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**PELLET ACCUMULATION, SEDIMENT SUPPLY, AND CROWDING AS
DETERMINANTS OF SURFACE DEPOSIT-FEEDING RATE IN
PSEUDOPOLYDORA KEMPI JAPONICA Imajima & Hartman
(POLYCHAETA : SPIONIDAE)¹**

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Abstract: *Pseudopolydora kempi japonica* Imajima & Hartman was exposed in the laboratory to varying frequencies of sediment supply and fecal pellet removal and to varying degrees of intraspecific crowding. When pellets were not removed, feeding rates were approximately halved after only four pellets had accumulated in the feeding areas of individual worms. Crowding and increasing temperature accelerated feeding-rate depression by decreasing the time required for such accrual. Pellet removal returned feeding rate to the initial level, even under crowded conditions. Over the short term of these experiments (16 h), the only strong effect of variation in sediment supply was seen at the highest supply rate, which depressed feeding. Pellet accrual thus was clearly dominant over both sediment supply and intraspecific crowding in determining feeding rates. These results suggest the need to determine both the frequency of fecal removal by sediment transport in the field and to match this frequency in future laboratory experiments when simulation of field conditions is attempted.

Key words: deposit-feeding; polychaetes; *Pseudopolydora kempi japonica*; sediment transport

INTRODUCTION

Several factors are now known or strongly suspected to affect deposit-feeding rates. Particle fluxes have been observed to influence feeding modes and feeding rates of benthic microphages in the laboratory (Taghon *et al.*, 1980; Dauer *et al.*, 1981; Dauer, 1983). Theoretical considerations of food supply further suggest that sediment transport is an important determinant of feeding rate in deposit-feeders (Miller *et al.*, 1984). Observations of aggressive interactions and their apparent consequences in the laboratory (Levin, 1981, 1982; Wilson, 1984), coupled with failure to observe some of those consequences in the field, suggest that sediment transport may ameliorate competitive interactions (Wilson, 1984). In a recent empirical effort to determine whether sediment transport does influence feeding rates both in the laboratory and the field, Jumars & Self (1986) showed that field deposit-feeding rates of *Pseudopolydora kempi japonica*, a spionid polychaete, were enhanced either by short pulses of sediment

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transport associated with the incoming tide or by some factor correlated with those pulses.

While this evidence and these arguments suggested that sediment movement does indeed affect subsequent deposit-feeding rates, they shed little light on the path from sediment dynamic stimulus to deposit-feeding response. Assuming food supply as the ultimate cause of increase in feeding rate following a sediment transport pulse, there were a multitude of possible proximate cues that could elicit enhanced feeding rates. Three seemed most likely to us on the basis of published work: influx of food, intraspecific interactions, and removal of wastes. Influx of food as both the ultimate and proximate cue appeared most likely a priori (appearing to be the cue for switching from deposit- to suspension-feeding while suspended transport is maintained: Taghon *et al.*, 1980; Dauer *et al.*, 1981; Dauer, 1983) and would alleviate exploitative competition, although it might or might not reduce interference competition. Intraspecific encounters might themselves be the strongest proximate cues (Levinton, 1979; Levin, 1981, 1982), and if so, we expected the effects of sediment supply and waste removal to be overridden by crowding. Alternatively, removal of pellets might provide a tactile or chemical cue. Pelletization by conspecifics can reduce available food supply and inhibit feeding on whole pellets (Levinton & Lopez, 1977). Feeding on mechanically dis-aggregated pellets can also be slow (Taghon *et al.*, 1984), apparently due to reduced food quality (Phillips & Tenore, 1984). All these cues and others might be used in combination.

We set as our goal to narrow the possibilities among proximal cues in one species and, in addition, to document that pulses of sediment transport can affect feeding rates without any switch from deposit- to suspension-feeding. The experiments also served as a crude sensitivity analysis for aspects of the simple scaling model of Miller *et al.* (1984). Their model assumes that export and import rates from and to the feeding area of a deposit-feeder are equal and that population effects can be predicted as the sum of individual effects. By manipulating crowding, sediment input and fecal removal independently, we examined the verity of these assumptions and the consequences of their violation. We chose a spionid polychaete, *Pseudopolydora kempji japonica* Imajima & Hartman, as the test animal because of background information available on it (Brenchley, 1981; Wilson, 1981, 1982, 1984; Jumars *et al.*, 1982; Taghon, 1982; Taghon & Jumars, 1984) and on its congeners (Levin, 1981, 1982), but particularly because of Jumars & Self's (1986) recent demonstration that field deposit-feeding rates in *P. kempji japonica* increased after sediment transport events. We opted for a laboratory approach to facilitate the controlled and independent manipulation of variables. To our surprise, a stimulus associated with fecal pellets appeared to be the dominant cue controlling the animal's feeding response to pulses of sediment movement.

MATERIALS AND METHODS

GENERAL PROCEDURES AND SIZE MEASUREMENTS

P. kempji japonica was collected from False Bay (48°29'N : 123°04'W) on San Juan Island, Washington, U.S.A., using a 0.5-mm sieve. Field densities at the collection site (≈ 1.3 m above M.L.L.W.) typically ranged from 0.4 to 3.3 individuals \cdot cm⁻² (Miller, unpubl.). Worms and macrofauna-free sediment passing through the sieve were transported to the nearby Friday Harbor Laboratories and maintained in sea-water tables (8–12 °C water temperature) for up to several days until used in experiments. Unfiltered sea water was used in maintenance and in all the experiments.

