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The effect of the quality of food patches on larval vertical distribution of the sea urchins *Lytechinus variegatus* (Lamarck) and *Strongylocentrotus droebachiensis* (Mueller)

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Abstract

Although most invertebrate larvae are weak swimmers and act as passive particles on horizontal scales, they may be able to regulate their vertical position in response to different factors, including increased food concentration. We examined the effect of the quality of food patches on larval vertical distribution for the sea urchins *Lytechinus variegatus* and *Strongylocentrotus droebachiensis*, and determined the effect of dietary conditioning on that response in the laboratory. We reared larvae on a mixed algal diet of *Dunaliella tertiolecta* and *Isochrysis galbana* under low (500 cells ml^{-1}) and high (5000 cells ml^{-1}) rations. Food patches were maintained in Plexiglas rectangular columns ($30 \times 10 \times 10$ cm) using a density gradient, where practical salinity in the bottom layer was 33, in the middle layer 30, and in the top layer 27. We examined the magnitude and mechanism of a behavioural response of larvae of *L. variegatus* in the four-arm stage, and on two developmental stages of *S. droebachiensis* (four- and six-arm), by manipulating patch quality. In the absence of a patch, larvae of both species and developmental stages swam through to the surface of the experimental columns. In the presence of algae, fewer larvae were present above the patch and more were at the patch than in control columns. More larvae swam through patches of "unflavoured" algal mimics than algal patches, and aggregated at the surface. Larval distribution relative to patches of algal filtrate without algal cells or of "flavoured" algal mimics in algal filtrate was not consistently different from that in either control or algal patches; thus, the magnitude of larval response to filtrate (with or without particles) was intermediate between that to control and algal patches. For *L. variegatus*, more larvae crossed the patches when reared on low than high rations, indicating that poorly conditioned larvae may be less responsive to environmental cues. Our results suggest that larvae can actively aggregate and maintain a vertical position in response to a food patch that

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depends on the quality and quantity of food. The response appears to be based mostly on a chemosensory rather than a mechanosensory mechanism.

Keywords: Algal mimics; Behavioural response; Echinoids; Food patch; Invertebrate larvae

1. Introduction

On horizontal scales, most invertebrate larvae act as passive particles, as their swimming cannot override advection by currents (for reviews, see Scheltema, 1986; Metaxas, 2001). In contrast, larvae and other small planktonic swimmers are able to exhibit effective displacement on vertical scales, both in the laboratory (e.g. scallop veligers: Manuel et al., 1996; urchin larvae: Metaxas and Young, 1998a) and in the field (e.g. scallop veligers: Tremblay and Sinclair, 1990; echinoderm larvae: Pedrotti and Fenaux, 1992). Potential reasons for vertical migration are not consistent among phyla and include horizontal transport, foraging and predator avoidance (Metaxas, 2001; Epifanio and Garvine, 2001). Dietary condition can influence the ability of echinoid larvae to maintain vertical position in the water column (Metaxas and Young, 1998a,b).

Dense blooms of phytoplankton, which is the main source of food for invertebrate larvae, are found at convergence zones (Cullen and Eppley, 1981; Sharples et al., 2001) and can last for days to weeks (Laws et al., 1988). This aggregation is due to hydrological properties (Sournia, 1993), such as advection, frontal isolation, tides and density discontinuities (Fortier and Leggett, 1982; Ashjian et al., 2001). Some zooplankton phyla aggregate in areas of increased concentrations of phytoplankton, both in the field (e.g. Raby et al., 1994; Ashjian et al., 2001; Lopez et al., 1998) and the laboratory (e.g. the euphausiid *Thysanoessa raschii*: Price, 1989; the echinoid *Echinometra lucunter*: Metaxas and Young, 1998a). In the laboratory, Metaxas and Young (1998a) showed that echinoid larvae aggregate in experimentally constructed food patches, and alter their swimming behaviour to remain within a patch. For the holoplanktonic copepod *Calanus pacificus*, the presence of food can influence diel migration (Huntley and Brooks, 1982). The relative importance of the physical environment and larval behaviour in generating observed distributions remains unclear (Pedrotti and Fenaux, 1996; Metaxas, 2001). However, although larvae are weak swimmers (Chia et al., 1984), their ability to aggregate and maintain position in an algal patch indicates controlled swimming, and thus a behavioural response to a stimulus.

For invertebrate larvae, food detection and capture may be influenced by mechanical or chemical cues and ingestion is determined by the quality of the food particles (Strathmann et al., 1972). Most echinoid larvae use cilia to filter food particles from the water column and direct them towards their mouth where ingestion occurs (Hart, 1991). A ciliary beat reversal, and thus initiation of food capture, can be induced mechanically by a physical disturbance (Hart, 1991). However, it is unknown whether larvae can detect food using a chemical cue. Echinoid larvae can select particles at the mouth on the basis of their chemical composition (Rassoulzadegan et al., 1984), as well as cell shape and size (Strathmann et al., 1972). Some suspension feeders, such as rotifers, graze strictly on a

mechanical cue (Hansen et al., 1997) while others, such as tintinnids, respond to chemosensory cues (Spittler, 1973).

