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Food quality and the heterogeneous spatial distribution of meiofauna

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ABSTRACT: Several different experimental approaches were used to examine recruitment of benthic meiofauna to patches of selected species of algae. In one approach algal-coated, baited slides were incubated in a salt marsh littoral benthos. The second approach employed patches of algae arrayed equidistantly around an inoculum of meiofauna in a petri dish. Meiofauna were shown to be selectively recruited to patches of some species of algae but not to others. The evidence obtained supports a hypothesis that selective recruitment of meiofauna can be one mechanism which establishes the spatial heterogeneity so often observed in natural collections of meiofauna.

INTRODUCTION

Spatial and temporal heterogeneity of abiotic resources and organisms, at various hierarchies of scale, are commonplace in the natural world. We must presume that interacting species and the communities in which they co-evolved function effectively in this environmental mosaic or else they would not persist today. Quite some time has passed since Hutchinson & MacArthur (1959) concluded that there was a continuous functional relationship between the size of the animal and the size of the mosaic elements of their environment. Though it would seem that the high species diversity of protozoa and small metazoa, their generally high reproductive rates and the mosaic nature of the environment at scales meaningful to them would have attracted many ecologists to use them to study mechanisms of community organization or structure, the specialized skills required for observation and manipulation and the proportionally greater time required in the identification of small organisms have not encouraged too many.

At present it seems easier to develop conceptual frameworks for understanding the mosaic structural and functional relationships in communities dominated by large sessile organisms (e.g. Pielou, 1975) than it does for communities with less, or relatively short lived, structural permanence (e.g. Steele, 1973). In those communities which

have been studied most intensively competition and predation seem to be the mechanisms which organize community structure (e.g. Connell, 1975). Through there is less documentation on this point, asexual reproduction and functionally similar phenomena (i.e. iteropary) seem to provide an additional major mechanism which operates in weaving communities from diverse assemblages of large numbers of small organisms with high reproductive rates.

Current ecological thinking suggests that resource partitioning by food type is more important for animals feeding on food that is large in relation to their own size than it is for animals feeding on relatively small food items (Schoener, 1974). Experimental evidence for protozoa (e.g. Fenchel, 1968; Lee, 1974; Rubin & Lee, 1976) and meiofauna (e.g. Provasoli et al., 1959; Tietjen et al., 1970; Lee et al., 1976) indicates that this concept is particularly applicable to the smallest animals. A conceptual framework for micro and meiofaunal resource optimization within an environmental mosaic could be based on successive responses of the animals to asexual blooms of different species of microflora. Species of littoral foraminifera, for instance, are known to feed, grow and reproduce quite rapidly in response to particular algal blooms (Lee et al., 1966; Lee & Muller, 1973). The explosive bursts of reproduction could lead to the extremely heterogeneous distribution of these animals which have been found in nature (Buzas, 1965, 1969; Lee et al., 1969; Matera & Lee, 1972).

Is it equally plausible that heterogeneity could develop in the small animal community as a consequence of selective recruitment of these animals to specific blooms of algae? At the onset of our experiments, we were unaware of any specific experiments which demonstrated that selective recruitment to algal patches could be a mechanism for structuring communities populated by very small animals.

MATERIALS AND METHODS

Two distinctly separate approaches were used in these experiments. In one approach algal slides were used as bait to attract meiofauna in the environment. The algae used were all isolated in axenic culture from littoral benthic habitats in North Eastern U.S. salt marshes. Algae were chosen for the experiment principally because they have been shown in previous experiments to be good food organisms for one or more species of salt marsh meiofauna (Lee et al., 1966, 1970, 1971; Muller & Lee, 1969; Tietjen & Lee, 1973, 1977; Muller, 1975). The algae used in both experimental approaches were: *Cylindrotheca closterium* (strain 9), *Amphora acutiuscula* var. *coffeaeformis* (Bl 17), *Achnanthes hauckiana* (110), *Nitzschia acicularis* (8), *Nitzschia* sp. (123), *Phaeodactylum tricornutum* (39), *Dunaliella salina* (13), *Chlamydomonas subcordiformis* (94), *Chlorococcum* sp. (38), *Nanochloris* sp. (41), and *Fragilaria* sp. (Bl 714 B). Sterilized microscope slides were aseptically dipped in sterile molten sea water agar (1.5 % agar [w/v] in local sea water) and then placed in sterile Coplin jars. When the agar hardened, a logarithmically growing algal culture was aseptically transferred to the Coplin jars. After 7 days incubation in the light (25° C; 18 h light/6 h dark) the slides were transferred to commercial microscope slide holders (made for staining 5 slides at a time) which gripped the slides at one end. The slides and slide