To control position and abundance while permitting construction of normal worm tubes, worms were allowed to burrow into sieved sediment in plastic test tubes (7.5 cm in length, 1.0 cm inside diameter, 1.2 cm outside diameter). The rims of the test tubes were buried beneath a veneer of sieved sediment in a large (30 cm \times 45 cm) plastic tray 11 cm deep. Worms have been maintained for several weeks in healthy condition in this experimental arrangement. A holding period of 2–7 days preceded each experiment. A very fine, silty sand of 78- μ m median grain size (nearly half silt by weight), a size range preferred by these worms (Jumars *et al.*, 1982), was used in the feeding-rate experiments. It came from the animal collection site, was passed through an additional 125- μ m sieve and was kept in the sea-water tables until used. It was applied as a slurry with a large turkey baster (pipette) onto the worm-tray sediment surface.

Size of individuals was estimated as body volume of fixed specimens from a multiple regression ($n = 30$ whole animals) of fluid displacement on three variables: distance from the front of the pigmented crescent on setiger two to the posterior of the J-shaped row of specialized hoods on setiger five, thickness of setiger five, and width of setiger five. Prior to fixation, the worms in this group were relaxed in an isotonic magnesium chloride solution. This regression was used in place of direct fluid displacement because worms often fragmented in handling and fixation.

When *P. kempji japonica* were maintained in trays for several days without application of fresh sediment, a circular, slight depressed (< 1 mm) area of differing surface texture (larger grain size) appeared about each worm. This region resulted from feeding, and its radius was easily measured with a ruler. The depositional flux from the unfiltered sea-water system thus clearly could not keep pace with individuals' feeding rates, was small compared with the magnitudes of experimental manipulations, and was present in both experiments and controls (so it could not account for experimental effects). We used the feeding area of isolated worms, characterized after several days without sediment addition, as a crude indicator of the spacing required to preclude direct intraspecific interaction; the feeding radius could be smaller with more frequent food supply, but our observations suggest not substantially so (the feeding depressions growing in depth rather than in radius with time). Measurements of feeding radius were done on 31 isolated worms which had not received sediment for 5 days. Also measured

were maximal outside dimensions of the tube opening. Two parametric, linear, least-squares regressions were calculated. A simple regression used outside tube diameter as the independent variable and feeding radius as the dependent variable, for application in estimating degree of feeding-area overlap among individuals. The relationship between preserved body volume and feeding radius was approximated by first estimating individual body volumes (from the measurements and the regression described in the preceding paragraph) then plugging those estimated body volumes as independent variables into a regression against the measured feeding radius for each of the 31 worms. The latter relation was calculated to determine whether feeding area in this species scales consistently with accepted allometric relations for other kinds of organisms.

Feeding rates were measured as weights or numbers of pellets produced per time. While the fact that deposit-feeders egest most of the mass and volume that they ingest makes input and output balance, it does not have to do so instantaneously. Taghon & Jumars (1984), for example, showed short bursts of rapid feeding in both *P. kempfi japonica* and *Hobsonia florida* (the latter being a sympatric ampharetid polychaete). By continuity, when ingestion and egestion do not balance, gut fullness must change (Jumars & Self, 1986). To avoid ambiguity, then, we chose 4 h as the basic measurement interval for fecal production. This period is a compromise, being generally long enough to allow complete clearance of gut contents (\approx three pellets in volume when full) but not so long that major changes in food quality (from microbial growth or local depletion) are likely.

All experiments were carried out in sea tables with minimal flow velocities ($< 5 \text{ cm} \cdot \text{s}^{-1}$ in the vicinity of the experimental containers) induced in the experimental containers by the flow of water past them or by thermal convection. Only when noted (i.e., for a few behavioral observations) were faster flows and sediment entrainment produced.

CROWDING EXPERIMENT

Test tubes were arranged in five separate trays to achieve varying mean worm densities (cm^{-2}). In each tray tubes were arrayed hexagonally (six surrounding one, for a total of seven tubes per tray). At the lowest three densities one worm inhabited each tube, and density was varied by adjusting spacing between centers of adjacent tubes from 5.0 to 2.7 to 1.2 cm to achieve, respectively, mean worm densities of 0.045, 0.10 and $0.21 \cdot \text{cm}^{-2}$. These means were calculated for the area of a circle, centered on the tube in the middle of the array and having a radius extending 1.4 cm beyond the distal edges of the six outlying tubes. The reason for this addition is that it accounts for the reach of a worm of typical size beyond the tube boundary. For the lowest density as an example, then, the circle was 5 cm plus a tube radius plus the palp reach ($= 5 + 0.6 + 1.4 = 7 \text{ cm}$) in radius and would contain seven individuals for a mean density of $0.045 \text{ individuals} \cdot \text{cm}^{-2}$. At the highest two densities (0.42 and $0.84 \cdot \text{cm}^{-2}$),

two and four worms, respectively, inhabited each test tube at a tube separation distance of 1.2 cm. Worms were assigned to tubes at random. The indicated mean densities thus should not be taken as precise measures of individual crowding, which varied with tube location (center versus peripheral tubes) and with the location of worms within tubes, but are certainly precise enough to give unambiguous ordering of the density treatments. The animals, 63 in total, were acclimated for 7 days with 1- to 2-mm "dustings" of fresh sediment from the turkey baster at irregular, 8- to 24-h intervals.

