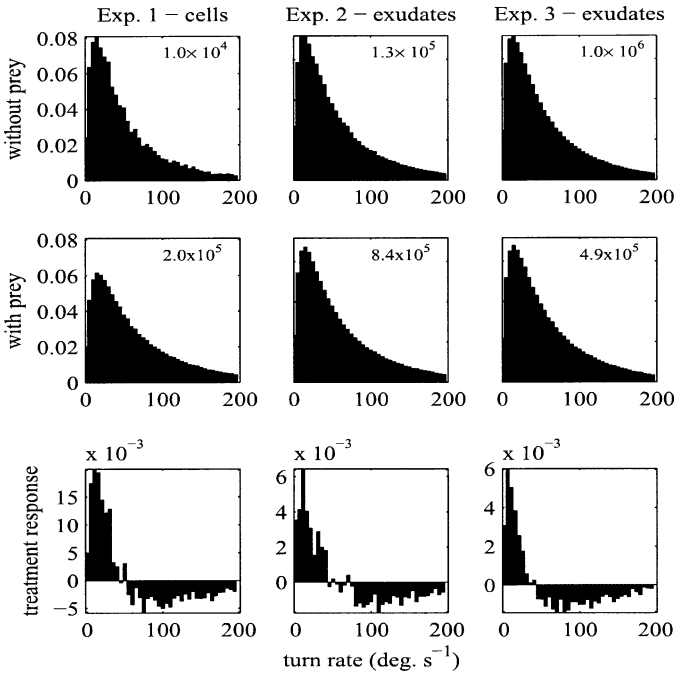

Fig. 3. Frequency distributions of turning rates of *O. marina* before (top row) and after (middle row) the introduction of a layer of *I. galbana* prey cells in three separate experiments (columns). The bottom row shows the difference between the two frequency distributions and is indicative of the behavioral response (note difference in *y*-axis ranges). Negative values indicate behaviors observed more frequently in the presence of prey. Thus, higher turning rates were observed more frequently in the presence of prey. The sample size, i.e., the total number of turns observed, is shown alongside each frequency distribution.

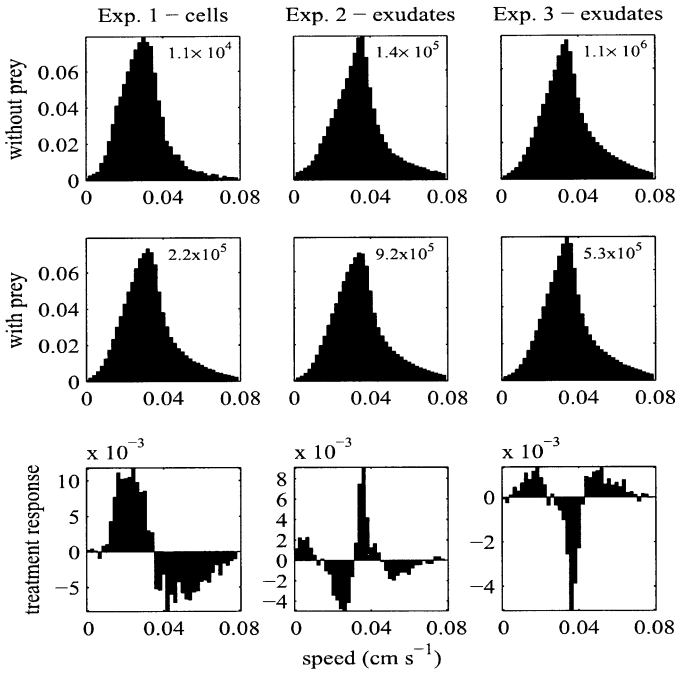

Fig. 4. Frequency distributions of swimming speeds of *O. marina* before (top) and after (middle) the introduction of a prey layer. The bottom row shows the difference between the two frequency distributions. For further explanation, see Fig. 3.

3). No significant differences in frequency distributions of turning rates were observed among pre-, peak, and postpeak aggregation periods.

