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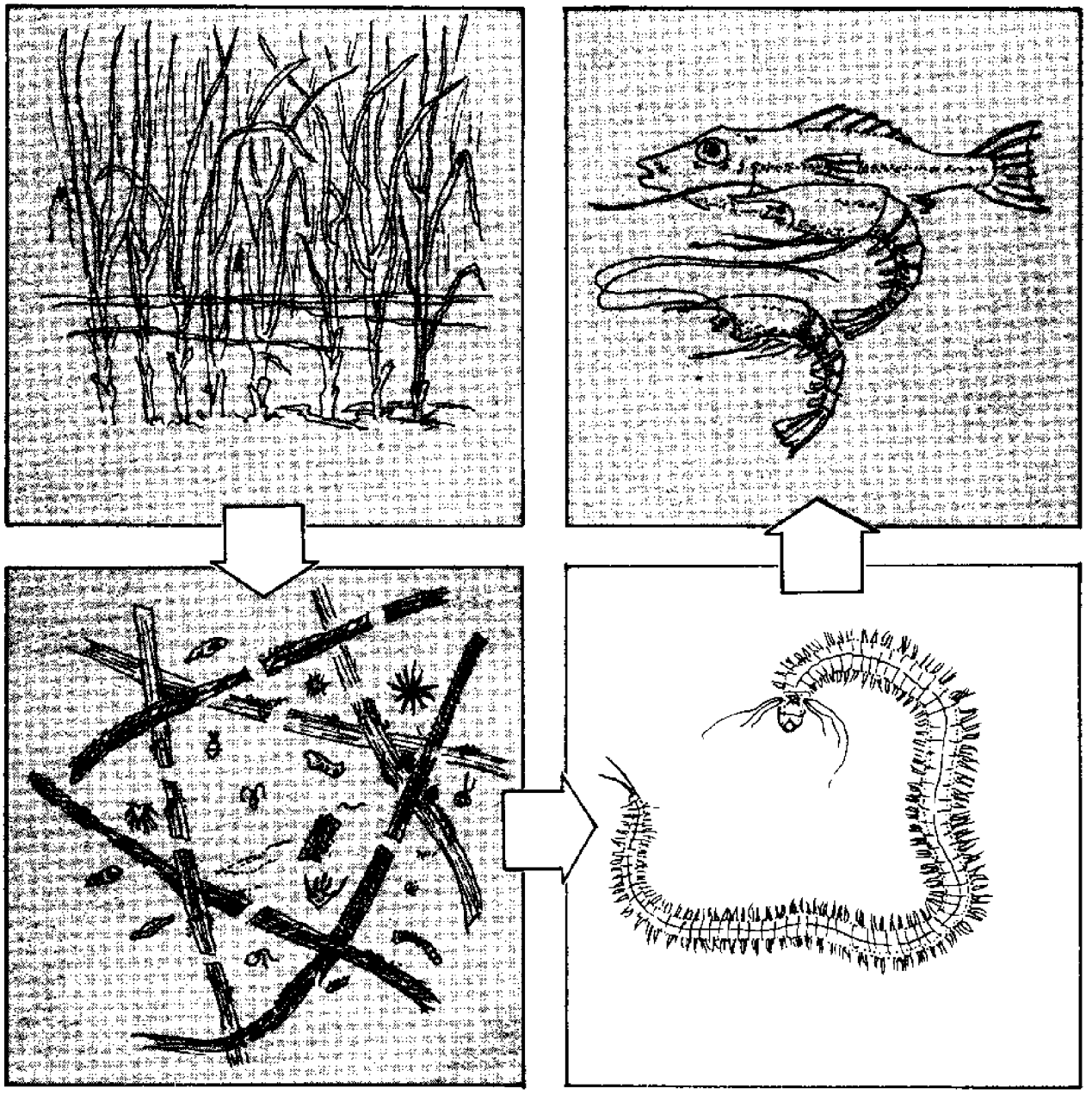

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ABSTRACT

The Significance of Microbial Carbon in the Nutrition of the Polychaete Nereis succinea and Other Aquatic Deposit Feeders.

In situ feeding rate of some infaunal deposit feeders can be determined without collecting feces by labeling the sediment with fluorescent particles and using these to trace ingested material through the gut of the animals. The feeding rate of the polychaete Nereis succinea, expressed as material ingested per body weight, increased with temperature and decreased with body size. Turnover times of the gut contents ranged from less than 30 min to over 6 hours. Total annual ingestion for a N. succinea population in a salt marsh near Beaufort, NC was estimated to be 5 kg of dry material m^{-2}, more than four times that reported for salt marsh epifaunal deposit feeders. Ingestion rate at 15 C for a wide variety of aquatic deposit feeders and detritovores was a function of body size and was inversely related to the organic content of the food.

A partial carbon budget was calculated for the N. succinea population. Annual consumption of microbial carbon was estimated to be 5.2 g m^{-2}; assimilation efficiency of bacteria was estimated to be 57% and if this value is used for all the microbial carbon, then total assimilation was 3.0 g C m^{-2}. Loss of carbon to the population was estimated by calculating annual production, 2.1 g C m^{-2}; respiration, 9.4 g; and release of dissolved organic carbon (DOC), none. The completed budget showed that even if assimilation of microbial carbon was complete, only 45% of the carbon requirement of N. succinea would have been satisfied;

with an assimilation efficiency of 57%, only 26% of the carbon requirement would have been satisfied. N. succinea was able to assimilate carbon from sterile plant detritus which suggests that some of the carbon needed to balance the budget may come from direct uptake of the plant substrate.

Ingestion and respiration were estimated from regression equations calculated from literature values for a variety of aquatic deposit feeders and detritovores. Based on sediment microbial carbon concentrations from the literature and the calculated ingestion rates and respiratory losses, it appears that detritovores do not consume enough microbial carbon to balance even respiratory losses, much less additional losses to production and DOC release. This implies that the accepted hypothesis of detrital utilization, that all uptake comes from digesting the microbes on the detritus, may not be true. Alternate sources of food such as direct uptake from the plant substrate, consumption of meiofauna, or uptake of DOM may be more important than uptake from microbes.

TABLE OF CONTENTS

TABLE OF CONTENTS (Continued)

SECTION I

THE ANNUAL INGESTION OF A NEREIS SUCCINEA POPULATION

Introduction

Deposit feeding invertebrates can strongly influence both the abiotic and biotic components of marine ecosystems. For example, manipulation and ingestion of sediment by deposit feeders may significantly affect the distribution of grain sizes, as well as altering other sediment properties such as porosity, water content, compaction and cohesion (Rhoads, 1967, 1973, 1974; Rhoads and Young, 1970; Aller and Dodge, 1974). Transfer of subsurface sediment to the sediment surface by deposit feeders may be important in recycling nutrients (Rhoads, 1973; Kraeuter, 1976). Resuspension of this sediment may exclude suspension feeders by clogging their feeding mechanisms; the physical instability of the sediment may discourage their larvae from settling and perhaps even cause newly settled larvae to be buried (Rhoads and Young, 1970; Aller and Dodge, 1974). Predation by deposit feeders on larvae of suspension feeders and tube builders may also be responsible for excluding these groups from areas where deposit feeders are particularly abundant (Woodin, 1976). In addition, at least one deposit feeder has been shown to stimulate bacterial respiration and benthic algal production, presumably by increasing nutrient recycling (Hargrave, 1970). The overall effects of deposit feeders on an environment are largely a function of their feeding and tube-building. Therefore, in order to understand and quantify these activities, it is necessary to have a measure of *in situ* feeding activity.

Information on feeding rates of infaunal deposit feeders is sparse, however, and virtually all studies to date have involved collection of

fecal material. The technique used most often has been to determine feeding rate indirectly by measuring fecal production rate of organisms which conveniently void their feces on the sediment surface or into the water, e.g., Pectinaria spp. (Gordon, 1966; Nichols, 1974), Clymenella torquata (Mangum, 1964; Rhoads, 1967), and Yoldia limatula (Rhoads, 1963); additional studies were summarized by Hargrave (1972) and Kraeuter (1976). Other workers have measured time of passage through the gut by dyeing material to be ingested with methylene blue (Fox et al., 1948; North, 1954) or Sudan III (Jacobsen, 1967), by intermixing colored chalk with the potential food (Hobson, 1967), and by labeling potential food with the radioisotope ^{51}Cr (Calow, 1975). However, feces were collected even in these tracer studies; the appearance of the first labeled material indicated complete passage through the gut.

Many deposit feeders do not egest their feces at the sediment surface and, in fact, it is often impossible to distinguish freshly produced feces from the surrounding sediment. For this reason, there are no satisfactory data on feeding rates for a large proportion of the benthic infauna. Although the colored tracers enable fecal material to be distinguished from sediment, it would be desirable to have a technique that would dispense entirely with collection of feces.

I present here a direct method for determining the feeding rate of some infaunal deposit feeders whose feces cannot be collected. The technique is a modification of that used by Hughes (1969) who was able to follow colored sediment through the bivalve Scrobicularia plana by periodic dissection of the gut. Fluorescent pigment particles are used as a tracer in the ingested material. The advantage of the fluorescent particles is that with a suitable light source they are visible through

the body wall of small invertebrates. The method is suitable for field or laboratory use on deposit feeders that satisfy the following conditions: (1) feeding must occur at the sediment surface; (2) feeding must not completely select against the fluorescent particles; and (3) ingested material must pass through the gut sequentially, i.e., there should be no mixing of newly ingested material with material already in the gut. Using this technique I have estimated yearly food ingestion for a Nereis succinea population in a salt marsh near Beaufort, NC.

Methods and Materials

Field Studies

The study area was a Spartina alterniflora marsh near the mouth of the Newport River estuary in North Carolina (34°43'N, 65°40'W). Salinity ranged from 22 to 36 °/₀₀ and water temperature from 5 to 32 C during the year of this study.

In situ feeding rates were determined by labeling sediment in the field with fluorescent particles, allowing the animals to feed on the labeled sediment, and then examining the gut contents to determine the amount of labeled sediment ingested in a given time. A suspension of fluorescent particles was made from 1 g Day-Glo Fire Orange (AG-14) powdered paint (Day-Glo Color Corp., Cleveland, OH), 1 liter distilled water and a few drops of the surfactant Tween 80 (following Haven and Morales-Alamo, 1966). Two to three hours before low tide two Plexiglas cylinders (22 cm diameter, 30 cm tall) were pressed into the sediment just enough to seal the edges. Water temperature within the cylinders was then recorded; water depth was 10-20 cm. A mixture of 150 ml of paint suspension and 300 ml of sea water taken near the cylinders was

poured slowly into each cylinder to minimize disturbance of the sediment surface. The resulting cloud of particles was dispersed throughout the cylinder by gentle stirring and the cylinders were left to incubate for 1 hour (14.4 and 19.5 C) or 30 min (28.0 C). The shorter time was necessary so that no labeled material would be egested. After the incubation was completed the top few centimeters of sediment within the cylinders were removed and placed in 20% formalin-sea water to kill the animals. All N. succinea were removed from the sediment by gentle washing followed by hand-sorting; only intact worms were used for the feeding rate determination.