In this study, we examined the effect of the quality of food patches on larval vertical distribution for two sea urchins (*Lytechinus variegatus* and *Strongylocentrotus droebachiensis*) in the laboratory, and determined the effect of dietary conditioning on that response. In previous experiments with the tropical sea urchin *E. lucunter*, the presence of a food patch had a pronounced effect on larval vertical distribution and that effect depended on the algal density in the patch and on dietary conditioning (Metaxas and Young, 1998a,b). Using a similar experimental system in this study, we extended our previous results by examining whether the mechanism of response to food patches is based on mechanical or chemical cues. While controlled experiments done in the laboratory cannot accurately reproduce conditions in the field, they provide an effective means of observing larval behaviour. Such experiments can provide a first estimate of the role of behavioural responses to cues, leading to hypotheses that can be tested directly in the field.

2. Materials and methods

2.1. Fertilization and larval culturing

Adults of *L. variegatus* were imported from Florida in August 2001, and adults of *S. droebachiensis* were collected from the subtidal zone near Halifax in February 2002. Urchins were induced to spawn by injection of ~ 2 ml 0.55 M KCl through the peristomial membrane. Females spawned into beakers containing 0.45-μm-filtered seawater, and males dry spawned to prolong sperm longevity. The eggs were rinsed gently through a 125-μm sieve, and embryos were obtained by mixing sperm and eggs. Fertilization success, determined as the proportion of eggs (250−500) with elevated perivitelline membrane, was between 94% and 99% for both species.

Larvae were reared under two rations of a mixed microalgal diet of *Dunaliella tertiolecta* and *Isochrysis galbana*, 500 cells ml^{-1} (low ration) and 5000 cells ml^{-1} (high ration). While the total number of algal cells remained constant, the ratio between species varied throughout development. In the two-arm stage, larvae received a combination of 50% *D. tertiolecta* and 50% *I. galbana* (by number), while in the four- and six-arm stages, the proportions were 66% and 33%, for each algal species, respectively.

Both larval rearing and experiments were conducted at 20 °C for *L. variegatus* and at 12 °C for *S. droebachiensis*. At the gastrula stage (day 2 for *L. variegatus*, day 4 for *S. droebachiensis*), feeding was initiated and larvae were transferred to 3.5-l jars containing 0.45-μm-filtered seawater, with practical salinity of 33, and stirred continuously with a motorized paddle. Larval concentration in the rearing containers was ~ 1 larva ml^{-1}. The water in the culture jars was changed and algae added every other day.

2.2. Experimental design—generation of experimental patches

Food patches were generated in plexiglas rectangular columns ($30 \times 10 \times 10$ cm) marked in 0.5-cm increments. Patch position was maintained in the middle of the water

column using haloclines as in Metaxas and Young (1998a). Practical salinity in the bottom layer was 33, in the middle layer 30 and in the top layer 27. Water of the lowest salinity was poured into the columns to a height of 8 cm. A 2- to 3-cm intermediate layer of water that contained the treatment (see below) was siphoned below the first layer. Lastly, a layer was siphoned to the bottom of the column until the water surface reached 20 cm. Once the treatments were established, salinity was measured in 0.5-cm increments to determine the exact position of the halocline (and, therefore, patch) with a temperature-compensated refractometer. We introduced 100–500 larvae to 3 cm above the bottom using a Pasteur pipette, and recorded their vertical position after 15 and 30 min. Previous studies have shown that halocline structure and patch composition (particle density) remain constant over 60–90 min (Metaxas and Young, 1998a,b). One set of experiments was conducted for *L. variegatus* in the four- to six-arm stage (4–5 days old) and two sets were conducted for *S. droebachiensis*, one in the four-arm stage (7 days old), and one in the six-arm stage (11 days old).

2.3. Experimental design—patch quality

The quality of food patches was manipulated to address the magnitude and mechanism of larval behavioural response. To examine the effect of algal density in a food patch on larval vertical distribution, we used two concentrations of the marine diatom *Thalassiosira pseudonana* (5000 and 10 000 cells ml^{-1}; "low algae" and "high algae", respectively). To determine whether the response was mechanically induced, we used 5-μm neutrally buoyant, spherical, polyamid seeding particles as algal mimics (*L. variegatus*: 5000 particles ml^{-1}; *S. droebachiensis:* 5000 and 10 000 particles ml^{-1}; "low particles" and "high particles", respectively). To ascertain whether larval response was chemically induced, we removed the algal cells from cultures of *T. pseudonana* by centrifugation, thus leaving only the culture medium (filtrate from two algal concentrations: 5000 and 10 000 cells ml^{-1}; "low filtrate" and "high filtrate", respectively). Lastly, to examine whether response was the result of a combination of mechanical encounter and algal chemical nature, we used flavoured particles (5000 and 10 000 particles ml^{-1}, "low flavoured particles" and "high flavoured particles", respectively), which were incubated for 24 h prior to experiment in the culture medium (*S. droebachiensis* only). We used four replicates for each treatment, and the experiments were run over a 2-day period for *L. variegatus*, a 4-day period for *S. droebachiensis* in the four-arm stage, and a 3-day period for *S. droebachiensis* in the six-arm stage.

2.4. Statistical analyses

To simplify the analysis, we pooled a number of 0.5-cm intervals to create three levels of the factor Position: (1) at the patch, (2) below the patch, and (3) above the patch. The patch was defined for each replicate column as the region between the two boundaries in the salinity gradient. The lower boundary was the greatest height above the bottom where practical salinity was 33 and the upper boundary was the smallest height above the bottom where practical salinity was 27. We then estimated the total number of larvae for all 0.5-cm

intervals within this region, as well as the total number of larvae above and below these boundaries.

