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Relevant scales in zooplankton ecology: Distribution, feeding, and reproduction of the copepod *Acartia hudsonica* in response to thin layers of the diatom *Skeletonema costatum*

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Abstract

We investigated the interaction of the copepod *Acartia hudsonica* in relation to thin layers of the diatom *Skeletonema costatum.* Thin layers have recently received much attention, since they are common and persistent features in the water column, often overlooked by traditional sampling methods. Their frequent abundance in coastal oceans and the high biomass associated with them has led to the assumption that they are important grazing sites of calanoid copepods. We employed 2-m tall tower tanks that allowed us to simulate thin layers. Three variables representative of three time scales were considered: the distribution of copepods in the tanks (time scale of minutes), fecal pellet production as a proxy for ingestion rate (time scale of hours), and egg production rate (time scale of >12 h). *A. hudsonica* responded significantly but very little to the thin layers in terms of their distribution. Given a choice, there was a slightly higher tendency to swim through a patch of diatoms than to swim around it. Fecal pellet production was slightly lower in the thin-layer treatments than in the homogeneous controls. Egg production was not influenced by differential distribution of diatoms in the tanks, which indicated that the copepods dealt equally well with patchy food as when the same numbers of cells were available in a homogeneous distribution. Time series experiments showed that ingested carbon is integrated over time scales of >12 h. Therefore, small-scale fluctuations of food in space and time do not necessarily translate into small-scale fluctuations in reproductive output.

The effect of heterogeneity in the spatial distribution of food continues to be a central issue in the study of trophic interactions between zooplankton and their prey. While prey may fluctuate randomly, as emphasized by classic studies (Fasham 1978), there is increased evidence that persistent small-scale features on the 10-cm scale exist over a wide range of environments (Mitchell and Fuhrman 1989; Bjørnsen and Nielsen 1991; Donaghay et al. 1992; Owen et al. 1992). An example of these small-scale features are thin layers of plankton, as recently documented for protected bays and the coastal oceans. These features occur over surprisingly large horizontal scales (>1 km) and frequently persist over weeks (Cowles et al. 1998; Dekshenieks et al. 2001). They can either consist of phytoplankton or zooplankton, or a combination of both. In many cases, thin layers are associated with physical features such as pycnoclines, but in others they are not (Dekshenieks et al. 2001). The existence of thin layers poses a new set of challenges for the accurate representation of trophic processes. First, if the sampling method is too coarse, a local maximum can easily escape detection and the average amount of prey is miscalculated (Cowles et al. 1998). This problem is not trivial, since water column averages have often shown to be below maintenance levels for zooplankton (Mullin and Brooks 1976). The second major challenge in understanding rate processes related to thin layers is that predator–prey interactions may change qualitatively due to the presence of dense and spatially confined layers of food. These changes may occur because of behavioral changes of plankton such as aggregation in, or avoidance of, these layers. Hence, conventional functional response models that derive from steady-state experiments may be inadequate when dealing with spatially limited, highly aggregated prey.

The first problem mentioned above, that of missing local prey maxima, can be dealt with by high-resolution sampling

Acknowledgments

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in both space and time (Jaffe et al. 1998). The examination of fine scale distributions alone, however, does not elucidate the effect of food heterogeneity on physiological processes such as feeding and reproduction. Co-occurrence of some zooplankter and their prey may simply be the result of passive accumulation due to physical features in the water column. Alternatively, coinciding predator and prey peaks may be the result of foraging strategies of the organisms (e.g., Tiselius et al. 1993; Leising and Franks 2002). Depending on the behavior of the individual zooplankter and the amount of time spent in a patch, the effect of this food patch may differ. The residence time in the patch may be too short to have a significant influence on feeding or growth, or it may provide the organism with surplus energy that can be allocated to growth and reproduction. Hence the appropriate assessment of the effect of patchy food distributions requires the understanding of relevant time and spatial scales in the behavior *and* the physiology of zooplankton.

A large body of literature on the effect of food heterogeneity on zooplankton deals with the relative distribution of zooplankton and their food in the field (Herman 1983; Napp et al. 1988; Holliday et al. 1998; Jaffe et al. 1998), with behavioral changes of zooplankton in response to changes in food concentration and quality (e.g., Buskey 1984; Price and Paffenhöfer 1986; Tiselius 1992; Leising and Franks 2002), or with simulated zooplankton behavior in response to food patches using models (e.g., Kremer and Kremer 1988; Tiselius et al. 1993; Leising and Franks 2000). In contrast, experimental information on the physiological responses of zooplankton to heterogeneity in the food environment is very sparse. Some calculations suggest that calanoid copepods may benefit from a patchy distribution of prey (McAllister 1971; Lasker 1975; Mullin and Brooks 1976; Dagg 1993), while others propose that the opposite may be true (Kremer and Kremer 1988). In the few experimental studies that deal with the heterogeneous distributions of food, results diverged considerably depending on the tested organism (Langton and McKay 1974; Davis and Alatalo 1992). Comparisons, however, are difficult to make because in most studies patchiness is confounded by a simultaneous change in total prey availability (Dagg 1977; Fancett and Kimmerer 1985; Lampert and Muck 1985; Marcus 1988).

The aim of this study was to investigate the changes in the distribution and physiological processes of the calanoid copepod *Acartia hudsonica* in response to differences in the relative distribution of diatoms in both space and time. The emphasis of these experiments was put on creating environments that are identical in all accounts (i.e., total amount of food available, food quality, and food type) except for the relative spatial distribution of the food itself. As a model for spatial heterogeneity we chose thin layers of *Skeletonema costatum,* an abundant bloom-forming diatom in the San Francisco estuary.

Material and methods

Water samples and copepods were taken approximately 0.5 km off the sea wall of the Romberg Tiburon Center for Environmental Studies in Central San Francisco Bay by means of a small boat or directly at the sea wall using the tidal current. Copepods were collected with a 0.5-m ring net (150-μm mesh) during 2-min tows at slow speed (<0.5 m s^{-1}) and were immediately diluted with freshly collected seawater from the same site. Fertilized females of *A. hudsonica* (i.e., with spermatophores) were individually transferred into oxygenated glass fiber filtered (GF/F) seawater and stored at a temperature of 15°C before the experiments.

We chose *A. hudsonica* because it was available during the entire year. Previous studies on the genus *Acartia* in the San Francisco estuary showed seasonal shifts in the species composition over the year (Ambler 1985). In general, it is difficult to distinguish species of the subgenus *Acartiura* when they are alive (Bradford 1976). However, by narrowing our search down to one particular morphotype (largest *Acartiura* in the sample, possessing three pairs of blue ventral dots, and characteristic shape of the genital segment) we minimized the risk of picking different species for our experiments. Detailed analysis of subsamples derived from our experiments showed that these individuals belonged to *A. hudsonica* according to Ueda (1986).