The worms were placed individually on glass slides and squeezed gently with another slide. They were observed at 100 X under epi-fluorescent illumination (wavelength of 490 nm) with a Leitz Ortholux microscope to determine the extent of labeling in the gut contents. The particles fluoresced a bright yellow-orange and were visible through the body wall of almost all the animals. For the largest individuals, it was necessary to make slits at intervals along the body and gut walls in order to see the fluorescent particles. All the worms were then cut into two pieces at the interface between labeled and unlabeled gut contents. The sediment anterior to the cut was removed from the gut by gentle prodding with tweezers. This sediment, which was ingested after the paint was introduced into the cylinders, was filtered onto tared Nuclepore filters (8 μm pore diameter), dried at 90 C and weighed to the nearest microgram.

Laboratory Studies

Feeding rates were also determined in the laboratory where the number of animals in each run could be controlled. N. succinea were

collected from the salt marsh by hand-sorting the top few centimeters of sediment. In the laboratory, 8 to 12 individuals were placed in each of two or three plastic pans (30 cm diameter) filled with about 7 cm of freshly collected marsh surface sediment. Aerated sea water was added slowly to the pans to a depth of about 6 cm; the flow continued at a rate low enough to prevent disturbance of the sediment surface. For two of the runs ambient temperature sea water (7.0 and 10.5 C) was used. The third run was carried out at 28.5 C when the ambient water temperature was 19.1 C; the temperature of the incoming water was raised initially to 23 C, raised to 26 C after 2 hours, and raised to 28.5 C 16.5 hours later; the paint was added 5 hours after the final temperature increase. Animals in the field are often exposed to similar temperature increases during low tide on a sunny day (Cammen, unpublished data). The worms had from 1 to 2 days prior to each run to construct burrows and otherwise adapt to the sediment. After the water supply was shut off, the fluorescent particles were added and mixed by gentle stirring. When the particles began to settle, the water flow was allowed to resume. Incubation times were 1.5 hours for the 7.0 and 10.5 C runs and 30 min for the 28.5 C run. Subsequent treatment of the animals was the same as for the field experiments.

Size of all worms was measured as width of the peristomium (PW), the first segment after the head; ash-free dry weight (AFDW) in micrograms was related to PW in millimeters as follows:

$$(1)\quad \log \mathrm{AFDW} = 2.842 + 2.769 \cdot \log \mathrm{PW} \qquad (r^2 = 0.97,\ N = 70).$$

The complete gut contents were removed from 18 worms, filtered, and dried and weighed as for ingested material. The relation between gut content weight (GC) in micrograms and PW in millimeters was:

$$(2)\ \log GC = 2.498 + 2.877 \cdot \log PW \qquad (r^2 = 0.89,\ N = 18).$$

Both these relationships are expressed as geometric mean (GM) regressions (Ricker, 1973).

Results

The feeding rate of N. succinea varied with both temperature and animal size. The overall relation between feeding rate (FR) in micrograms hr^{-1}, peristomial width (PW) in millimeters, and temperature (T) in °C was:

$$(3)\ \log FR = 0.815 + 2.216 \cdot \log PW + 1.274 \cdot \log T$$
$$(R^2 = 0.81,\ N = 43).$$

This relationship was derived from combined data for all laboratory and field experiments (Table 1), but was based only on those worms which ingested the label. While 80% or more of the worms ingested the fluorescent particles at 28.5, 19.5 and 14.4 C, the percentage dropped to 50% at 10.5 C and 35% at 7.0 C. The interaction between log T and log PW was not significant ($F = 1.18$, $P < 0.28$), indicating that the effect of animal size on feeding rate was not affected by temperature.

Discussion

Suitability of the Fluorescent Pigment Method

The feeding habits and gut structure of N. succinea are suitable for this method. N. succinea is thought to be a nonselective deposit

Table 1. Summary of the feeding rate determinations on *Nereis succinea*. Coefficients are given for the expression log FR = a + b · (log PW) where FR is the feeding rate in μg hr^{-1} and PW is the peristomial width in mm.

Location	Temp. (°C)	N	b	a	r^2	Significance
Laboratory	7.0	6	2.719	1.815	0.96	**
Laboratory	10.5	11	2.368	2.085	0.66	**
Field	14.4	7	1.773	2.338	0.75	*
Field	19.5	7	2.124	2.435	0.30	NS
Field	28.0	1	--	--	--	--
Laboratory	28.5	11	1.803	2.832	0.73	**

*Significant at the 95% level.

**Significant at the 99% level.

NS = not significant.

feeder consuming mainly sediment with associated detritus, microbes, algae and occasional meiofauna (Teal, 1962; Odum and Heald, 1972; personal observation). Although it possesses a pair of formidable jaws and will readily feed on dead animal tissue (personal observation), there are no literature reports of adult N. succinea being an active predator. Typically, when feeding the worms periodically extend their heads out of their burrows, search the area around the burrow mouth for a brief period, ingest a quantity of sediment, and quickly retract completely into their burrows. Although another nereid species has been reported to filter feed (Harley, 1950), this behavior has not been observed in N. succinea. However, since part of the paint remained in suspension and part settled to the sediment surface, the worms could pick up the label by either feeding method. The actual feeding behavior would have had no effect on measurement of their feeding rate. Aside from the pharynx, the gut of N. succinea appears to be unstructured. Mixing of gut contents is minor since there was a clear distinction between labeled and unlabeled material in most of the animals examined.

The reduction in the proportion of N. succinea ingesting particles at lower temperatures might be explained in two ways: (1) Surface feeding might be reduced at lower temperatures with an increase in feeding at a depth in the sediment where there were no fluorescent particles available. Most of the animals had sediment throughout the gut at the end of each experiment, suggesting that they were continuing to feed but were ingesting unlabeled sediment; therefore, I have assumed this explanation is correct. (2) Feeding could become more sporadic at lower temperatures with the percentage of actively feeding worms being reduced.

This technique should be useful with many additional species. For example, both the small polychaete Streblospio benedicti and an unidentified oligochaete ingested fluorescent particles during this study; conceivably the same type of experiments could have been carried out on them. The method is relatively simple and does not require the collection of feces. Although any type of fluorescent light may be used, the stronger the light source the easier it is to observe the particles. With smaller animals it may be possible to calculate the volume of the gut which contains labeled particles, thus eliminating the need for dissection and weighing of minute quantities of sediment.

Turnover Rate and Total Annual Consumption

Turnover time for the gut contents of N. succinea ranged from over 6 hours for large worms at 10 C to less than 30 min for small worms at 30 C (Figure 1). The calculations were made from values for gut contents derived from Equation 2 and feeding rates derived from Equation 3. Daily turnover (total consumption/body weight) was 10.0-20.5 for N. diversicolor weighing 5-15 mg dry weight (Veltishcheva and Karzinkin, 1970) and 4.6-6.4 for N. succinea weighing 6-24 mg (Yablonskaya, 1952, as cited in Veltishcheva and Karzinkin, 1970). For animals of this size (5-24 mg), I calculated daily turnover to be 1.7-2.2 at 10 C, 4.1-5.3 at 20 C, and 6.9-8.9 at 30 C. Veltishcheva and Karzinkin (1970) used silt labeled with ^{14}C in a manner analogous to this study; no method was given for Yablonskaya's work. No mention was made of the temperature used for either set of experiments and it is not clear whether the animals were allowed to establish burrows.

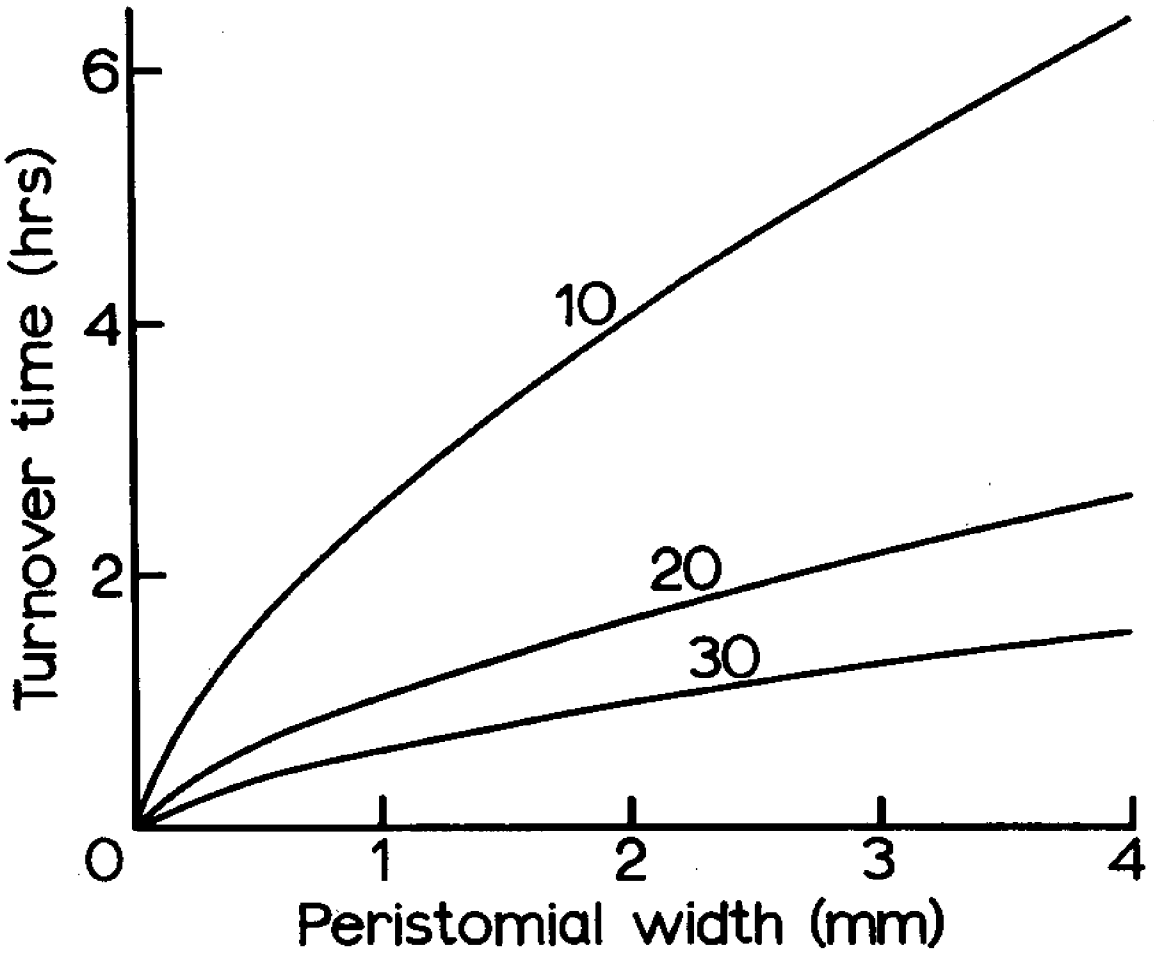

Figure 1. Model curves for turnover times of the gut contents of Nereis succinea at 10, 20 and 30 C calculated from Equation 2 relating feeding rate to peristomial width and temperature.

