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# Sulphide as a larval settlement cue for *Capitella sp I*

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**Key words:** *Capitella*, sulphides, larval settlement, pioneers

**Abstract.** Pioneering marine benthic invertebrates are capable of locating and colonizing newly created and recently disturbed mud bottoms within a few days. The results of this study demonstrate that sulphides – naturally occurring products of anaerobic organic matter decomposition – promote the larval settlement of the pioneering polychaete *Capitella sp I* in both laboratory and semi-natural conditions.

Settlement was enhanced both in sediments enriched with sulphides and in sulphidic, sediment-free conditions when compared with controls. A sulphide concentration ranging between 0.1 mM and 1.0 mM elicited optimal settlement with subsequent metamorphosis and survival of the settled worms.

This is the first time a geochemically-mediated larval settlement response has been demonstrated.

The initial colonization of new and/or recently disturbed marine fine-grained sediments by larvae of small, pioneering polychaetes has been documented world-wide (Grassle and Grassle, 1974; McCall, 1975, 1977; Dauer and Simon, 1976; Rhoads et al., 1977; Pearson and Rosenberg, 1978; Poore and Kudenov, 1978; Rhoads et al., 1978; Sanders et al., 1980; Knox and Fenwick, 1981; Raman and Ganapati, 1983; Tsutsumi and Kikuchi, 1983). Questions remain, however, regarding the mechanism(s) driving primary colonization on marine soft-sediments. It is important to attempt to resolve this point, as pioneering polychaetes play an important role in structuring the soft-sediment benthic community. They are a food source for many demersal fish and crustacea (Virnstein, 1977). Their presence promotes the oxidation of the upper 2–3 cm of marine sediments, altering pore water chemistry and, in turn, affecting mineralization processes occurring in sediments (Aller, 1977). Dense aggregations of pioneering polychaetes have been shown to increase sediment stability and affect fluid boundary conditions at the sediment-water interface; these then affect sediment and larval entrainment, sediment erosion, and sediment deposition (Rhoads and Young, 1970; Rhoads et al., 1978; Eckman, 1979, 1983). Finally, some pioneers are employed as indicators of highly stressed regions (Pearson and Rosenberg,

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1978). One such pioneer, the polychaete *Capitella capitata* Fabricius, is often reported from organic-rich, sulphidic sediments (Pearson and Rosenberg, 1978). As these environments appear to be favorable for the survival and reproduction of adult *Capitella*, larvae of these organisms may be capable of locating and settling in such organic-rich environments.

Factors which have been experimentally determined to induce settlement and/or metamorphosis of marine benthic organisms include biological ones – i.e. the presence of certain flagellates and bacterial exudates (Wilson, 1953a, 1953b, 1954, 1955; Scheltema et al., 1981), physical ones – i.e. sediment grain size (Wilson, 1948) and chemical ones – i.e. specific molecules adsorbed on shells (Crisp and Meadows, 1962, 1963). Other studies have implicated oxygen deficiency (Arntz, 1977), tidal periodicity (Dauer and Simon, 1975), general and local hydrodynamic conditions (Pearson, 1970; Tyler, 1977; Eckman, 1979, 1983; Hannan, 1981; Nerini and Oliver, 1983), proximity of adult populations (Dauer and Simon, 1976), the nature of the sediment and its susceptibility to disturbance (Jumars, 1975; McCall, 1975; Santos and Simon, 1980), the presence of decaying organic matter (Gerlach, 1977) and specific microfloral associations (Thorson, 1966) as factors promoting the aggregation of settling larvae. Researchers have also determined that the following inhibit the successful settlement of some benthic larvae: oxygen deficiency (Arntz, 1977), sediment instability (Rhoads and Young, 1970; Rhoads et al., 1978), predation (Riese, 1977; Cowden et al., 1984), and pollution (Bellan et al., 1972). No study prior to the present one has examined the role of the sedimentary geochemical environment as a specific mediator of larval settlement behavior.