Swimming speeds increased significantly ($p < 0.01$) in the presence of *I. galbana* cells (experiment 1) but did not change significantly in the presence of cell-free *I. galbana* filtrate (experiments 2 and 3, $p = 0.185$ and $p = 0.082$, respectively, Fig. 4). It is noteworthy that swimming speed in experiments 2 and 3, before the introduction of exudate thin layers, was already 20% higher than in experiment 1. Increased swimming speeds were also observed in other experiments, whenever *O. marina* were exposed to prey concentrations >5,000 *I. galbana* mL^{-1} (data not shown). Our results are, therefore suggestive, but further replication is needed to fully interpret them. In all experiments, lowest swimming speeds were observed during postpeak aggregation phases. Highest swimming speeds were observed during the peak aggregation phase (Fig. 5).

O. marina were introduced at the bottom of the water column and immediately swam upward. Consequently, *O. marina* showed a strong bias toward upward swimming before the introduction of the layer (Fig. 6), indicated by positive vertical velocities. Vertical velocity decreased significantly ($p < 0.01$) once *O. marina* encountered prey thin layers. This shift in vertical velocity was also evident in changes in the swimming direction of *O. marina*, which

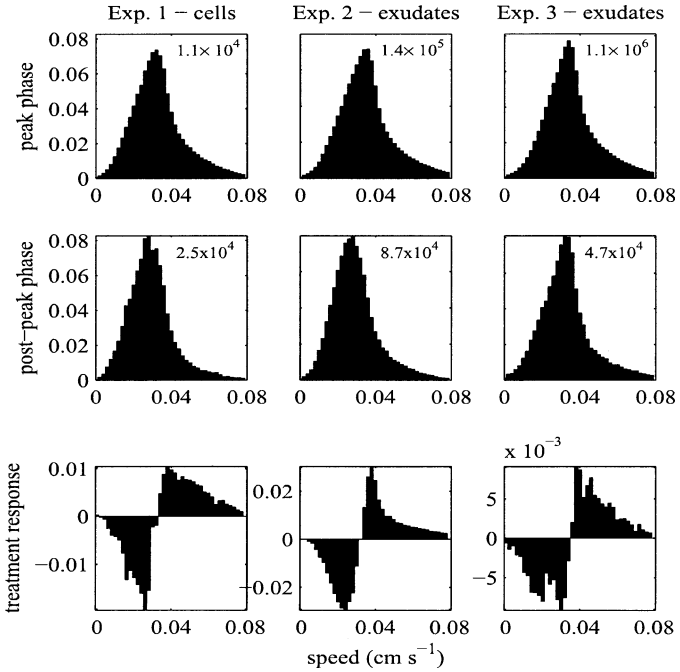

Fig. 5. Frequency distributions of swimming speeds of *O. marina* during the peak (top) and postpeak (middle) aggregation phases. The bottom row shows the difference between the two frequency distributions. For further explanation, see Fig. 3.

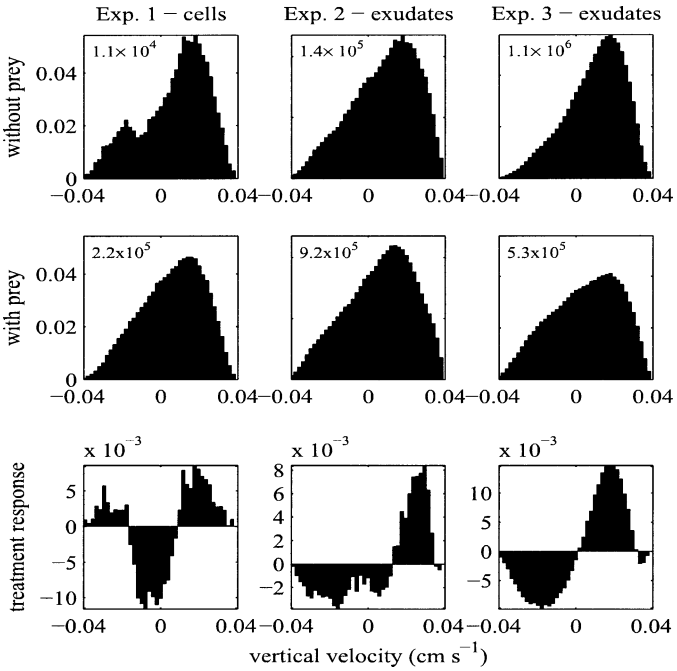

Fig. 6. Frequency distribution of vertical velocities of *O. marina* before (top) and after (middle row) the introduction of a prey layer. The difference between the two frequency distributions is shown in the bottom row. Positive values indicate upward swimming, negative values downward swimming. For further explanation, see Fig. 3.

shifted from predominantly upward swimming to more horizontal swimming (Fig. 7). However, a distinct upward bias in swimming direction persisted even after the introduction of prey, compared with the expected frequency distribution for random swimming directions. No significant differences were observed between the vertical-velocity frequency distributions observed during the different phases of aggregation.