On each of 2 consecutive days, feeding rates of the density-treatment worms were measured over four feeding bouts. These periods began with the removal of fecal pellets by gentle suction with a pipette, followed by the application of fresh sediments. Application was by turkey baster and achieved an even covering of 1- to 2-mm thickness in each density treatment for each bout. This thickness was chosen on the basis of pre-test feeding rates to preclude depletion of food during the 4-h feeding bouts. At the end of each feeding bout, the number of worm tube openings visible on the surface (an estimate of the number of active worms) and the number of fecal pellets were counted. Fecal pellets were collected by pipette, dried (40 °C), and weighed on tared cellulose filters. Tube opening counts were used to normalize pellet counts and weights on a per-worm basis. These counts were either six or seven for arrays with seven worms and varied over at most four counts in higher-density worm arrays. (The results would not have differed significantly if we had added the number of inactive worms, but the illustrated mean pellet production rates could have been misleading.) Water temperature was recorded at the beginning and end of each feeding bout. To test for worm-density and feeding-bout differences, the feeding rates as weight or number of pellets per worm (a single datum for each worm-density group and feeding bout) were analyzed as a two-way analysis of variance (ANOVA) without replication (Sokal & Rohlf, 1969). Data were transformed to logarithms to the base ten (testing a multiplicative, rather than additive model) as pre-tests showed this transformation homogenized variances and reduced greatly the interaction sum of squares in Tukey's test for non-additivity (Snedecor & Cochran, 1979).

DEPOSITION-FREQUENCY EXPERIMENT

Three groups of worms at each of two densities (low = 1 per test tube or $0.21 \cdot \text{cm}^{-2}$ and high = 4 per test tube or $0.84 \cdot \text{cm}^{-2}$) were prepared as described above. At each density, the worm groups were randomly assigned to a deposition-frequency treatment, consisting of counting (visually) and collecting (by gentle suction with a pipette) fecal pellets and depositing fresh fine sediment at intervals of 1, 2 or 4 h. Deposition again was of a 1- to 2-mm layer each time. Feeding rates measured as the mean over the whole 4-h feeding bout (as both pellet numbers and weights per individual) for four consecutive bouts were log-transformed and analyzed as a three-way ANOVA (worm density, deposition frequency, and feeding bouts being the treatments) without replication (Sokal & Rohlf, 1969).

PELLET DEPOSITION EXPERIMENT

The three high-density groups from the previous experiment were subsequently assigned randomly to the following treatments for 1-h feeding bouts: (1) pellets counted and removed by gentle suction with a pipette, and fine sediment applied in a 1- to 2-mm layer; (2) pellets similarly counted and removed, but no fine sediment applied; and (3) pellets counted, removed, combined with those removed from all the other groups, dis-aggregated by repeated shearing in the orifice of a pipette, and re-applied over the entire worm array to this third treatment group, without any fresh-sediment addition. The fecal application, ranging among the feeding bouts from 129 to 171 mg of pelletal material, equalled $\approx 4\%$ of the mass applied in the usual 1- to 2-mm, fresh-sediment dustings. Counts of pellet production were log-transformed and analyzed as a two-way ANOVA without replication.

PELLET REMOVAL AND ACCUMULATION EXPERIMENTS

To test the hypothesis that accrual of fecal material in the feeding area depresses feeding rate, pellets were either removed within 10 min after defecation or were allowed to accumulate, each of these two treatments continuing over a 4-h feeding bout. Treatments were assigned randomly to isolated, individual worms, 24 per treatment, as well as to low- and high-density worm groups (0.21 and $0.84 \cdot \text{cm}^{-2}$) prepared as above. Pellet production by each worm was censused every half-hour. Pellet counts from the individual-worm experiment, totalled for the entire feeding bout and log transformed, were analyzed as a one-way ANOVA (Sokal & Rohlf, 1969). Half-hour pellet production counts in the low- and high-density groups were regressed against time since the start of the feeding bout to detect trends in feeding rate over time.

RESULTS

SIZE DETERMINATIONS AND QUALITATIVE OBSERVATIONS OF BEHAVIOR

Animal sizes (in preserved condition) for the full suite of experiments, estimated via the multiple regression on anterior length, width and thickness measures, ranged from 0.72 to 4.3 mm^3 ($r^2 = 0.91$ for the regression with $n = 30$). Feeding radius in still water was linearly related to maximal, outside tube diameter: foraging radius (mm) = $(9.52 \times \text{tube diameter (mm)}) + 4.8$ ($r = 0.66$, $P < 0.001$, $n = 31$). The regression of log feeding radius versus log estimated body volume for the same 31 individuals gave the following equation: log feeding radius (mm) = $(0.248 \times \log \text{body volume (mm}^3)) + 1.04$ ($r = 0.69$, $P < 0.001$). The first-order coefficient in the latter equation is marginally ($P = 0.05$) lower than the predicted one-third value from simple isometric scaling. The mean value of 1.4 cm for feeding radius (corresponding to a circular feeding area of 6.2 cm^2) indicated that at population densities $> 0.16 \cdot \text{cm}^{-2}$ neighboring worms' feeding areas would overlap.

Defecation began when the palps ceased their normal surface deposit-feeding and particle-selection activities (lashing the sediment surface with the palps, picking up selected particles, and transporting them along the palps to the mouth) and were pulled nearly completely inside the tube. The palps then re-emerged, together with a pellet held between them, midway along the palps. When the palps were fully extended, the pellet fell off onto the sediment surface, landing (in the absence of a substantial current) in the inner half of the feeding area (i.e., within a pellet's length of the tube opening). The palps then resumed normal feeding activities. Pellets accumulated in the feeding area, either in a radial pattern (in very still water) or in piles to one side (downstream, in flows of a few $\text{cm} \cdot \text{s}^{-1}$ in free-stream velocity). No attempts to pick up or ingest fecal material were ever observed. At imposed flow velocities $> 10 \text{ cm} \cdot \text{s}^{-1}$ (observed in the flume used by Miller, 1984) pellets were swept downstream directly from the palps (at a height of a few mm from the bed), and out of the feeding area of the worm, but under these conditions the animal tended to suspension- rather than deposit-feed as described by Taghon *et al.* (1980). Hence the description of feeding area via a palp radius scribed on the deposit would no longer have been applicable.