Aller (1977) and Westrich (1983) have demonstrated that deep-burrowing (>3 cm), deposit-feeding organisms (Stage III of Rhoads and Boyer 1982) enhance rates of anaerobic organic matter decomposition (OMD) by continually supplying highly labile organic matter to bacterial colonies present in the sediment. The products of this degradation, however, are either oxidized within the burrow or are precipitated around the burrow walls associated with irrigating macrofauna. In pioneering assemblages (burrow depth <3 cm) the products of OMD (i.e. $H_2S$, $HS^-$, $NH_4^+$, $CH_4$) accumulate in sediment pore waters. The rate of loss of these reduced products to the overlying water column is controlled by molecular diffusion without much pore water oxidation. This results in measurable quantities of $H_2S$ (including $HS^-$) and other OMD products present in the waters immediately in contact with the sediments. Natural disturbances, such as storms and current scour, may disturb the upper cm of oxidized sediment and enhance the concentration of reduced OMD products in the water near the sediment-water interface. Man-induced perturbations, such as sewage sludge and dredge spoil dumping, result in organically-enriched sediments and are also associated with high concentrations of OMD products near the sediment-water interface. All of the above create biologically 'open' space for pioneering macrofauna settlement.

The association of *Capitella capitata* with sediments of high organic content and the resulting end-products of the anaerobic decomposition of such material, has been reported in many field studies (McCall, 1975, 1977; Pearson and Rosenberg, 1978; Sanders et al., 1980; Tsutsumi and Kikuchi, 1983). This paper describes a series of experiments designed to test the hypothesis that $H_2S$, a major anaerobic OMD product, does not promote the settlement of larvae of the pioneering polychaete, *Capitella sp I.* This polychaete was determined by Grassle and Grassle (1976) to be the most opportunistic of the sibling species complex previously identified as the single species *Capitella capitata* Fabricius.

## Materials and methods

A total of 4 experiments were performed to ascertain the influence, if any, of $H_2S$ on larvae of *Capitella sp I.* All sulphide solutions were made by dissolving crystals of $Na_2S \cdot 9H_2O$ in 0.22 $\mu$m filtered deoxygenated seawater. Sulphide measurements were made using a sulphide electrode (Berner, 1963) or colorimetrically, employing the methods of Gilboa-Garber as modified by Howarth et al. (1982). Temperature and pH recordings were kept for each experiment. Animals, when preserved, were fixed in a solution of buffered formalin and then transferred to 70% isopropyl alcohol and stained with rose bengal.

### *I. Settlement choice experiment*

Thirty Dispo® weighing dishes (7.5 cm x 7.5 cm) were filled to a depth of 2 cm with acid-cleaned sand passed through a 125 $\mu$m sieve. Fifteen of these dishes had several small (~ 1 cm) $Na_2S \cdot 9H_2O$ crystals placed beneath the sand covering to serve as a source of diffusing sulphides. Fifteen control and fifteen experimental dishes were randomly placed in each of two 60 cm x 45 cm seawater tanks which collected the outflow from 4 *Capitella sp I* rearing tanks. Sulphide measurements were made in the water surrounding and up to 1 cm above the experimental and control dishes with a sulphide electrode. Temperature was kept at 20 °C; pH was 7.4. The dishes were left in the tank for a period of 8 days, long enough to insure that larvae were released from the rearing tanks but short enough to prevent settled and metamorphosed juveniles in the control and experimental dishes from reproducing. At the conclusion of the experiment the contents of each dish were elutriated with Ludox®. The elutriate was passed through a 0.35 $\mu$m sieve and all retained organisms were preserved, stained and counted.

The results of this experiment are given in Table 1. A greater number of larvae settled and metamorphosed in the sulphide dishes when compared to the control dishes (Mann-Whitney U-test $p < 0.001$). The sulphide values directly above the experimental dishes ranged between 0.1 mM and 0.01 mM sulphide for the duration of the 8 days. They decreased below 1.0 $\mu$M at a

Table 1. Results of the settlement choice experiment

| Treatment type | # Metamorphosed *Capitella sp I* |
|---|---|
| Control | 2 |
| Control | 7 |
| Control | 14 |
| Control | 15 |
| Control | 23 |
| Control | 30 |
| Control | 34 |
| Control | 34 |
| Control | 37 |
| Control | 41 |
| Sulphide | 41 |
| Sulphide | 41 |
| Sulphide | 59 |
| Control | 61 |
| Control | 62 |
| Control | 67 |
| Sulphide | 81 |
| Sulphide | 83 |
| Sulphide | 86 |
| Sulphide | 96 |
| Sulphide | 106 |
| Sulphide | 114 |
| Sulphide | 120 |
| Sulphide | 165 |
| Sulphide | 180 |
| Sulphide | 318 |