The animals for each tank were kept in 100 ml GF/F seawater for several hours until we started the experiments. All experiments followed approximately the same time line: the copepods were collected between 1000 and 1200 h. Individuals were picked between 1300 and 1600 h. The experimental tanks were set up between 1600 and 2100 h, and the copepods added to the tanks or jars between 2100 and 2200 h. The incubations were terminated after 12 h and processed for postincubation. The incubation temperature was 15°C in all experiments, close to the in situ temperature (13°C to 17°C) in Central San Francisco Bay during collection.

We used the diatom *S. costatum* as a prey, since it is one of the most dominant bloom-forming diatoms in the San Francisco estuary (Cloern et al. 1985; Lehman 2000). According to previous studies, *Acartia* readily fed on this diatom and produced large numbers of eggs (Verity and Smayda 1989; Ederington et al. 1995). Cultures were inoculated with *S. costatum* strain CCMP 1332 (Provasoli-Guillard National Center for the Culture of Marine Phytoplankton, Bigelow Laboratory) and grown in f/2+ medium (Guillard 1983) at 21 psu and light–dark cycle of 12 : 12 h. Since diatoms lose their buoyancy quickly when nitrogen limited (Richardson and Cullen 1995), the cells were harvested during the early or middle exponential phase. In addition, we allowed the cultures to settle for at least 2 h and decanted the cultures so that only buoyant and healthy cells were employed in the experiments. The diatoms were diluted with seawater that was collected at the same time and location as the copepods and that had been filtered through a felt bag with a nominal pore size of 1 μm (bag filtered). Salinity was adjusted by adding deionized water or Instant Ocean (Aquarium Systems).

The core experiments consisted of treatments in which the same quantity of food was presented to the copepods but in two very different distributions. In one set, the diatoms were mixed homogeneously into the tanks, in the other, thin layers of diatoms were established in the center of the tanks. The incubations were performed in 2-m tall tower tanks (76 $\times$ 50.5 mm inside dimensions) made out of acrylic glass and

described in Lougee et al. (2002) and Clay et al. (in press). In preparation for the experiments, seawater collected at the same sites as the copepods was bag filtered and the salinity adjusted as described above. The tanks were slowly filled through valves attached to the sides of the tanks with 3.5 liters of 25 salinity on the bottom, 1 liter of 21 salinity in the center, and 3.5 liters of 17 salinity water on the top. This was done identically for both the homogeneous and the thin-layer treatments. For the homogeneous treatment, the diatoms were mixed evenly into all three parts of the water column at a final concentration of 25 μg C L^{-1} prior to filling the tanks. For the thin-layer treatment, the same amount of diatoms was added, but it was mixed only into the center of the water column at eight times higher concentration (200 μg C L^{-1}). These concentrations were chosen according to the results of the preliminary experiments, showing the response of egg production to changes in food concentration (*see below*). Calculations of carbon concentrations were based on 15 pg C $cell^{-1}$ (Strathmann 1967). Treatments were distributed evenly across tanks over the experimental series in order to avoid tank effects. Tungsten lights were suspended above each tank and automatically switched off at 2100 h and switched on at 0600 h using an X-10 system on a personal computer. The light intensities were ca. 9 μmol s^{-1} m^{-2} at the top and ca. 1.5 μmol s^{-1} m^{-2} at the bottom of the tanks. The position of the copepods was monitored by means of a panning video system mounted parallel to each tank. It consisted of infrared light-emitting diodes (LEDs), lenses that project the infrared light evenly through the tanks, and black and white video cameras. The cameras were equipped with zoom lenses (18–108 mm/f2.5) and infrared filters (Wratten 87) to reduce interference from the visible light at the top of the tanks. Each pan took 6 min, recording the shadow images of the copepods every 2 h during the experiments. The videos were analyzed by counting the number of copepods in 10-cm segments (quadrats) through the entire depth of the tanks. The quadrats on the top and the bottom of the tanks were excluded from analysis because upward and downward moving zooplankton naturally aggregate due to the impenetrable interfaces (bottom and air). We calculated three indices from the raw counts of copepods in each quadrat for each pan. The index of mean crowding was calculated according to (Lloyd 1967)

$$m^* = m + \left(\frac{\sigma^2}{m} - 1\right)$$

where m^* is the mean crowding, m the mean, and σ^2 the variance of the number of copepods in the average quadrat. This index reflects the number of copepods in the near vicinity of each copepod. It is therefore a density measure based on individuals and not on area. An index of 2 means that there are on average two other copepods for each copepod per quadrat. Another index suggested by Lloyd is the index of patchiness (P),

$$P = \frac{m^*}{m}$$

If the variance equals the mean, the index P is 1. Indices larger than 1 are considered characteristic for overdispersed

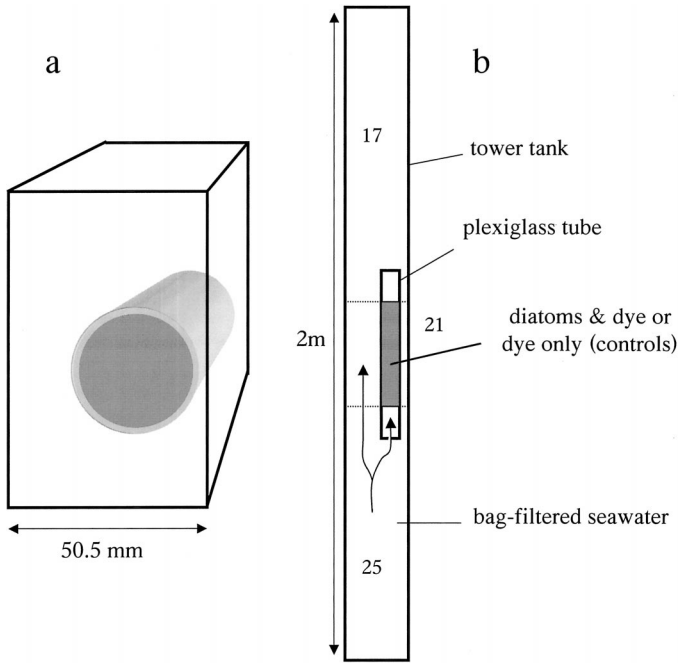

Fig. 1. Experimental setup for the choice experiments. An acrylic glass tube with an inner diameter of 32 mm was suspended in the center of the tanks with nylon threads. (a) An upward view of the tube in the tanks drawn to scale. (b) Diatoms and water without diatoms were slowly added simultaneously inside and outside the tube, respectively, in order to maintain the same salinity gradients (25, 21, and 17).

populations. For densities, Bez (2000) suggested the use of an index of aggregation (I_a) calculated as

$$I_a = \frac{\sum_i z_i^2}{S \times \left(\sum_i z_i\right)^2}$$

where I_a is the index of aggregation, z_i is the density of copepods in each quadrat, and S is the sample area. Like Lloyd's crowding (Eq. 1), I_a is domain (i.e., scale) independent (Bez 2000). We could therefore use I_a for the comparison of fluorescent values to copepod counts.