While sensitive to the flux of suspended material (Taghon *et al.*, 1980), *P. kempfi japonica* adapted remarkably well to laboratory conditions. It habituated quickly to routine operations, such as fecal pellet removal by pipette, often exploring the pipette tip with one palp while continuing to feed with the other. Pellet removal was always done via gentle suction to avoid production of suspensates as a behavioral cue; production of "puffs" of sediment generated active exploration and feeding activity of the palps.

CROWDING EXPERIMENT

Results from the experiment designed to test the effect of worm density on feeding rate were consistent (Fig. 1) with the preceding calculation of feeding overlap. Two-way ANOVA of these log-transformed data (both total pellet weight and pellet number) indicated significant differences among worm-density groups ($F_{4,28} = 7.51$ by wt, $P < 0.001$; $F_{4,28} = 11.72$ by number, $P < 0.001$): crowding significantly depressed feeding rate when feeding areas overlapped. Mean feeding rate was 35% lower in crowded than in isolated worms, i.e., 3.5 pellets per worm in 4 h compared with 5.5. There also were feeding-bout differences ($F_{7,28} = 6.65$ by wt, $P = 0.0011$; $F_{7,28} = 5.29$ by number, $P = 0.0062$). Subsequent examination of these results indicated that the bout effect was correlated with the mean feeding-bout temperature ($r = 0.80$, $P = 0.02$, temperature ranging from 9.0 to 13.2 °C), with faster feeding at higher temperature. Four of the eight feeding bouts were run on each day of the experiment, and temperature peaked in each day's third bout (late afternoon). Estimates of the strength of the crowding effect (the slope of feeding rate plotted against worm density) were correlated both with water temperature and with mean bout feeding rate. The faster the worms fed, the greater was the relative effect of crowding; this feedback explained the wedge-shaped envelope of data points indicated by the range bars of Fig. 1. At higher (than

Crowding Experiment - Pellet Counts

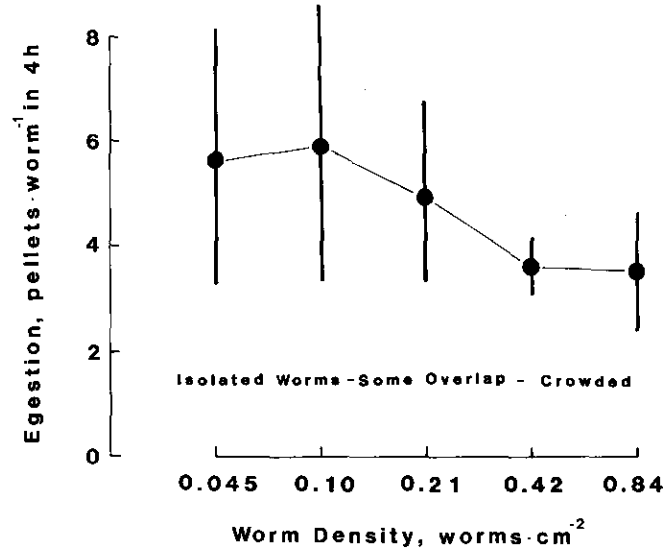


Fig. 1. *P. kempji japonica*'s feeding rate as a function of worm density: ● indicate means, vertical bars are ranges, for eight feeding bouts; the degree of crowding and feeding-area overlap is also indicated, with 0.16 worms · cm⁻² being the estimated threshold where overlap begins; field densities fall toward the right edge of the graph and reach four times the highest shown here.

the mean) feeding rates (high temperatures) the crowding effects were more severe (larger negative slope compared with the mean line shown in Fig. 1), while at the lowest feeding rates the crowding effect was ameliorated (smaller negative slope). Similarities in the experimental results for both feeding-rate variables, due to a good correlation between total pellet weight and number produced per worm ($r = 0.92$, $n = 40$), justified the use of the far easier pellet counts for assessing feeding rate in further analyses.

DEPOSITION-FREQUENCY EXPERIMENT

This experiment tested the effect of crowding, of simultaneous fecal material removal and sediment deposition at three frequencies, and of time (feeding bout) on feeding rate. The three-way ANOVA showed strong interaction between worm density and deposition (and fecal removal) frequency ($F_{2,6} = 27.27$, $P < 0.001$). Main effects tests for density and deposition frequency were also significant ($F_{1,3} = 15.87$, $P = 0.03$; $F_{2,6} = 13.44$, $P = 0.007$, respectively) as is the feeding-bout effect ($F_{3,6} = 5.67$, $P = 0.035$). The other two interaction tests were not ($P > 0.24$). Additional insight was gained from plotting the results (Fig. 2). At high worm density, feeding rate increased as deposition frequency increased; at the 1 · h⁻¹ deposition frequency, the worms fed at a rate statistically indistinguishable from the most rapid observed in isolated worms.

