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Individual physiological responses
to environmental hypoxia and organic enrichment:
Implications for early soft-bottom community succession

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ABSTRACT

Infaunal inhabitants of coastal marine sediments occupy environments along a continuum from extremely food-rich, low-oxygen regions to food-poor habitats with relatively high levels of available oxygen. In organic-rich sediments, efficient utilization of available organic matter by deposit-feeding macrofauna may often be limited by the supply of oxygen. Specific feeding rate, growth, and production efficiency were measured on single individuals of the polychaete *Capitella* species 1 to determine whether previously measured declines in growth rates in response to hypoxia were due to decreased feeding, decreased conversion efficiency, or both.

Under otherwise constant conditions, feeding rate was determined by the nitrogen content of the sediment, with a greater nitrogen content generally leading to higher specific feeding rates in a manner consistent with recent interpretations of optimal foraging theory. However, the relationship between feeding rate and growth was influenced by oxygen concentration such that in relatively nitrogen-poor sediment, greater growth rates were observed at the lower oxygen level. Simultaneous measurement of growth and feeding rates indicated that the effect of oxygen was due to a decrease in the efficiency with which ingested sediment was converted to tissue under low nitrogen, high oxygen conditions. We suggest that the decreased conversion rate of ingested sediment to body volume under the higher oxygen regime reflected an aerobic metabolic system poised to rapidly exploit available oxygen supplies.

The physiological responses measured in our experiments are consistent with the classical faunal successional sequence occurring in a deposit following organic enrichment. When viewed temporally, these faunal changes parallel geochemical changes such that high organic matter, low oxygen conditions give way to higher oxygen levels and decreased concentrations of organic matter. Thus environmental conditions typically change toward those under which *Capitella* sp. 1 would be expected to perform most poorly. We suggest that an underlying physiological mechanism in *Capitella* spp. may strongly influence the early successional changes observed following the organic enrichment of soft-bottom benthic environments.

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1. Introduction

Maximum efficiency in the production of phosphate-bond energy in heterotrophic organisms requires both chemical energy in the form of food and a source of molecular oxygen. From the perspective of an infaunal inhabitant, coastal marine sediments can generally be placed along a continuum from extremely food-rich regions with no oxygen to food-poor regions with relatively high levels of available oxygen. Due to active microbial respiration of sedimentary organic matter, aerobically respiring infaunal macroinvertebrates inhabiting organically-enriched sediments must often compete with microbes for both organic matter and oxygen. Unless active ventilation activity is maintained, burrow oxygen concentrations can decrease to values below detection within a few seconds to minutes. The rate of depletion depends on burrow diameter and organic matter reactivity (Kristensen, 1983; Aller, 1988). Many of the adaptations revealed by animals that have adopted sediment-dwelling lifestyles have probably evolved in response to this fundamental tradeoff (Forbes, 1989; Forbes and Lopez, 1990a).

The dilemma faced by infauna attempting to obtain and burn food efficiently is particularly acute for pioneering animals colonizing organically-enriched habitats. Regions of the seafloor defaunated by organic enrichment fall at one extreme of the oxygen-food continuum. Food is abundant but the oxygen needed for efficient combustion is extremely scarce. The initial stages of benthic community development in sediments following disturbance through organic enrichment are often dominated by small, threadlike polychaetes belonging to the sibling species complex of *Capitella capitata* (Grassle and Grassle, 1976). These populations frequently reach extremely high densities but, if the level of enrichment declines, are succeeded by larger, more slowly growing species (Pearson and Rosenberg, 1978; Tsutsumi, 1990; Tsutsumi *et al.*, 1990).

An important earlier hypothesis stated that the pronounced numerical dominance exhibited by *Capitella* spp. and other functionally similar organisms during the initial stages of succession was a result of two fundamental features of their biology: a generally high tolerance of polluted conditions and specific life history characteristics allowing a rapid response to organic enrichment events (e.g. Gray, 1979; 1981).

In the first case the inital occupation of organically enriched habitats by pioneering species was made possible by a general ability to withstand harsh geochemical conditions including environmental hypoxia and high levels of sulfide. Experimental work on the pioneering species *Capitella* spp. and *Streblospio benedicti* suggests that these species are not unusually tolerant of sulfide and environmental hypoxia. Survival times of both *Capitella* spp. and *Streblospio benedicti* under hypoxia are indistinguishable from those of polychaete species such as *Arenicola marina, Nereis virens, N. diversicolor* and *Scoloplos armiger* which are typically thought to characterize later successional communities (Reish, 1966; Tsutsumi, 1987; Ueno and Yamma-

moto, 1982; Forbes and Lopez, 1990a, Llansò, 1991, Bromander et al., 1993 and references therein).

The life history characteristics thought to be most important in enabling rapid response to organic enrichment include a widespread dispersal ability followed by rapid individual growth, early maturation and thus a very great potential for rapid population growth. Poor competitive ability was hypothesized to lead to a species' inability to maintain habitat space in the face of the later arriving colonists (e.g. discussions in Grassle and Grassle, 1974; McCall, 1977; Gray, 1981).

