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Stimulation of feeding behavior in three species of fiddler crabs by hexose sugars

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Abstract. Feeding responses to five hexoses were examined in three closely related species of fiddler crabs, *Uca minax*, *U.pugnax* and *U.pugilator*. Hexoses tested were glucose, galactose, sorbose, fructose and mannose. Intact crabs and eyestalk-ablated crabs were tested. Responses to sugars were species specific. Eyestalks are directly involved in vision and overall neural integration as well as with chemosensory and metabolic pathways associated with feeding. Overall, eyestalk-ablated crabs were more sensitive than intact crabs. Studies of responses of individuals within a population to hexoses showed there are individual *U.pugnax* that respond to galactose and others that do not. Similarly, there were *U.pugilator* individuals that were mannose responsive and others that did not respond to mannose. An additional study of differences in population responses to hexoses would provide valuable tools in studying geographic relationships between fiddler crab populations.

Introduction

Fiddler crabs of the genus *Uca* are obvious semiterrestrial members of low energy intertidal environments in many parts of the world (Crane, 1975). Fiddler crabs usually forage on exposed substrata in large groups (Teal, 1958; Miller, 1961). Fine grained sand or mud is brought to the buccal region with the chelae and sorted into material that is either swallowed or rejected. The rejected feeding pellets (Miller, 1961) have been used to quantify feeding activity and to test for chemosensory responses (Robertson *et al.*, 1980, 1981). Among living prey, diatoms, ciliates and bacteria stimulate feeding (Robertson *et al.*, 1981).

Robertson *et al.* (1981) showed that chemical components in the substratum upon which sand fiddler crabs (*U.pugilator*) walk elicit feeding responses. On natural substrata, crab foraging intensities were well correlated with food levels (Robertson *et al.*, 1980). Amino acids, proteins (casein) and especially sugars and sugar polymers such as dextrin were found to be strong stimulants of feeding activity (Robertson *et al.*, 1981). Although individual compounds were effective in eliciting feeding responses, mixtures were more effective (Robertson *et al.*, 1980).

Robertson *et al.* (1981), and others (Hazlett, 1971a,b; Hartman and Hartman, 1977; Zimmer-Faust *et al.*, 1979) have suggested crustaceans orient to specific chemicals that reflect major dietary components. Thus, differences in response by different species of fiddler crabs might reflect differences in quantity or quality of food in the habitat that each species occupies. Hexoses are specific excretion products and components of the exopolymers of food items such as diatoms (White and Benson, 1984). Crabs could use hexoses to detect food.

In contrast to most aquatic crustaceans whose antennules are central to food search behavior (Hazlett, 1971a; Carr and Derby, 1986) fiddler crab antennules are separated from the food containing substratum by air. Thus, food search is mediated by dactyl chemoreception rather than antennule chemoreception (Robertson *et al.*, 1981). Antennular chemoreception is known to be mediated by neurosecretory complexes in

the eyestalks. These neurosecretory complexes are involved in sexual displays (Gleeson *et al.*, 1987) and feeding (Hazlett, 1971a). Hazlett (1971a) showed that crab responses to antennular stimulation were reduced in eyestalk-ablated animals and reported that there was an increase in chewing of inedible objects by ablated animals. The effect of eyestalk ablation on dactyl mediated feeding responses of deposit feeding crabs such as the *Uca* species (Robertson *et al.*, 1981) has not been investigated. Crustacean eyestalks are central to vision, neural integration and chemosensory as well as metabolic pathways. Studies with ablation are an initial step in determining if and how this major crustacean control center is involved in feeding behavior.

Here, we report studies of the feeding responses of three locally abundant species of fidder crabs, *U.minax*, *U.pugilator* and *U.pugnax* to five hexoses. We show differences in responses both within and between species. We also show that response thresholds of intact crabs are higher than those of eyestalk-ablated crabs, but that the patterns of response are similar. The latter information should be useful in probing the genetic basis and hormonal control of feeding behavior in fiddler crabs.

Materials and methods

Test animals

Uca pugilator were collected from Bird Shoals, Beaufort, NC, USA. *Uca minax* and *U.pugnax* were gathered from the banks of a tidal creek on US Highway 70, three miles east of Beaufort, NC. Crabs were held in 150 × 75 × 30 cm water tables. Each water table contained a 20 × 75 × 5 cm strip of substrate from the collection environment. Fresh seawater flowed continuously into the table and was maintained at a depth of several mm. The temperature of the room was ~23°C and the photoperiod was ~12:12.