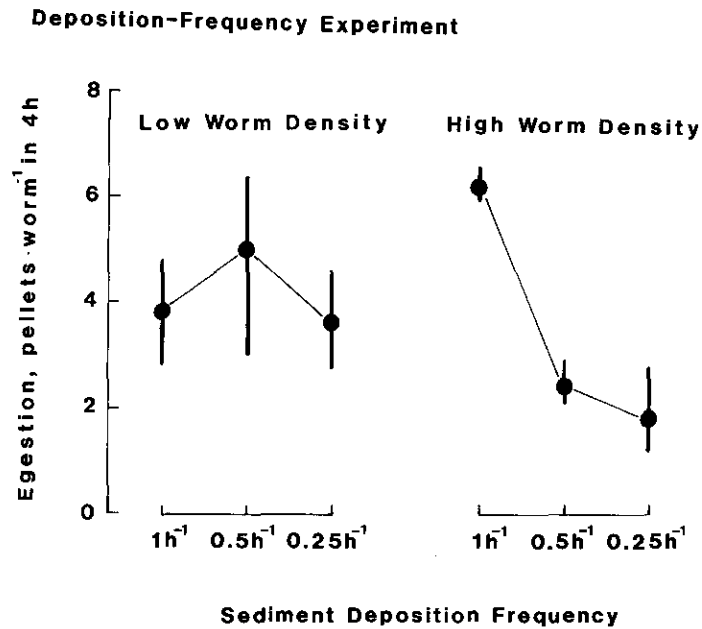


Fig. 2. *P. kempji japonica*'s feeding-rate response to frequency of sediment deposition for low- ($0.21 \cdot \text{cm}^{-2}$) and high- ($0.84 \cdot \text{cm}^{-2}$) density worm groups: ● are means, vertical bars, ranges, for four feeding bouts.

At low worm density, feeding rate increased from the $0.25 \cdot \text{h}^{-1}$ to $0.5 \cdot \text{h}^{-1}$ deposition-frequency treatments, but decreased at the $1 \cdot \text{h}^{-1}$ treatment. The feeding-bout means were negatively correlated with temperature ($r = -0.72$, over a range from 9.6 to 11.4 °C), which also covaried with feeding-bout order (increasing linearly over the four bouts).

As a post-experiment check on the possibility that treatment differences found in the above experiment were due solely to differences among the worm groups (unlikely due to the strictly random assignment of individual worms to groups, but a potential problem in an unreplicated ANOVA) a follow-up experiment was done on the next day. It was identical in design to the above experiment except that all worm groups received fresh sediment at 4-h intervals (i.e., the deposition-frequency main treatment effect became a worm-group effect). Statistical analysis of these results indicated no worm-group effect ($F_{2,6} = 1.90$, $P = 0.23$), but significant worm-density ($F_{1,3} = 1398$, $P < 0.001$) and feeding-bout effects ($F_{3,6} = 8.55$, $P = 0.014$; there were no significant interactions ($P > 0.66$). Thus, the evidence was firmly against the idea that the deposition-frequency treatment effects of the previous experiment might have been attributable to worm-group differences. Again much of the variance among feeding bouts was correlated with temperature ($r = 0.95$, over the range from 11.2 to 14.0 °C).

Weights of pellets were also recorded for the deposition-frequency experiment. The

three-way, log-transformed ANOVA gave nearly identical results to the pellet-count analysis (F -test for interaction of worm density and deposition frequency $F_{2,6} = 26.49$, $P = 0.0011$; feeding-bout main effect $F_{3,6} = 8.42$, $P = 0.014$; other interaction tests non-significant, $P > 0.67$). As was found in the crowding experiment, there was a good correlation ($r = 0.98$) between pellet counts and weight of fecal material, further validating the use of pellet counts as a measure of feeding rate for *P. kempji japonica*. The pellets are elongate cylinders that scale isometrically with body size (cf. Hargrave, 1972).

PELLET-DEPOSITION EXPERIMENT

Pellet removal and sediment deposition were separated in this experiment (Fig. 3). Analyzed as a two-way ANOVA with log-transformed data, the results indicated a significant treatment effect ($F_{2,6} = 14.79$, $P < 0.0048$) but no feeding-bout block effect ($F_{3,6} = 1.52$, $P = 0.30$). Feeding rate when pellets were removed every hour and fresh sediment deposited was about the same as that when pellets are removed without sediment replacement, and about that of uncrowded worms (cf., Figs. 1 and 2 converted to a 1-h rate). Notably, the group receiving fresh sediment appeared to have lower

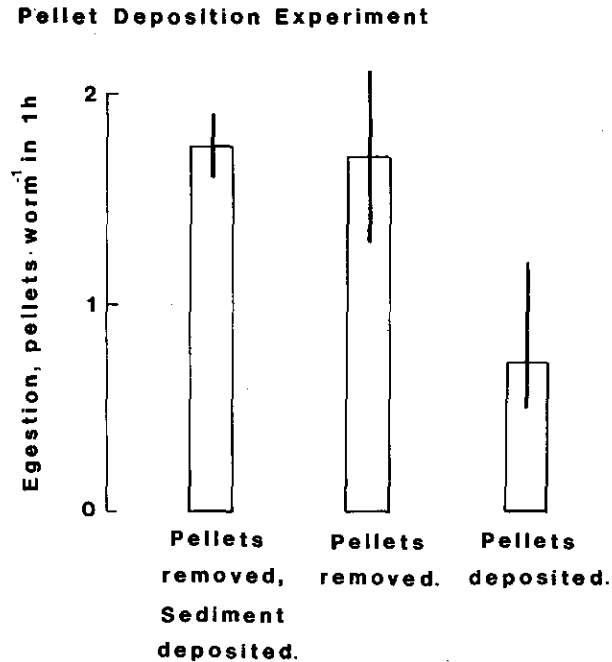


Fig. 3. *P. kempji japonica*'s feeding rate for three treatment combinations of pellet removal, deposition of fresh sediment, and deposition of dis-aggregated pellets: wide bars indicate means, narrow bars are ranges, for four feeding bouts.

variance in feeding rates. Deposition of dis-aggregated pellets was associated with feeding rates less than one-half those of the other two treatments. The lack of a significant feeding-bout effect was not surprising since water temperature varied only 0.5 °C over this experiment. The experiment was repeated twice so that each worm group received systematically each treatment in a modified Latin squares design. In each repetition the results were as above and not attributable to worm-group differences. The results of high feeding rate when pellets were removed, but low when dis-aggregated pellets were deposited, suggested that the presence of fecal material in the feeding area accounted for the crowding effect and that other means of inter-individual interaction (e.g., direct aggression) were of minor influence over the short-term duration of our experiments.