Run length is a measure of the distance covered between significant changes in direction and is a frequently used parameter in analyses of foraging behaviors such as area-restricted searches (e.g., Leising 2001). We defined run length as the distance between direction changes of 30°, after a sensitivity analysis determined that results did not change substantially over a range of 15–60°. Run length decreased significantly after the introduction of thin layers of *I. galbana* cell-free filtrate ($p < 0.01$, experiments 2 and 3), but not after the introduction of a thin layer of *I. galbana* cells ($p = 0.104$, experiment 1; Fig. 8). In all experiments, run lengths were shortest during the postpeak aggregation phase (data not shown).

The combined effect of changes in individual movement characteristics resulted in significantly ($p < 0.01$) increased path curvatures, i.e., changes in the overall geometry of swimming paths (Fig. 2). The lower the curvature of a path, the more it resembles a straight line. Increased path curvatures in the presence of prey imply more convoluted paths that lead to relatively smaller overall displacement and increased contact rates within a localized volume. Curvatures of *O. marina* paths in the absence of prey were lower (i.e.,

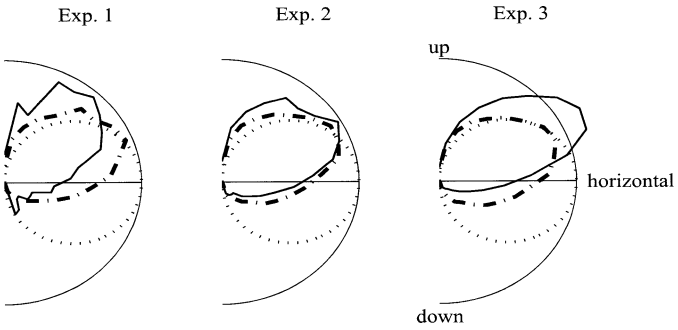

Fig. 7. Circular histograms showing the frequency distributions of swimming directions before (solid line) and after (dash-dot) the introduction of a prey layer in experiments 1–3. The circle (dotted line) indicates the expected frequency of randomly distributed swimming directions. The axes were fixed to the same range for all three graphs.

paths were straighter), compared with the more convoluted and helical paths observed in the presence of prey (Fig. 9). Analysis of path curvature over time showed that curvature increased continuously and was highest during the postaggregation phases.

Discussion

Simultaneous observations of both movements of *O. marina* individuals and overall predator population distributions enabled us to link variations in individual-level swimming behaviors to spatial variations in prey as well as changes in