In another suite of experiments, we explored the possibility that *Acartia* is able to find and exploit patches of diatoms at close range. These experiments were set up as choice experiments that gave the copepod the option to swim through a patch of diatoms or to pass around it. The experimental setup is shown in Fig. 1. Thirty-centimeter long acrylic glass tubes with an inner diameter of 31.5 mm were suspended in two tanks (Fig. 1). In one tank, diatoms were mixed at 500 μg C L^{-1} with a dilute solution of neutral red dye (Sigma-Aldrich) and added into the tubes while the tanks were slowly filled. In the control tank, the dye without diatoms was added to the tubes. Neutral red is a vital stain that did not reveal any toxic effects in laboratory tests with copepods (Anstensrud 1989). The salinity gradient was the same throughout all tanks: 25 in the bottom, 21 in the center, and 17 in the top of the tank (Fig. 1). The copepods were

added to the top of the tank and incubated for 12 h. At the end of the incubation, the water was gently siphoned from the tank into a bucket using Tygon tubing with an inner diameter of 8 mm. All of the water was then gently poured through a submersed sieve with a 30-μm Nitex screen to collect the copepods. The live copepods and the red stained copepods were counted.

Two preliminary experiments established the relationship between diatom concentration and egg production. The copepods were starved in GF/F seawater 24 h prior to the experiments to cease egg production. In one experiment, the copepods were incubated in 1-liter polyethylene jars on a plankton wheel for 20 h at eight different food concentrations (i.e., 10, 20, 40, 60, 80, 100, 150, and 200 μg C L^{-1}). In another experiment, animals were incubated in the tower tanks at four distinct concentrations (i.e., 20, 40, 80, and 160 μg C L^{-1}) for 20 h.

The postincubations in all experiments were performed with individual copepods placed into 20-ml scintillation vials, which were filled with reoxygenated GF/F seawater. For consistency among experiments, no food was added. This also ensured that the various egg production rates reflected the treatments during the main incubations and the signal was not diluted by new material and energy entering the organism. As a consequence, egg production was relatively low in our experiments and should not be compared to egg production rate measurements on freshly collected, actively feeding copepods. The postincubation period of 24 h was informed by the time series experiments that indicated that a time interval of a minimum of 12 h was necessary to see a differential egg production in response to a food treatment. After postincubation, the condition of the animals was assessed. Only eggs from actively swimming copepods were included in our analyses. The postincubation was terminated by adding 4% buffered formaldehyde stained with Rose Bengal (Stearns et al. 1989). Eggs were counted directly in the scintillation vials on an inverted microscope at 40× magnification. To avoid refraction of light on the bottom of the scintillation vials and to obtain a clear image, the vials were placed in a Petri dish containing immersion oil. This way we did not lose eggs due to additional transfers.

Four time series experiments were performed in order to establish the dynamics of egg production following differential food treatments. In an initial experiment, copepods were starved for 24 h until they ceased egg production. They were then individually transferred into 20-ml scintillation vials containing diatoms in order to determine the time it takes from a food pulse to the beginning of egg production. In the other four time series experiments, eight egg collectors (Fig. 2) were employed. Ten fertilized females were added into each of the columns. In time intervals of 2–4 h (depending on the trial) eggs were flushed into the Petri dishes by bleeding air into incubator tubes through the valves on top of the containers. This way, eggs were removed with a minimum amount of disturbance to the animals. An additional advantage of these devices was that the water in the container could be removed and recharged with a new concentration of food simply by immersing the tubes into a container with the new concentration of food. In order to not damage the animals during water changes and transfer, a residual amount

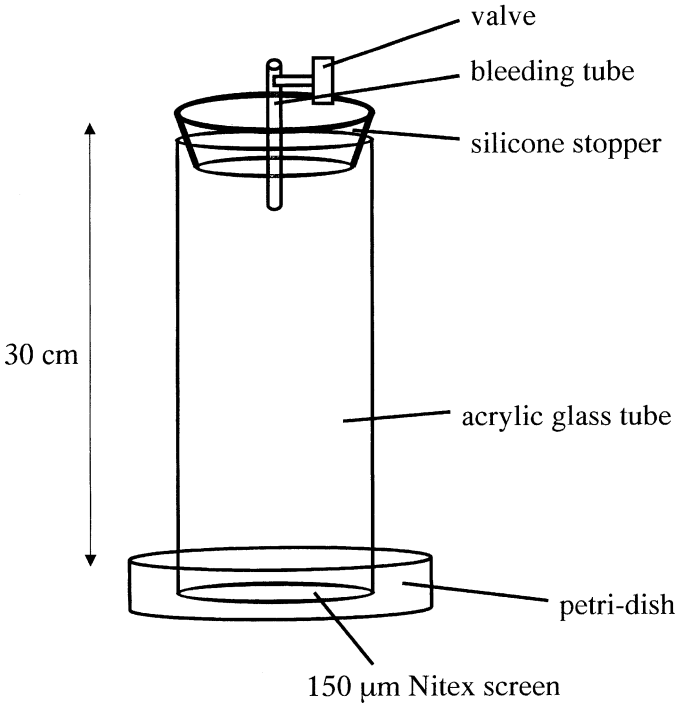

Fig. 2. Egg collectors used in the time series experiments. Animals were added by immersing the tubes in buckets of water containing the experimental food suspension. Before lifting the tubes from the bucket, we replaced the stopper and closed the bleeding valve. The tubes were put in a rack standing upright in Petri dishes. The surface tension of the net (150-μm mesh) and the stopper held the water in the tube. Eggs were rinsed into the Petri dish by bleeding air into the top of the tube.

(1 cm) of water must be left on top of the screen. Whenever copepods were switched from one extreme concentration to another (e.g., from high food concentration to filtered seawater), additional rinses with the new concentration were performed by repeatedly ($n = 3$) filling and emptying the columns in the target concentrations. The eggs that dropped into the Petri dishes were rinsed onto a 30-μm screen and subsequently into scintillation vials. Copepods, eggs, and fecal pellets were preserved in 4% buffered formaldehyde containing Rose Bengal (Stearns et al. 1989).

Results

Over the duration of the core experiments (12 h), the diatom layers stayed intact and remained suspended on the pycnocline, although the layer tended to sink slightly (Fig. 3). The distribution of copepods showed a significant but ephemeral effect of thin layers of food (Fig. 3, Table 1). Our hypothesis was that the copepods would show an increase in the indices of aggregation in response to the aggregated food in the thin layer and would show a lesser degree of aggregation in the homogeneous food treatments. Table 1 shows the summary of Lloyd's crowding, the Lloyd index of patchiness, and the index of aggregation (I_a) across all experiments for each of the time periods after the start of the experiments. When all times (except the time at the re-