Recent work has brought to light several important problems and inconsistencies regarding the life history scenario. Firstly, the sibling species capable of exhibiting the highest rates of initial population increase are the lecithotrophic forms, such as *Capitella* species 1, which brood a relatively small number of large, yolky eggs with a very short (hours to a few days) planktonic period (Tsutsumi and Kikuchi, 1984; Tsutsumi et al., 1990). This is also the case for other early colonists of organically enriched habitats including the species *Polydora ligni* and the lecithotrophic form of *Streblospio benedicti* (Zajac, 1986; Levin, 1984). Thus the strategy of long-range dispersal to newly enriched habitats is not used by some of the most opportunistic of the colonizing species. This observed lack of a consistent relationship between dispersal ability and high rate of population growth in newly-opened habitats has been demonstrated experimentally in investigations by Levin and colleagues using *Streblospio benedicti*. Under controlled laboratory conditions Levin et al. (1987) demonstrated greater finite rates of population increase for the lecithotrophic as opposed to the planktotrophic mode of development. This result stands in contrast to predictions based solely on the apparent opportunistic nature of planktotrophic life history traits.

A second inconsistency concerns the frequently observed temporal stability of *Capitella* spp. populations occurring within highly enriched sediments. When a high rate of organic matter input is maintained over time, these populations tend to persist, often dominant both with respect to biomass and numbers of individuals (e.g., Pearson and Rosenberg, 1978). This observation suggests that, if *Capitella* spp. are not particularly tolerant of the geochemical harshness of the habitat, they may in fact be fairly good competitors for high concentrations of labile organic matter. If true, this would be in contrast to standard interpretations of classical r and K theory formulated with regard to benthic successional dynamics (e.g. McCall, 1977). It may in fact be that *Capitella* spp. require highly labile organic matter to maintain positive population growth rates. For example, following a detailed series of field studies, Tsutsumi and coworkers suggested that the association of *Capitella* spp. with organically enriched areas indicated what they termed a 'physiological requirement' for highly organic food. This conclusion followed from the observation that a very high sedimentary protein content was required for the presence of reproductively functional females in the local population (Tsutsumi, 1990).

Experiments at the individual organism level with *Capitella* sp. 1 indicated that the twin constraints of oxygen and food availability can interact in complicated ways to control organism growth. When individual *Capitella* sp. 1 were exposed to oxygen concentrations below approximately 35 μM (ca. 9% saturation), they ceased feeding and became quiescent, with body volume shrinkage rates of up to 20% d^{-1} (Forbes and Lopez, 1990a). Forbes and Lopez (1990a) also found that when O_2 level was decreased from 187 to 35 μM, individual worm growth rates were consistently decreased by up to 20% to 35% d^{-1}; again leading to high rates of shrinkage for some animals. Simultaneous manipulations of oxygen and food concentrations revealed that the effect of food level on growth was dependent on oxygen concentration and vice versa. Changes in oxygen concentration within the range of 35–187 μM were as important as changes in food level in determining worm growth rates (Forbes and Lopez, 1990a). However, because feeding rates were not measured, the above studies were unable to determine the extent to which the decreases in growth were due to decreased feeding, decreased conversion of food to tissue, or some combination of both.

In this study we have concentrated on an organism typically inhabiting the low-oxygen, high-food extreme of the habitat continuum. We have measured individual growth and feeding rates and the efficiency with which *Capitella* sp. 1 is able to convert ingested sediment into tissue under a carefully selected set of oxygen and food concentrations. We originally hypothesized that decreased oxygen availability would be especially critical under conditions of food limitation. Thus, under conditions in which food is limiting, oxygen must be present in sufficient quantity to achieve maximally efficient production of phosphate bond energy. Given the fact that infaunal benthos typically excrete and therefore lose access to the energy contained in anaerobic metabolic endproducts (Livingstone, 1983), oxygen can be considered equivalent to food when oxygen is in short supply. Decreased access to molecular oxygen equates directly with decreased ATP production per unit mass of food catabolized. Thus we predicted that if worms were food-limited, decreasing the oxygen concentration would amplify the effect of low energy intake by decreasing the efficiency with which ATP is produced. Thus, on top of any behavioral changes in feeding rate or physiological compensation from changes in respiratory pigments, we expected that decreasing the ambient oxygen concentration would decrease the efficiency with which ingested sediment was converted to tissue.

We found that feeding rate was positively and asymptotically related to nitrogen content in the offered sediment at both environmental oxygen levels. However, growth rate was positively related to feeding rate at 200 μM O_2 but not at 100 μM. The relation between growth and feeding rate was modulated by sedimentary food concentration with higher mean growth rates at 100 μM O_2 at the lowest food concentration. This decrease in efficiency is in direct contrast to predictions based on the arguments outlined above. The implications of these results are discussed in the

context of a 'physiological requirement' for highly labile organic matter by *Capitella* sp. 1 and the general problems faced by benthic infauna colonizing the low oxygen extreme of the food-oxygen continuum in coastal sediments.