X ± S.E. : Controls = 32.85 ± 5.83
: Sulphides = 114.62 ± 20.49

*Note*: Four samples were lost in transport

radial distance less than 1 cm from the experimental dishes. No sulphides were detected in waters above or immediately surrounding the control dishes. Bacterial mats developed on a number of the sulphide dishes; none were present on control dishes. The results could reflect the following: (a) bacterial mats associated with sulphides may enhance larval settlement and metamorphosis, (b) the sulphides themselves enhance larval settlement and/or metamorphosis, or (c) sulphides trigger settlement by physiologically shocking the larvae, yielding adults which are abnormal in some manner. The microcosm experiment addressed, in part, this last point.

*II. Microcosm experiment*

Two (36 cm x 25 cm x 8 cm) trays were filled to a depth of 8 cm with acid-cleaned sand passed through a 125 $\mu$m sieve. One tray was 'seeded' with 453.6 gms of $Na_2S \cdot 9H_2O$; the second tray was not. These trays were placed in a sea table and 0.22 $\mu$m filtered seawater flowed over them to a depth of 8 cm for one week prior to the introduction of larvae. This permitted the build-up of sulphides in the pore waters of the experimental tray sediments

Table 2. Results of the microcosm experiment

| Treatment type | # Metamorphosed *Capitella sp I* |
|---|---|
| Control | 1 |
| Control | 1 |
| Control | 1 |
| Control | 2 |
| Control | 3 |
| Control | 3 |
| Control | 3 |
| Control | 4 |
| Control | 4 |
| Sulphide | 4 |
| Sulphide | 4 |
| Sulphide | 5 |
| Control | 6 |
| Control | 6 |
| Control | 6 |
| Sulphide | 7 |
| Sulphide | 15 |
| Sulphide | 31 |
| Sulphide | 32 |
| Sulphide | 33 |
| Sulphide | 36 |
| Sulphide | 39 |
| Sulphide | 82 |
| Sulphide | 106 |

$\bar{X} \pm$ S.E. : Controls $= 3.33 \pm 0.56$
: Sulphides $= 32.83 \pm 9.23$

and was observed as a blackening of the sediment surface. Sulphide measurements were made at a distance of 1 cm above both the sulphidic and control trays and in the water surrounding both trays. Runoff from a *Capitella sp I* rearing tank flowed into the sea table containing the two trays. No food was introduced into the sea table containing the experimental trays for the duration of the experiment. At the end of the 2 month experimental period, 12–1 cm deep (2.5 cm diameter) cores were taken from the center of each tray and preserved. Whole sediments were examined for larvae, juveniles, and adults of *Capitella sp I.*

Sulphide concentrations in the water in contact with the experimental trays were in excess of 1.0 mM initially and remained in the 0.1 mM range for the entire duration of the experiment. Concentrations of sulphide in supernatant water over the control trays and in the ambient sea table water were negligible. Results of this experiment are given in Table 2. A significantly greater number of metamorphosed worms (juveniles and adults) were found in the sulphide tray when compared with the control tray (Mann-Whitney U-test $p < 0.001$). Of the adults present in the sulphide tray, many females contained eggs and some had well-developed brood cases. Several of these females and brood cases were isolated prior to preservation and allowed to develop in order to ascertain the viability of the larvae produced. No brood cases were found in the control tray sediments. The presence of different age classes of *Capitella sp I* in the sulphide tray indicates that multiple or continuous settlement can occur in this species. I did not detect any apparent negative effect of the sulphides on the reproduction of *Capitella sp I*. The results here do not allow a distinction to be made between sulphide as a potential energy source (bacterial growth as food) for juvenile *Capitella sp I* and as a settlement cue for the larvae. The next experiment was designed to isolate the effects of sulphides on *Capitella sp I* larvae in the absence of bacterial mats or other sediment-related influences.