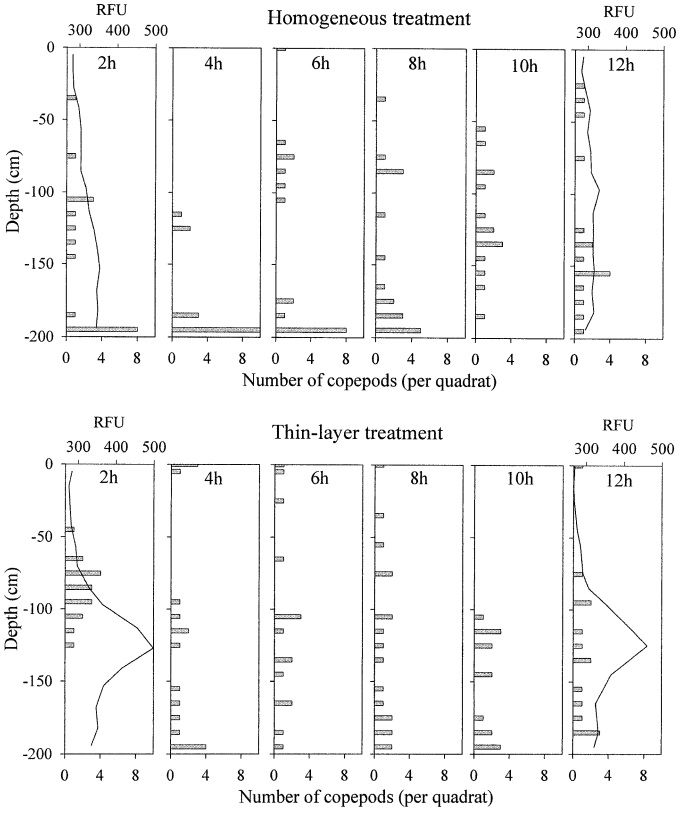

Fig. 3. Representative example of the distribution of copepods (bars) in relation to the distribution of Chl *a* experiments in 2-h intervals. Upper panel, example of homogeneous treatment; lower panel, example of thin-layer treatment. Solid lines, distribution of diatoms (relative fluorescent values).

lease of the animals) were pooled (t2–t12), there was a significant effect of treatment on the Lloyd index of crowding (analysis of variance [ANOVA] with treatment nested in experiment, df = 119, $F = 5.64$, $p < 0.0001$) and the Lloyd index of patchiness (ANOVA with treatment nested in experiment, df = 119, $F = 2.32$, $p = 0.020$). However, the more conservative index of aggregation (Bez 2000) was not significantly different between thin layer and homogeneous treatments (nested ANOVA, df = 119, $F = 0.87$, $p = 0.55$). When the samples were split into intervals of elapsed time after the introduction of the copepods, the Lloyd index of mean crowding was significantly affected by treatment at 2 and 4 h after the introduction of the copepods but not at the remaining time periods (t0 and t6–t12) (Table 1). The Lloyd index of patchiness was significantly affected by treatment at $t = 2$ only. The index of aggregation (I_a) was the least sensitive of the three indices, since treatment did not significantly influence I_a of the copepods at any point in time (Table 1). Plotting I_a of the copepods against I_a of the diatoms did not yield a significant regression (Fig. 4).

Treatment (thin layer or homogeneous food) significantly influenced the average depth at which the copepods were found in the tanks. Accounting for a decrease of average depth with elapsed time, the copepods remained significantly shallower in the thin-layer treatments than in the homogeneous treatments (Fig. 5). The effect was subtle, however,

Table 1. Lloyd's index of mean crowding, Lloyd's index of patchiness, and Bez's index of aggregation I_a (Bez 2000). Mean ± standard deviation are shown for 2-h time intervals after the introduction of copepods into the tanks. H = homogeneous distribution of *Skeletonema costatum* in the tanks, TL = thin layers of *S. costatum* in the tanks. 0 = first pan approximately 10 min after the introduction of the copepods. Sample size was 20 for each row. Probability values reflect significance levels when nesting treatment within experiment * $p < 0.05$; *** $p < 0.001$. Means shown are overall means across all experiments not accounting for differences between experiments.

Elapsed time (h)	Index	H	TL	$p < 0.05$
0	crowding	2.83±1.28	2.60±1.22	
	patchiness	2.76±1.09	2.81±1.05	
	I_a	0.20±0.05	0.21±0.052	
2	crowding	1.17±0.70	1.49±0.49	*
	patchiness	1.51±0.76	1.79±0.41	*
	I_a	0.16±0.03	0.16±0.03	
4	crowding	1.06±0.63	1.34±0.93	*
	patchiness	1.48±1.18	1.80±1.00	
	I_a	0.16±0.09	0.18±0.05	
6	crowding	0.98±0.70	1.37±0.87	
	patchiness	1.22±0.78	1.72±0.77	
	I_a	0.13±0.04	0.17±0.04	
8	crowding	1.51±0.63	1.22±0.74	
	patchiness	1.71±0.62	1.46±0.85	
	I_a	0.16±0.03	0.15±0.05	
10	crowding	1.99±1.62	1.52±1.01	
	patchiness	2.37±2.31	1.81±0.74	
	I_a	0.19±0.13	0.17±0.03	
12	crowding	1.67±1.16	1.72±1.01	
	patchiness	1.79±1.03	1.98±0.85	
	I_a	0.16±0.05	0.17±0.04	
All times	crowding	1.60±1.15	1.61±0.98	***
	patchiness	1.84±1.28	1.91±0.89	*
	I_a	0.17±0.07	0.17±0.04	

with an average distance between treatments of only 12.7 cm in the 2-m water columns (df = 139, $t = 3.27$, $p = 0.006$; General Linear Model (GLM) using experiment, $p < 0.0001$, elapsed time $p < 0.0001$; and treatment as independent variables, $p = 0.0019$). There was no detectable tank effect ($p = 0.26$) and ''tank number'' was removed from the model for further analysis.

The relationship between egg production of the postincubations and the concentration of diatoms at various initial food treatments is shown in Fig. 6. Egg production was low at concentrations up to about 30 μg C L^{-1} and reached saturation at approximately 100 μg C L^{-1}. As a result of these incubations, we chose 25 and 200 μg C L^{-1} as the two food concentrations at the extreme end of the spectrum in order to maximize the sensitivity of the method to the two treatments (homogeneous at 25 μg C L^{-1} and thin layer at 200 μg C L^{-1}; arrows in Fig. 6).

It took 12 h for egg production to resume after starvation and a subsequent food pulse of *S. costatum* (Fig. 7). The results of cumulative egg production in the time series experiments are shown in Fig. 8a–c. When *Acartia* was fed on the two different food concentrations for 12 h, the egg production curves gradually drifted apart 6–12 h after the co-