2. Methods

a. Biovolume as a response variable. The central questions addressed in this investigation dealt with organism performance as a function of two critical environmental parameters, oxygen level and food concentration. The need for repeated measurements on small individual animals led us to choose body volume for the size estimates. Volume measurements have the advantage that animals can be sized while full of sediment obviating the need for long periods in which the worms are removed from sediment for gut evacuation. The additional weight due to sediment within the gut for worms of this size can be significant. For a 1.5 mm^3 worm, the dry weight of sediment within the gut can be greater than 50% of the dry weight of the worm itself (Forbes and Lopez, 1987). The option of obtaining wet weights for the worms was rejected for two reasons. First, the long periods (ca. 0.5–1 d) necessary for complete emptying of the gut were unsatisfactory in growth rate experiments employing animals often turning over more than 10% of their body carbon per day (Forbes, 1989; Forbes and Lopez, 1995). Second, the process of measuring wet weights in worms of this size can be damaging to the worms. The ability to relate changes in volume to changes in such parameters as dry weight, carbon, nitrogen or energy content depends primarily on the carbon or nitrogen density of worm tissue. Differences in lipid content due to egg production or water content due to hypo or hyper-osmotic culture conditions seemed most likely, *a priori*, to create problems. Thus a salinity of 28.0 ‰ was carefully maintained for all seawater coming in contact with the animals. The problem of egg production was handled by carefully and randomly assigning worms to treatments. Thus any differences in volume growth rates due to differences in worm lipid content were considered to be an added random component of the total variance. We have assumed that worm bulk density did not change as a function of food or oxygen treatment.

Worm responses were not converted to wet weight, dry weight or carbon content because this does not solve the problem that these variables cannot be measured on the same worm before and after the experimental manipulation. The assumption that worm bulk density did not change as a function of treatment would still be required for interpretation of the statistical analysis. Nevertheless, the biovolumes reported here may be used to predict worm dry weights using the following relationship. Worm dry weight (μg) = 216.21 volume (mm^3) − 48.32 ($n = 7$, $P = 0.004$, T.L. Forbes, unpubl). Worm dry weights may be further converted to carbon by noting that organic carbon content is approximately 37.1% of worm dry weight for this sibling species of *Capitella* (Cammen, 1985).

b. General design. Forty-eight *Capitella* sp 1 were grown individually in 20 ml scintillation vials for 48 h. A factorial design was used which allotted 24 worms to each oxygen treatment. Each oxygen treatment in turn consisted of 6 individual worms at each of 4 food concentration levels yielding an overall $2 \times 4 \times 6$ ($O_2 \times$ food $\times$ replicate) design. Experimental sediment was added to each vial forming a layer 2–3 mm thick. This volume of sediment was sufficient to prevent the worms from ingesting or otherwise processing all of the sediment during the 48 h experimental period and thereby limiting feeding rate. To control for the effect of body size on growth and feeding rate, 48 worms were chosen to be approximately 1–2 mm³ in body volume and randomly assigned to the experimental vials. This size class of worms falls on or near the plateau region in which both growth and feeding rates are relatively independent of body size (Forbes and Lopez, 1990b).

The entire system was closed and recirculating. Water containing oxygen at the appropriate concentration was distributed by two 24-channel peristaltic pumps from holding reservoirs through each of the 48 experimental vials (28‰, 22 ± 1°C). The 5 liter reservoirs were continuously and vigorously gassed to achieve the desired oxygen concentration. Pumping rate was adjusted such that the residence time of water in each reservoir was 20–24 h in order to oxidize any small amounts of H_2S or other reduction products that may have been generated within the system (Morse *et al.*, 1987). Circulation time for water from the seawater reservoir to the scintillation vials containing individual worms was kept low with calculated residence times in the worm vials of approximately 10 minutes.

Growth rate, feeding rate, and the conversion efficiency of ingested sediment into body tissue were chosen as response variables. All three variables were calculated from measurements made simultaneously on individual worms.

c. Growth rate measurements. Growth rates were measured as changes in worm body volume and calculated with the formula: G (% d^{-1}) = {[ln(BV_f) − ln(BV_i)]/d} $\times$ 100 where BV_f is the final body volume (mm³), BV_i the initial body volume and d is the time in days (Kaufmann, 1981).

Worms were assumed to be cylindrical and volumes were estimated in the manner described previously (Forbes and Lopez, 1987). Each worm size estimate used in the analysis was the mean of 3 replicate volume determinations. The additional replication and use of the mean values in the subsequent calculations significantly reduced the variability over previous efforts. Estimates of average size over the 2 d growth intervals were calculated as geometric mean volumes (*GMV*) where *GMV* = $(BV_i \times BV_f)^{1/2}$.

d. Food and oxygen concentration manipulations. Experimental sediments were collected from Kærby Fed, a shallow cove in the inner reaches of Odense Fjord, Denmark. Organic carbon content of the offered food treatments was designed to

Table 1. Volume-percent added glass beads and weight percent carbon, nitrogen, and carbon to nitrogen ratio for the experimental sediments.

Food level	% Beads (vol:vol)	%N	%C	C:N
1	0	0.992	9.348	10.139
2	50	0.224	2.009	8.969
3	67	0.122	1.158	9.492
4	80	0.014	0.147	10.500

approximate the range (0.1 to 10%) of organic carbon found in unpolluted estuarine and coastal shelf sediments (Mayer, 1989). Food concentration was manipulated by sieving sediment to <40 μm and blending the wet sediment with clean, dry glass beads (<50 μm) to achieve the four volume proportions given in Table 1. Thus all particles were <50 μm in size and clearly within the range of ingestible particle diameters for the size range of animals used (Forbes, 1984). Percentages of C and N were determined on a Hewlett-Packard 185B CHN-analyzer equipped with an HP 3380A integrator. The carbonate content of the unamended experimental sediment was between 0.02 and 0.03% of sediment dry weight (M. Holmer, unpubl.).