The N. succinea population in a salt marsh near Beaufort, NC was estimated to consume about 5 kg dry weight of sediment m^{-2} in one year (Table 2). This calculation was made with size-frequency data determined from monthly core samples and water temperatures measured weekly or biweekly (Section II). For each day, the population of each of the 22 size classes of the N. succinea population and the water temperature were estimated by interpolating between the data points; using Equation 3, daily sediment ingestion was estimated for each size class. I assumed that all worms were feeding throughout the day. As discussed above, temperature decreases within the range used in these studies may have affected the depth of feeding but probably did not decrease the total number of actively feeding individuals. All feeding experiments presented here were necessarily carried out while the marsh surface was submerged; however, the worms probably feed continuously since all worms collected during low tide for gut analysis had full guts and several worms were observed feeding in the marsh at low tide. In addition, a few observations of worms at night in the laboratory always revealed full guts. Since the marsh is intertidal, sediment temperature (and feeding rate) changed with the tides. I assumed, however, that the water temperature represented an average temperature since the exposed sediment would be warmer than the water during the day and cooler at night.

Total ingestion by the N. succinea population appears to be far greater than that reported for other salt marsh invertebrate species. A population of the fiddler crab Uca pugnax was estimated to consume 0.6 kg dry weight m^{-2} of sediment and detritus in one year (Krebs and Valiela, in preparation); 0.4 kg was consumed by the older crabs

Table 2. Monthly sediment ingestion by a Nereis succinea population in a salt marsh near Beaufort, NC. Numbers are for 1 m^2. See text for various assumptions which have been made.

Month	Mean water temp. (°C)	Mean Nereis biomass (g AFDW)	Total ingestion (g dry wt)
August[a]	30.8	2.2	785
September	29.4	1.6	568
October	23.0	1.1	305
November	18.3	0.9	179
December	11.0	1.1	113
January	8.9	2.1	173
February	13.7	2.6	329
March	15.4	2.8	424
April	22.2	2.3	554
May	24.9	2.5	755
June	26.4	1.7	523
July	29.5	1.1	426
August[b]	29.8	1.0	404
Total (using August mean)			4944

[a]Extrapolated from last 18 days.

[b]Extrapolated from first 13 days.

(carapace widths >1 cm). In a Georgia marsh the same size class of older U. pugnax and U. pugilator was estimated to consume 1.1 kg m^{-2} of sediment and detritus, while the marsh periwinkle Littorina irrorata consumed only 0.1 kg (Kraeuter, 1976).

It is apparent that in this salt marsh, at least, it is the smaller infauna that ingest and process most of the sediment, not the larger epifauna. The average biomass of N. succinea found in this marsh was 2.1 g ash-free dry weight m^{-2}; populations were lower in two other North Carolina salt marshes, averaging 0.2 and 0.8 g dry weight m^{-2} (Cammen, 1976), and in a Louisiana marsh, averaging 0.2 g ash-free dry weight (Day et al., 1973). Even with these reduced abundances the amount of sediment ingested would approach or surpass that estimated for the fiddler crabs. If the meiobenthos living in the sediment are included, the disparity between infaunal and epifaunal sediment ingestion becomes even greater. Previous studies which have concentrated on the more obvious and accessible fauna in the marsh may have overlooked animals that significantly influence community structure.

Ingestion by Aquatic Invertebrates as a Function of Body Weight and Organic Content of the Food Material

Previous workers have found a correlation between consumption of food and body size for various invertebrates. When plotted against log of body weight, log of food consumed fell on a straight line for 11 terrestrial arthropod species feeding on a forest floor (Reichle, 1968) (Figure 2); slope of the line was 0.68. Daily rations and body weights were related similarly for 10 aquatic crustaceans, including filter feeders and scavengers (Sushchenya and Khmeleva, 1967). In addition, log of egestion rate appeared to be related to log of body size for 20

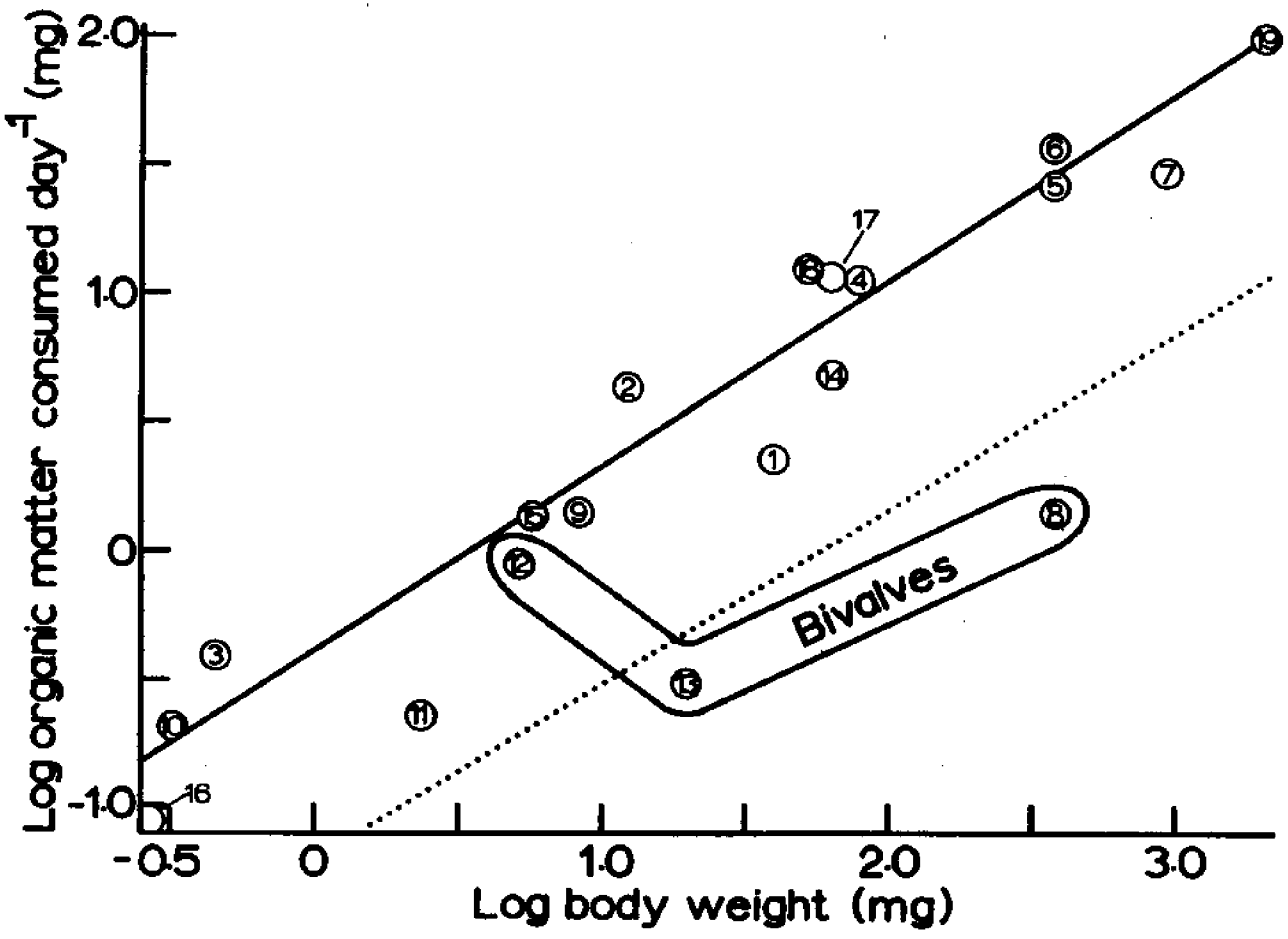

Figure 2. Relation between consumption of organic matter and dry body weight for various aquatic invertebrates. Numbers refer to species listed in Table 3. Only the geometric mean weights of those species with a range of values were used to compute the regression line (——). For comparison the line calculated by Reichle (1968) (····) has been included. Data for the bivalves were not included in calculation of the regression line (see text).

aquatic deposit feeders (Hargrave, 1972) although the relation was not strong enough to warrant statistical treatment.

In order to examine further the relation between feeding rate and body size for aquatic deposit feeders, I looked at species where data were available for feeding rate at or near 15 C, for body size, and for organic content of food material (Table 3). Most of these species are from Table 2 in Hargrave (1972); some additional data, including those for N. succinea, were included.

Feeding rate of these deposit feeders was explained almost entirely by body size and organic content of the food. The relation for the 13 species from Table 3 where organic content of the food was available (excluding the three bivalve species--see below) was:

$$(4)\quad \log FR = -0.483 + 0.691 \cdot \log W - 1.030 \cdot \log OM \qquad (R^2 = 0.98)$$

where FR is mg dry matter consumed hr^{-1}, W is mg dry body weight, and OM is the fraction of organic matter in the food.