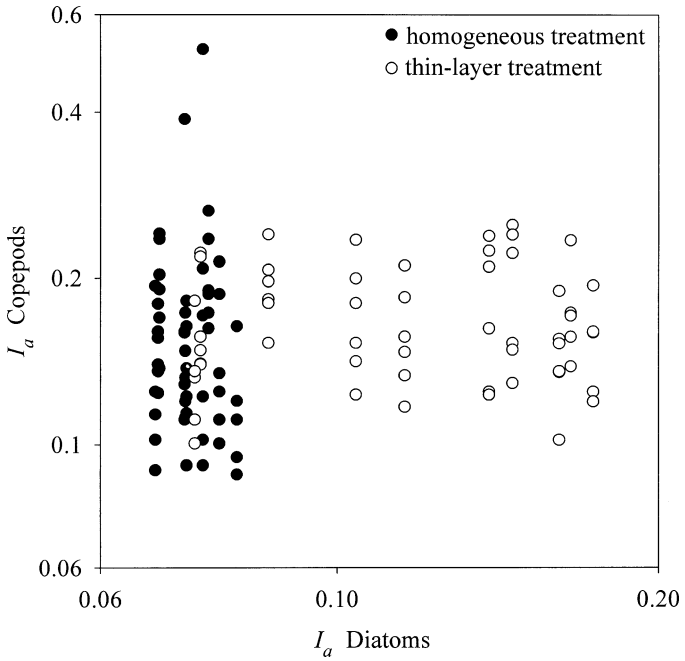

Fig. 4. Index of aggregation (I_a) for diatoms and copepods. Dark circles = homogeneous treatment, light circles = thin-layer treatment. There was a clear distinction in the distribution of diatoms between treatments; however, copepods did not aggregate significantly more in the thin-layer treatments than in the homogeneous treatments. Linear regression: df = 119, r^2 = 0.001, F = 0.25, p = 0.615.

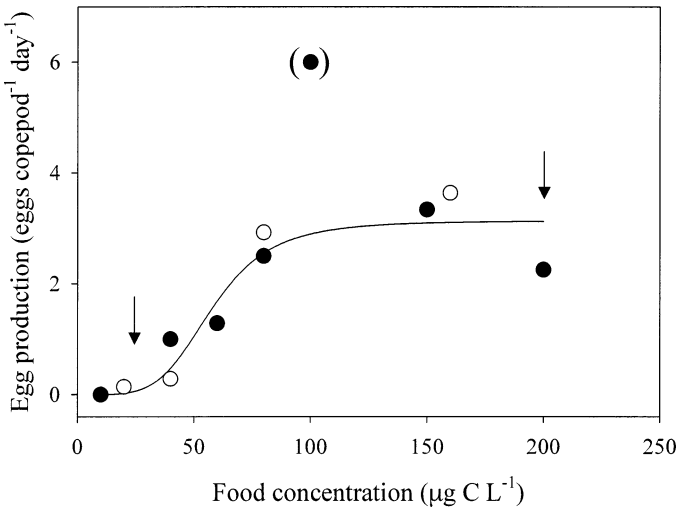

Fig. 6. Egg production of *A. hudsonica* in response to 24-h incubations at nine different concentrations of homogeneously distributed diatoms. Four incubations were performed in the tower tanks (open circles), the remainder of the trials in 1-liter jars put on a rotating wheel (dark circles). The equation was fit to the data excluding one outlier (parentheses): EPR = $(3.13 \times C^{4.59})/(58.10^{4.59} + C^{4.59})$, where EPR = egg production rate (copepod^{-1} d^{-1}) and C is the concentration of *S. costatum* cells (μg C L^{-1})

pepods were transferred into the same treatment (Fig. 8a–c). When copepods were transferred from differential feeding conditions into filtered seawater for 24 h, the copepods that originally fed at 25 μg C L^{-1} produced in total approximately 30% fewer eggs than those that fed at saturated concentrations at 200 μg C L^{-1} (Fig. 8b). The slope (egg production rate) was 0.10 eggs copepod^{-1} h^{-1} after incubation in the low food concentration and was significantly lower than the slope after incubation in the high concentration treatment (0.15 eggs copepod^{-1} h^{-1}) (analysis of covariance [ANCOVA] homogeneity of slopes, df = 95, F = 7.46, p = 0.0076, Fig. 8b). When the copepods were fed at the two different concentrations but subsequently transferred into a saturated food concentration of *S. costatum*, the egg production continued and a separation of the signal occurred a few hours into the incubation. However, after approximately 38 h, the difference between the two treatments was also only

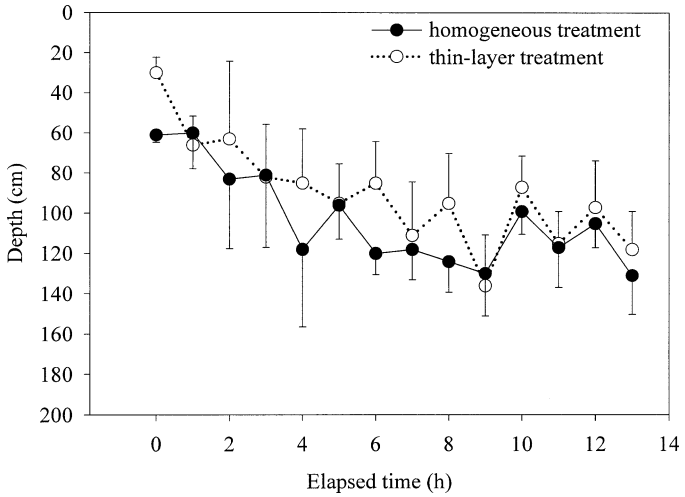

Fig. 5. Average depth of the copepods across all thin-layer experiments. Copepods stayed significantly higher in the water column when a thin layer was present between 2 to 8 h counted from the start of the experiments. Bars: 0.5 standard deviation.

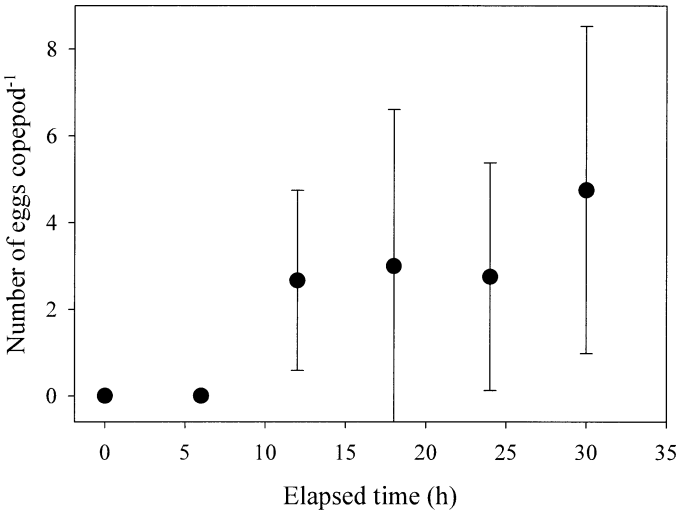

Fig. 7. Number of eggs produced by *A. hudsonica* after a 24-h starvation period when fed on a saturated concentration (>200 μg C L^{-1}) of *S. costatum.* Diatoms were added at time = 0. Egg production resumed ca. 12 h after the addition of diatoms.