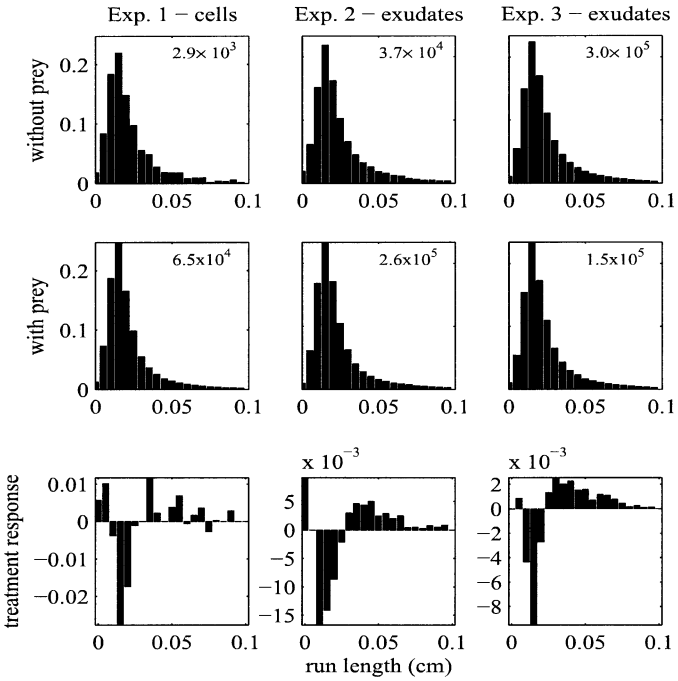

Fig. 8. Frequency distributions of run lengths of *O. marina* before (top) and after (middle) the introduction of a phytoplankton thin layer. The bottom row shows the difference between the two frequency distributions. Note differences in *y*-axis scales of bottom row. For further explanation, see Fig. 3.

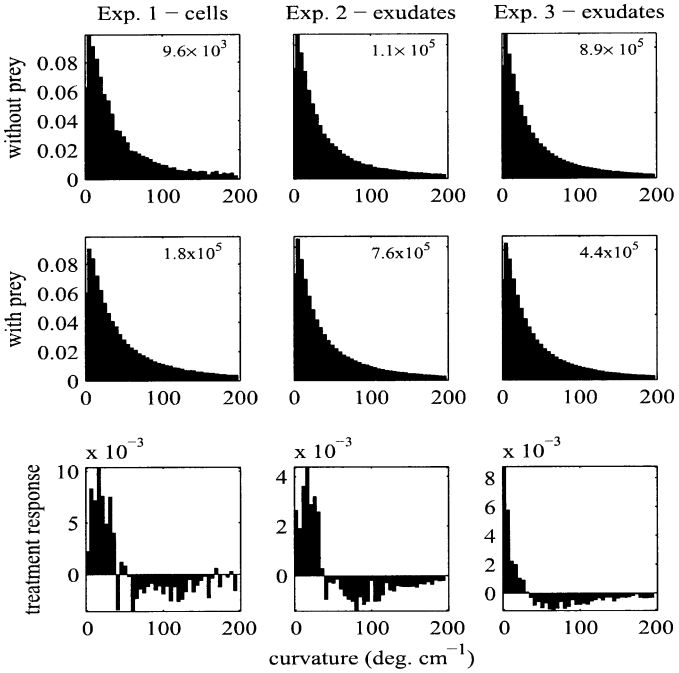

Fig. 9. Frequency distributions of path curvature of *O. marina* before (top) and after (middle) the introduction of a phytoplankton thin layer. The bottom row shows the difference between the two frequency distributions. Note differences in *y*-axis scales of bottom row. For further explanation, see Fig. 3.

predator population distributions within a relatively large experimental volume. The population-level distribution data provide a quantitative assay of how effectively predators aggregate to resource patches and how much time they require to do so. Individual movement observations give an indication of which behavioral mechanisms *O. marina* cells actually employ, from among the many alternatives that could theoretically give rise to aggregation in resource patches. These observations provide a basis for speculations about how well-suited *O. marina*'s behavioral responses are to exploit different types of resource distributions (e.g., horizontal thin layers) and for hypotheses about the ecological consequences and evolutionary advantages or disadvantages of the observed behaviors.

Aggregation of protist populations to prey patches: scaling and trophic impacts—In all experiments, *O. marina* responded with rapid and prolonged aggregations to the introduction of prey thin layers. Predators required only a few minutes to accumulate in thin layers, and large numbers remained for several hours within the 5-mm prey patches. The 0.3-m-tall experimental tank is at the lower end of what might be considered a relevant spatial scale for trophic interactions of populations in the water column under field conditions. What do our observations imply for resources distributed over larger scales? Rough estimates drawn from a scaling analysis in Grünbaum (2001) suggest that, for predators employing biased random-walk foraging behaviors, the effective availability of patchily distributed prey is indicated by the Frost number.

$$\mathcal{F}r = \frac{c^2 T \tau}{L^2}$$

where c is a typical forager speed, τ is a typical turning interval, L is a typical distance between prey patches, and T is a typical prey patch longevity. Prey distributions characterized by Fr $\gg 1$ are available because foragers can find and exploit prey patches before they disappear. Conversely, prey distributions characterized by Fr $\ll 1$ are unavailable because prey patches disappear before foragers can find them.