Regulation of organic matter consumption may be a general phenomenon for aquatic deposit feeders. According to Equation 4 feeding rate was inversely proportional to the organic content of the food since the coefficient for log OM, -1.030, was not significantly different from -1. Previous studies support the idea that consumption of organic matter is actively regulated in benthic invertebrates. Feeding rates of the polychaete Pectinaria gouldii were lower when feeding on sediment richer in organic matter and pigments than when feeding on less nutritious sediment (Gordon, 1966); ingestion rates of the snails Ancylus fluviatilis and Planorbis contortus varied inversely with their assimilation efficiency for various foods (Calow, 1975). The mechanism behind this regulation is not clear, however. For example,

Table 3. Daily organic matter consumption of various invertebrate species. For those species where consumption was determined from a regression equation, data are given for the lowest, highest, and geometric mean weights of the size range considered. Organic carbon was converted to organic matter by multiplying by 1.9 (Bader, 1954) for species 3 and 4; organic nitrogen was converted to organic matter by multiplying by 20.5 (Bader, 1954) for species 17, 18, and 19. Methods used in the studies were to measure ingestion (I), egestion (E), or gut contents and turnover time of the gut (T). All weights are in mg.

Species	Source	Method	Dry wt	Total ingestion animal^{-1} day^{-1}	% Organic matter in food	Organic matter ingested day^{-1}	Comments
1) Thoracophalia mucronata	Fox et al. (1948)	T	40	230	1	2.3	Yearly average; polychaete
2) Orchestia grillus	Lopez (1976)	E	12.4	4.4	88	3.9	15°; feeding on detritus; ash content from Cammen (unpublished data); amphipod
3) Potamopyrgus jenkinsi	Heywood & Edwards (1962)	E	0.46	2.7	14.4	0.39	20°; dry wt without shell; snail
4) Pectinaria gouldii	Gordon (1966)	E	80	1667	0.70	11.6	18-20°; dry wt from Hargrave (1972); estimate of biodeposition reduced by 2/3 to give feces, see Rhoads (1967); polychaete
5) Abarenicola pacifica	Hobson (1967)	E	380	3400	0.8	27.2	10-13°; dry wt calculated as 17% of wet weight; polychaete
6) Abarenicola claparedi	Hobson (1967)	E	380	9400	0.4	37.6	10-13°; dry wt calculated as 17% of wet weight; polychaete
7) Arenicola marina	Jacobsen (1967)	E	930	4700	0.64	30.1	17.5°; dry wt calculated as 17% of geometric mean of wet weight (given as 3-10 g); polychaete

Table 3 (Continued)

Species	Source	Method	Dry wt	Total ingestion animal^{-1} day^{-1}	% Organic matter in food	Organic matter ingested day^{-1}	Comments
8) *Scrobicularia plana*	Hughes (1969, 1970)	E	380	43	3.4	1.47	15°; dry wt without shell; bivalve; organic content calculated assuming value of 4.45 kcal/g dry organic matter in sediment (mean of values for detritus and benthic algae in Cummins & Wuycheck, 1971)
9) *Pteronarcys scotti*	McDiffett (1970)	E	2 8.4 35	0.41 1.49 5.40	93	0.38 1.39 5.02	15°; feeding on dead leaves, ash content assumed to be 7% (Cummins & Wuycheck, 1971); stonefly nymph
10) *Hyalella azteca*	Hargrave (1972)	E	0.10 0.32 1.0	0.25 0.43 0.32	50	0.125 0.21 0.16	15°; amphipod
11) *Pontogammarus maeoticus*	Soldatova (1970)	I	0.57 2.32 9.46	0.22 0.53 1.27	41	0.09 0.22 0.52	20°; feeding on *Cladophora* sp.; data calculated assuming 2.12 kcal/g dry wt *Cladophora* and ash content of 59% (Cummins & Wuycheck, 1971); amphipod
12) *Macoma balthica*	Bubnova (1972)	I	2.2 5.1 8.8 14.3	2.52 4.49 6.52 9.10	--	0.56 0.90 1.23 1.61	6°; bivalve
13) *Portlandia arctica*	Bubnova (1972)	I	9.3 14.0 19.9 36.6	1.97 2.70 3.54 5.66	--	0.19 0.24 0.31 0.46	15°; feeding on dead leaves, ash content assumed to be 7% (Cummins & Wuycheck, 1971); stonefly nymph

Table 3 (Continued)

Species	Source	Method	Dry wt	Total ingestion animal^{-1} day^{-1}	% Organic matter in food	Organic matter ingested day^{-1}	Comments
14) *Uca pugnax*	Krebs & Valiela (in prep.)	E	3.3 63.3 1215	3.5 19.9 114.7	23.7	0.82 4.73 27.2	No temperature given; organic matter concentration from Valiela *et al.* (1974); decapod crab
15) *Nereis succinea*	This paper	I	0.86 5.8 38.1	3.91 20.2 103.7	6.8	0.27 1.38 7.06	15°; polychaete
16) *Tubifex tubifex*	Ivlev (1939)	E	0.27	0.43	20.8	0.09	16-18°; organic matter concentration calculated assuming 1.52 kcal/g dry wt of organic matter from eutrophic lake sediments (Cummins & Wuycheck, 1971); oligochaete
17) *Scopimera globosa*	Ono (1965)	I	65	50	--	11.8	No temperature given; decapod crab
18) *Ilyoplax pusilla*	Ono (1965)	I	53	300	--	12.6	No temperature given; decapod crab
19) *Macrophthalmus japonicus*	Ono (1965)	I	2050	4680	--	99.0	No temperature given; decapod crab

the animals may sense the "organic quality" of their food (the sediment) and adjust their feeding rates accordingly in order to maintain a constant assimilation of organic matter with a minimum expenditure of energy (see Calow, 1975). Alternatively, the substrate quality which cues the feeding rate may only be indirectly related to organic content. Of course, the relation between ingestion rate and organic content of the sediment can be explained without resorting to actual "regulation". A given species population with an inherent feeding rate may be found only in a certain substrate and be incapable of adjusting the feeding rate if transferred to a different substrate; the relation shown here may represent only long-term adaptation to different environments by many populations.

It is useful to express consumption of total organic matter as a function of body weight (Figure 2). The equation for this least squares regression was highly significant:

$$(5)\quad \log C = -0.451 + 0.729 \cdot \log W \qquad (r^2 = 0.93,\ N = 16)$$

where C is mg organic matter consumed day^{-1} and W is mg dry body weight. It was necessary to make two assumptions:

(1) Egestion rates were equivalent to ingestion rates.

The error introduced by this assumption is equal to the percent of the food that is assimilated; for an adult Hyallela azteca, for example, consumption of organic matter would be underestimated by 7.5% (calculated from data in Hargrave, 1972). Since most of the taxa considered were feeding on material substantially poorer in organic matter than that fed upon by H. azteca, the error from this assumption would be less than for H. azteca.

(2) The organic content of the surrounding sediment was the same as that of the material ingested by the deposit feeders.

For some taxa (2, 9, 11, 12, 13, 17, 18, 19 from Table 3) data were available for the actual amount of organic matter ingested; for the remaining taxa, however, the only data available were organic content of the surrounding sediment and dry weight of the total ingested material. In order to calculate the organic matter ingested, it was necessary to assume that no selection for organic matter occurred during feeding. This assumption probably was not valid for all the taxa considered, but the error introduced to the calculations must have been relatively small since feeding rates agreed well for both groups of taxa (Figure 2). In addition, much of the data were not in satisfactory form and many conversions and calculations were made with varying degrees of confidence; these calculations were listed in Table 3. In particular, the use of a conversion factor for organic nitrogen to total organic matter in sediments has been criticized (Bader, 1954).

Consumption of organic matter by two of the three bivalve species was much less than that predicted by this relation (Figure 2). Comparison of bivalve respiration with respiration values from other taxa (Table 4; Figure 3) indicates that the reduced ingestion rates of bivalves cannot be attributed to lower metabolic requirements. Consumption rate for Portlandia arctica was studied at 6 C, but even assuming a Q_{10} of 2 to estimate the rate at 15 C does not correct the low value; consumption rate of Scrobicularia plana was calculated for 15 C. The explanation for the low ingestion rate of S. plana may be a highly selective feeding behavior which results in ingestion of material much richer in organic material than the surrounding sediment; feces of

Table 4. Respiration of various invertebrate species. Coefficients are given for the expression $\log R = \log a + b \cdot \log W$ where R is $\mu\ell$ O_2 consumed $animal^{-1}$ hr^{-1} and W is mg dry body weight.

Species	Source	Dry wt (mg)	$\mu\ell$ O^2 consumed $animal^{-1}$ hr^{-1}	Coefficients a	Coefficients b	Comments
3) *Potamopyrgus jenkinsi*	Heywood & Edwards (1962)	0.46	0.8	1.45	0.71	20°; calculated from Figure 4 in Heywood & Edwards (1962)
5) *Abarenicola pacifica*	Hobson (1967)	380	70.4	1.88	0.61	12-14°; calculated from Figure 5 in Hobson (1967)
6) *Abarenicola claperedi*	Hobson (1967)	380	107.8	3.65	0.57	12-14°; calculated from Figure 5 in Hobson (1967)
8) *Scrobicularia plana*	Hughes (1970)	380	102.4	1.19	0.75	13.5°
9) *Pteronarcys scotti*	McDiffett (1970)	8.4	6.5	1.08	0.84	15°
10) *Hyalella azteca*	Hargrave (1970)	0.32	0.4	1.44	1.13	15°
12) *Macoma balthica*	Kennedy & Mihursky (1972)	5.1	4.3	1.75	0.55	20°
14) *Uca pugnax*	Shanholtzer (1973)	63.3	13.1	0.69	0.71	15°
15) *Nereis succinea*	Cammen (Section II)	5.8	3.18	0.88	0.73	15°