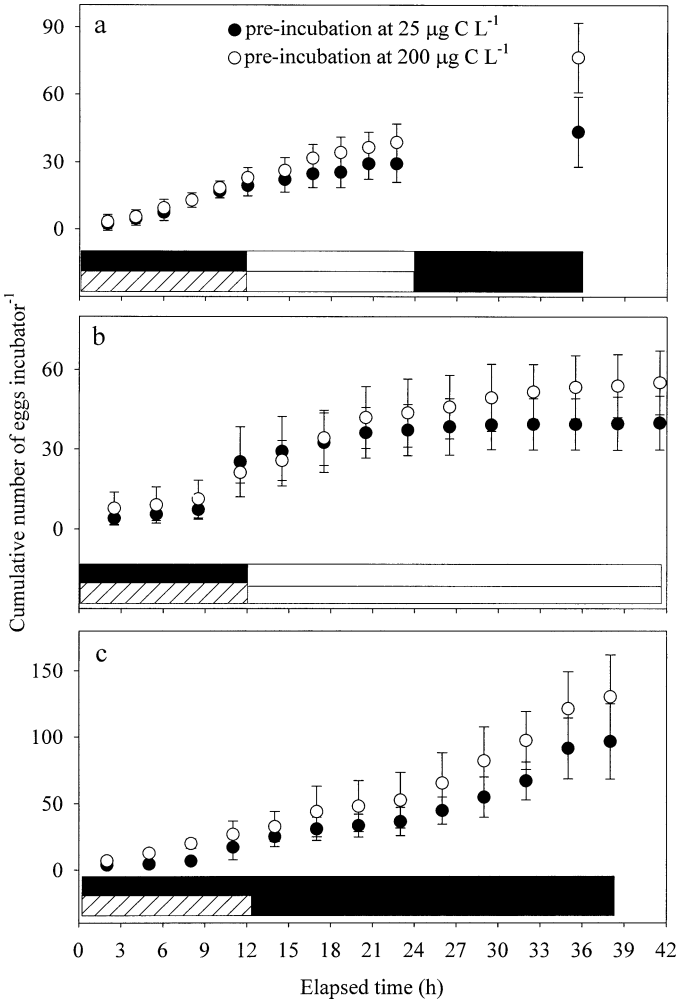

Fig. 8. Time series experiments: Cumulative number of eggs produced during exposure to varying food concentrations. Dark circles = first 12 h at low concentration (25 μg C L^{-1}). Light circles = first 12 h at high concentration (200 μg C L^{-1}). After the initial 12 h the animals were treated identically. As a reference, the bars near the *x*-axis indicate the concentration of diatoms in the two treatments during experimental incubations. Dark = 200 μg C L^{-1}, hatched = 25 μg C L^{-1}, clear = bag-filtered (1 μm) seawater.

ca. 30%. The egg production in the postincubation was significantly higher when the copepods were initially fed at high concentration (0.39 eggs copepod^{-1} h^{-1}) than when they were initially fed at low concentration (0.29 eggs copepod^{-1} h^{-1}) (ANCOVA test for homogeneity of slopes: df = 79, F = 4.52, p = 0.0368, Fig. 8c).

Except for one experiment, fecal pellet production was slightly higher in the homogeneous treatment than in the thin-layer treatment (Table 2, mean difference between treatments = 8 fecal pellets copepod^{-1} over the 12-h interval; ANOVA with treatment nested in experiment, df = 19, F = 6.29, p = 0.0041). The average egg production in the postincubation was significantly influenced by experiment number and tank but not by treatment in four out of five experiments (homogeneous and thin layer, Table 3). Overall, there was no significant difference on egg production between the two treatments (Table 3). Even when egg-laying copepods only were considered, there was no significant effect of treatment on egg production (Table 3). There was also no detectable effect of treatment on the number of egg-laying females (Table 3).

Table 2. Fecal pellet production per copepod in each tank and experiment during 12-h incubations. Overall shows means of experimental means (nested) ± standard deviation.

Experiment	Homogeneous	Thin layer
1	38.15	27.97
	47.33	33.71
2	60.55	33.19
	50.83	44.27
3	43.00	37.92
	58.93	42.98
4	43.56	47.79
	33.84	45.39
5	25.00	20.40
	29.31	21.00
Overall	43.05±11.11	35.46±9.98

The choice experiments revealed that the copepods were able to respond to diatom patches over short (i.e., centimeter) distances. There was a significantly higher percentage of copepods stained red in the treatments with diatoms (60% ± 13 standard deviation [SD] of the total) than in the dye-only controls (45% ± 10 SD) (paired one-tailed *t*-test, n = 14, t = 2.97, p = 0.013).

Discussion

Despite multiple transfers, the copepods were in excellent shape at the end of the experiments. This high level condition of the copepods was a result of 13 preliminary experiments that were not included in the analysis but allowed us to improve our transfer and incubation protocols. As a result, >90% of the individuals could still respond with a fast escape response after the experimental treatments and the 24-h starvation period. While in the tanks, and judging from the shadow images of the copepods on the tapes, the animals were very active and showed normal sequences of jumping and feeding bouts (Tiselius 1992). The cruising speed of these animals was approximately 0.3 m per min, which is within the range of vertical displacement speeds of 0.18–0.36 m min^{-1} for the closely related *Acartia clausi* (Leising and Franks 2002). The height of our tanks was of great advantage because we saw copepods aggregating as far as 30 cm away from the surface and bottom of the tanks. Given that the average depth of San Francisco Bay, including San Pablo Bay, Central Bay, and South Bay, is approximately 3.6 m (U.S. Geological Survey), the spatial scales in our experiments are much closer to reality than traditional extrapolations from jars to the coastal ocean.

Another important question is the suitability of *S. costatum* as food for *A. hudsonica*. *Acartia* feeds raptorially and selects for microzooplankton (e.g., Wiadnyana and Rassoulzadegan 1989). It is therefore possible that the observed lack of aggregation response toward the diatoms is because these

Table 3. Egg production rates (eggs copepod^{-1} d^{-1}) during the 24-h postincubation interval in the thin layer (tl) and homogenous (h) treatments across experiments, including overall mean. *F* and *p* values according to a one-way ANOVA.

Analysis	No.	n_h	Average$_h$ ± SD	n_{tl}	Average$_{tl}$ ± SD	*F*	*p*
All individuals	1	19	2.30±3.00	23	2.51±2.86	<0.01	0.950
	2	11	6.00±4.12	13	3.52±2.11	4.38	0.048*
	3	30	2.60±3.43	38	2.28±3.47	0.13	0.715
	4	42	2.93±2.94	34	4.28±4.71	2.39	0.127
	5	23	0.88±1.43	29	0.69±1.36	0.04	0.836
	Overall	135	2.49±3.15	137	2.57±3.68	0.04	0.847
Egg-laying females only	1	10	4.50±3.37	13	4.31±3.54	0.02	0.897
	2	11	6.00±3.69	12	3.58±2.50	3.43	0.078
	3	16	4.88±3.32	20	4.35±3.79	0.19	0.666
	4	27	4.37±2.65	21	6.81±4.46	5.58	0.023*
	5	13	2.23±1.42	10	2.30±2.54	0.01	0.935
	Overall	77	4.36±3.04	76	4.63±3.86	0.23	0.634
Percentage of egg-laying females	1		53		57		
	2		100		92		
	3		53		53		
	4		64		62		
	5		57		34		
	Overall	5	65.40±18.09	5	58.83±18.86		

diatoms are not preferred food. However, chain-forming diatoms are often a major component of phytoplankton patches that can be potentially used by grazers (Sieracki et al. 1998), and diatom blooms, in general, form the basis for seasonal secondary production (Irigoien et al. 2002). *Acartia* co-occurs with *S. costatum* during the spring bloom in San Francisco Bay (Rollwagen Bollens pers. comm.) and *Acartia* produced tenfold more eggs in response to feeding on this diatom species than on ciliates (Ederington et al. 1995). For these reasons, understanding the interaction of one of the most important copepod species in Northeast Pacific estuaries with an important bloom-forming diatom is critical.