Feeding assays

Fiddler crabs test the substratum with their dactyls and chelae. The minor cheliped is brought to the buccal region and the feeding movement completed by removal of material on the cheliped by the mouth parts (Miller, 1961). Chemical stimulation of the dactyls or chelae increases the frequency of this feeding movement. Feeding assays were conducted on intact and eyestalk-ablated crabs. Usually 30 mature crabs of each species and in each condition (intact or eyestalk-ablated) were tested. Data presented for no additions and glucose are based upon 60 crabs. Preliminary tests showed the sex of the crab did not affect assay responses. Five hexoses were tested: fructose, galactose, glucose, mannose and sorbose. Ambient seawater (32 p.p.t.) filtered to remove particles >100 kd was used for hexose dilutions from 0.004 to 1.0 M. The filtered seawater was also used to rinse crabs and to test for background feeding activity. The water contained <12 μM hexose equivalents per liter by the phenol sulphuric acid technique (Ashwell, 1955). Stock sugar solutions were stored frozen at −20°C. Dilutions were tested immediately after mixing.

Assays on intact crabs

Because sighted fiddler crabs are skittish and show an alarm response (Herrnkind, 1968), crabs were observed through a 4.0 × 0.5 cm slit in a blind. Preliminary trials showed that crabs could be reproducibly tested in groups of 5–10 in a 19 cm diameter finger bowl since crabs maintained position and could be identified individually. After a 15 s interval in which the alarm response due to handling passed, 20 ml of test solution was introduced through pipettes previously positioned 1.5 cm above the bottom of the finger bowl. Crabs were observed for 2 min. A positive feeding response was recorded for each individual that brought its minor cheliped to its buccal region more than once. Each individual crab was scored as responding positively or not responding in each test solution. The background response was that observed upon introduction of 100 kd filtered seawater. Hexose solutions were tested from lowest to highest concentration. Crabs were rinsed for 5–10 s in filtered seawater between tests in each solution. Approximately 90 min were required to observe feeding responses of 30 crabs to a dilution series of a hexose.

Assays on eyestalk-ablated crabs

Eyes were ablated at the base of the stalk with a pair of forceps. At least 12 h elapsed after ablation and before testing. This interval was sufficient for competition of visual changes in chromatophores due to eyestalk ablation to occur. Spontaneous feeding activity was reduced by rinsing crabs and storing them in 100 kd filtered seawater for 30 min prior to conducting experiments. Blind crabs did not show an alarm response. In tests, individual crabs were placed in 10.5 cm diameter finger bowls containing 10 ml of the test solution, and observed for 20 s. Movement of a cheliped to the buccal region more than once was considered to be a positive feeding response. Crabs were rinsed for 5–10 s in 100 kd filtered seawater and then placed in the next higher concentration. All hexoses were tested from lowest to highest concentration. The background response was that recorded in response to introduction into 100 kd-filtered seawater.

Analyses

Thresholds for responses were determined for the five hexoses. Threshold is defined as the first concentration at which the feeding response is significantly greater than background using the proportions test. Contingency analyses generating a G statistic were used to compare responses between species (Sokal and Rohlf, 1981).

Results

Background feeding

Intact and eyestalk-ablated fiddler crabs of all three species were exposed to filtered seawater and observed in order to determine the background level of feeding movements. Feeding movements of intact crabs of all three species were low. From 0–6% of the intact crabs responded in the 2 min test interval. Statistical analyses comparing background feeding responses of intact crabs both between and within species showed

Table I. Feeding thresholds (mM) of three species of fiddler crabs

Species	Hexose				
	Glucose	Sorbose	Galactose	Mannose	Fructose
Uca pugilator					
Intact	16	16	16	125	None
Ablated	8	4	8	8	None
Uca minax					
Intact	16	32	16	None	None
Ablated	4	8	8	16	None
Uca pugnax					
Intact	16	16	125	1000	None
Ablated	8	8	250	None	None

that the responses were similar. Eyestalk ablation dramatically increased the background feeding responses of all three species. Background feeding responses in a 20 s interval for ablated animals were 15% for *U.minax*, 25% for *U.pugilator* and 30% for *U.pugnax*. In spite of the shorter assay interval and holding in filtered seawater, background feeding responses of ablated crabs of all species were significnatly higher than their intact counterparts [z-test of proportions (Walpole, 1974) all $z > 2.35$, $P > 0.01$].