Oxygen concentration was manipulated following the general protocol outlined in Forbes and Lopez (1990a). Briefly, pure N_2 and air were mixed in one of two reservoirs, one for each O_2 concentration. Oxygen concentrations were measured with a microelectrode mounted in the reservoir flask. Total O_2 exposure for each experimental treatment was quantified in the manner previously described by Forbes and Lopez (1990a). The oxygen concentration reported for each of the two treatments was calculated as the area under the curve of O_2 concentration versus time divided by the area that would have been attained under 100% air saturation. The peristaltic pumping rate was set higher at the start of the experiment so that the predetermined exposure concentration for each treatment was achieved within 5 hours.

e. Measurement of feeding rate and the calculation of growth efficiency. Accurate determination of growth efficiency necessitated measurement of the total amount of sediment passing through each animal. At the end of the 48 h experiment all fecal pellets egested by an individual were collected on a 50 μm sieve and preserved in 70% ethanol. Pellets were then counted under a dissecting microscope. Because all animals were within the size range in which specific feeding rate and pellet bulk density are nearly independent of size (Forbes and Lopez, 1990b; Forbes, 1984), (V_{er}) was defined as: (mm³ sediment egested)/(mm³ worm volume) per day. Total volume of sediment egested during the experiment was calculated from the total number of fecal pellets defecated by each worm, employing the relationship: mm³ (fecal pellet)$^{-1}$ = 0.0025 worm volume$^{0.7}$ (mm³) (Forbes, 1989). Feeding rates are thus equivalent to body volumes d^{-1}.

As a measure of the efficiency with which ingested sediment is converted to worm tissue, gross production efficiency (GPE) was defined as worm volume change divided by the total amount of sediment egested for the 2 day growth interval (GPE = (mm³ growth)/(mm³ sediment egested)). This measure of production efficiency will serve as a consistent measure of organism performance as long as feeding selectivity, worm density, and fecal pellet density do not change as a function of experimental treatment.

3. Results

a. Food and oxygen concentration manipulations. Food concentration treatments consisted of sediment diluted with clean glass beads and ranged from 20% to 100% natural Kærby Fed sediment (vol:vol) (Table 1). The percent nitrogen increased over 70 times from 0.014 to 0.992 %N (wt:wt). Percent carbon similarly increased 64-fold from 0.147 to 9.348 %C across food treatments. Thus C:N remained relatively constant (mean = 9.775) and was uncorrelated with %N (Pearson product-moment $P = 0.847$) indicating that the glass bead dilutions did not systematically distort the C:N among treatments (Table 1). Integrated oxygen concentrations for the low and high O_2 treatments were 103 μM and 206 μM respectively. Hereafter they will be referred to as the 100 μM and 200 μM [O_2] treatments.

b. Response of feeding rate. At both the high and low oxygen concentrations, feeding rate (V_{er}) was influenced by food concentration (Fig. 1, Table 2). However, the precise nature of this effect differed between the two oxygen treatments (ANOVA; [O_2] × Food interaction $P = 0.042$). The shape of the positive response depended on the oxygen concentration (Fig. 1). This effect can be seen clearly in Figure 1 by noting that the stepwise shift from lower to higher feeding rates occurred at a lower food concentration in the low compared to the high oxygen treatment.

Overall feeding rate (V_{er}) averaged 3.3 body volumes d⁻¹ (=3.3 mm³ sediment (mm³ worm)⁻¹ d⁻¹) and mean rates among treatments ranged from approximately 2 to 4.5 body volumes d⁻¹ (Fig. 1). Food concentration exerted a very strong effect on V_{er}, causing a doubling from approximately 2 to 4 body volumes d⁻¹ as nitrogen level in the offered food increased from 0.014% to 0.992% (wt:wt) for both oxygen treatments (Fig. 1, Table 2). Feeding rate responded to changes in food concentration by shifting in a stepwise fashion from approximately 2–2.5 to 4 body volumes d⁻¹ as %N increased from 0.122 to 0.224% (Fig. 1). The shift to higher feeding rates was accompanied by a reversal in the ranking of V_{er} with respect to oxygen treatments. Below a food concentration of 0.1 %N, mean V_{er} was greater for the low oxygen treatments, whereas at nitrogen levels greater than 0.1%, V_{er} was greater for the higher oxygen treatments (Fig. 1). Thus worms fed most rapidly at the highest food and oxygen levels. The one-step shift of the food concentration response indicated
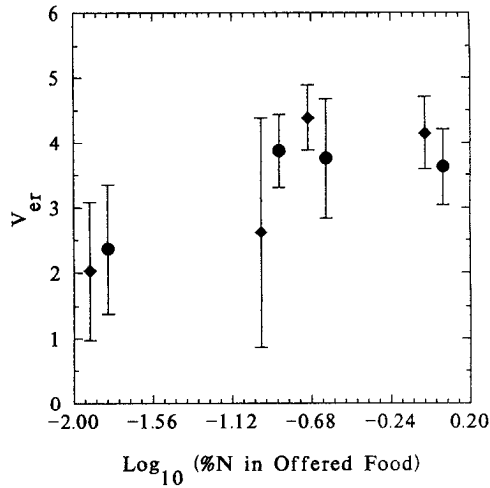
Figure 1. Plot of volume-specific feeding rate (body volumes d^{-1}: V_{er} = (mm^3 sediment egested) (mm^3 worm volume)$^{-1}$ d^{-1}) versus log$_{10}$ (%N) (wt:wt) in the offered experimental sediment. Filled circles: low oxygen (100 μM) treatment; filled diamonds: high oxygen (200 μM) treatment. Error bars are 95% confidence limits for the sample mean. Due to overlap, means have been offset ±0.05 log units to facilitate viewing the confidence limits.