There are two studies that are closely related to ours and that were used to guide our initial experimental setup. Tiselius (1992) studied the behavior and fecal pellet production of *Acartia tonsa* in response to thin layers of the diatom *Thalassiosira weissflogii,* and Saiz et al. (1993) investigated the effect of thin layers of the same diatom on *A. tonsa* egg production. In the first study, *A. tonsa* spent significantly more time in the food layers compared to homogeneous controls (Tiselius 1992). Fecal pellet production in these experiments was equally high in the thin-layer treatments and the homogeneous treatments (Tiselius 1992). Our experiments showed a different trend. Significantly fewer fecal pellets were produced in our thin-layer treatments than in the homogeneous treatments. There is another explanation for the observed discrepancy besides possible species-specific differences. First, the spatial scales at which our experiments were performed were an order of magnitude larger than the scale in the experiments by Tiselius (1992). Instead of 20-cm tanks and 3-cm thick food layers, we used 2000-cm tanks and 25-cm thick layers. This difference in scale may be important because copepods in our setup could move sufficiently far away from the layer as to not bounce back into the food layer by chance (*see below* for perceptive ranges, retention strategies, and choice experiments).

Fecal pellet production rate is a useful proxy for ingestion rate when *Acartia* feeds on diatoms (Besiktepe and Dam 2002). It is remarkable that the copepods produced more fecal pellets in the homogeneous treatment than in the thin-layer treatment, although the difference was small. We did not consider fecal pellet size (Dagg and Walser 1986) or fecal pellet density (Urban et al. 1993). Both could potentially increase at higher ingestion rates. Since we based ingestion rates on fecal pellet counts, we may have slightly underestimated ingestion rates in our thin-layer treatments.

In the second study similar to ours, Saiz et al. (1993) recorded the egg production of *A. tonsa* in response to thin layers of the diatom *T. weissflogii.* As in our study, their results showed no significant difference between homogeneous and thin layers in terms of egg production. In contrast to Saiz et al. (1993), however, we used the same total amount of food between treatments and could compare egg production directly, whereas Saiz et al. extrapolated their egg production data using a functional response curve published in an earlier paper (Paffenhöfer and Stearns 1988). Extrapolation from a functional response model derived from experiments under steady-state bottle incubations is likely to be inaccurate for patchy food distributions. In addition, the short 6-h postincubation used by Saiz et al. (1993) is of concern. As we have shown in our experiments, it took the copepods' egg production between 12 and 20 h to respond to the differential food treatments (Figs. 7 and 8). Tester and Turner (1990) found considerable variability in the time that elapsed from feeding to a subsequent peak in egg production within the genus *Acartia.* The egg production delay ranged from 9.5 h for *A. tonsa* to 91 h for *A. ornata.* Our results corroborate field studies that show that there is a significant correlation of egg production with food concentrations 24–27 h prior to the egg incubations (Stearns et al. 1989), although a slight effect may already be noticeable after a few hours (Dagg 1988). The 6-h incubations used by Saiz et al. (1993) may therefore have been insufficient to resolve the

relatively subtle expected differences between the two treatments.

Overall, there was no treatment effect on egg production in our experiments. The means across all experiments between homogeneous and thin-layer treatments were 2.49 ± 3.15 ($n = 135$) and 2.57 ± 3.68 ($n = 137$), respectively. An a posteriori power test using our sample size and the observed variance showed that we would have been able to distinguish a difference between treatments of as little as 30% with a power >0.80 (effect size $d = 0.26$). Any substantial difference in egg production would therefore have been apparent. The slight benefit that the homogeneous distribution might have had over the thin-layer treatments in terms of ingestion (i.e., fecal pellet production) disappeared in the egg production. This highlights the fact that nutrients are not put into egg biomass at once but rather spread out over physiological time scales. In order to have increased benefit from a patchy food distribution, individuals would need to stay within a thin layer much longer than they did according to our video observations: a minimum of 12 h as our time series experiments suggested (Fig. 8), or at least 20 h for a maximal effect (Fig. 6).

The Lloyd index of mean crowding was the most sensitive index for detecting differences in the distribution of copepods between treatments. According to the analysis shown in Table 1, the copepods were highly aggregated on the top of the water column shortly after they were introduced into the tanks. After 2 and 4 h they were significantly more aggregated in the thin-layer treatment than in the homogeneous treatment. After 6 h, they were equally dispersed in the thin-layer and homogeneous treatments. This observation is consistent with the average depth distribution during the time course of the experiments (Fig. 5). The presence of the thin layer of diatoms seemed to have retarded the dispersion of the copepods in the tanks in comparison to the treatments in which food was homogeneously distributed. The difference between treatments, however, was subtle and ephemeral. These findings correspond to earlier findings by Tiselius (1992), who showed that copepods slow down their average swimming speed due to increased feeding activity.

This pattern of increased retention in a food layer can result from an area-restricted search strategy in which the step length of an individual hop decreases and the turn angle increases when entering a food patch (Leising 2000). However, differences in behavior were only found between feeding copepods and unfed controls but not at different food levels (Leising and Franks 2002). Uchima and Hirano (1988) reported that changes in swimming as a response to changes in food level depended on acclimation conditions. Copepods in that study (*Oithona davisae*) responded less sensitively when they were acclimated at high versus low concentrations of food. The strongest changes in behavior (i.e., decreased motility) are usually observed when the copepods are in direct contact with food cells (Williamson 1981; Buskey 1984). These examples highlight the diversity of copepod behavioral responses toward patchy food distributions, depending on species, food type, and feeding history (Donaghay 1988). It would be very valuable to compare the response to patchy food of phylogenetically more ancient copepod superfamilies such as the Centropagoidea, to which the genera *Acartia* and *Centropages* belong, to the more modern copepod genera such as *Clausocalanus*, *Eucalanus*, and *Calanus*, since there are systematic differences in sensory abilities between these two groups (Lenz et al. 2000).