Assuming similar foraging responses are used in different prey distributions, so that c and τ are constant, the availability of prey of a given distribution characterized by L_a and T_a is equivalent (indicated by equal Frost numbers) to a different prey distribution characterized by L_b and T_b if

$$\frac{T_a}{L_a^2} = \frac{T_b}{L_b^2}$$

That is, prey patches are equally available if their longevity increases with the square of the typical distance between those patches. If we use this scaling to perform an extrapolation of our experimental results for a comparable experiment using a 3-m water column, this reasoning suggests that meter-scale prey concentrations would be available to *O. marina* and similar predators if they last more than a few hours. However, for a prey layer embedded within a 30-m water column to be available, its longevity must be 10,000-fold greater than the aggregation times we observed in our 0.3-m column, implying that aggregation of predators over 10s of meters would require days or even weeks. Over such long time scales, growth and mortality can no longer be ignored and are likely to have a greater impact on population size than movement behaviors. Refined estimates of how observed behaviors and aggregation patterns scale up to resources distributed over meters or 10s of meters will require detailed spatially explicit modeling and are the subject of on-going research. However, the present analysis does suggest that real prey distributions probably include both those that can be quickly located by *O. marina,* implying high resource–consumer correlations and trophic rates, and also those that cannot be quickly located, implying low correlations and trophic rates.

Consequence of aggregation behaviors for trophic and demographic rates—Further estimates can be used to assess the potential trophic impacts of the observed patterns of aggregation to prey patches. We used published numeric and functional responses (Goldman et al. 1989; Jeong et al. 2001) to estimate the quantitative consequences of spatial structure in prey distributions and predator behavioral responses on *O. marina* growth and ingestion rates in three scenarios: (1) a uniform prey distribution in which total number of prey cells is the same as in experiment 1, so that prey concentration is low and constant regardless of predator location; (2) a heterogeneous prey distribution corresponding to experiment 1, in which prey cells are concentrated in a 5-mm thin layer, but in which predators do not respond be-

haviorally to food and so do not aggregate in the food layer; and (3) a heterogeneous prey distribution corresponding to experiment 1, with predators that respond by aggregating to the prey thin layer as observed.

In scenario 1, the uniform prey distribution has a concentration of 135 *I. galbana* mL^{-1}, which is close to *O. marina*'s feeding threshold (Jeong et al. 2001). Thus, *O. marina* would do little or no feeding, suggesting the predator population could not grow based on a prey cell distribution lacking a pronounced, concentrated structure. In scenario 2, the patch structure is present; however, only approximately 1.25% of predators would be located within the thin layer, resulting in an overall population growth rate of roughly 0.02 divisions d^{-1}. With such low *O. marina* concentration in the food patch, it would take almost 3 d for the predators to ingest the prey biomass available within the thin layer (neglecting predator and prey growth over that time). Scenario 3 corresponds to the experimental conditions, where prey was concentrated in a thin layer and predators aggregated to that layer. In this scenario, peak abundance of predators within the thin layer exceeded background by up to 2,000%. Estimates of total population growth rate for aggregating predators increase to 0.38 divisions d^{-1}, and at peak predator concentration, it would take only approximately 3.3 h to consume all prey within the thin layer. We note that the estimated removal of prey cells, and thus reduction in stimulus concentration, is consistent with the relatively short duration of the aggregation observed in experiment 1.

These calculations, though preliminary, suggest strongly that spatial structure of phytoplankton prey and the associated behavioral responses by protistan predators are likely to affect, by an order of magnitude or more, the intensity of trophic interactions involving *O. marina,* and similar protist predators, in planktonic communities.