Because there were no pronounced differences in the vertical distribution of *L. variegatus* and four-arm *S. droebachiensis* between 15 and 30 min after larval introduction, we only present results for 30 min for these two taxa. Also, since there were no pronounced differences between dietary conditionings for four- and six-arm *S. droebachiensis*, we only present results for high rations for this species. Specifically, we examined the independence of quality of the food patch (Patch; six levels for *L. variegatus* and nine levels for *S. droebachiensis*), position relative to the patch (Position; three levels), and replicate (four levels) by three-way loglinear models. For *L. variegatus*, we included dietary conditioning (Diet; two levels), and for six-arm *S. droebachiensis*, time since larval introduction (Time; two levels) as a fourth factor in the loglinear models. For both species and developmental stages, firstly, we tested the homogeneity of the four replicates within each level of Diet × Patch (*L. variegatus*), Patch (four-arm *S. droebachiensis*), or Patch × Time (six-arm *S. droebachiensis*) treatment combination using two-way models with Replicate and Position as the two factors, to determine whether vertical distributions from replicate columns could be pooled (Sokal and Rohlf, 1981). These two factors were not independent in most cases, and thus Replicate was included as a factor in the loglinear models.

A loglinear model fits the data well when *G*-values are low and there is no significant difference between the predictions by the model and the observed data (Fienberg, 1970). When there are no significant interactions, the effects of each factor are independent from one another. None of the four-way and most of the three-way models that we tested fit the data for either species or developmental stage (in most cases, *G* highly significant, $p < 0.0001$). Thus, two-way models were used to examine: (1) the independence between the factors Patch and Position (within each level of: Diet for *L. variegatus*; and Time for six-arm *S. droebachiensis*); (2) the independence of the factors Diet and Position within each level of Patch for *L. variegatus* only; and (3) the independence between the factors Time and Position within each level of Patch for six-arm *S. droebachiensis* only. Because of the large number of comparisons with each model, we used $\alpha_{critical}$=[0.05/(no. of comparisons within each species and developmental stage using a type of model)] to avoid an increased probability of type I error. Statistical analyses were done using SPSS version 11 for Windows.

3. Results

Sharp haloclines were generated in the experimental columns that maintained the patches in position for the duration of the experimental period. Patches were generally 2–3 cm thick, and were positioned approximately in the middle of the columns, 8–10 cm above the bottom (Figs. 1–3).

For both species and developmental stages, there were complex interactions between larval vertical distribution in the experimental columns and dietary conditioning, quality of the food patch, and replicate as indicated by multi-way loglinear models. Only the vertical distribution of six-arm larvae of *S. droebachiensis* varied pronouncedly with time since

larval introduction into the experimental columns (Fig. 3). While significant patterns between larval vertical distribution and patch quality were recorded after 15 min, most were no longer present after 30 min. At 30 min, most larvae were present in the layer above the patch for all levels of Patch and all replicates. Thus, our presentation of the effects of patch quality on larval vertical distribution for six-arm *S. droebachiensis* focuses on 15 min after larval introduction.

Larval vertical distribution varied with patch quality, as indicated by the dependence of Position and Patch in two-way loglinear models done within each level of Diet × Replicate combination for *L. variegatus*, Replicate for four-arm *S. droebachiensis*, and Time- × Replicate combination for six-arm *S. droebachiensis* (G_{16} was highly significant and $p < 0.0001$, in 19 out of 20 tests). For *L. variegatus*, more larvae were present at or below the patch in "low algae and "high algae" than in "control" treatments, but there was no difference between algal treatments (Fig. 1; Table 1). Similarly, for four-arm *S. droebachiensis*, fewer larvae were above and more were at the patch in "high algae" than in "control" (Fig. 2; Table 2). For six-arm *S. droebachiensis*, fewer larvae were above and more were present at the patch in "low algae" than in "control" and in "high algae" than in "low algae" treatments (Fig. 3; Table 3).

For *L. variegatus* and six-arm *S. droebachiensis*, more larvae were found either above or below the patch in "low particle" than "low algae", and in "high particle" than in "high algae" treatments in at least three replicates (Tables 1 and 3). The detected differences between "low particle" and "control" treatments were not in a consistent direction among replicates. There were no differences among any of these treatments for four-arm *S. droebachiensis.*

For both stages of *S. droebachiensis*, there were no differences in larval distribution between "control" and "low filtrate" treatments (Tables 2 and 3). However, for *L. variegatus*, more larvae were at the patch in "low filtrate" than "control" treatments in two and three replicates for the high and low rations, respectively. Differences between "low algae" and "low filtrate", and "high algae" and "high filtrate" treatments were not detected consistently for all replicates, but when present they most frequently indicated that more larvae were above filtrate than algal patches.

For four-arm *S. droebachiensis*, there were no differences between "control", "low algae" and "low flavoured particle" treatments (Table 2). For six-arm *S. droebachiensis*, there was no difference in larval distribution between "control" and "low flavoured particle" treatments, but differences between "low flavoured particle" and "low algae" treatments were not consistent among replicates (Table 3). Larval distribution did not differ consistently among replicates between "high algae" and "high flavoured particle" treatments for either stage.