PELLET REMOVAL AND ACCUMULATION EXPERIMENTS

Comparison of the two treatment groups of isolated individuals over the whole feeding bout by one-way ANOVA indicated that worms for which pellets were removed had significantly higher feeding rates ($F_{1,46} = 6.85, P = 0.012$). Total egestion of pellets

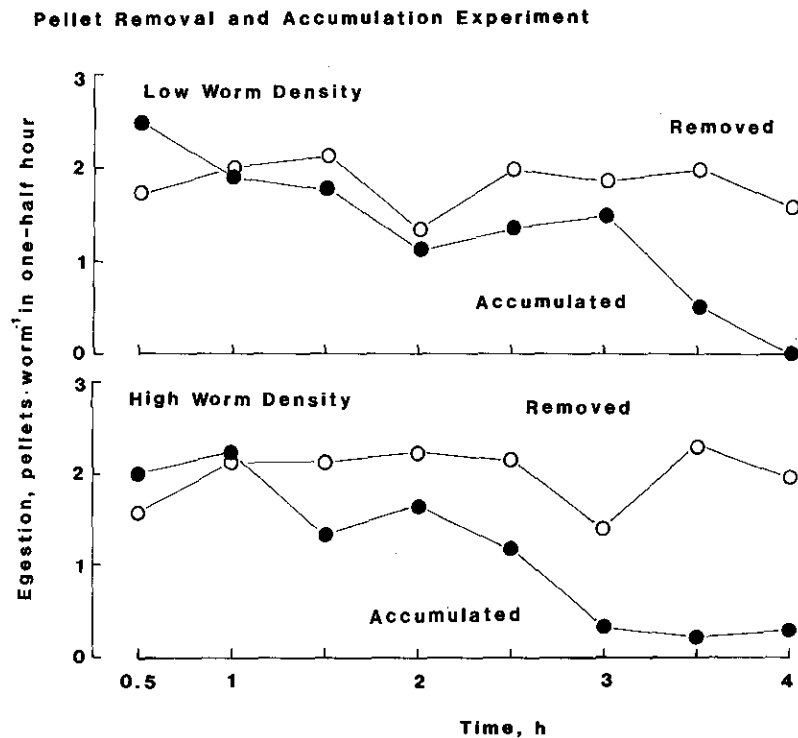


Fig. 4. *P. kempji japonica*'s feeding rate over 4 h for low- and high-density worm groups for which pellets were removed every 10 min (○) or allowed to accumulate (●).

in 0.5 h by the 24 worms in each treatment was negatively correlated with time since the start of the experiment for the accumulation group ($r = -0.84$, $P < 0.0096$, $n = 8$ time periods), but not for the removal group ($r = 0.13$, $P = 0.78$). Feeding rate slowed noticeably when four or more pellets accumulated in an individual's feeding area.

When the same experimental removal-accumulation procedure was run with low- and high-density worm arrays (Fig. 4), the same results are found: a steady decrease in feeding rate with time when pellets accumulated, but no such decrease when pellets were removed. When pellets were removed, high-density worms fed at rates as high as those of uncrowded worms.

DISCUSSION AND CONCLUSIONS

All these results are consistent with primary control of deposit-feeding rate in *P. kempji japonica* by the accumulation of fecal pellets. In comparison, sediment supply rate and crowding had negligible direct effects, with the crowding effect being predictable from its influence on fecal accrual. Over the short time scales of these experiments, feeding rate is depressed by accumulation of as few as four fecal pellets in the feeding area, and this effect is completely eliminated by their removal. The cue appears to be chemical rather than mechanical, as it is still effective when dis-aggregated pellets are substituted for whole ones. Observations of similar feeding-rate depression by dis-aggregated fecal material in *Amphicteis scaphobranchiata* (Polychaeta : Ampharetidae) (Taghon *et al.*, 1984) suggest that this phenomenon might be widespread. They add additional impetus to the study of degradation of pellets under realistic fluid dynamic conditions (Taghon *et al.*, 1984) and of the specific identity and persistence of the feeding depressant. Our casual observations suggest that the pellets of *Pseudopolydora kempji japonica* in still water remain intact for ≈ 1 day before dissolution of the mucous matrix and attack by microbes and meiofauna causes disaggregation. Within a few hours, it becomes impossible to pick the pellets up in a pipette without damage, but these observations give little insight into the possible persistence of a chemical cue or the distance over which it can act.

The significant regression of feeding radius on tube opening diameter made it possible, however, to predict the extent of feeding area overlap, and this prediction was consistent with the crowding threshold observed in Fig. 1. These results suggest that the chemical cue either diffuses very slowly (requiring contact) or diffuses so quickly that it reaches an ineffective concentration at distances beyond the feeding radius. It may similarly be possible from laboratory or field photographs or by video image analysis to estimate the potential for interaction among tentaculate surface deposit-feeders. To be so, clearly the area over which interactions occur must be predictable from something measurable in the image (e.g., from size of the tube or burrow opening). Less obviously, the extent to which movement from burrow to burrow occurs or multiple burrow openings are used must be established. Interaction distance would appear to scale with

body size if mediated either by pellet accrual, as in deposit-feeding *P. kempji japonica*, or by interference or exploitation via tentacles. If interaction distance changes substantially with environmental conditions, as it might in animals sensitive to the supply rate of new sediments (perhaps including *P. kempji japonica* in its suspension-feeding mode), then its prediction will require more complex calculations than a simple regression of tentacle reach on burrow opening as well as supplementary environmental data (e.g., on suspensate flux).