Threshold of intact crabs to hexoses

Responses of crabs to the different hexoses were specific. None of the three species responded to fructose. *U.pugilator* was equally sensitive to glucose, sorbose and galactose and ~eight-fold less sensitive to mannose. *U.pugnax* was equally sensitive to glucose and to sorbose, eight-fold less sensitive to galactose and 64-fold less sensitive to mannose. *U.minax* was equally sensitive to glucose and galactose, two-fold less sensitive to sorbose and insensitive to mannose. Threshold concentrations for the most potent sugars for all species were 16 mM (Table I).

Threshold of eyestalk-ablated crabs to hexoses

Thresholds for responses of eyestalk-ablated crabs were determined for the five hexoses. None of the three species responded to fructose. *U.pugilator* had its lowest threshold to sorbose and was equally sensitive to glucose, galactose and mannose. *U.pugnax* was equally sensitive to glucose and sorbose, 30-fold less sensitive to galactose and did not respond to mannose. *U.minax* was most sensitive to glucose, equally sensitive to sorbose and galactose and least sensitive to mannose. Threshold concentrations for the most potent sugars were 4–8 mM. In nine out of 10 instances, eyestalk ablation lowered thresholds primarily two- to four-fold. Only in the case of the response of *U.pugnax* to galactose was the concentration threshold increased (Table I).

Rank-order of intact crabs to hexoses

Overall, intact and ablated crabs responded similarly to the different hexoses. The major differences between intact and ablated crabs were the general increase in background

Table II. Percentage of intact fiddler crabs responding to three hexoses. At least 30 crabs of each species were tested at each concentration

Species	Glucose (M)							Sorbose (M)							Galactose (M)						
	0.016	0.032	0.064	0.125	0.25	0.5	1.0	0.016	0.032	0.064	0.125	0.25	0.5	1.0	0.016	0.032	0.064	0.125	0.25	0.5	1.0
Uca minax	20	33	47	70	73	87	95	7	10	13	27	47	63	83	10	10	10	20	33	30	47
Uca pugilator	20	33	67	90	100	100	100	17	37	47	87	97	100	97	20	23	40	57	70	83	80
Uca puganax	70	77	90	97	100	100	100	50	47	47	57	70	93	90	3	7	10	30	50	60	60

Table III. Percentage of eyestalk-ablated fiddler crabs responding to three hexoses. At least 30 crabs of each species were tested at each concentration

Species	Glucose (M)									Sorbose (M)									Galactose (M)								
	0.004	0.008	0.016	0.032	0.064	0.125	0.25	0.5	1.0	0.004	0.008	0.016	0.032	0.064	0.125	0.25	0.5	1.0	0.004	0.008	0.016	0.032	0.064	0.125	0.25	0.5	1.0
Uca minax	47	60	80	87	90	95	95	97	97	5	43	63	65	73	70	75	87	87	30	50	57	60	60	60	67	73	70
Uca pugilator	35	55	77	81	83	100	100	100	100	45	63	70	83	90	90	90	90	100	45	53	70	87	87	93	93	97	93
Uca pugnax	45	80	85	93	93	93	93	90	90	33	50	43	45	65	75	80	80	87	25	30	33	35	40	37	55	53	50

feeding and increase in sensitivity to the sugars that evoked feeding responses. However, response patterns to hexoses were species- and hexose-dependent.

Intact crabs were differentially sensitive to hexoses. Glucose was the only hexose that evoked >95% response in all species. At the three highest concentrations of glucose tested, 100% of *U.pugnax* and *U.pugilator* fed. *U.minax* were the least responsive to all concentrations tested although 95% fed at 1.0 M glucose (Table II).

Sorbose ranked second in potency, evoking ≥80% response in all three species. Percentage response of *U.pugnax* to lower concentrations were significantly higher than for the other two species ($G > 11.5$, 2 *dF*, $P < 0.1$). One of the three species, *U.pugilator*, responded in highest percentage to sorbose. *U.minax* were the least responsive to all sorbose concentrations tested although 83% fed when exposed to 1.0 M sorbose (Table II).