For *L. variegatus* and four-arm *S. droebachiensis*, the few detected differences in larval distribution between "low particle", "low filtrate" and "low flavoured particle", and between "high particle", "high filtrate" and "high flavoured particle" treatments were not consistent among replicates (Tables 1 and 2). For six-arm *S. droebachiensis*, more larvae were above and fewer were below "low filtrate" and "low flavoured particle" than "low particle" patches (Table 3). Also, more larvae were at the patch in "high filtrate" and "high flavoured particle" than "high particle" treatments for most replicates.

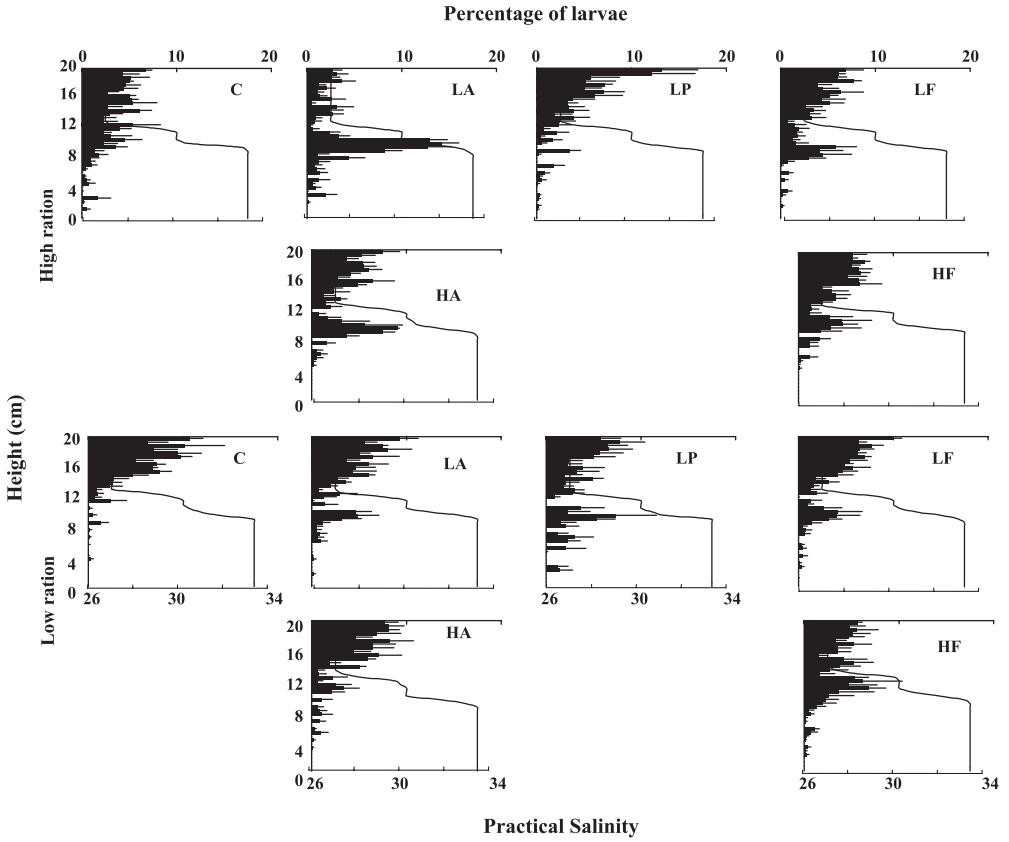

Fig. 1. *L. variegatus*. Vertical distribution in experimental columns of four-arm larvae reared under a high or low food ration, 30 min after introduction, and exposed to food patches of six different qualities (C: "control"; LA: "low algae"; HA: "high algae"; LP: "low particle"; LF: "low filtrate"; HF: "high filtrate"). Line indicates mean salinity. Error bars are standard errors of the mean, $n = 4$.

Table 1
L. variegatus. Analysis by two-way loglinear models of the independence between larval position in experimental columns 30 min after larval introduction (Po) and patch quality (P) (model: P + Po) within each level of the factor Diet (high ration and low ration) and Replicate

Treatment comparison	High ration								Low ration							
	Replicate 1		Replicate 2		Replicate 3		Replicate 4		Replicate 1		Replicate 2		Replicate 3		Replicate 4	
	G_2	p	G_2	p	G_2	p	G_2	p	G_2	p	G_2	p	G_2	p	G_2	p
C vs. LA	186.6	< 0.0001*	5.13	0.077	274.4	< 0.0001*	138.3	< 0.0001*	4.88	0.087	136.6	< 0.0001*	3.89	0.143	142.3	< 0.0001*
C vs. HA	17.18	0.0002*	54.85	< 0.0001*	11.23	0.004	8.86	0.012	208.1	< 0.0001*	45.99	< 0.0001*	63.28	< 0.0001*	3.30	0.192
LA vs. HA	114.4	< 0.0001*	48.27	< 0.0001*	113.9	< 0.0001*	98.17	< 0.0001*	256.9	< 0.0001*	21.98	< 0.0001*	43.04	< 0.0001*	122.0	< 0.0001*
C vs. LF	52.15	< 0.0001*	22.56	< 0.0001*	4.18	0.124	5.08	0.079	32.56	< 0.0001*	22.10	< 0.0001*	73.32	< 0.0001*	6.04	0.049
C vs. LP	71.39	< 0.0001*	74.51	< 0.0001*	31.22	< 0.0001*	38.51	< 0.0001*	1.24	0.538	63.21	< 0.0001*	14.60	0.0007*	100.1	< 0.0001*
LA vs. LF	310.2	< 0.0001*	6.81	0.033	252.4	< 0.0001*	177.2	< 0.0001*	27.51	< 0.0001*	65.65	< 0.0001*	63.23	< 0.0001*	133.2	< 0.0001*
LA vs. LP	471.9	< 0.0001*	57.90	< 0.0001*	115.2	< 0.0001*	328.5	< 0.0001*	18.68	0.0001*	30.18	< 0.0001*	11.18	0.0037	69.08	< 0.0001*
LF vs. LP	66.45	< 0.0001*	48.64	< 0.0001*	44.11	< 0.0001*	13.57	0.0011*	95.20	< 0.0001*	28.61	< 0.0001*	150.3	< 0.0001*	67.46	< 0.0001*
HA vs. HF	4.60	0.100	299.4	< 0.0001*	465.9	< 0.0001*	271.3	< 0.0001*	25.36	< 0.0001*	411.6	< 0.0001*	521.1	< 0.0001*	998.9	< 0.0001*