The only situation in which sediment supply frequency appeared to have a major effect on deposit-feeding *P. kempji japonica* was in isolated worms at very high supply frequencies, and that effect was negative (Fig. 2). The experimental treatment for this group consisted of applying each hour 1–2 mm of fresh sediment; only a small fraction of this layer could be consumed (and removed, when feces were collected) in the allowed feeding bout. Excess sediment accumulated, causing the sediment surface in the worm container to rise appreciably over the course of the experiment. These worms spent relatively more time in tube construction and maintenance and less time feeding than those at high worm density, where the newly deposited sediment layer was nearly completely consumed in 1 h by the four-fold larger number of worms. The 1-h^{-1} deposition treatments represented a deposition rate of about $2\text{ cm}\cdot\text{day}^{-1}$, similar to that found by Brenchley (1981) to cause mortality in laboratory experiments with this same species, so the negative effect observed here on feeding rate is not surprising.

We had expected to remove temperature effects on feeding rate and effects correlated with duration of the experiment (e.g., starvation or acclimation to experimental conditions) through the surrogate variable “feeding bout” in the ANOVA’s. Efficiency of such removal was in fact the reason for choosing these experimental designs. We had anticipated, however, neither the effect of pelletal accumulation nor its interaction with crowding and temperature: the faster a worm or group of worms fed, the sooner feeding rate was depressed by pelletal accumulation. Consequently, the length of a feeding bout influenced the strength of the correlation between feeding-bout means and animal density or temperature. Given the importance of the fecal-accrual feedback, the potential for stronger interactions should be taken into account in designing future experiments, if confounding of variables is to be avoided.

While the apparent temperature effects were not our major focus and confounding with them was avoided by experimental design, the appearance of large changes in feeding rates over small ranges of temperature bears some scrutiny. Small temperature variations are inherent in most sea-water supply systems and thus probably have occurred during many previous measures of feeding rates. We do not believe that all the correlations we observed with temperature are, however, straightforward, direct effects of temperature on the motor and digestive systems of *P. kempji japonica*. The crowding experiment may bear this simple interpretation because the bouts went through two diurnal cycles of temperature and a comparatively large range ($4.5\text{ }^{\circ}\text{C}$). The deposition-frequency and pellet-deposition frequency experiments, on the other hand, went through temperature ranges of $2.8\text{ }^{\circ}\text{C}$ or less and through only a part of the phase

of increasing temperature. Thus, any factor that changed monotonically with time also would correlate unavoidably with temperature. That the simple interpretation does not hold for the deposition-frequency experiment is apparent from the opposite sign of the temperature correlation in this case. What we suspect is that the microbial flora on which *P. kempji japonica* feeds changed over the series of feeding bouts and that this change was accelerated at higher temperature, producing food-quality changes of either sign, depending on the flora. This interpretation is consistent with subsequent experiments with this species (Penry, unpubl.; Jumars, unpubl.). While the rate changes are rapid, it must be remembered that recruitment of bacteria in this (Eckman, 1985) and other open sea-water systems can occur not only by local growth but also by immigration. Alternatively, feeding-rate changes may be produced by time-varying chemical cues in the sea-water system, a possibility seemingly more likely after our own observations of feeding-rate depression by pellets. Thus experimental precision with *P. kempji japonica* and other deposit-feeders may be more a problem of food-quality control or control of chemical cues than of temperature control. Until the mechanism is resolved, blocked designs to remove its unintended effects will continue to be essential in experiments concerning deposit-feeding rates.

Although we did not anticipate the overriding importance of pelletal accumulation in determining feeding rate, in hindsight we can provide some tentative explanations. *P. kempji japonica* ingests a diversity of particles (Jumars *et al.*, 1982) of widely varying chemical and physical characteristics. Since the pellets are produced by the animal itself, their coatings and matrix are much less variable and more easily recognizable than are diverse potential food particles. If times of pellet removal and of new particle supply coincide (i.e., if sediment transport usually serves both functions simultaneously), then there is little selective advantage in keying on the (more difficult to recognize) supply side as a cue.

Experimental data on critical erosion thresholds of pellets versus food of *P. kempji japonica* (Nowell *et al.*, 1981) suggest that slightly greater shear stresses are required to move pellets than to move ambient sediments, but critical erosion stress for already deposited pellets may not be the relevant criterion for the feeding rate of individuals. The manner in which pellets are held aloft during defecation allows them to move considerable distances downstream, even during flows incompetent to erode them once they do come to rest. In other words, pellets during defecation are easily removed from the feeding area by free-stream currents stronger than $\approx 10 \text{ cm} \cdot \text{s}^{-1}$. The forces required to move fecal material out of the feeding radius as it is defecated remain unquantified either in the field or the laboratory, and the relative frequencies of transport into, compared with out of, an animal's feeding area remain unknown for the field. Thus, we do not yet know the validity of the simplifying assumption made by Miller *et al.* (1984) that these fluxes are equal, but our results do focus greater attention towards the removal side of the process in future observations.

The present results have additional implications for the interpretation of past and future laboratory experiments, especially those carried out under still-water conditions.