Galactose ranked third in potency, evoking ≥45% response in *U.minax*, 60% response in *U.pugnax* and >80% response in *U.pugilator*. The highest percentage response was to 0.50 M galactose by *U.pugilator* (83% response)—significantly greater than the response of the other two species ($G > 10.5$, 2 *dF*, $P < 0.01$). *U.pugnax* showed a 60% response at 0.5 and 1.0 M galactose. Total percentage responses of *U.minax* were lower than the other species at all concentrations tested. Less than 50% of *U.minax* fed at 1.0 M galactose (Table II).

Responses of intact crabs to mannose were weak at best. *U.pugilator* was the most sensitive to mannose. Responses of *U.pugilator* to mannose concentration from 0.125–0.50 M were all significantly greater than control (z test of proportions $z > 1.65$, $P < 0.05$). *U.pugnax* responded significantly (test of proportions $z > 1.65$, $P < 0.05$) only at 1.0 M mannose. *U.minax* did not respond significantly to mannose. The highest response to any concentration of mannose by any species of fiddler crab was 20%. *U.pugilator* responded at 20% to 0.5 M mannose. *U.pugnax* responded at 20% to 1.0 M mannose (data not shown).

Tests with fructose showed that the hexoses span the spectrum of possible responses. Fructose did not evoke feeding responses in any of the three species of fiddler crabs.

Rank-order of eyestalk-ablated crabs to hexoses

Eyestalk-ablated crabs showed patterns of responses to the hexoses that were similar to those of intact crabs. At least 80% of the crabs of each species responded to 0.032 M or greater glucose (Table III). At least 85% of the crabs of each species responded to sorbose. However, only at 1.0 M sorbose did >80% of all three species respond. Maximum percentage responses by *U.pugilator* were consistently higher than those of the other species at all concentrations tested. Galactose evoked responses that ranged from a maximum of 55% for *U.pugnax* to 73% for *U.minax* and 97% for *U.pugilator*. In contrast to the results for intact crabs, the percentage response of ablated *U.minax* to galactose was higher than that of *U.pugnax* for all concentrations tested (Table III).

Of the eyestalk-ablated crabs, *U.pugilator* was the most sensitive to mannose. Responses of *U.pugilator* to mannose concentration of 0.008 M and from 0.064–1.0 M were all significantly greater than background levels of response (z test of proportions $z > 1.65$, $P < 0.05$). Ablated *U.pugnax* did not respond significantly to mannose. Ablated *U.minax* responded significantly (z test of proportions $z > 1.65$, $P < 0.05$)

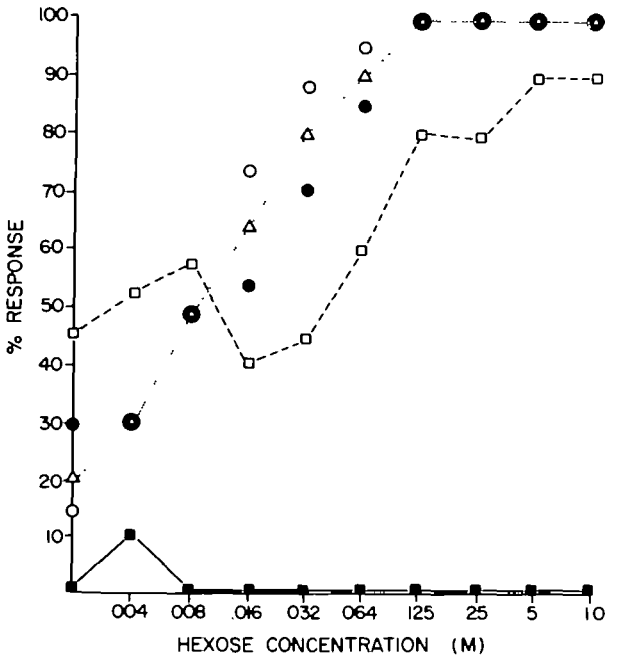

Fig. 1. A comparison of feeding responses of eyestalk-ablated *U.pugnax* to galactose. Thirty crabs were divided into two groups based on responses to galactose; 20 responding to galactose and 10 not responding to galactose. Both groups responded similarly to glucose. △, total glucose response; ○, galactose responders tested with glucose; ●, galactose nonresponders tested with glucose; □, galactose responders tested with galactose; ■, galactose nonresponders tested with galactose.

to mannose at 0.016, 0.032 and 1.0 M. The highest percentage response was 53% by *U.pugilator* at 0.25 M mannose (data not shown). Feeding responses of crabs to mannose were generally less than twice the background feeding response. As was the case with intact crabs, fructose did not evoke an increase in feeding responses in any species.