Shown are pairwise comparisons between levels of the factor Patch (C: "control"; LA: "low algae"; HA: "high algae"; LF: "low filtrate"; LP: "low particle"; HF: "high filtrate"). $\alpha_{critical} = 0.0014$; $df = 2$; *= significant difference between treatments.

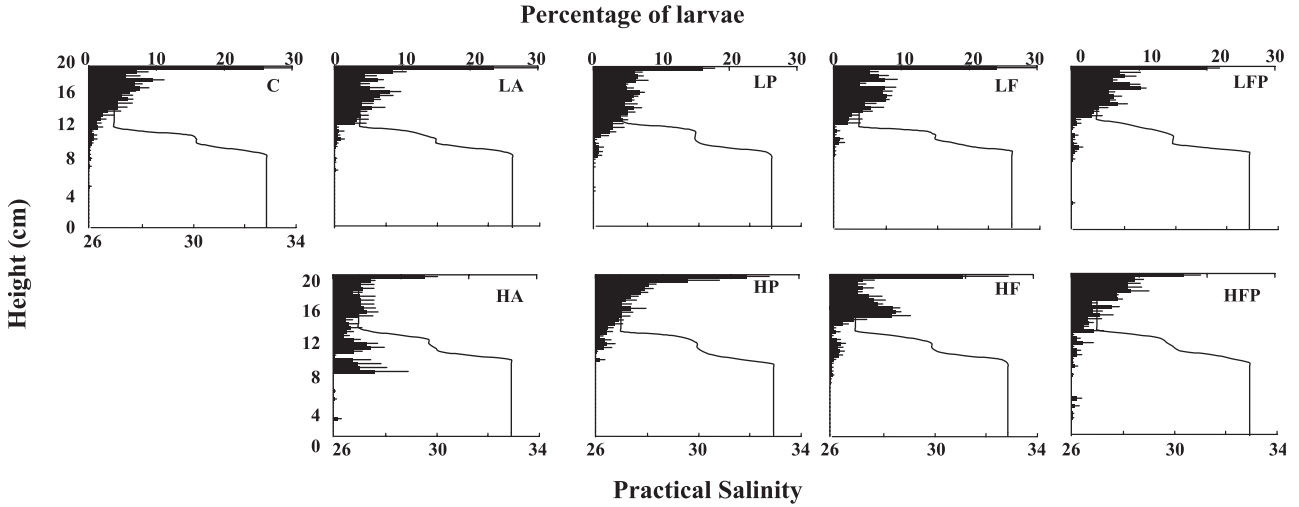

Fig. 2. *S. droebachiensis*. Vertical distribution in experimental columns of four-arm larvae reared under a high food ration, 30 min after introduction, and exposed to food patches of six different qualities (C: "control"; LA: "low algae"; HA: "high algae"; LP: "low particle"; HP: "high particle"; LF: "low filtrate"; HF: "high filtrate"; LFP: "low flavoured particle"; HFP: "high flavoured particle"). Line indicates mean salinity. Error bars are standard errors of the mean, $n = 4$.

Table 2
S. droebachiensis (four-arm). Analysis by two-way loglinear models of the independence between larval position in experimental columns 30 min after larval introduction (Po) and patch quality (P) (model: Po + P) for each Replicate