that, with regard to feeding rate, the worms clearly experienced and responded to at least two different food concentration treatments.

c. Response of growth rate. The nature of the growth rate data was such that we were unable to discover a transformation which would homogenize the cell variances for the growth response as a function of the food and oxygen concentrations. All attempted transformations led to cell variances which strongly violated ANOVA assumptions (Barlett's test for homogneity of variances, P's < < 0.05). We therefore constructed asymmetric 95% confidence limits for the cell means using the bootstrap method. This method makes no distributional assumptions yet is more powerful than standard nonparametric ranking procedures (Crowley, 1992; Press *et al.*, 1992). Confidence limits for each cell mean were based on 10,000 bootstrapped samples. Cell means were considered different if their 95% confidence limits did not overlap.

Table 2. ANOVA results for the response of specific feeding rate to manipulations of environmental oxygen and food concentration. Due to the significant main effect interaction, a table is given for each oxygen level. See text for treatment details.

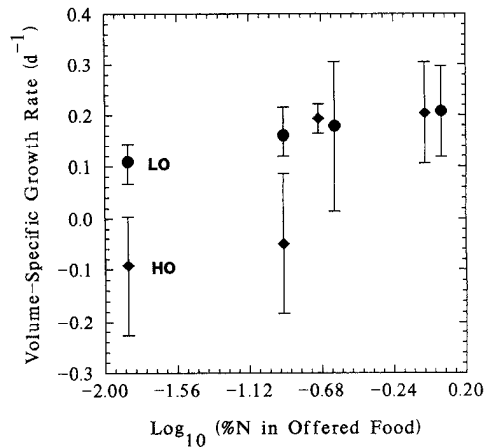| [O$_2$]	Source	*df*	Mean square	*F*-ratio	*P*
200 μM	Food	3	7.7502	9.4029	0.0005
	Error	19	0.8242		
100 μM	Food	3	2.8075	5.6603	0.0065
	Error	18	0.4960		

Figure 2. Plot of mean individual growth rate versus $\log_{10}$ (%N) (wt:wt) in the offered experimental sediment. Filled circles: low oxygen (100 µM) treatment; filled diamonds: high oxygen (200 µM) treatment. Error bars are 95% confidence limits for the sample mean. Due to overlap, the means for the highest two food treatments have been offset ±0.05 log units to facilitate viewing the confidence limits.

Using this approach we were able to test for an interaction between the effects due to food and oxygen concentration, although no probability level can be attached to the effect.

The effect of food concentration on growth was strongly dependent on oxygen concentration (Fig. 2). At the low oxygen concentration, growth rate was independent of food concentration. Mean values at low oxygen varied between approximately -10% to 20% d^{-1}. In the high oxygen treatment, growth rate showed a large single-step increase from mean values of -9% d^{-1} to 20% d^{-1} (Fig. 2). The lowest observed growth rates in our study were measured for animals in the two lowest food concentrations at the high oxygen concentration. At an oxygen concentration of 100 µM, mean growth rates approximately doubled, increasing from 11% d^{-1} to 21% d^{-1} as a function of nitrogen in the offered sediment, although all 95% confidence limits overlapped (Fig. 2). In contrast, in the 200 µM [O_2] treatment, mean growth rates nearly tripled, increasing from -9% d^{-1} to 20% d^{-1} across food concentrations (Fig. 2). Thus increases in food concentration positively influenced growth most strongly at [O_2]'s near 200 µM. The relationship between growth rate and food concentration was unaffected by oxygen concentration at the highest two food levels (Fig. 2).

Geometric mean body sizes for this experiment ranged from 0.70 to 2.04 mm³. As planned, the values clustered closely about the plateau region of the *Capitella* sp. 1 growth trajectory (Forbes and Lopez, 1990b). To confirm that growth rates were indeed independent of worm size, we calculated regressions and visually examined plots of growth rate on body size for the eight possible food and oxygen combinations
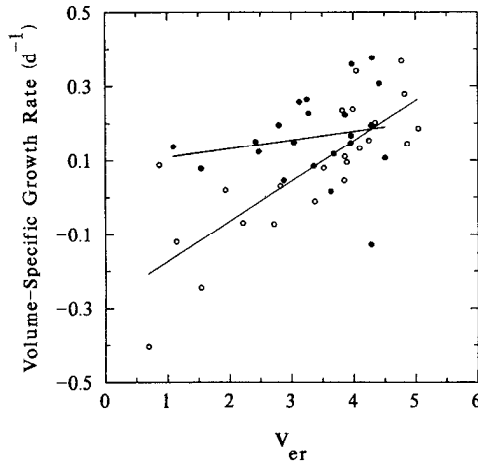
Figure 3. Plot of mean individual growth rate versus volume-specific feeding rate (body volumes d^{-1}: V_{er} = (mm^3 sediment egested) (mm^3 worm volume)$^{-1}$ d^{-1}). Filled circles: low oxygen (100 μM) treatment; open circles: high oxygen (200 μM) treatment. The upper line is a LOWESS smooth through the points for the low oxygen treatment (details in text). The lower line is a least squares regression fit to the points for the high oxygen treatment where growth = 0.11 (V_{er}) − 0.28, N = 23, R^2 = 0.64, and $P << 0.001$.