holders in turn were inserted into a set of in situ incubators which we fabricated from lucite cylinders and flat sheets of the same plastic. The incubators were designed to hold 4 slide holders (Peel-a-Way Sci Div., W. Glen Wunderly Co., South el Monte, California) (with each 3 slides) in immediate contact with the benthic substratum. The walls of the incubators were perforated with small holes (0.5 cm) to permit free exchange of sea water without exposing the slides to macrofauna, and the bottom of the incubators were surrounded with a wide flange which prevented them from sinking into the substratum. There were 4 incubators to a set which were tied by means of nylon ropes to each other and staked so that each incubator was in a quadrant of m^2. In order to study both recruitment and reproduction, incubation times were varied from 2 days to several weeks. Control slides (sea water-agar controls) were randomized with experimental slides and were present in all subsets. At harvest the slide holders were gently removed from the incubators and individual slides were inserted into plastic cytological slide mailing tubes filled with a sodium bicarbonate buffered Rose Bengal-formalin mixture. The organisms on the surface of the slides and in the mailing tubes were examined under a dissecting microscope and when necessary under a compound microscope. The organisms were enumerated only to major group.

The second approach ("cafeteria") to the problem was basically a laboratory one. Large petri dishes (150 mm × 15 mm) were the experimental vessels. They were very carefully filled on a perfectly level surface with 40 ml of sea water agar. Stock cultures of the same experimental algae were grown on similarly prepared plates except that the medium was richer ("S" agar; Lee et al., 1970). An alcohol sterilized # 10 cork borer was used to remove a central and 8 equidistant peripheral plugs of agar from the experimental plates. A template placed under the plates aided the processes. Number 10 plugs of algae from the stock plates were aseptically placed in four alternate peripheral holes in the experimental plates. The alternate spaces between algal patches were filled with plugs of "S" medium agar. Control plates were filled with plugs of "S" agar in all 8 positions. Two series of experiments were conducted in the petri dishes. In the first series synxenic cultures of individual meiofaunal species. *Chromadorina germanica* (nematode), *Nitocra typica* (harpacticoid copepod), *Leptocaris brevicornis* (harpacticoid copepod), *Allogromia laticollaris* (foraminifera) and *Rhabditis marina* (nematode) were inoculated into the central well. In the second series of experiments, 1 ml of freshly collected meiofauna (sieved through 500 μm mesh) from littoral aufwuch communities in the greater Sippewissett salt marsh (Falmouth, Mass., USA) was used as inoculum. After the experimental animals were introduced into the central wells, 20 ml of sterile sea water was very carefully pipetted onto the surface of the petri plates to make a thin aqueous film above the plates. (The special care was necessary to prevent dislodging and distribution of the meiofauna from the central well during the flooding of the plates.) The plates were incubated on a laboratory bench which had a bank of fluorescent lamps ~ 30 cm above it. The lights were cycled every 12 h. The experiments were harvested at either 4 or 10 days. A # 15 cork borer was used to remove an area slightly larger than the original algal or control patches. The plugs were harvested into small vials containing a buffered Rose Bengal-formalin solution. During incubation and harvest great care was exercised not to agitate the experimental vessels. Each experiment was replicated twice.

Table 1

Recruitment to baited slides

Species	Experiment I 7/5 – 7/8	Experiment II 7/17 – 7/24	Experiment III 7/30 – 8/13
Spatial controls I*	179 – 17 – 14**	709 – 49 – 46	2304 – 95 – 58
II	106 – 7 – 18	477 – 28 – 50	480 – 11 – 1
III	78 – 5 – 17	510 – 38 – 52	1038 – 58 – 20
IV	27 – 6 – 1	414 – 55 – 51	404 – 8 – 2
Chlorococcum sp. (38)	60 – 5 – 18	520 – 14 – 24	904 – 39 – 35
Dunaliella salina (14)	136 – 4 – 17	447 – 18 – 52	1217 – 51 – 52
Nanochloris sp. (41)	140 – 20 – 13	507 – 19 – 52	929 – 62 – 63
Nitzschia acicularis (8)	65 – 7 – 16	463 – 48 – 63	555 – 39 – 21
Chlorophyte (50)		655 – 44 – 50	402 – 19 – 16
Amphora acutiuscula (RF 8)	134 – 19 – 21	608 – 94 – 70	369 – 13 – 13
Chlamydomonas sp. (94)	136 – 4 – 18	478 – 29 – 50	914 – 27 – 29
Phaeodactylum tricornutum (39)	60 – 3 – 12	576 – 106 – 62	898 – 41 – 12
Amphora sp. (BL 17)	164 – 6 – 31	536 – 54 – 38	825 – 47 – 21
Nitzschia acicularis (8)	194 – 10 – 18	1004 – 51 – 56	523 – 22 – 23
Amphora sp. (BL 15)	113 – 15 – 20	596 – 50 – 30	477 – 17 – 35
Amphora acutiuscula (RF 8)	66 – 9 – 2	536 – 55 – 58	225 – 8 – 11