Galactose and mannose as special cases

The level of response of *U.pugnax* to galactose and of *U.pugilator* to mannose enabled more detailed analysis since in both instances the maximum response was significantly less than 100% at all concentrations tested, but with responses to a number of concentrations sufficiently above control levels. The response to glucose by the same individuals was used as a positive control for confirming responsiveness of individual crabs (Figures 1 and 2).

U.pugnax individuals were divided into two groups based upon their responses to galactose. These groups were termed galactose responders and galactose nonresponders (Figure 1). The division was made by separating crabs that responded to at least two concentrations of galactose from those that did not. There were significant responses to galactose in the galactose responding group ($z > 1.65$, $P < 0.05$). Background feeding responses of galactose responders were also significantly higher than those of nonresponders ($z > 2.85$, $P < 0.01$). Finally, although the percentage response of

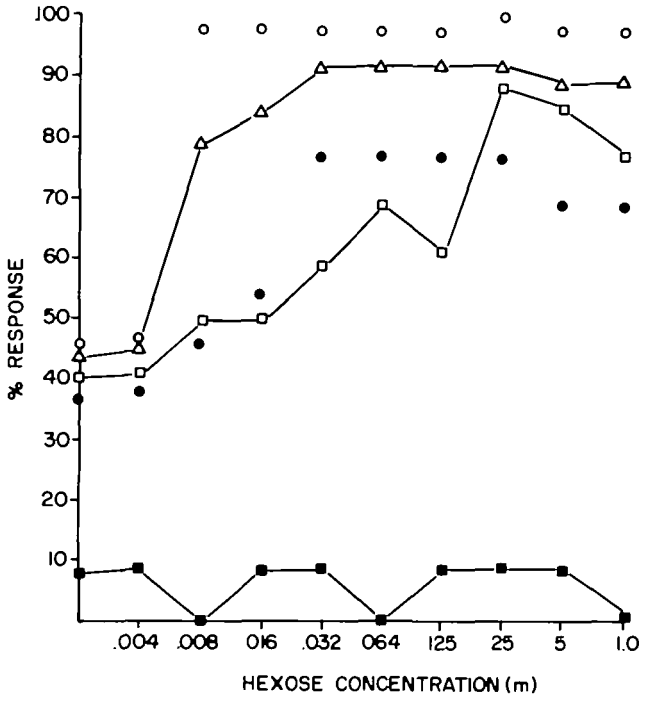

Fig. 2. A comparison of feeding responses of eyestalk-ablated *U.pugilator* to glucose and mannose. Thirty crabs were divided into two groups based on responses to mannose; 20 responding to mannose and 10 not responding to mannose. Both groups responded similarly to glucose. △, total glucose response; ○, mannose responders tested with glucose; ●, mannose nonresponders tested with glucose; □, mannose responders tested with mannose; ■, mannose nonresponders tested with mannose.

galactose responding animals to glucose was always higher than that of the galactose nonresponsing group, both groups responded significantly and in high percentage to glucose.

Similarly, *U.pugilator* individuals were divided into groups of mannose responders and mannose nonresponders (Figure 2). This division was made by separating crabs that responded to at least two concentrations of mannose from those that did not. There were significant responses to mannose in the mannose responding group ($z > 1.65$, $P < 0.05$). Control feeding responses of mannose responders were also significantly higher than those of nonresponders ($z > 2.85$, $P < 0.01$). Finally, the percentage responses of both groups to glucose were similar.

Discussion

Of the three species tested, intact and ablated *U.pugilator* in general were the most responsive. *U.pugilator* responded more to higher concentrations of the stimulating hexoses and at least as well as the other species to lower concentrations. Exceptions were that intact *U.pugnax* responded more to the lower concentrations of glucose and sorbose and, of the ablated crabs, *U.minax* had a lower threshold to glucose than did *U.pugilator* (see Tables II and III).