*III. In vitro experiment*

*Capitella sp I* larvae were isolated on hatching. Individual 35 mm diameter glass petri dishes were filled with 10 ml of 0.22 μm filtered deoxygenated seawater. No sediment was present in these dishes. Larvae were pipetted into each dish and allowed to acclimate for 10 min prior to the introduction of the test stimulus. Larval density per dish ranged from a minimum of 15 to a maximum of 169. The exact number depended on the availability of larvae hatched on a particular experimental day. Hatching was accomplished in one of two ways. Either individual females with brood cases were isolated and checked daily for larval hatching or the brood cases were visually staged and manually torn open when hatching appeared imminent. This latter method often resulted in the production of larvae which were not totally competent to settle. One ml of either filtered aerobic seawater or 0.1 mM sulphide solution was added to each dish at the start of a run. Each dish was then covered with a glass cover and observations of swimming and settling behavior were made immediately after the test solution was added and at 3 h intervals for a 24 h period. The pH was monitored and ranged between 6.9 and 7.2; the higher pH was recorded in the experimental dishes. Each run was conducted under a uniform epi-illumination field and at constant temperature.

The concentration of sulphides intially experienced by the larvae was 0.01 mM, measured colorimetrically. After 24 h, the concentration had diminished to μm levels. The 0.1 mM–0.01 mM range is representative of concentrations measured in nature in areas where *Capitella capitata* have been reported (Theede et al., 1969; Kolmel, 1978; Pearson and Eleftheriou, 1981). Table 3 contains the results of 7 runs conducted between August 1982 and May 1983. Enhanced larval settlement and metamorphosis were observed in dishes containing sulphides relative to controls (Kolmogorov-Smirnov Test, $p < 0.001$ and $p < 0.008$). At the end of each run, all metamorphosed animals were counted and transferred to sediments. The results from this experiment demonstrate that *Capitella sp I* larvae respond positively to sulphides in the absence of sediment and/or bacterial mats. They do not imply that worms could survive long-term without sediment and a food source. A final experiment was designed to ascertain the range of sulphide

Table 3. Results of the *in vitro* sulphide response experiment

| Date | Run | Trial | Controls | | | | Sulphides | | | | Notes |
|---|---|---|---|---|---|---|---|---|---|---|---|
| | | | # Larvae | % Set | # Meta[1] | % Meta[1] | # Larvae | % Set | # Meta[1] | % Meta[1] | |
| 8–82 | I | 1 | 33 | 55 | 7 | 21.21 | 43 | 100 | 7 | 16.28 | a, g, +, * |
| | | 2 | 19 | 26 | 0 | 0.00 | 39 | 100 | 17 | 43.59 | |
| | | 3 | 12 | 17 | 0 | 0.00 | 88 | 85 | 10 | 11.36 | |
| 5–83 | II | 1 | 123 | 2 | 0 | 0.00 | 169 | 100 | 139 | 82.00 | b, f, *** |
| 5–83 | III | 1 | 18 | 67 | 1 | 5.56 | 28 | 100 | 21 | 75.00 | c, f, *** |
| 5–83 | IV | 1 | 88 | 5 | 2 | 2.27 | 40 | 100 | 34 | 85.00 | d, f, *** |
| 5–83 | V | 1 | 24 | 0 | 0 | 0.00 | 30 | 97 | 13 | 43.33 | d, g, *** |
| | | 2 | 35 | 0 | 0 | 0.00 | 23 | 78 | 12 | 52.17 | |
| | | 3 | 42 | 2 | 0 | 0.00 | 33 | 100 | 11 | 33.00 | |
| 5–83 | VI | 1 | 58 | 43 | 8 | 13.79 | 64 | 100 | 55 | 86.00 | d, h, * |
| 5–83 | VII | 1 | 86 | 0 | 0 | 0.00 | 58 | 97 | 0 | 0.00 | e, f, ** |
| $\bar{X} \pm$ S.E.: | | | | 19.73 ± 7.43 | | 3.89 ± 2.15 | | 96.09 ± 2.25 | | 47.98 ± 9.36 | |

(a) hatched 8/15/82
(b) hatched 5/21/83
(c) hatched 5/22/83
(d) hatched 5/23/83
(e) hatched 5/24/83