(2 oxygen by 4 food levels). None of the treatment cells showed a strong relationship between growth and body size ($P > 0.11$ for all cells). We therefore removed body size as a variable from further consideration.

d. The relationship between growth and feeding rates. One of the mechanisms by which changes in oxygen and food levels may have influenced growth rates is through effects on feeding rates. Thus feeding rate was also considered to be an independent variable in the growth rate response. Worm growth rates were strongly affected by feeding rate (Fig. 3). The effect of feeding rate was in turn dependent on sedimentary nitrogen concentration (Fig. 1). The effect of feeding rate on growth was modulated by environmental oxygen concentration (cf. Table 3, Figs. 1, 2 & 3). At high O_2 levels, growth was linearly related to feeding rate (linear regression, N = 23, $P << 0.001$, Fig. 3); whereas for the low oxygen treatment, growth was independent of feeding rate (linear regression, N = 22, P = 0.418, Fig. 3). Because there was no

Table 3. ANOVA results for the response of specific growth rate as a function of specific feeding rate (V_{er}) and oxygen concentration.

Source	df	Mean square	F-ratio	P
$[O_2]$	1	0.1325	10.3925	0.0025
V_{er}	1	0.2081	16.3173	0.0002
$[O_2] \times V_{er}$	1	0.0886	6.9464	0.0118
Error	41	0.0128		

Table 4. ANOVA results for the response of specific growth rate as a function of specific
   feeding rate (V_{er}) and oxygen concentration.

Source	df	Mean square	F-ratio	P
$[O_2]$	1	0.1325	10.3925	0.0025
V_{er}	1	0.2081	16.3173	0.0002
$[O_2] \times V_{er}$	1	0.0886	6.9464	0.0118
Error	41	0.0128		

strong linear relationship between growth and feeding rates at the low oxygen
treatment the data were modeled using the robust smoothing procedure, LOWESS
(Cleveland, 1979). This avoided making the assumption of no relationship at all; an
assumption that is questionable given that the probability of detecting a non-zero
correlation coefficient with the current design was 0.51 (Cohen, 1988; Dallal, 1988).
Figure 3 indicates that at low feeding rates, worms grew best in the low oxygen
treatment. Thus the factors that acted to lower feeding rates from their maximum
values (primarily decreases in food concentration) had a greater negative impact on
growth at the high oxygen levels (Fig. 3).

An interesting feature of these data is that at the lowest two food concentrations,
the worms grew at greater rates at 100 μM O_2 than they did at 200 μM O_2 (Fig. 2).
For the treatment with 0.122 %N in the offered food, worm growth rates were
16% d^{-1} at 100 μM O_2 as opposed to the slight shrinkage rate of -0.05% d^{-1} at
200 μM O_2. A similar decrease in growth rates to even greater absolute negative
values (-9% d^{-1}) was observed for the 0.014% N food with the highest growth rates
in the 100 μM O_2 treatment.

e. Growth efficiency response. As was the case for the growth rate data, we were
unable to transform the data for the growth efficiency response to create reasonably
homogeneous variances (Bartlett's test for homogeneity of variances, $P < < 0.05$,
for all transformations). Thus the same analytical approach has been adopted as with
the growth data, and analyses are based on bootstrapped 95% confidence limits for
the cell means. The method used was identical to that outlined above for the growth
data.

At 100 μM oxygen there was no effect of food concentration on the efficiency with
which worms turned ingested sediments into increased tissue volume (GPE) (Fig. 4).
The response was flat across food treatments and GPE fluctuated within the narrow
range of 4.4% to 5.7%. The worms converted ingested sediment to tissue (Vol:Vol)
at a mean efficiency of 5.2%.

At 200 μM oxygen, food concentration exerted a strong effect on GPE (Fig. 4).
Mean GPE increased from -11.9% to 4.9% as a function of food concentration and
leveled off at the two highest food values. At the two highest food concentrations
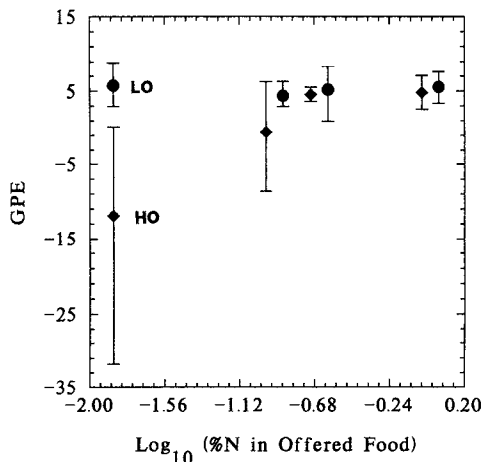production efficiencies were indistinguishable with respect to the effect of oxygen

Figure 4. Plot of gross production efficiency (GPE = (mm^3 growth) (mm^3 sediment egested)$^{-1}$) versus log$_{10}$ (%N) (wt:wt) in the offered experimental sediment. Filled circles: low oxygen (100 μM) treatment; filled diamonds: high oxygen (200 μM) treatment. Error bars are 95% confidence limits for the sample mean. Due to overlap, the means for the highest three food treatments have been offset ±0.05 log units to facilitate viewing the confidence limits.