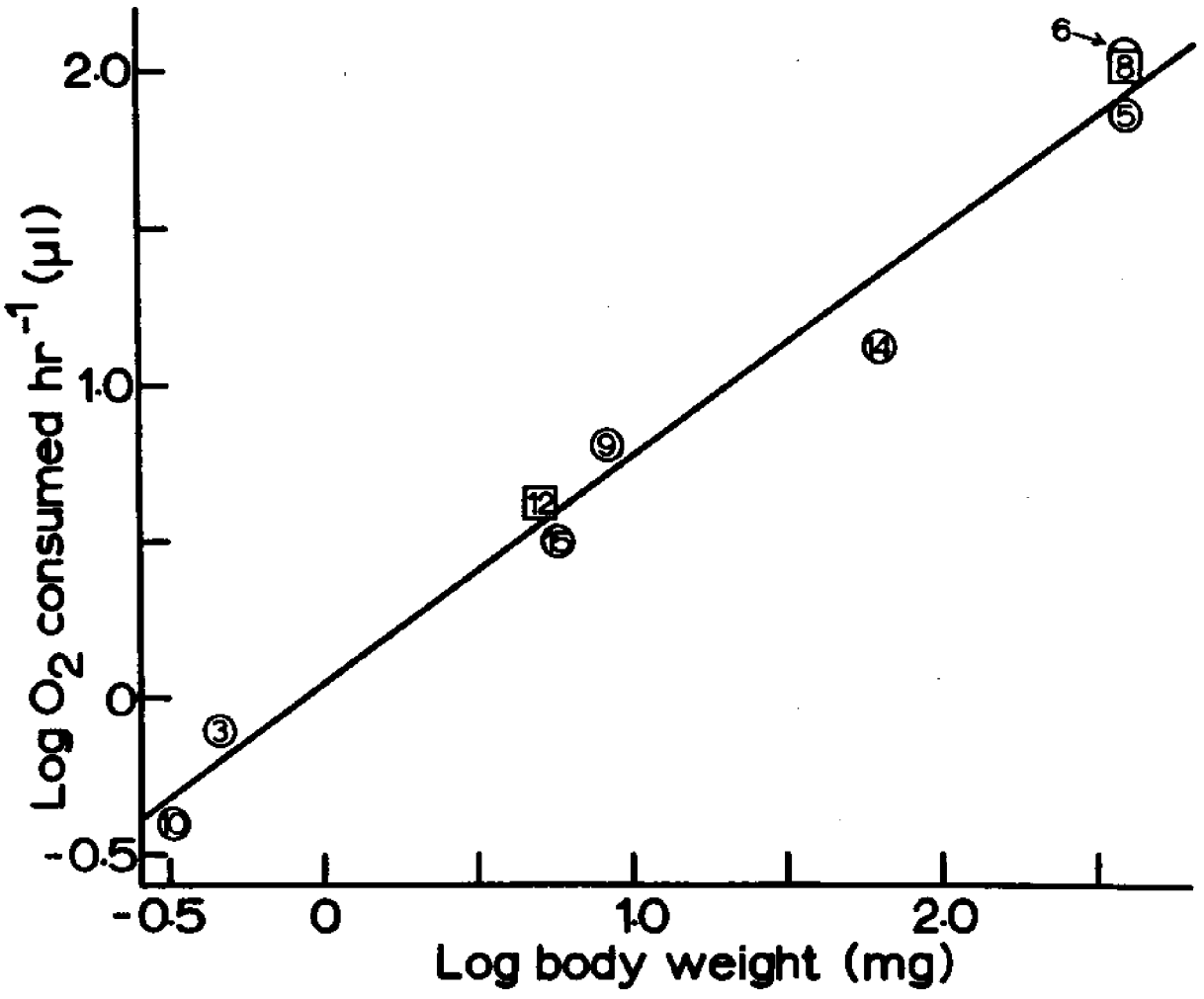

Figure 3. Relation between respiration and dry body weight for various aquatic invertebrates. Numbers refer to species listed in Table 4. For clarity the two bivalve species are square points. Where a range of weights were available, only the dry weight equal to that used in calculating the regression for Figure 2 was plotted. The equation of the regression line is

$\log R = 0.043 + 0.727 \cdot \log W \qquad (r^2 = 0.98, N = 8)$

where R is µl O_2 consumed $animal^{-1}$ hr^{-1} and W is mg dry body weight.

S. plana had 1.8 times the concentration of organic matter as the sediment (Hughes, 1970). However, selective feeding of P. arctica was accounted for by Bubnova (1970) and the numbers in Table 3 represent the actual ingestion of organic matter. Since these two bivalves evidently did not fit the same line as the other taxa, I excluded all three bivalves from the calculation of the regression line. Future studies may indicate whether or not bivalves should be included with the other taxa.

Could this relation be used to predict consumption of organic matter from body size for aquatic invertebrates? If the extent of selection of organic matter by a given species is known, this relation may be useful in predicting an order of magnitude figure. In the future, as additional data become available, it may even be possible to predict feeding rates within acceptable confidence limits for aquatic deposit feeders.

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SECTION II

THE SIGNIFICANCE OF MICROBIAL CARBON IN THE NUTRITION OF THE POLYCHAETE *NEREIS SUCCINEA* AND OTHER AQUATIC DEPOSIT FEEDERS

Introduction

With recognition of the importance of detritus-based food webs in shallow water aquatic ecosystems (Darnell, 1967; Mann, 1972; Odum *et al.*, 1972; Odum and Heald, 1975) an increasing amount of study has been made of the trophic structure within these food webs. One of the basic questions has been the actual source of the carbon and energy obtained by detrital consumers--do they utilize the plant material of the detrital particles directly, or must they rely on bacteria, fungi, and other microbes to convert the plant tissue to microbial biomass before it can be utilized?

Most evidence and published opinion favor the hypothesis that detrital plant material must be converted to microbial tissue before it can be utilized by consumers (Newell, 1965; Fenchel, 1970, 1972; Odum and Heald, 1975; Wetzel, 1975; Berrie, 1976; Hargrave, 1976; Yingst, 1976; Lopez *et al.*, 1977). The accepted view is that the plant substrate is first colonized by microorganisms, forming detritus, and then consumed by a detritovore which digests the microbiota off the particles without affecting the plant substrate; after these denuded particles are defecated, they are recolonized by microbes and reingested by consumers (Newell, 1965 and others).

The main evidence for this view has come from the high assimilation efficiencies found for organisms fed bacteria and the low assimilation efficiencies found for organisms fed sterile plant detritus. However, no one has shown conclusively that the amount of microbial carbon (or

energy) available to a detritovore is sufficient to satisfy its carbon (or energy) requirement. Due to the vast amounts of detrital plant material passing through deposit feeders or detritovores, even a low assimilation efficiency might result in significant uptake of carbon (or energy).

I have attempted to determine whether the ingestion and assimilation of microbes are sufficient to meet the carbon requirement of a population of the detritus feeding polychaete Nereis succinea (Frey and Leuckart) in a North Carolina salt marsh. I have estimated annual production, respiration, loss of dissolved organic carbon (DOC), and consumption and assimilation efficiency for N. succinea. Using data from Rublee (in preparation) on microbial populations in the same marsh, I have attempted to balance the carbon budget for the polychaetes in order to determine whether the microbial carbon supply was adequate.

Study Site

The study area was a Spartina alterniflora marsh near the mouth of the Newport River estuary (34°43'N, 65°40'W). The marsh, about 2000 m^2, bordered a shallow embayment with a maximum depth of approximately 1 m at low tide; tidal range in this region was about 1 m. Water temperature in the embayment varied from 5 to 32 C and salinity from 22 to 36 $^{\circ}/_{\circ\circ}$ (Figure 1).

The marsh was covered with a uniform stand of medium Spartina. Average standing stock in September 1976 was 457 $\pm$ 158 g dry weight m^{-2}; annual production was estimated as 566 $\pm$ 181 g dry weight m^{-2} using the equation developed by Williams and Murdoch (1969) for marshes in the Beaufort area.

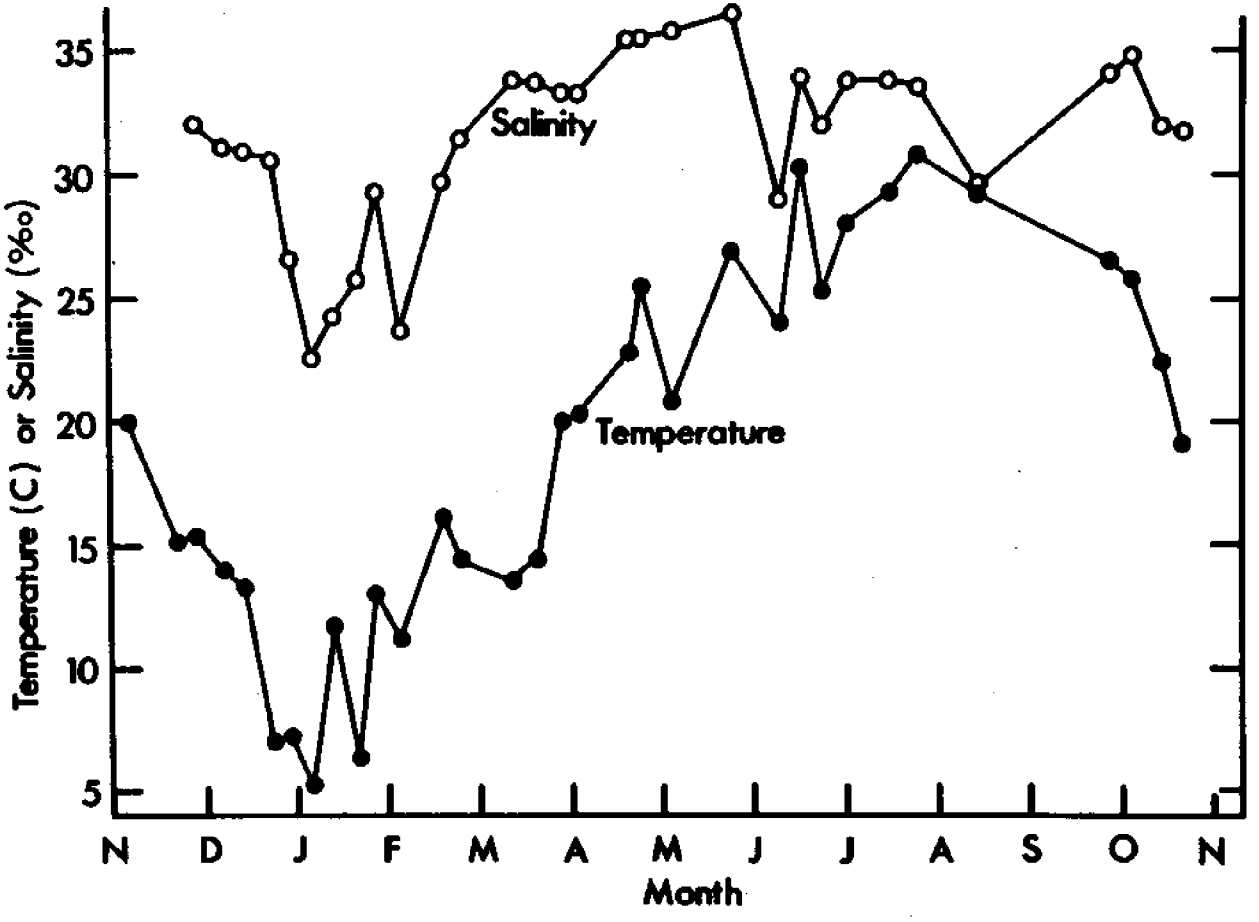

Figure 1. Temperature and salinity of water in the marsh embayment.