Treatment combination	Replicate 1		Replicate 2		Replicate 3		Replicate 4	
	G_2	p	G_2	p	G_2	p	G_2	p
C vs. LA	<0.01	1.000	3.30	0.192	1.30	0.522	4.41	0.110
C vs. HA	254.2	<0.0001*	0.441	0.802	26.03	<0.0001*	60.43	<0.0001*
LA vs. HA	252.6	<0.0001*	2.31	0.315	24.14	<0.0001*	51.66	<0.0001*
C vs. LF	7.20	0.027	3.46	0.178	1.92	0.383	2.91	0.233
C vs. LP	26.14	<0.0001*	12.92	0.002	32.39	<0.0001*	13.86	0.001
C vs. LFP	9.92	0.007	16.36	0.0003*	5.27	0.072	1.58	0.453
LA vs. LF	7.14	0.003	<0.01	1.000	3.81	0.149	1.67	0.433
LA vs. LP	25.90	<0.0001*	6.68	0.035	23.95	<0.0001*	3.82	0.148
LA vs. LFP	9.83	0.007	6.00	0.050	3.14	0.208	0.555	0.758
LF vs. LP	13.02	0.002	6.59	0.037	32.54	<0.0001*	4.64	0.098
LF vs. LFP	7.53	0.023	5.88	0.053	10.80	0.005	1.25	0.536
LP vs. LFP	7.61	0.022	1.47	0.480	23.27	<0.0001*	5.99	0.050
HA vs. HF	221.0	<0.0001*	2.86	0.240	21.95	<0.0001*	42.90	<0.0001*
HA vs. HP	221.9	<0.0001*	2.30	0.316	2.59	0.274	40.68	<0.0001*
HA vs. HFP	195.6	<0.0001*	6.90	0.032	32.69	<0.0001*	4.41	0.111
HF vs. HP	<0.01	1.000	7.48	0.024	14.37	0.0008	1.51	0.471
HF vs. HFP	10.68	0.005	11.83	0.003	36.27	<0.0001*	20.91	<0.0001*
HP vs. HFP	351.5	<0.0001*	391.0	<0.0001*	359.2	<0.0001*	221.5	<0.0001*

Diet = High ration. Shown are pairwise comparisons between levels of the factor Patch (C: "control"; LA: "low algae"; HA: "high algae"; LF: "low filtrate"; LP: "low particle"; LFP: "low flavoured particle"; HF: "high filtrate"; HP: "high particle"; HFP: "high flavoured particle"). $\alpha_{critical} = 0.0002$; $df = 2$; * = significant difference between treatments.

For *L. variegatus*, larval vertical position was consistently dependent on dietary conditioning. More larvae were present above the patch if reared under low than high rations in 17 out of 24 tests (Fig. 1; Table 4).

4. Discussion

For both *S. droebachiensis* and *L. variegatus*, there was a pronounced effect of the presence of a food patch on larval vertical distribution. In the absence of algae, larvae of both species swam to the surface and aggregated in the top 8–10 cm of the water column. In the presence of algae, fewer larvae were present above the patch and more were at the patch than in control columns without algae. For six-arm *S. droebachiensis*, more larvae were present in patches of high than low algal density. The ability to detect food particles also has been recorded for larvae of the sea urchin *E. lucunter* (Metaxas and Young, 1998a). For this species, larval distribution relative to food patches depended on algal density in the patch: larvae aggregated just below a "high algae" patch and within a "low algae" patch. Similarly, changes in swimming behaviour have been recorded for holoplankton, such as the marine tintinnid *Favella* sp. (Buskey and Stoecker, 1989) and the euphausiid *T. raschii* (Price, 1989). Interestingly, in our study, larval vertical