(Fig. 4). Thus there is a strong interaction between the effects of oxygen and food concentration on GPE.

4. Discussion

a. Physiological considerations. The primary cause of decreased growth rate of *Capitella* sp. 1 at the higher oxygen concentration was clearly lowered conversion efficiency as opposed to lowered specific feeding rate (cf. Figs. 1 and 4). At oxygen concentrations in which some degree of feeding activity is maintained (i.e. down to at least 100 μM O_2), decreased growth can to a large extent be accounted for by lower gross rates of conversion of ingested sediment into tissue.

While modulated to some degree by oxygen concentration, percent nitrogen in the offered food nonetheless exerted the predominant effect on feeding rate (Fig. 1). Animals feeding at the lowest rates tended to be feeding on sediment with the lowest nitrogen content. In contrast, the growth response was strongly influenced by available oxygen, though only at the lowest two food concentration treatments (Fig. 2). The net effect of these interactions was the unexpected result that worm growth per unit sediment ingested was strongly dependent on oxygen concentration with the lowest growth efficiencies observed in the high oxygen, low nitrogen treatment.

In the discussion below we have made two assumptions. The first is that the worms did not lose more 'energy dense' tissue under the low food, low oxygen conditions than they did under the high food, high oxygen treatment. It is known that *Capitella*

sp. 1 has very little in the way of stored energy reserves. Species 1 has no peritoneal or coelomic cell reserves and unlike other sibling species, has no lipid and only moderate amounts of glycogen in the ovarian follicle cells (Eckelbarger *et al.,* 1984). This suggests that the ability to sustain a loss of energy dense tissue such as lipid is unlikely. This hypothesis could be tested by investigations combining volume and carbon loss measurements. The second assumption is that absorption efficiency did not vary across treatments such that the lowest absorption rates occurred solely as a function of oxygen concentration. That is, absorption efficiencies in the low oxygen, low food versus the high oxygen, low food treatments differed only due to differences in feeding rate ($=$gut residence time^{-1}). It is well-known that absorption efficiencies are closely related to feeding rates in deposit feeders and predictive models have been developed to quantify the expected relationships (e.g. Kofoed *et al.,* 1989). The influence of other environmental variables, such as oxygen concentration, on this important energetic process are unknown.

Given the validity of the above assumptions, we hypothesize that the worms maintain relatively high metabolic rates under conditions of high oxygen availability. That is, heat production or energy turnover rates are maintained at high levels in the absence of food and the presence of relatively high levels of oxygen. Under low food conditions this could be maintained only through utilization of biomass, leading to the high observed rates of shrinkage.

Under the present experimental conditions, it is most likely the aerobic component of metabolism that was maintained at high levels. We suggest that high metabolic rates are maintained in the presence of oxygen, independent of the level of available food. This would be expected if molecular oxygen, or a correlate, triggered high rates of metabolism and thus functioned as the rate limiting substrate. A metabolic system 'poised' in this way for aerobic respiration should allow a much more rapid change from low activity to high activity metabolic states than a analogous system responding solely to changes in the availability of fuel substrates. Metabolic systems poised for the rapid initiation of glycolysis in vertebrate muscle tissues have been known for some time (e.g. Hochochka, 1976).

The highest population densities of *Capitella* sp. 1 as well as other enrichment opportunists occur in environments in which oxygen, rather than food, is in short supply. These organisms are generally not found at high densities in oxygen-rich environments with relatively low levels of sedimentary organic matter. Thus under the environmental conditions enabling high rates of population growth, a metabolic system responding rapidly to changes in available oxygen would not tend to run short of fuel. Calculations based on organic matter reactivity and burrow diameter indicate that an infaunal animal the size of a pioneering polychaete can expect the concentration of oxygen in burrow water to change from near saturation to complete anoxia on the order of a few seconds to (at most) minutes once irrigation activity ceases. A metabolic system poised to rapidly exploit the appearance of oxygen would clearly be

advantageous to an organism in competition with aerobic microbes and reduced chemical species present within the burrow microenvironment. Finally, a great deal of experimental evidence concerning aerobic respiration rates in polychaetes (including *Capitella* spp.) demonstrates that many are indeed oxyconformers, at least when isolated from their burrows in laboratory studies (e.g. Mangum and van Winkle, 1973). Thus many polychaetes do respond to increased oxygen availability with an increased metabolic rate.

Finally, in a review and analysis of metabolism and respiratory physiology of thiobiotic meiofauna, Powell (1989) demonstrated theoretically that a first-order respiration strategy makes sense if maximization of energy turnover rate (and presumably growth rate) is a goal; even under extremely hypoxic conditions. We add the caveat that this strategy is sound only if enough food is available to maintain a positive energetic balance.