Sediment was mainly medium to fine sand with an organic matter content of 4-12% (Table 1).

Methods and Materials

Production

The standing stock of N. succinea was measured at approximately monthly intervals between August 1975 and August 1976. Random samples were taken within the study area with a can corer (173 cm^2, 20 cm deep). Fifteen cores were taken the first month and 12 the second, but due to the excessive time required for processing, six cores were taken each month for the remainder of the study.

Cores were returned to the laboratory and processed according to Frey et al. (1973). A 0.8 x 0.6 mm mesh was used to retain the animals along with macro-detritus and root matter. The animals were stained with rose bengal and removed by hand. The width of the peristomium (the segment immediately behind the head) was measured to 0.05 mm for each individual of N. succinea and then the worms were dried at 55 C for 4 days, weighed to the nearest microgram, ashed at 500 C, and reweighed to give ash-free dry weight (AFDW). Since the worms fragmented readily during sieving, heads were counted to give the number of individuals per core. The relation between peristomial width (PW) and AFDW was determined by geometric mean (GM) regression (Ricker, 1973) on a total of 70 measurements of intact worms taken throughout the year. Twelve worms were dried, ground, and analyzed for carbon content using an F and M Model 185 CHN analyzer.

Annual production was calculated following the methods in Crisp (1971). Monthly PW-frequency distributions were graphed and cohorts were separated using probability paper (Harding, 1949; Cassie, 1954).

Table 1. Sediment data from cores taken near the north end (I), middle (II), and south end (III) of the study area. Organic matter was determined by loss of weight during ignition.

Station	Depth (cm)	% Granules	% Very coarse	% Coarse	% Medium	% Fine	% Very fine	% Silt-clay	% Organic matter	Dry wt cm^{-3}
I	0-2	0.1	0.1	13.8	21.9	39.2	9.4	15.6	6.84	0.56
	2-4	0.1	0.3	12.1	23.1	38.4	10.4	15.4	5.36	0.57
	4-6	0.0	0.1	12.2	24.2	41.7	10.5	10.5	7.39	0.52
II	0-2	0.0	0.1	13.5	27.0	36.6	10.7	12.2	7.31	0.59
	2-4	0.0	0.1	15.3	28.7	35.1	9.6	11.1	7.20	0.64
	4-6	0.0	0.3	12.2	26.8	38.1	11.1	11.4	4.63	0.72
III	0-2	0.1	0.5	15.0	16.4	37.2	13.8	17.0	6.81	0.59
	2-4	--	--	--	--	--	--	--	7.27	0.66
	4-6	0.0	0.3	13.1	15.1	46.4	11.4	13.8	7.84	0.66

Production of each cohort between successive samples was calculated as $\bar{N} \cdot \Delta w$, where $\bar{N}$ was the mean number of individuals sample^{-1} and Δw was the change in mean individual weight between samples. Production of cohorts prior to settlement was taken as the standing stock of the first month the cohorts appeared in the samples. Production was calculated on both the raw cohort data and data derived from smoothed mortality and growth curves.

Respiration

N. succinea were collected from the marsh when the ambient water temperature was approximately 33 C. Individuals were placed into covered plastic petri dishes (8.5 cm diameter) along with fresh marsh sediment and sea water to a depth of 1 cm. The animals were allowed to acclimatize for 1-2 days for the 30 C experiment, 10 days for the 20 C experiment, and 15 days for the 10 C experiment.

All respiration experiments were carried out with a Gilson Differential Respirometer. Since measurements were taken simultaneously for O_2 consumption and release of dissolved organic carbon (DOC) (see next section), Gulf Stream surface water was used for all experiments to take advantage of its low DOC content. At the time these experiments were carried out, the salinity of the water flooding the marsh was 36 $^{o}/_{oo}$, essentially the same as that of the Gulf Stream water. In order to test for an effect due to the use of the Gulf Stream water, two experiments were carried out at 30 C using the same animals, one with estuarine water filtered through a 0.2 µm pore size membrane filter and one the following day with Gulf Stream water.

Prior to the start of each experiment the worms were placed in petri dishes with the appropriate water at the experimental temperature

and allowed to clear their guts for 4-6 hours. Feces were rarely voided after this time. The worms were then rinsed twice and placed in 20-ml respiration flasks with 3 ml of water. After the flasks were sealed, the animals were given 1.5 hours to acclimatize at 30 C, 2.25 hours at 20 C, and 3 hours at 10 C. Readings were taken over 2.25 hours at 30 C and 1.5 hours at 20 and 10 C.

The flasks were not shaken during the experiments since shaking tossed the worms from side to side in the vials. In order to measure the difference between shaken and non-shaken rates of O_2 consumption, the run at 30 C in estuarine water was extended for 45 min while the flasks were shaken.

Respiration data were converted from microliters O_2 consumed to micrograms C released as CO_2. Gardner (1972) gave respiratory quotients (RQ: CO_2 evolved/O_2 consumed) of 1 for carbohydrates, 0.71 for fats, and 0.93 for proteins and amino acids (if the nitrogen is metabolized to ammonia). Since N. succinea feeds on detritus and associated microbiota rich in carbohydrates and protein, I assumed an RQ of 0.9. Using this value the conversion was

1 µl O_2 consumed (STP) ≡ 0.482 µg C released.

DOC Release

DOC release was measured at the same time as respiration at 10, 20, and 30 C. At the end of each respiration experiment the water was taken from each flask, pipetted into a test tube with 0.25 ml of 10% phosphoric acid and bubbled for 5 min with nitrogen to remove any inorganic carbon. Replicate 1.0 or 1.5 ml aliquots were then sealed in ampoules with 0.1 g $K_2S_2O_8$. The ampoules were autoclaved to oxidize the organic

carbon (Menzel and Vaccaro, 1964) which was then measured with a CMA Model FT-1 Carbon Micro-Analyzer. Blank flasks which contained sea water but no worms were included in all experiments.

Some organic carbon might have been present on the surface of the worms at the beginning of each run and might have contaminated the water. As a control, a separate group of eight large worms were allowed to clear their guts, rinsed twice in Gulf Stream water (as for the respiration experiments), placed in the respiration flasks with 3 ml Gulf Stream water and immediately removed. Water samples were taken from these flasks and analyzed for organic carbon as above.

Ingestion

Ingestion rate was determined using fluorescent pigment as a tracer in marsh sediment. Experiments were carried out at 7.0, 10.5, 14.4, 19.5, 28.0, and 28.5 C. The fluorescent pigment was mixed into the water overlying the sediment; some of the pigment settled onto the sediment surface while some remained in suspension. The worms were allowed to feed for 0.5 to 1.5 hours and then killed and examined under fluorescent light to determine the amount of sediment ingested after the pigment was introduced. This sediment was removed from the worms and weighed. Complete details of the method were given in Section I.

Ingestion was calculated from ingestion rates and size-frequency data of the N. succinea population and temperatures of the water flooding the marsh. First, a multiple regression was calculated from the combined data relating ingestion rate of N. succinea to body size and temperature. Based on the peristomial width, the worms were then divided into 22 size classes each with a range of 0.2 mm. Population data for each size class were plotted over the year for the 12 samples

and daily numbers in each class were calculated by linear interpolation between sampling dates. Water temperature data were treated similarly with linear interpolation between sampling dates to give daily values. Ingestion was calculated each day for each size class and summed over all size classes to give total daily ingestion; these values were then summed to give total annual ingestion for the population.

Assimilation Efficiency

Experiments were designed to estimate assimilation efficiency of N. succinea for both the detritus and its associated microbiota. Spartina alterniflora grown in the laboratory or harvested from the field was used as the source of detritus.

Carbon-14-labeled Spartina was grown in the laboratory using the growth chamber described by Ferguson and Williams (1974). $Ba^{14}CO_3$ with a specific activity of 0.8-1.3 mCi $(gC)^{-1}$ was introduced into the chamber. A $^{14}CO_2$ atmosphere was created by addition of HCl. At first, plants were brought in from the field, leaves were removed and Miquel's solution as modified by Rice (1953) was added to provide nutrients (Ferguson and Williams, 1974). Later, intact cores were brought in from the field, the plants were cut off at the surface to force new growth, and a modified Hoagland's solution was used to provide nutrients. The latter method provided better growth.

Three types of experiments were run to determine the assimilation efficiency of N. succinea for the various components of the detrital system. First, assimilation of water-extracted Spartina and assimilation of the microbiota associated with detritus were estimated in separate experiments by double-labeling the Spartina or microbes with ^{14}C and ^{51}Cr and feeding to the worms; the ^{51}Cr acted as an unassimilated

tracer. Second, assimilation of detrital plant material by N. succinea was examined qualitatively by extracting the readily available components from ^{14}C-labeled Spartina, feeding the remaining material to the worms, and then monitoring respired $^{14}CO_2$. Third, assimilation of bacteria by the worms was estimated by following bacterial numbers through the gut of several worms with the use of direct counting techniques.

Digestion of Water-Extracted Spartina and Detritus Microbiota (^{14}C and ^{51}Cr). Assimilation efficiencies for the water-extracted Spartina and for the microbial component of the detritus system were estimated using the ^{51}Cr-^{14}C double-labeling technique of Calow and Fletcher (1972) as modified by Wightman (1975); an error in that modification has been corrected (Cammen, 1977).

Assimilation of Spartina by N. succinea was measured using ^{14}C-labeled Spartina. The labeled Spartina was freeze-dried, ground with a Wiley mill so the fragments passed a 0.37 x 0.33 mm mesh, sterilized with ethylene oxide gas, leached in autoclaved sea water for 15 days, and then rinsed thoroughly with filtered sea water; all sea water referred to as "filtered sea water" was filtered through a 0.2 μm pore size membrane filter. The Spartina was incubated with ^{51}Cr for 2 hours with filtered sea water; since the ^{51}Cr was added as $^{51}CrCl_3$ in 0.5 N HCl, NaOH was added simultaneously to prevent a pH shift. After the incubation was completed, the Spartina was rinsed several times with filtered sea water to remove excess ^{14}C and ^{51}Cr.

The feeding experiments were carried out in the laboratory at 25 C in the dark with individual sterile petri dishes for each worm. Each dish contained 1 g dried autoclaved marsh sediment and 0.2 g Spartina. The worms fed for 3 hours, food samples (Spartina-sediment mixture) and

feces were collected for each worm, the worms fed for 12 hours more, and food samples and feces were again collected. Feces were collected in 30 ml of filtered sea water; after they were collected, 4 ml of water were taken in order to measure $DO^{14}C$.