Eyestalk ablation is known to dramatically alter levels of hormones including hyperglycemic hormone in crabs (Fingerman, 1970) as well as to alter crustacean chemoreceptive behavior (Hazlett, 1971a; Gleeson *et al.*, 1987). Hyperglycemic factor or the concentration of hemolymph sugars on higher neural integration (Hazlett, 1971a) could control feeding activity and the behavioral threshold of sugar detection. The eyestalk ablation technique provided information that complemented the work of Hazlett (1971a) and provided possible clarification of the meaning of his observations on chewing of inedible objects as explained below. Ablation may result in decreased antennular sensitivity and increased dactyl sensitivity.

Hazlett (1971a) reported that antennular sensitivity was reduced upon eyestalk ablation and that chewing on inedible objects was increased. The present study shows that background feeding responses and the overall behavioral sensitivity to chemical stimulation are increased upon eyestalk ablation. Whilst handling the crabs, it was discovered that there were sufficient chemicals on bare hands (presumably serine) so that any object touched by human hands elicited feeding responses in the crabs. This coupled with the demonstrated increased sensitivity to sugars suggests that what Hezlett (1971a) referred to as chewing of inedible objects could be due to altered chemical sensitivity to levels of chemicals on the surface of inedible objects. Thus, while antennular sensitivity is decreased upon eyestalk ablation, dactyl sensitivity appears to be increased. Background feeding responses may be due to increased sensitivity to chemical stimulation.

The sediments upon which fiddler crabs feed are rich in bacteria and diatoms that are either coated with exopolymers that contain high percentages of hexoses or that specifically secrete hexoses such as glucose (White and Benson, 1984). Robertson *et al.* (1981) showed that cultures of diatoms and bacteria induced feeding in fiddler crabs when mixed in clean sand. Therefore, the sensitivity of crabs to hexoses suggests that free or polymer-bound hexoses could be used as indicators of food and to mediate feeding activity (Robertson *et al.*, 1981). Extrapolation from the laboratory data on pure hexoses to field conditions is premature because the availablity of compounds for stimulation of feeding in natural sediments cannot be related directly to chemical measures of specific compounds.

Each species of fiddler crab occupies a different habitat (Teal, 1958). The species differences in behavioral response thresholds may be adaptations to the dietary items normally found in individual habitats. If this hypothesis is true, *U.pugilator* is acutely sensitive to glucose, *U.pugnax* to sorbose and *U.minax* to galactose. Feeding thresholds of the various species to sugars may be partially responsible for the species distributions observed in the field. Although the quality of food in all habitats seems sufficient for survival (Teal, 1958), utilization of that food is based upon the ability to detect and respond immediately.

Our finding that fiddler crabs do not respond to fructose corresponds with that of Robertson *et al.* (1981) for *U.pugilator*. Trott *et al.* (1984), using a similar assay, showed that *Ocypode quadrata*, a close relative of fiddler crabs, is strongly responsive to both fructose and mannose. *U.pugilator* was reported to be unresponsive to mannose (Robertson *et al.*, 1981). However, our feeding assay showed that a small but significant number of intact crabs responded to mannose. Work with the more responsive eyestalk-ablated crabs showed that there were crabs that responded to mannose at relatively low

concentrations and crabs that did not respond to mannose at any concentration. Thus there is plasticity in the response to sugars. If differences between fiddler crabs and ghost crabs represent differences in feeding strategies (Trott *et al.*, 1982), differences in responses within a species over its geographic range could reflect differences in food quality.

The feeding responses of *U.pugilator* to mannose and of *U.pugnax* to galactose are examples of potential genetic variation in feeding behavior within a species. Although 100% of the crabs tested responded to glucose, only 50% of *U.pugilator* responded to mannose and only 50% of *U.pugnax* responded to galactose. Additional study of differences in population responses to hexoses would provide valuable tools in studying geographic relationships between fiddler crab populations. The gene flow between populations is a result of dispersal and recruitment of planktonic larvae that are virtually impossible to trace. However, an understanding of the relationships between the genetics of taste reception provide an insight by quantitative investigation of feeding responses of recruiting organisms.

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