In summary, at the level of whole organism physiology the following relationships were observed. Under otherwise constant conditions, feeding rate was determined by the nitrogen content of the available sediment, with a greater nitrogen content generally leading to higher specific feeding rates. This result has often been observed in studies of deposit feeders and is consistent with recent interpretations of optimal foraging theory (Cammen, 1989). However, the relationship between feeding rate and growth was influenced by the level of available oxygen such that when the nitrogen content of the food was low, greater growth occurred at the lower oxygen level. Simultaneous measurement of growth and feeding rates indicated that oxygen influenced the efficiency at which ingested sediment was converted to body volume. We hypothesized that the decreased conversion rate of ingested sediment to body volume under the higher oxygen regime reflected an aerobic metabolic system poised to rapidly exploit available oxygen supplies.

b. Ecological considerations. Discussions of the factors that may limit both individual and population growth and production rates of deposit feeders have generally neglected oxygen as a resource (Forbes and Lopez, 1990a). The experiment reported here demonstrates that access to oxygen can be important even when environmental oxygen concentrations are relatively high. The degree of environmental hypoxia maintained in these experiments was not severe. Data on capitellid respiratory physiology (Wells and Warren, 1975), *in situ* measurements of oxygen penetration into organic-rich sediments (Jørgensen and Revsbech, 1985; Mackin and Swider, 1989), and community-level field investigations (e.g. Tsutsumi, 1987, 1990; Dauer *et al.*, 1992; Llansó, 1992) suggest that infauna inhabiting low-oxygen, high food habitats must often experience lower O_2 concentrations in nature than have been used here. Even so, the effect of low oxygen concentration on the critical bioenergetic parameters of growth, specific feeding rate, and gross production efficiency observed in this experiment were readily measurable and would be expected to have

significant life history consequences. Possession of a metabolic system responding rapidly to an increase in oxygen concentration without regard to available food is strategically sound only if the system evolved in order to efficiently exploit an environment consistently rich in food but low in oxygen.

The physiological responses observed in our experiments are entirely consistent with the classical faunal successional sequence occurring in a deposit following organic enrichment. These faunal changes consistantly co-occur with geochemical changes. The initial geochemical stages are typified by high organic matter levels coupled with extremely low oxygen concentrations. This pattern occurs whether one is observing spatial changes along a chronic enrichment gradient or following a discrete loading event over time (Pearson and Rosenberg, 1978; Rhoads *et al.*, 1978; Rhoads and Boyer, 1982). As succession proceeds, or as one moves outward along the gradient, the labile organic matter in the surface sediment declines and oxygen penetration into the sediment increases. This is paralleled by a well-documented and characteristic faunal pattern which is similar regardless of whether the decrease in organic enrichment occurs over spatial or temporal scales. We refer to these as the 'one-shot' (temporal scale) and 'gradient' (spatial scale) forms of organic enrichment respectively.

Under one-shot enrichment conditions, the geochemical evolution of a deposit is influenced to a large extent by the activity and behavior of the infauna (Rhoads, 1974). Due to the burrowing and feeding activities of *Capitella* sp. 1, there will be a natural tendency for increased oxygen penetration into the sediment and decreased levels of labile organic matter near the sediment-water interface. Our experiments suggest that these are exactly the environmental conditions under which *Capitella* sp. 1 would be expected to perform poorly. The physiological results observed in our study are wholly consistent with the 'boom and bust' population dynamics frequently observed under one-shot enrichment. Without a high influx of labile organic matter the system will evolve toward conditions which are unfavorable for population persistence. The sequence proposed above is thus very similar to the facilitation model of succession outlined by Connell and Slatyer (1977).

In contrast, under gradient enrichment conditions a steady supply of highly labile organic matter allows the formation of steady state conditions near the enriched end which are capable of supporting persistent high population densities of *Capitella* spp. (e.g. Pearson and Rosenberg, 1978). The often-observed temporal stability of these populations combined with an apparently unexceptional ability to tolerate low oxygen and high sulfide conditions suggests that it may be most productive to view *Capitella* sp. 1 and perhaps other enrichment opportunists as very successful competitors for labile organic matter. We are inclined to regard the temporal persistence of high population densities at a point along an enrichment gradient as prima facie evidence of good competitive ability.

A recent study by Tsutsumi (1990) of a *Capitella* sp. population in the vicinity of a

fish farm found that the population was maintained throughout the year without reliance on recolonization from other habitats. Due to organic enrichment from the fish farming activities, this locality experienced severe anoxia, including high sedimentary sulfide concentrations, for several months each year during the summer and autumn (Tsutsumi and Kikuchi, 1983; Tsutsumi, 1990). *Capitella* sp. populations declined dramatically during the summer months and consistently recovered during winter and early spring. Small 'seed' populations (<100 m^{-2}) remained viable throughout the summer months when conditions were most hostile due to anoxia and very high sedimentary sulfide levels (>2 mg total sulfide/g dw sediment; Tsutsumi and Kikuchi, 1983). These seed populations were able to respond very rapidly by producing lecithotrophic larvae when more favorable oxygen and sulfide levels returned.

In summary, the experiments described here suggest that the mechanism behind the decline of *Capitella* spp. populations in nature may be strongly influenced by a physiology well adapted to exploit the low oxygen, high food end of the soft bottom benthic habitat continuum.

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