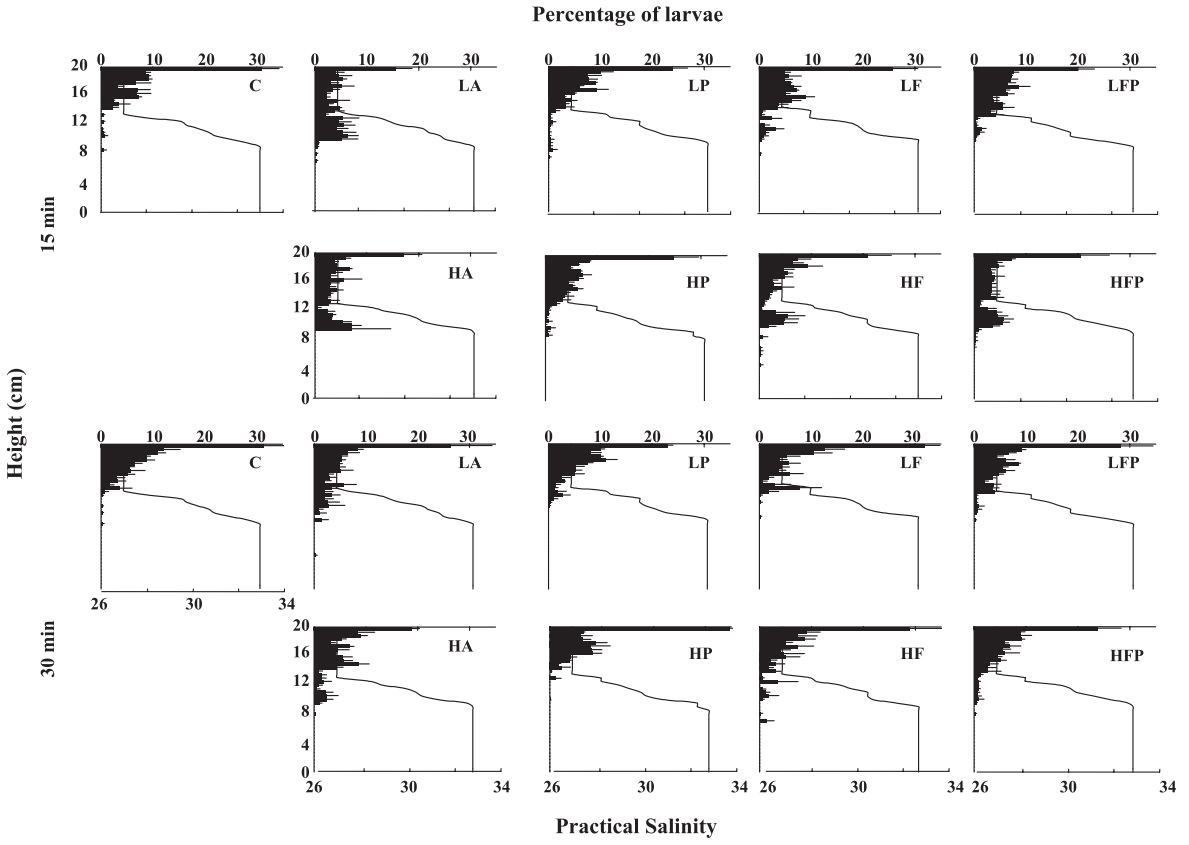

Fig. 3. *S. droebachiensis*. Vertical distribution in experimental columns of six-arm larvae reared under a high ration, 15 or 30 min after introduction, and exposed to food patches of six different qualities (C: "control"; LA: "low algae"; HA: "high algae"; LP: "low particle"; HP: "high particle"; LF: "low filtrate"; HF: "high filtrate"; LFP: "low flavoured particle"; HFP: "high flavoured particle"). Line indicates mean salinity. Error bars are standard errors of the mean, $n = 4$.

Table 3
S. droebachiensis (six-arm). Analysis by two-way loglinear models of the independence between larval position in experimental columns (Po) and patch quality (P) (model: Po + P) for each Time after larval introduction and Replicate

Treatment comparison	Time = 15 min								Time = 30 min							
	Replicate 1		Replicate 2		Replicate 3		Replicate 4		Replicate 1		Replicate 2		Replicate 3		Replicate 4	
	G_2	p	G_2	p	G_2	p	G_2	p	G_2	p	G_2	p	G_2	p	G_2	p
C vs. LA	175.4	< 0.0001*	8.13	0.017	34.37	< 0.0001*	15.98	0.0003	97.66	< 0.0001*	4.30	0.116	2.58	0.775	1.26	0.532
C vs. HA	61.14	< 0.0001*	65.31	< 0.0001*	50.19	< 0.0001*	23.05	< 0.0001*	11.23	0.0036	3.43	0.180	23.84	< 0.0001*	28.40	< 0.0001*
LA vs. HA	75.16	< 0.0001*	33.91	< 0.0001*	4.09	0.130	0.716	0.699	69.61	< 0.0001*	8.34	0.016	16.32	0.0003*	26.68	< 0.0001*
C vs. LF	39.62	< 0.0001*	2.35	0.309	0.034	0.983	2.17	0.339	< 0.01	1.000	1.24	0.538	< 0.01	1.000	2.78	0.249
C vs. LP	137.5	< 0.0001*	117.7	< 0.0001*	105.0	< 0.0001*	95.82	< 0.0001*	6.19	0.045	5.12	0.078	1.42	0.492	6.32	0.043
C vs. LFP	< 0.01	1.000	8.14	0.017	0.238	0.888	3.10	0.212	2.54	0.281	1.12	0.570	< 0.00	1.000	12.68	0.002
LA vs. LF	78.69	< 0.0001*	3.40	0.183	25.64	< 0.0001*	6.99	0.030	63.31	< 0.0001*	3.96	0.138	1.73	0.420	1.38	0.502
LA vs. LP	140.1	< 0.0001*	87.90	< 0.0001*	158.2	< 0.0001*	149.9	< 0.0001*	80.17	< 0.0001*	0.02	0.992	0.222	0.895	4.26	0.119
LA vs. LFP	171.9	< 0.0001*	3.08	0.215	35.78	< 0.0001*	13.55	0.001	90.78	< 0.0001*	3.56	0.169	2.03	0.362	10.11	0.006
LF vs. LP	113.7	< 0.0001*	118.3	< 0.0001*	106.5	< 0.0001*	98.75	< 0.0001*	0.16	0.925	10.91	0.004	6.35	0.042	5.17	0.078
LF vs. LFP	84.10	< 0.0001*	2.89	0.235	44.89	< 0.0001*	18.19	< 0.0001*	0.437	0.804	2.74	0.248	9.12	0.010	1.52	0.468
LP vs. LFP	133.9	< 0.0001*	101.2	< 0.0001*	96.22	< 0.0001*	126.3	< 0.0001*	1.22	0.542	4.20	0.122	1.12	0.570	2.34	0.310
HA vs. HF	2.15	0.342	22.95	< 0.0001*	37.30	< 0.0001*	24.98	< 0.0001*	13.13	0.001	11.58	0.003	18.09	< 0.0001*	18.61	< 0.0001*
HA vs. HP	21.99	< 0.0001*	75.95	< 0.0001*	71.26	< 0.0001*	34.44	< 0.0001*	9.86	0.007	< 0.01	1.000	21.79	< 0.0001*	28.79	< 0.0001*
HA vs. HFP	24.54	< 0.0001*	34.78	< 0.0001*	9.10	0.010	4.18	0.124	3.06	0.217	1.32	0.517	8.09	0.018	4.32	0.115
HF vs. HP	16.14	0.0003*	92.68	< 0.0001*	7.84	0.020	1.09	0.581	31.43	< 0.0001*	11.29	0.004	0.882	0.643	2.71	0.259
HF vs. HFP		0.023	31.80	< 0.0001*	33.55	< 0.0001*	22.05	< 0.0001*	20.74	< 0.0001*	10.43	0.005	8.74	0.013	6.62	0.037
HP vs. HFP	27.01	< 0.0001*	25.29	< 0.0001*	63.43	< 0.0001*	24.51	< 0.0001*	3.87	0.144	1.29	0.526	8.45	0.015	14.27	0.0008

Diet = High ration. Shown are pairwise comparisons between levels of the factor Patch (C: "control"; LA: "low algae"; HA: "high algae"; LF: "low filtrate"; LP: "low particle"; LFP: "low flavoured particle"; HF: "high filtrate"; HP: "high particle"; HFP: "high flavoured particle"). $\alpha_{critical} = 0.0007$; $df = 2$; *= significant difference between treatments.