* average of 5–9 slides
** nematodes – forams – copepods

Those experiments involving field work were done in 2 successive summers while in residence at the Marine Biological Laboratory, Woods Hole, Mass., USA.

Some additional laboratory experiments were performed with the foraminifer *Allogromia laticollaris* and 2 species of algae, *Nitzschia acicularis* and *Dunaliella parva*. Plates were either uniformly inoculated with either organism, divided into uniformly inoculated algal alternating quadrants, or 4 or 8 algal patches of one species in a uniform background of the other species. Uninoculated discs of media were used as controls.

Analysis of variance was performed with the aid of the UCLA Health Sciences Computer Program BMDOLV.

RESULTS AND DISCUSSION

Both experimental approaches clearly demonstrated that selective recruitment of meiofauna by particular algal patches is a mechanism which can establish spatial heterogeneity in meiofaunal populations. Our conclusion is based on the distribution of nematodes, foraminifera and copepods which are the most frequently encountered meiofauna in our field locations. Ostracods, large ciliates, gastrotrichs, rotifers, nauplii and other invertebrate larvae occur in too few numbers to yield statistically significant information on these organisms. In the baited slide experiments we enumerated the organisms from a total of 144 control and experimental slides in 3 separate experiments. Great variance was found in the absolute numbers of animals recovered from both control slides and experimental slides coated with the same algal species both incubated in different quadrants of the experimental meter in the same experiment or in successive experiments (Table 1). We judge this to be due to differences in populations of organisms available for recruitment at the fairly well separated ($\sim$ 0.7 m) experimental sites. We, therefore, based our analysis of variance on differences between replicate baited slides and control slides in the same experimental set. The number of meiofauna recovered per slide increased with incubation time. For example we recovered a mean of 110.5 ($\pm$ 49.6), 564.7 ($\pm$ 140.7) and 780.8 ($\pm$ 495.2) nematodes per slide for slides incubated 3, 7 and 14 days respectively. Corresponding values for forams were 9.1 ($\pm$ 4.77), 50.4 ($\pm$ 35.1), 34.8 ($\pm$ 24.0) and for copepods 15.7 ($\pm$ 7.2), 50.3 ($\pm$ 11.7) and 25.8 ($\pm$ 18.7) respectively for the same time periods. In many instances we noted juvenile forms on the slides, indicating possible meiofaunal reproduction in situ. The decline in numbers of forams and copepods recovered from the slides incubated for the longest time may indicate migration of juveniles away from their sites of production or depletion or changes in algal resources on the experimental slides. Because it is extremely time consuming we have not yet analyzed the algal populations on the slides to check this latter point, but we have prepared replicate microscope slides for future analysis. Analysis of variance between replicate slides coated with the same algal species and control slides from the same experimental subsets yielded F ratios of 19.762, 10.653 and 27.062 for nematodes, forams and copepods respectively indicating significant differences between them ($F_{.99} \approx 5.03$). We noted that in various subsets slides baited with particular algal species had recruited

more meiofauna than those baited with other species but when we compared the slides from different subsets and those incubated at different times we found no significant differences. We interpret these results again as a reflection of the match between the meiofauna available at the experimental site for recruitment and the algal species being tested at the time. This could be checked in future experiments by identifying the individual meiofaunal species recovered on each baited and control slide. We also noted that on several occasions small polychaetes and haustoriid amphipods had established burrows on our slides. Although not numerous enough to test statistically, we generally recovered many more nematodes and forams from the walls of the polychaete burrows than on other areas of the slides. There were fewer meiofauna recovered on slides with amphipod burrows.