Feces and food samples were placed separately in scintillation vials with 1 ml NCS solubilizer (New England Nuclear) and digested for 30 min in an ultrasonic bath (Tompkins et al., 1968). Four drops of glacial acetic acid were then added and the vials were replaced in the bath for an additional 30 sec. Each vial was counted for gamma emissions using a 128-channel Nuclear Data counting system. A scintillation cocktail of 11 ml Aquasol-2 (New England Nuclear) and 4.5 ml distilled water was then added to each vial and shaken; this produced a gel which suspended all undigested material. These vials were left for 5 days to equilibrate and were then counted with a Beckman LS-200B liquid scintillation system. Water samples were not digested but were otherwise treated identically to the feces and food.

Quench curves for ^{14}C and ^{51}Cr were determined for the scintillation counter using digested Spartina as a quenching agent; counting efficiency for the gamma counter was also measured. The overall procedure was to use the gamma counter to determine the ^{51}Cr DPM, calculate the ^{51}Cr CPM that would result on the scintillation counter, determine the ^{14}C CPM by subtraction, and convert to ^{14}C DPM with the quench curve. DPM were used for all subsequent calculations.

The ^{51}Cr:^{14}C ratios from the food dishes were averaged to give a single food ratio. The ^{14}C DPM released as DOC were added to the ^{14}C DPM in the feces and the ^{51}Cr:^{14}C ratio was then calculated; this allowed estimation of actual assimilation, not just digestion or loss

from the Spartina. These ratios were also averaged to give a single feces ratio. The food and feces ratios were then substituted in the following expression to give assimilation efficiency (AE) (Cammen, 1977):

$$AE = 100 \times \{1 - [(^{51}Cr \text{ DPM}:^{14}C \text{ DPM food})/(^{51}Cr \text{ DPM}:^{14}C \text{ DPM feces})]\}.$$

Assimilation of the microbial component of the detritus system was estimated by the use of both sterile and non-sterile detritus as food sources for N. succinea. Artificial detritus was produced from Spartina harvested from the field in late September by air drying and grinding with a Wiley mill so the fragments passed a 0.37 x 0.33 mm mesh. One portion of the ground Spartina was sterilized with ethylene oxide or by autoclaving. The remaining portion was incubated for 3 days with microbes; these were obtained by mixing decaying Spartina leaves collected from the field with sea water in a high speed blender and letting the particulate matter settle out. Both the sterile detritus and the non-sterile detritus were then incubated for 24 hours with sterile ^{14}C-labeled leachate prepared from ground ^{14}C-labeled Spartina which was added to filtered sea water, left for 2-3 days, and autoclaved. Chromium-51 was added to the incubating detritus after 22 hours for the first experiment and along with the leachate for the second experiment. After the incubations were completed, the detritus was rinsed several times with filtered sea water. Each petri dish contained 0.4 g wet weight detritus mixed with 2 g dried autoclaved marsh sediment for the first experiment and 0.2 g detritus mixed with 2 g wet autoclaved marsh sediment for the second experiment. For the first experiment the worms fed for 6 hours, food samples and feces were collected, the worms fed for 12 hours more, and food samples and feces were again collected. For the second experiment, the worms fed for 12 hours and then food samples

and feces were collected. Subsequent treatment of the samples and data analysis were the same as above.

Since the success of the ^{51}Cr-^{14}C method depends on the ^{51}Cr passing through the animal without being assimilated, two experiments were devised to measure ^{51}Cr assimilation. In the long-term experiment worms fed on sediment with ^{51}Cr-labeled detritus for periods of 6, 12, or 24 hours. The worms were then allowed to clear their guts and the ^{51}Cr was measured in the feces. The worms were rinsed in 10% HCl to remove adsorbed ^{51}Cr and then counted in the gamma counter. Using turnover times for gut contents derived from Section I, the total amount of ^{51}Cr potentially available for assimilation was estimated and assimilation efficiencies were calculated. For the short-term experiment the worms fed on sediment that had been mixed with $^{51}CrCl_3$ and then allowed to settle. The worms were allowed to feed for only 1 hour and then placed in filtered sea water to clear their guts; since this time interval was less than the turnover time for the gut contents, no feces were lost. Since production of feces was low, the worms were allowed to feed for an additional 2 hours and feces were again collected. The worms were rinsed in 10% HCl and then counted for ^{51}Cr along with the feces. Assimilation efficiency was calculated as

body burden/(feces burden + body burden).

Only those worms where the feces CPM were at least twice background were considered in the analysis.

Refractory Detrital Assimilation (^{14}C). The refractory portion of detritus was simulated by extraction of the more labile compounds from ^{14}C-labeled Spartina following Wetzel (1975). Ground-labeled Spartina

was first added to a 1:1 (by volume) mixture of chloroform and methanol and left for 1 hour in a refrigerator. Following filtration, the remaining material was then placed in 1 N NaOH in a boiling water bath for 30 min. The extracted Spartina was rinsed with filtered (0.2 μm pore size) distilled water and acidified briefly by addition of CO_2. The chloroform-methanol extraction removes the lipids and the NaOH extraction removes water-soluble compounds, amino acids, proteins, and nucleic acids (Holland and Gabbott, 1971); the remaining material is largely cellulose and lignin.

Four groups of worms were used in this experiment. The first group fed on the extracted Spartina, the second group fed on labeled Spartina that had been leached in distilled water for 18 hours but not extracted, and the third and fourth groups were controls with the extracted and nonextracted Spartina. The heads were removed from the worms in the control groups to prevent feeding; any uptake would have been due to uptake of $DO^{14}C$ through the integument of the worms or by the microflora growing on the worms.

This experiment was run twice with varied design. Each dish contained 0.2 g wet weight of either extracted or nonextracted Spartina mixed with 1 g dried autoclaved marsh sediment for experiment I, and 0.1 g of Spartina mixed with 2 g of wet autoclaved marsh sediment for experiment II. The worms were alternately allowed to feed and to clear their guts in filtered sea water. Experiment I had three periods of feeding--31.5, 9.5, and 24 hours; fecal production was not adequate for the analysis until after the final feeding period. The worms were given 10.5 hours to clear their guts after the final feeding period and then placed in unlabeled sediment for 13.5 hours. Experiment II had two

feeding periods, 6 and 11 hours; the worms were then given 4 hours to clear their guts. After the worms had cleared their guts of labeled material, they were placed into individual 50-ml flasks with 25 ml filtered sea water for collection of respired $^{14}CO_2$ (Hobbie and Crawford, 1969). Strips of filter paper were folded and placed in small plastic cups suspended in the flasks when the worms were introduced. The worms remained in the flasks for 24 and 12 hours for experiments I and II, respectively. The experiments were terminated by injecting H_2SO_4 into the water to kill the worms and to remove any $^{14}CO_2$ from solution and then injecting phenethylamine on to the filter papers to adsorb the respired $^{14}CO_2$. The filters with the adsorbed $^{14}CO_2$ were counted in a toluene-PPO-POPOP scintillation cocktail; counts were corrected for background but not for quench since only relative comparisons were to be made and quench was virtually identical for all samples. Feces were collected for both runs, digested, and counted as in the previous section.

Since the respired CPM were a function of worm size, all worms were weighed after drying at 55 C and the weights were used to convert to respiration for a "standard worm" with a peristomial width of 3.3 mm and a weight of 19.0 mg. All respiration rates (CPM) were multiplied by

$$19.0^{0.730} \times w_E^{-0.730}$$

where w_E was the weight of the worm and 0.730 was the exponent relating body weight to respiration for N. succinea (see Results--Respiration).

Digestion of Bacteria (Direct Counting). Eight N. succinea were collected from the study area and nearby marsh at low tide, placed in 10% formalin-sea water, and brought back to the laboratory where they

were kept refrigerated. Within 24 hours they were cut into 7 to 10 sections depending upon the size of the worm. Gut contents were removed from each section, mixed with a micro-blender, and a portion counted for bacteria using acridine orange direct counting (Daley and Hobbie, 1975; Hobbie et al., 1977; Rublee, in preparation). The remaining gut contents were dried at 90 C and weighed.

Results

Production

Nereis succinea was most abundant in early spring (Figure 2). Both biomass and number of individuals followed similar patterns with minimum values in December (0.9 g AFDW, 616 individuals m^{-2}) and maximum values in February (3.6 g AFDW, 1375 individuals m^{-2}). Mean biomass for the year was 2.1 g AFDW m^{-2}.

Peristomial width (PW) in millimeters was related to AFDW in micrograms by

$$\log \text{AFDW} = 2.842 + 2.769 \cdot \log \text{PW} \qquad (r^2 = 0.97,\ N = 70)$$

and the AFDW of N. succinea was found to be 50.72 $\pm$ 0.33% carbon. These relations were used to convert PW to grams carbon for the production calculation.

Three major periods of recruitment were identified from the PW-frequency data (Figure 3), two in the spring (SP1 and SP2) and one in the fall (F). Each of these recruitments gave rise to a cohort of worms which could be identified for three year-classes, the 0+, 1+, and 2+. Using the three year-classes, hypothetical life histories (mortality and growth curves) were constructed for each cohort (Figure 4).