(f) Adults and larvae at 15 °C
(g) Adults and larvae at 20 °C
(h) Adults reared at 15 °C; larvae kept at 20 °C
(+) Experiment interrupted after 3 hrs
(1) Metamorphosed

(*) Natural hatch, trochophores
(**) Forced hatch, trochophores
(***) Natural hatch, pre-trochophores

Table 4. Results of the optimal concentration range experiment

| Date | Concentration[a] | # Larvae[b] | % Set | # Meta[c] | % Meta[c] | Notes |
|---|---|---|---|---|---|---|
| 8–83 | Control | 90 | 45.56 | 4 | 4.44 | * |
| | 0.01 mM | 90 | 56.63 | 7 | 7.78 | |
| | 0.10 mM | 90 | 52.81 | 9 | 10.00 | |
| | 1.00 mM | 90 | 91.96 | 19 | 21.11 | |
| | 10.00 mM | 90 | 100.00 | 24 | 26.67 | 13 dead |
| 9–83 | Control | 65 | 3.08 | 2 | 3.08 | ** |
| | 0.01 mM | 65 | 12.31 | 8 | 12.31 | |
| | 0.10 mM | 65 | 16.92 | 11 | 16.92 | |
| | 1.00 mM | 65 | 100.00 | 65 | 100.00 | |
| | 10.00 mM | 65 | 100.00 | 55 | 84.62 | 45 dead |
| 9–83 | Control | 36 | 0.00 | 0 | 0.00 | ** |
| | 0.01 mM | 36 | 0.00 | 0 | 0.00 | |
| | 0.10 mM | 36 | 0.00 | 0 | 0.00 | |
| | 1.00 mM | 36 | 100.00 | 33 | 91.67 | |
| | 10.00 mM | 36 | 100.00 | 1 | 2.78 | 36 dead |

(a) Initial concentrations; final concentrations were an order of magnitude lower (i.e. 1.00 mM initial was 0.10 mM after 24 h)
(b) Adults were reared at either 15 °C or 20 °C
(c) Metamorphosed
(*) Metatrochophores used in this study had hatched 12 h prior to the initiation of this experiment
(**) Natural hatch; trochophore larvae

concentrations to which *Capitella sp I* larvae respond and the optimal concentration for promoting larval settlement and/or metamorphosis.

*IV. Optimal concentration range experiment*

This experiment employed the same techniques as the preceding one. 10 ml of either filtered aerobic seawater, 0.1 mM, 1.0 mM, 10 mM, or 100 mM sulphide solution was added to each dish at the start of a run. The experimental concentrations of sulphides produced in the dishes were: zero, 0.01 mM, 0.1 mM, 1.0 mM, and 10 mM. The pH ranged from 6.8 in the controls to 8.0 in the 10.0 mM dishes. The higher pH was corrected to 7.0 by the addition of 5% HCl. At the conclusion of the experiment, the number of larvae settled, metamorphosed, and alive were counted.

A gradual oxidation of sulphides occurred over the 24 h experimental period. The final concentrations of sulphides, measured colorimetrically, were an order of magnitude lower (1.0 $\mu$M, 0.01 mM, 0.1 mM, 1.0 mM) than the initial concentrations employed. The results, given in Table 4, show a significant difference (Friedman's Test, $p < 0.05$) between larvae settling in initial concentrations $\geqslant 1.0$ mM and those in the lower sulphide concentrations and the controls. It should be noted that although high settlement was recorded for the maximum sulphide concentration (10 mM initial) most of these settled larvae died within the 24 h experimental period. Those in the next concentration (1.0 mM initial) had a higher settlement proportion than larvae exposed to initial sulphide concentrations $< 1.0$ mM. Adult worms developed from the settled larvae in the 1.0 mM initial sulphide concentration and successfully reproduced in the months following the conclusion of this experiment, yielding viable larvae. These results indicate that a sulphide concentration range of 1.0 mM–0.1 mM represents the threshold concentration for the promotion of larval settlement in the polychaete *Capitella sp I.*

## Discussion

The experiments presented here demonstrate that *Capitella sp I* larvae settle, metamorphose and are able to successfully reproduce in the presence of $H_2S$ and its related chemical species.