Table 2

Selective recruitment of nematodes to patches of algae in petri dishes

Algal species in patches	Experiment A* incubation 10 days	Experiment B** incubation 10 days	Experiment B** incubation 20 days
Nematodes in inoculum	842	2495	2495
Chlorococcum (38)	15	568***	327***
Chlamydomonas sp. (94)	69***	100***	274***
Dunaliella parva (14)	127***	471***	378***
Amphora acutiuscula (RF 8)	290***	785***	727***
Phaeodactylum tricornutum (39)	38	1076***	246***
Nanochloris sp. (41)	28	103***	102***
Nitzschia acicularis (8)	75***	95***	56***
unidentified chlorophyte (50)	39	959***	310***
Dunaliella salina (13)	69***	6***	127***
Control plate patches	15	4	5
Typical interpatch control (e.g. between algal species 50/13)	40	22	9

* inoculated 30 July
** inoculated 8 August
*** indicates significant difference from random occurrence

A total of 8 "cafeteria" experiments with fresh natural collections of meiofauna were performed in 2 successive summers. In each experiment there were 128 or 138 control or experimental disks which were examined. Inocula varied numerically from experiment to experiment. Because of the fragility of many of the organisms involved, no attempt was made to compact inocula. There were generally larger numbers of meiofauna available for recruitment in inocula from experiments later in both summers than those done earlier. A typical mid-June inoculum had 192 nematodes, 26 forams, 167 copepods, 223 nauplii, 5 ostracods and 1 polychaete worm while in late July a typical inoculum had 1714 nematodes, 10 forams, 95 copepods, 46 nauplii, 11 large ciliates, 3 ostracods, 1 amphipod and 2 gastropods. The numbers declined later in the summer so that a typical mid-August inoculum contained 775 nematodes, 64 forams, 55 copepods, 35 nauplii, 36 large ciliates, 19 ostracods and 12 hydrozoans. Taken as a whole there were no significant differences between replicate algal patches

in the same experiments (F ratio 2.02, $F_{.99}$ 5.3). There were very significant differences between the animal populations on experimental algal patches and control areas (nematodes $F_{.99} = 2.64$; forams $F_{.98} = 2.01$; copepods $F_{.95} = 1.97$; nauplii $F_{.95} = 2.12$; large ciliates $F_{.95} = 2.16$; other groups insufficient data). As in the baited slide experiments, there were significant differences in the fauna recruited by patches of various species of algae (overall F ratio 25.3; significant at the 5 % level) but the attractiveness of a particular algal species varied in successive experiments presumably as a function of the specific animals available in the community for recruitment at the time of each experiment (Table 2). We observed microscopically that there were often changes in the animal populations of patches over a period of several days (Table 2). In some cases populations gradually built up by recruitment and then declined. In other cases reproduction was noted temporarily building up the populations and was followed by dispersal of the offspring.

The "cafeteria" experiments with gnotobiotic laboratory cultures were quite reproducible and in general they gave results consistent with previous tracer feeding and gnotobiotic grown experiments (Lee et al., 1966, 1969; Tietjen et al., 1970; Tietjen & Lee, 1973, 1977). Since the experiments were relatively short (less than the generation times of the meiofauna tested) recruitment to algal patches was the main source of the heterogeneous distribution of the animals. The 4 algal eating species of meiofauna each favored particular algal patches over others (Table 3). *Leptocaris brevicornis* was the most selective of the meiofauna tested; 80 % of the inoculum was found in patches of *Nanochloris* sp. while few were found in patches of *Chlamydomonas subcordiformis, Phaeodactylum tricornutum, Cylindrotheca closterium* or *Dunaliella parva. Chlamydomonas subcordiformis,* on the other hand, attracted more *Allogromia laticollaris* than did the other species of algae tested. When the algal patches were expanded, or when the plates were sectored, *A. laticollaris* showed even stronger tendencies for attraction to particular patches and heterogeneous distribution. *Chromadorina germanica* was most strongly attracted to *Phaeodactylum tricornutum* and *Cylindrotheca closterium.* The distribution of *Rhabditis marina,* a bactivorous species, was very interesting. It seemed to strongly avoid patches of 3 species of algae, *Cylindrotheca closterium, Dunaliella parva* and *Nanochloris* sp., but otherwise is was randomly distributed on both control and experimental patches.

Because of the economic and medical importance of nematodes, their behavioral responses to various types of stimuli have received significant attention (recently reviewed by Croll, 1970; Nicholas, 1976). There is considerable evidence that plant parasitic nematodes are attracted to the roots of particular species of plants. In an experiment similar to our first approach, but without controls, Meyers & Hopper (1967) found that mats of 2 species of marine fungi, *Dendryphiella arenaria* and *Halosphaeria mediostigera* staked out on sand flats for several days attracted large numbers of *Metoncholaimus* sp. and lesser numbers of *Monhystera, Prochromadorella, Araeolaimus, Acanthonchus, Diplolaimella, Chromadora, Symplocostoma* and *Viscosia.* Recently students of behavioral genetics have been attracted to study chemotaxis and the sensor anatomy of *Caenorhabditis elegans* (Dusenberry, 1973, 1975, 1976; Ward et al., 1975; Ware et al., 1975). *C. elegans,* a not too distant relative of *Rhabditis marina,* avoids D-trypthophan with a threshold in the range of 10^{-3}–10^{-4}M but