Aggregation in response to dissolved amino acids was reported in an earlier study for *A. hudsonica* and *Eurytemora herdmani* (Poulet and Quellet 1982). However, it is unlikely that the receptors of the copepods are suitable to detect particles over large distances (Jonsson and Tiselius 1990). The results from our choice experiments confirm this, since only 60% of the copepods came in contact with the dye if diatoms were present (treatment), as opposed to 45% that swam through the dye by chance (controls). The difference between controls and treatments was significant but not large and is probably linked to small changes in the swimming behavior upon encountering the scent of nearby diatoms around the rim of the tube. Minimal aggregation in response to food patches in our experiments may even be the result of complex behavioral engagement of *A. hudsonica* with its environment. Other than locating food, copepods face multiple trade offs ranging from tidal vertical migrations in order to maintain their preferred longitudinal position in the estuary (Kimmerer et al. 1998) to vertical migrations to avoid predators (Bollens and Frost 1989, 1991). Overall, and for all the species of the genus *Acartia* for which the response to patchy food distributions have been investigated so far (*A. clausi*, *A. hudsonica*, and *A. tonsa*), the observed effects ranged from subtle (behavior) to negligible (egg production).

Although the copepods did not remain aggregated for prolonged periods in response to the food layers, they must have taken advantage of the layer to a certain extent or they would not have been able to produce the same number of eggs as in the homogeneous food distributions. We can therefore rephrase this spatial question as a temporal one. A copepod that swims through a patch of food encounters a brief pulse of food. Indeed, many copepods seem to gorge feed after periods of starvation (e.g., Frost 1972; Mackas and Bohrer 1976), and some budget calculations suggest that temporally limited encounter with prey may even be advantageous for nocturnally migrating copepods (McAllister 1971). In most experiments, different amounts of food were given in pulse and in continuous treatments so that the results were confounded by a simultaneous effect of total food availability (Dagg 1977; Fancett and Kimmerer 1985; Marcus 1988). In one of the few experiments in which the same total amount of food was made available to animals, oyster spat did better when food was given in pulses rather than at low concentrations that were spread over time (Langton and McKay 1974). In a study on the copepod *Centropages typicus*, Davis and Alatalo (1992) found that this copepod was able to integrate nutrient acquisition over daily fluctuations in their food supply at amplitudes comparable to those found in their natural environment. When Davis and Alatalo (1992) pulse-fed dinoflagellates at frequencies of 7 and 14 h, respectively, *C. typicus* displayed the same growth rates and produced as many eggs as when feeding continuously on the same total amount of food. A potential problem of pulsed food availability is that recovery from starvation is associated with additional energetic costs (Kremer and Kremer 1988; Thor 2003) probably due to increased energy requirements to re-

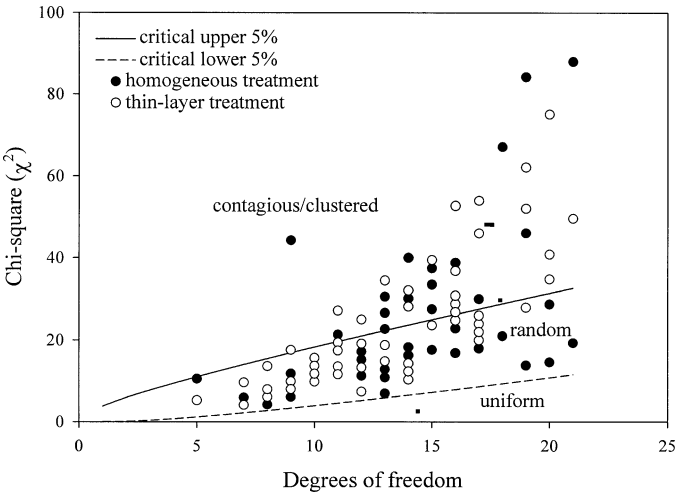

Fig. 9. Chi-square distribution of *A. hudsonica* in the video observations. The solid line traces the upper 5%, the dashed line the lower 5% critical chi-square values for each degree of freedom. This method allows for the distinction of three domains: uniform, random, and contagious distributions of copepods in the tanks (Brower and Zar 1984).

start growth and egg production and increased specific dynamic action (Kiørboe et al. 1985). Any benefits from a sudden high food pulse could therefore be lost. In our experiments, the copepods seemed neither to benefit nor to be at a disadvantage from patchy food distributions. Given that we offered two extreme food environments, it is quite remarkable that the mean egg production was so similar (Table 2). This points toward a capacity of *A. hudsonica* to efficiently deal with small-scale variability in its food environment.

Distributions of copepods in response to their food environment can be complex and often unpredictable (Conover et al. 1988). As with most complex behaviors, the influences are multifactorial and can rarely be modeled via simple algorithms. This notion corresponds closely to field studies by Daro (1988), who showed that the vertical distribution varied depending on the species, the stage, and the availability of food. There are examples in which copepod abundance peaks coincided with either subsurface Chl *a* maxima (Sameoto 1984) or productivity maxima (Herman 1983; Napp et al. 1988) in the sea. Others show that abundance peaks of small pelagic crustaceans did not co-occur with the maxima of fluorescence in the water column (Jaffe et al. 1998) but instead with a more persistent chlorophyll peak with a weaker fluorescent signal. It is often difficult to separate physical from biological effects in the field, a fact that highlights the importance of supplementary laboratory tests under controlled conditions. For instance, in approximately half our experiments the copepods were more aggregated than expected by chance alone (Fig. 9). Since we used identical salinity stratifications in all our tanks, we could distinguish biological and physical effects and show that the diatoms themselves affected the distribution of copepods only slightly. In the field, similar coinciding copepod and phytoplankton peaks could easily be interpreted as copepods actively tracking their prey. Aggregation of plankton in the vicinity of pycnoclines is a well-known phenomenon (Harder 1968). Recently, Lougee et al. (2002) showed that this also holds true for *A. hudsonica* using our experimental setup. As Cowles et al. (1998) pointed out, there is little benefit for a grazer population if the prey organisms are randomly distributed in a heterogeneous food environment. A certain amount of predictability is required for the development of behavioral adaptations and foraging strategies over evolutionary time scales. Since thin layers are often associated with steep density gradients, they make excellent candidates as targets for behavioral adaptations. In order to increase the probability of consistently finding more food, it may therefore be more advantageous for copepods to respond to physical cues rather than chasing after ephemeral food patches.

In conclusion, *A. hudsonica* responded significantly to various states of aggregation of diatoms in terms of their distribution. There was also an increased tendency to swim through a patch of food when presented at close range (instantaneous behavioral response). These behavioral effects, however, were small and ephemeral. Feeding rates were slightly higher in the homogeneous than in the thin-layer treatments. These differences in behavior and feeding, however, were lost over longer physiological time scales representative of egg production. The result is a dampening effect—at least in this trophic link—in which small-scale patchiness of prey does not translate into variability in secondary production. Conversely, centimeter-scale variability may be critical for motile microplankton that aggregate in patches of prey (i.e., larvae, rotifera, ciliates, flagellates; Fenchel and Blackburn 1999). Thus, more detailed experimental studies are required in order to compare relevant scales among species and groups of plankton and across various prey types. For *A. hudsonica,* food concentrations integrated over the entire water column may be more representative than local prey maxima, as long as these peaks of high prey densities are sampled at sufficiently high resolution (Cowles et al. 1998). The relevant spatial and temporal scales of secondary production of these actively migrating copepods may therefore lie in the meter and day range, rather than the centimeter and second range.

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