There are ecological advantages to be gained by a species if it is able to settle and metamorphose in highly sulphidic areas. First, as $H_2S$ excludes most macrofauna, *Capitella sp I* and perhaps some other pioneers are able to exploit relatively non-competitive open space. This is an advantage for those pioneers which may be poor competitors (Vermeij, 1978). Competition with meiofauna in such regions, however, is a possibility. Secondly, as $H_2S$ is usually indicative of anaerobic OMD, it is a chemical cue which reflects the presence of available detritus for near-surface deposit-feeders. Additionally, sulphides may indicate the presence of bacterial mats which may also be a food source for some pioneers. This last statement is supported by evidence from both the settlement choice and the microcosm experiments.

The physiological basis for the settlement behavior exhibited by *Capitella sp I* larvae needs to be further investigated. Cavanaugh (personal communication) has examined *Capitella sp I* for enzymes commonly associated with chemautotrophic symbionts found in several hydrothermal vent species (Cavanaugh et al., 1981). Her results indicate that *Capitella sp I* adults do not possess chemautotrophic symbionts. Whether *Capitella sp I* physically excludes sulphides or renders them non-toxic in some other manner (actual utilization?) remains to be investigated.

Additionally, it is not known whether *Capitella sp I* possess a sulphide receptor cell. The results from the concentration range experiment suggest that some form of chemoreception is functioning. The nature of the response – the 1.0 mM threshold – suggests that the receptor cell, if it exists, has a high excitation threshold. The fact that a concentration of 10 mM is lethal does not necessarily imply that the hypothesized receptor cell functions in a narrow band. The larvae readily set in this high concentration, therefore, it is possible that the receptor cell was functioning. Death occurred post-settlement and may be related to an inability on the worms' part to detoxify such high sulphide concentrations.

Once pioneering organisms, such as *Capitella sp I*, are established on a mud surface, the sediments may become oxidized as the pioneers irrigate the mud via small tubes and burrow openings. This process subsequently decreases the flux of sulphides and other anaerobic OMD products out of the sediment and eventually terminates the settlement cue ($H_2S$ for *Capitella sp I*). The aerobic surface may then become colonized by other macrofauna who are less tolerant of high concentrations of anaerobic OMD products. This autogenic succession (Rhoads and Boyer, 1982) could only occur in the absence of any further disturbance or organic enrichment.

Anaerobic OMD products as settlement cues for some of the earliest macrofaunal pioneers on marine mud bottoms (i.e. *Capitella sp I*) may reflect the evolutionary 'roots' of these animals in primitive low-oxygen marine basins (Cuomo, 1984). The macrofaunal marine benthos, therefore, may be viewed as consisting of obligatory aerobes and those organisms which are adapted to life in extreme geochemical environments; the latter, in some cases, being the more primitive. This last idea is somewhat similar to the concept of the 'sulphide biome' described by Fenchel and Riedl (1970).

## Summary and conclusions

The results of the studies presented here have led me to reject the hypothesis that $H_2S$ does not promote larval settlement in the polychaete *Capitella sp I.* Instead, the following conclusions have been drawn:

1. *Capitella sp I* larvae settle in response to the presence of sulphides. Although sulphides may not be necessary for settlement, significantly more larvae settle in their presence than in their absence. A concentration between 1.0 mM and 0.1 mM sulphide elicits optimal settlement. Adults developed from larvae which had settled in response to sulphide produced larvae which settled and developed into reproductively viable adults.
2. Settlement can be initiated in sulphidic, sediment-free conditions, suggesting that the behavioral response to sulphide is independent of other sediment-related parameters.
3. Although other products of anaerobic OMD are released into the water column, the presence of sulphides alone is sufficient to induce settlement of *Capitella sp I* larvae.
4. Sulphides in marine sediments are associated with the presence of anaerobic or facultative bacteria and decaying labile organic matter. Both of these may be a food source for *Capitella sp I.* The ability to settle in sulphidic areas allows for the exploitation of such food resources in relatively non-competitive regions and therefore, may have a significant effect on the post-larval survival and growth of some pioneering organisms.

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