Table 3

Recruitment of individual species of meiofauna to algal species

Algal species in patch	Number of animals in patch				
	Chromadorina germanica *	*Rhabditis marina* **	*Nitocra typica* **	*Leptocaris brevicornis* **	*Allogromia laticollaris* ***
Amphora acutiuscula (RF 8)	128	54	8	61	623
Nitzschia acicularis (8)	288	16	10	15	640
Chlamydomonas subcordiformis (94)	151	26	14	1	1036
Phaeodactylum tricornutum (39)	440	27	8	3	529
Cylindrotheca closterium (9)	414	1	10	3	569
Dunaliella parva (13)	26	1	5	0	714
Nanochloris sp. (41)	120	4	9	144	527
Achnanthes hauckiana (110)	182	63	10	20	640
Interpatch control****	48 ± 21	19 ± 42	1 ± 2	1 ± 4	169 ± 78
Control plate (no patches)****	28 ± 13	23 ± 88	1 ± 1	1 ± 2	78 ± 23
Duration of experiment	8 d	11 d	11 d	11 d	11 d
# animals in inoculum	1,000	1,000	95 adults	175 adults	1,000

* average of 12 replicates
** average of 6 replicates
*** average of 3 replicates
**** average of 24 replicates

was insensitive to concentrations up to 10^{-2}M of L-tryptophan. Though Dusenbery (1976) wondered about the adaptive value of this response to the organism in its natural environment there are some possible explanations. Since many bacteria incorporate D-amino acids into their cell walls and capsules we suggest that *C. elegans* may have an adaptation to avoid microhabitats especially heavily colonized by particular species of bacteria containing or releasing large quantities of D-tryptophan. This type of problem might be more easily studied using *Rhabditis marina* since we have already identified patches of 3 species of algae which the worm avoids. Release of various metabolites including amino acids and carbohydrates by the algae is quite well known and much of the methodology required is now quite routine (Hellebust, 1974).

While we feel we have obtained strong evidence to suggest that algal colonies or blooms can selectively attract meiofauna and can be a factor causing the non-random distribution of these animals, with obvious cost-benefit advantages for the growth and reproduction of these animals, we cannot yet assess the importance of this phenomenon relative to other community organizing factors. We have found, for instance that many species of littoral foraminifera are more fecund on mixed diets of particular species of algae than on monalgal ones (Muller & Lee, 1969). Evidence indicates that this may be the case for at least some copepod species as well. Forams can have feeding nets up to several cm which could be feeding in several algal patches at the same time.

Many species of littoral benthic foraminifera are algal patch makers themselves. They gather and transport captured algae from the edges of their feeding webs to their tests and often build huge balls or clumps of algae around themselves. Only a small fraction of the algae is used immediately as food. A part of the algal mass is used from time to time by the forams as surface on which to construct new test chambers or reproductive chambers (Grell, 1973).

Compared to other physical environments (i.e. rocky shore) the salt marsh littoral is relatively benign. In common with many benign environments (i.e. forest floors) the biota of the littoral is seasonal, relatively transient, but predictable. Many selective forces are operating in time and space as the assemblages in the littoral go through their annual successional trajectories. Because so many questions remain, there is not yet sufficient evidence to build a conceptual framework which would clarify the tradeoffs of the various selective factors which shape the biotic assemblages of the lower and intermediate steps in the salt marsh detrital food webs. Those meiofauna and microfauna which have been carefully studied seem to segregate by partitioning the available microflora (Fenchel, 1968; Lee et al., 1966, 1975; Muller, 1975). How often do they encounter blooms of "ideal" food organisms in nature? How do consumption rates and efficiencies vary with abundance and time? What are the relative replacement or turnover rates of these small plants and animals in time and in space? What role does competition among the various organisms play in the 4-dimensional spacing of the organisms in the community successional trajectory? What role do the macrofauna play in structuring the assemblages of smaller organisms? Do the macrofauna selectively harvest the smaller animals? Are the initial colonizations of *Spartina*, *Zostera*, and macrophytes selective or stochastic? How readily acceptable are new recruits to these communities? While the major abiotic and biotic factors which help to establish and maintain relatively permanent communities (i.e. rocky shores and

northern temperate forests) seem to be known, we must for the moment, content ourselves by asking and answering many more questions.

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