Foraging strategies in Oxyrrhis marina—One effective behavioral mechanism for aggregating in resource concentration is reduction in swimming speed in response to increased recent exposure to prey cues (Schnitzer et al. 1990; Davis et al. 1991; Visser and Thygesen 2003). Our results suggest that *O. marina* does not employ this mechanism. On the contrary, while swimming speeds did not change in the presence of *I. galbana* exudates, they increased significantly after exposure to intact prey cells. Theory predicts that this behavior could cause long-term movement of predators away from concentrations of prey cells. However, this potentially counterproductive behavior may be beneficial in increasing prey contact and capture rates over the short term. Investigations of encounter rates between predators and prey suggest that, when prey move relatively slowly and turbulence is weak, contact rates are limited by predator swimming speed (Gerritsen and Strickler 1977; Rothschild and Osborn 1988). In such cases, reductions in predators' swimming speeds would result in reduced prey encounter rates. We hypothesize that a trade-off exists favoring short-term benefits from increased prey encounters over the longer term risk of exiting the prey patch, and that *O. marina* has apparently adopted the foraging strategy of increasing short-term contact rates through faster swimming when prey cells are present.

Our observations further suggest that several other elements of *O. marina*'s foraging strategy act to mitigate the potential long-term cost of more rapid swimming. Recent exposure to either prey cells or prey exudates also elicited increases in turning rates and curvature and decreases in run length (Table 1). Each of these responses has been shown in theoretical studies to promote aggregation in concentrations of the associated cue (e.g., Okubo and Levin 2001).

We also observed a reduction in the initially strong vertical components of swimming directions in the absence of prey to a distribution with stronger horizontal components in the presence of a horizontal layer of prey. This shift in preferred swimming directions may directly mitigate the increased risk of departing patches by swimming at increased speeds. A foraging response that includes directional bias is interesting because it may have different consequences for different patch geometries. For patches that are relatively large in horizontal extent, such as the thin layers observed by McManus et al. (2003), a vertical movement bias is likely to increase the rates of patch encounters, while a horizontal bias is likely to increase retention once in patches. These modulations of swimming behaviors would need to be reversed for organisms that forage for patches that are relatively larger in the vertical extent, such as the wakes of sinking or rising particles (Thygesen and Kiørboe 2002; Jackson and Kiørboe 2004). The observed shifts in swimming directions suggest the hypotheses that *O. marina* specializes in exploiting horizontally extensive prey patches, such as thin layers and Ch1 *a* maxima, and has evolved behavioral strategies that promote efficient exploitation of these types of resources even at the cost of decreased ability to profit from other patch geometries.

Extended periods of aggregation were observed irrespective of whether the thin layer contained *I. galbana* prey cells or cell-free *I. galbana* filtrate. A chemotactic response to phytoplankton exudates could explain the similarities in aggregation patterns. Behavioral responses to chemical cues are well established for protists and some of the cellular mechanisms of signal transduction are known (Machemer 1989; Van Houten 1994). Phytoplankton exudates form one of the largest pools of organic carbon on earth (Hedges 1992). Thus, exudates could be a useful stimulus for phytoplankton predators, indicating the distribution and concentration of prey. Nonetheless, intact prey cells stimulated behavioral responses that chemical cues alone did not, suggesting that multiple cues are involved in *O. marina*'s foraging behaviors and that movement characteristics can be modulated in different combinations.

We hypothesize on the basis of all these observations that: (1) *O. marina* has a hierarchical set of behavioral responses to prey cues that distinguishes between prey cells and prey-derived odors; (2) exposure to chemical cues elicits a primary response to decrease overall cell displacement based on modulation of turning rate, curvature, and/or run length, which are responsible for initial aggregation in food patches; (3) direct contact or some other stimulus requiring close proximity of intact prey cells elicits a secondary response in the form of increased speed, which increases short-term contact rates; (4) the potential negative long-term consequences of increased speed require that this response is only em-

ployed when prey cells are present and thus an immediate payoff is likely; and (5) swimming direction and vertical velocity are modulated to further decrease the probability of leaving horizontal resource patches.

Overall, these results suggest that *O. marina*, and possibly many other planktonic predators, have effective behaviors to exploit spatially structured resources. These behaviors affect both the population distribution of the predators as well as their encounter rates with prey. Subsequent effects on community composition and biological rates are likely. It is noteworthy that estimates of growth and ingestion rates ignoring predators' foraging behaviors, irrespective of prey distribution, would maximally have resulted in very low population growth and ingestion rates. In contrast, estimates accounting for actual prey distributions and observed prey behaviors resulted in more than an order of magnitude increase in estimated population growth and ingestion rates.

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Received: 17 March 2005
Accepted: 10 August 2005
Amended: 24 August 2005