Table 4
L. variegatus. Analysis by two-way loglinear models of the independence between larval position in experimental columns 30 min after larval introduction (Po) and Diet (D) (model: Po + D) within each level of the factor Patch (P) (C: "control"; LA: "low algae"; HA: "high algae"; LF: "low filtrate"; HF: "high filtrate"; LP: "low particle") and Replicate (R)

Treatment combination		G	*p*
P = C	R = 1	42.91	< 0.0001
	R = 2	302.5	< 0.0001
	R = 4	62.49	< 0.0001
P = LA	R = 1	369.7	< 0.0001
	R = 2	46.46	< 0.0001
	R = 3	201.7	< 0.0001
	R = 4	237.3	< 0.0001
P = HA	R = 2	25.26	< 0.0001
	R = 3	21.17	< 0.0001
	R = 4	82.31	< 0.0001
P = LF	R = 1	65.48	< 0.0001
	R = 2	162.2	< 0.0001
	R = 3	81.69	< 0.0001
P = HF	R = 1	50.15	< 0.0001
	R = 2	42.20	< 0.0001
P = LP	R = 3	45.74	< 0.0001
	R = 4	68.47	< 0.0001

Shown are only models that indicated a significant dependence between the two factors ($df = 2$) (out of 24 possible models tested).

distributions were bimodal, with one mode centered in the upper water layer, and another in the middle layer containing the patch. This suggests that response to a food patch may not be a population-wide (or even offspring-wide) characteristic, but rather an adaptive behaviour of some individuals.

We explored the potential mechanism for patch detection by manipulating the quality of the food patch. By comparing larval distributions between "algae" and "particle" patches, we assessed the presence of a potential mechanosensory mechanism of detection. In most cases, more larvae swam through the "particle" than the algal patches. Further, the distributional differences between "particle" and "control" patches were not consistent. Thus, the evidence that a response to food patchiness is mediated solely by a mechanical detection of cells or particles is weak.

A chemosensory mechanism for patch detection (in the absence of a mechanosensory one) can be explored by comparing distributions between "algae" and "filtrate" patches. Larval distribution relative to "filtrate" patches was not consistently different from either "control" or "algae" ones, suggesting that the magnitude of larval response to filtrate is intermediate between that to control and algal patches. Larvae in poor dietary conditioning were slightly more responsive to filtrate patches. The "flavoured particle" patches allowed us to determine whether detection of food is determined by a combination of mechanical encounter and chemical cue, or whether some other algal-specific characteristic is required for food recognition and subsequent behavioural response. Both species and developmental stages displayed a response to "flavoured particle" patches that was similar to that to "filtrate" patches.

Our results suggest that chemical cues alone appear to elicit some level of response to food patches by echinoid larvae, whereas mechanical cues do not. It is possible that larval response to a food patch may involve two processes: initial detection by chemical cues diffusing beyond the patch, followed by mechanical encounter. It is also likely that larvae have the ability to determine the "nutritional quality" of cells they ingest. For example, echinoid and asteroid larvae are known to preferentially ingest both algal cells to polystyrene algal mimics (Rassoulzadegan et al., 1984; Okaji et al., 1997) and flavoured to non-flavoured algal mimics (Appelmans, 1994).

The most pronounced effect of dietary conditioning on the response to food patchiness was recorded for *L. variegatus*. More larvae crossed the patches when reared on low than high rations, indicating that poorly conditioned larvae may be less responsive to environmental cues. A similar effect was detected for *E. lucunter* (Metaxas and Young, 1998a). The mechanism by which dietary conditioning affects larval behaviour is unclear.

The effects of patch quality on larval vertical distribution varied between 15 and 30 min, but only for six-arm *S. droebachiensis*. Most differences between treatments detected at 15 min were no longer present after 30 min. This temporal change in larval vertical distribution may denote an optimal foraging behaviour, where larvae do not remain within a food patch (particularly of poor quality, such as algal mimics or filtrate) for more than a few minutes. In the field setting, it is unlikely that echinoid larvae are able to maintain their position for longer periods.

Larval aggregation near food patches varied with species and developmental stage, and was strongest for six-arm *S. droebachiensis*. In previous studies, *E. lucunter* showed pronounced aggregation near food patches (Metaxas and Young, 1998a,b). These three species occupy a wide range of habitats: *E. lucunter*, tropical intertidal rocky substrates with high wave action, *S. droebachiensis*, subtidal temperate rocky bottoms and *L. variegatus*, tropical sandy bottoms (Hendler et al., 1995; Meinkoth, 1998). Thus, their larvae are also likely to be exposed to different conditions while in the plankton, both in terms of food abundance and hydrodynamics. In combination, these studies suggest that the magnitude of response to food patchiness may be genus-specific. However, it appears that this behavioural response is induced mainly by chemical cues across echinoid taxa.

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