Fecal accumulation provides an alternative or more mechanistic explanation to the unsteady (decreasing) feeding rates in *P. kempjaponica* and in the ampharetid *Hobsonia florida* compared with steady feeding rates in *Amphicteis scaphobranchiata* observed by Taghon & Jumars (1984). Of the three, only *A. scaphobranchiata* ejects its fecal material out of its feeding radius (Nowell *et al.*, 1984). Similar behavior may be widespread in animals (e.g. *Yoldia limatula*, Bender & Davis, 1984) from environments lacking the physical energy to move fecal pellets frequently. Aggressive encounters also seem to vary with time during fecal accumulation. We observed aggressive behavior (e.g., tentacle

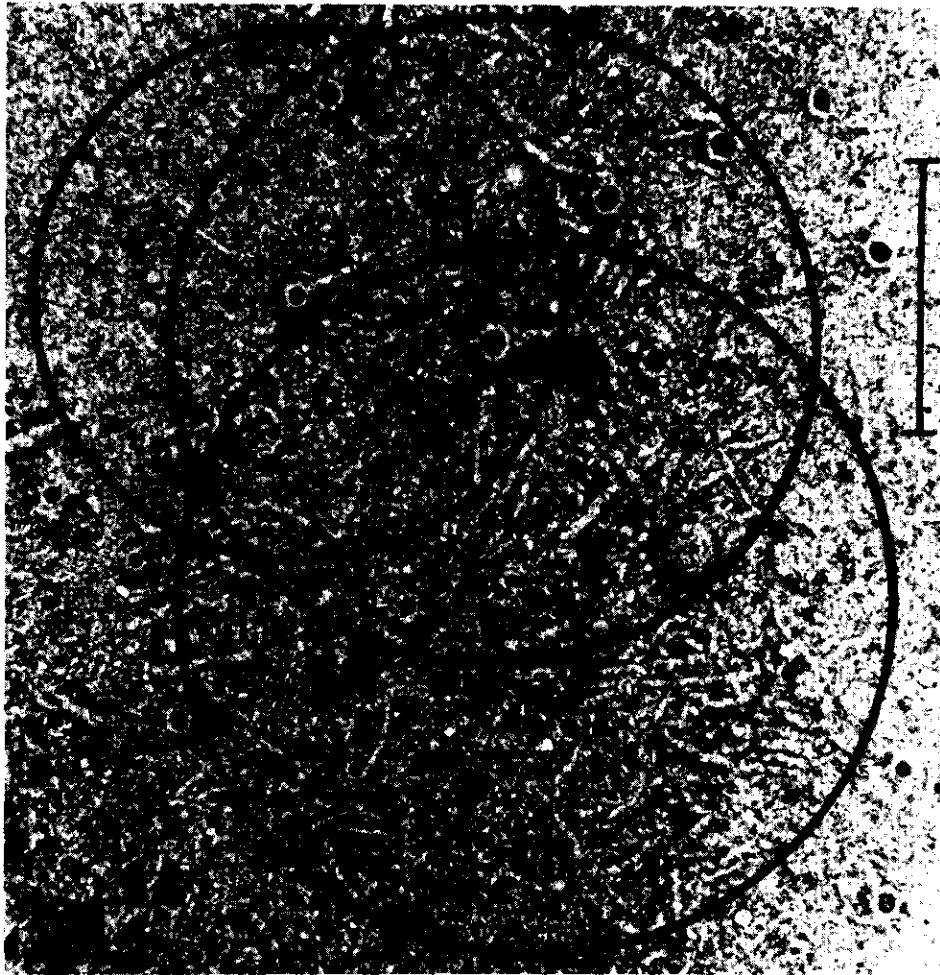


Fig. 5. Photograph of *P. kempjaponica* tubes and accumulated fecal pellets taken in a ripple trough of a tide-pool in False Bay on 2 October 1984: estimated feeding areas (superimposed circles), based on the empirical regression determined in the laboratory, have been drawn around three tubes to indicate the extent of areal overlap in feeding and defecation; scale bar = 1 cm.

fighting and pulling of one worm from its tube by another, as observed by Levin, 1981) only in animals that did not experience frequent exchange of sediments (fecal removal and sediment resupply). Left undisturbed in sea-water tables for 1 wk or more, worms on the periphery of a closely spaced array orientated their tubes outward, away from other worms, presumably to minimize overlap with other worms' feeding and defecation areas (pers. obs.). As indicated by the accumulation of fecal material, worms on the periphery continued to feed and defecate directly in front of the tube opening, although apparently at a slower rate than during the experiments. Worms in the center of the array appeared to cease feeding altogether. While not so severe in the short duration of our experiments, positional differences in pellet production rate within our experimental arrays were observed and appeared in rough accord with the degree of feeding-area overlap among worms. More generally, fecal accrual rates and patterns must be matched in the laboratory and the field if field relevance is to be assured.

Our results particularly serve to focus attention on the frequency of pelletal removal from the feeding area and away from the initial, steady-state approach of Miller *et al.* (1984). The laboratory results suggest that feeding-rate depression will occur within 2–4 h in still water at field temperatures, but they provide an under-estimate for higher field densities, which reach four times the highest used in our experiments. Qualitative field observations document that pellets do accumulate in tide-pools (Fig. 5). Wave activity as the tide exposes or just covers the flat at False Bay usually appears able, however, to move both ambient sediments and fecal pellets. Pellets, for example, are rarely in evidence in the vicinity of tube openings as the tide recedes. This qualitative impression of frequent transport events is being tested with in situ measurements (Miller & Sternberg, in prep.). A crucial question is whether feeding-rate depression due to the accumulation of fecal material routinely occurs during periods of immersion in False Bay, in intertidal environments generally, and in subtidal environments as a whole.

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