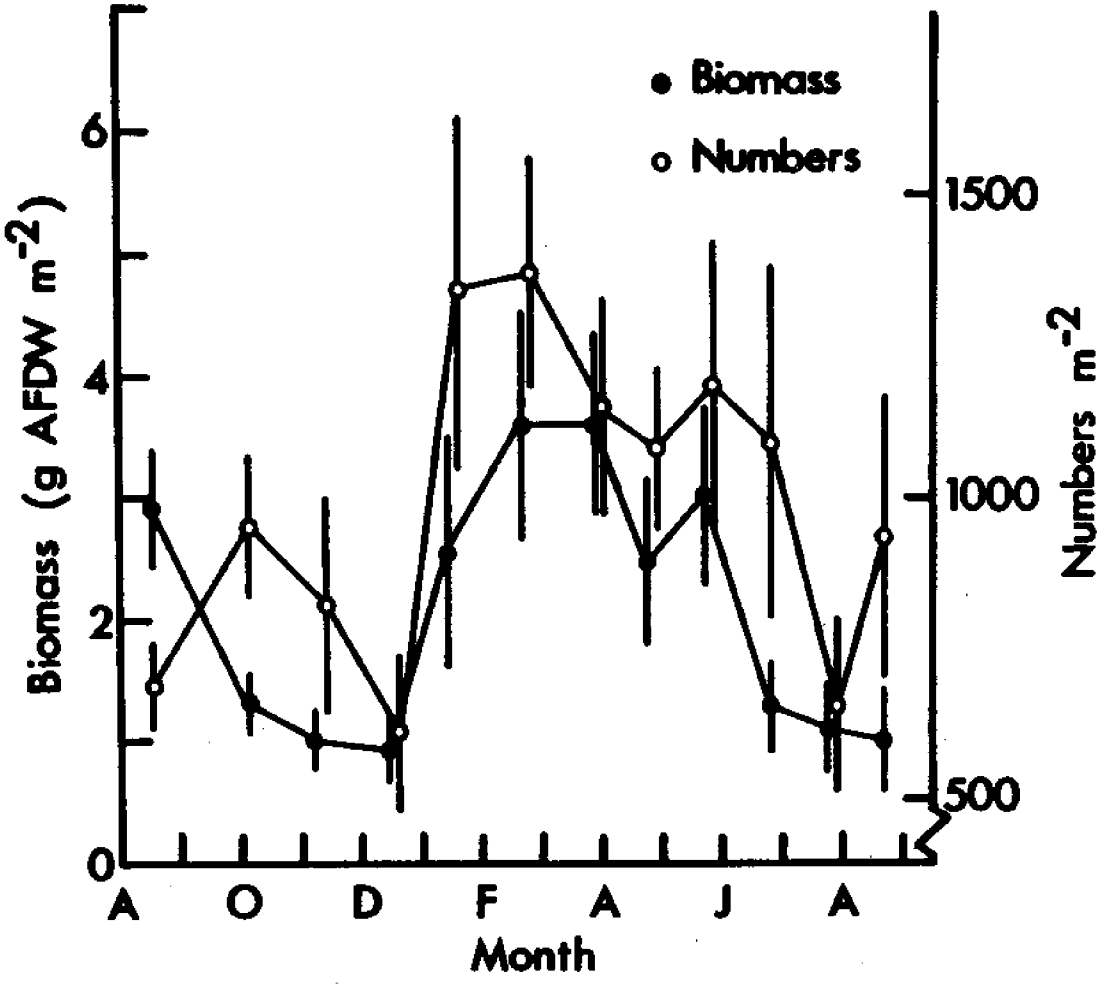

Figure 2. Population numbers and biomass of N. succinea in the study area.

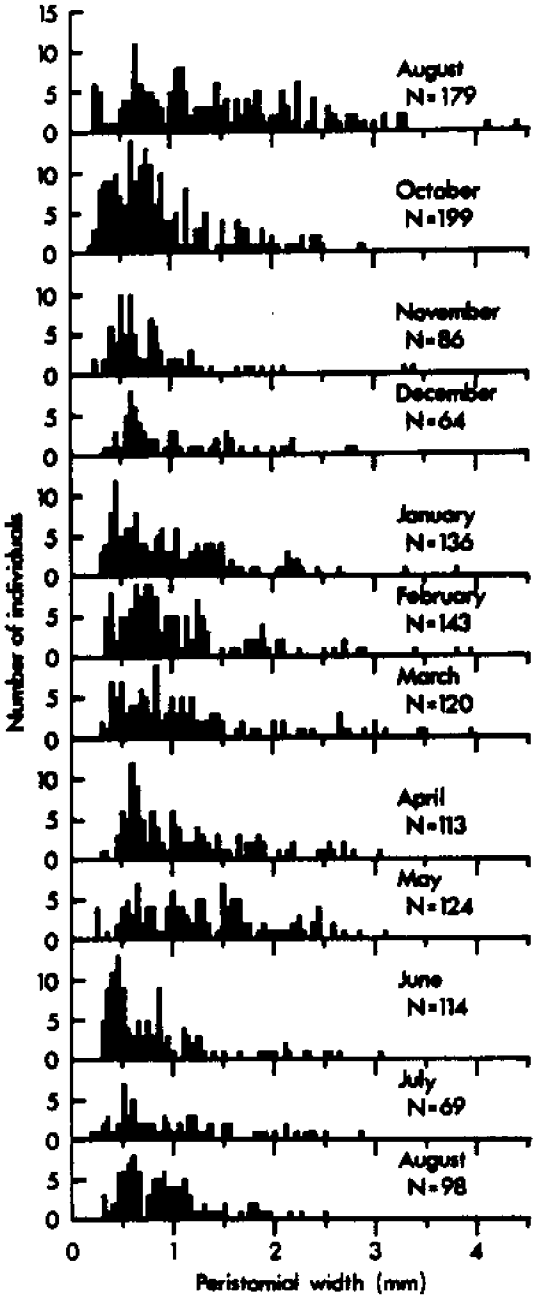

Figure 3. Peristomial width-frequency diagrams for the monthly samples of N. succinea from the study area. N is the total number of individuals collected each month.

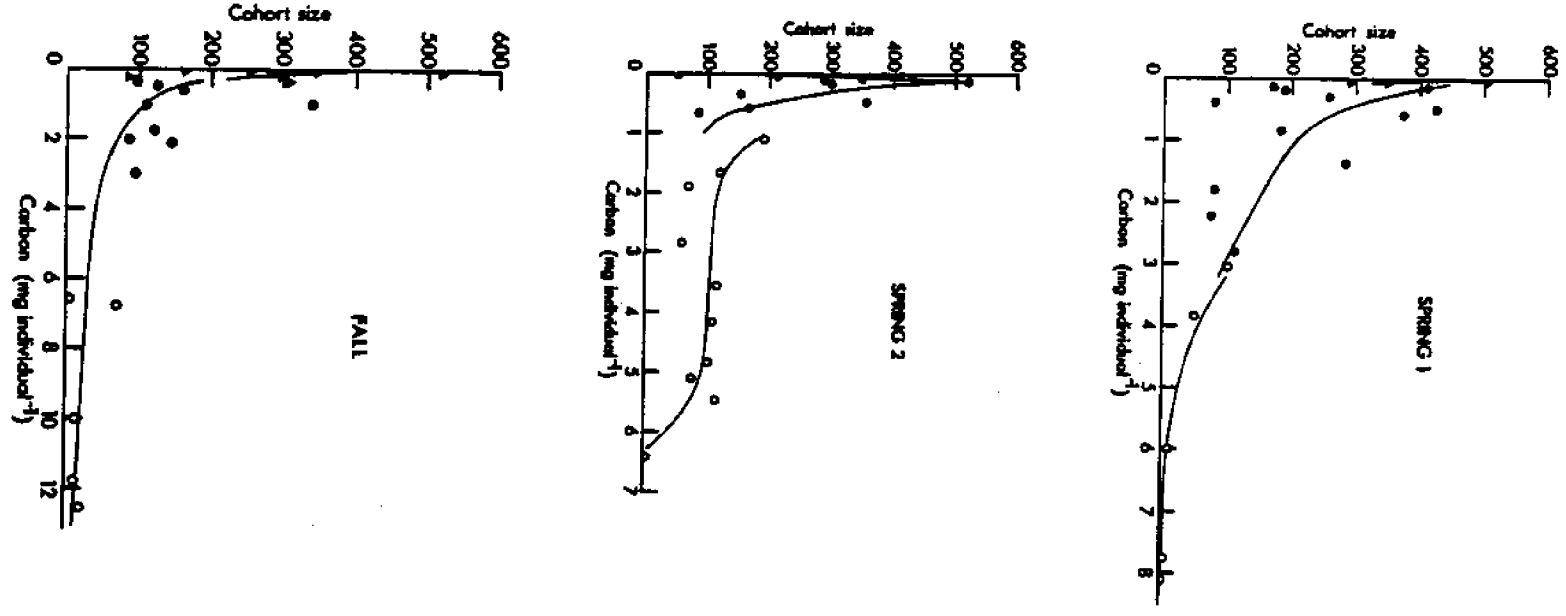

Figure 4. Allen curve of N. succinea cohorts. Two year-classes were present when sampling began (○ and ●); a third class (▲) was recruited during the sampling period for the Spring 1 and Fall cohorts.

Production estimates were identical for both the raw and the smooth data. Using the cohorts established from the PW-frequency distributions (Figure 3) with no attempt to smooth the life history curves (Figure 4), annual production was calculated as 2.1 g (Table 2); using smoothed life history curves (Figure 4) annual production was also 2.1 g (Table 2). Total production over the life span of each cohort was similar for both calculations with the spring cohorts producing about 20% more than the fall cohort (Table 2); production was virtually identical for the two spring cohorts. Monthly production figures varied between the two calculations (Table 3) and neither calculation could account for the sudden increase in biomass between December and February (Figure 2).

Respiration

Respiration increased with both size of the worms and temperature (Figure 5). Equations for each of the least squares regression lines were:

$$10\ C\ (GS)\ \log R = -2.963 + 0.773 \cdot \log W \qquad (r^2 = 0.91,\ N = 15)$$

$$20\ C\ (GS)\ \log R = -2.569 + 0.760 \cdot \log W \qquad (r^2 = 0.93,\ N = 14)$$

$$30\ C\ (GS)\ \log R = -1.838 + 0.648 \cdot \log W \qquad (r^2 = 0.94,\ N = 14)$$

$$30\ C\ (EST)\ \log R = -1.694 + 0.637 \cdot \log W \qquad (r^2 = 0.89,\ N = 15)$$

where R is µg carbon released hr^{-1} as CO_2, W is µg dry body weight, GS is unfiltered Gulf Stream water, and EST is 0.2 µm filtered estuarine water. Analysis of covariance showed no significant difference in respiration at 30 C when measured in Gulf Stream and estuarine water ($F = 0.018$, $P < 0.99$). Shaking increased the measured rate of O_2 consumption in 12 of the 15 animals tested; the mean change was an increase of 13.6%.

Table 2. Annual production of N. succinea estimated from both raw and smoothed population data for two spring and one fall cohorts.

Cohort	Annual production ($g\ C\ m^{-2}$)	
	Raw	Smoothed
Sp 1	0.73	0.75
Sp 2	0.73	0.76
F	0.62	0.61
Total	2.08	2.12

Table 3. Estimated monthly production of N. succinea.

Month	Production ($g\ C\ m^{-2}$)	
	Raw	Smoothed
August	0.18	0.19
September[a]	--	0.17
October	0.14	0.17
November	0.18	0.16
December	0.09	0.17
January	0.35	0.15
February	0.24	0.13
March	0.14	0.18
April	0.28	0.23
May	0.34	0.23
June	0.09	0.18
July	0.05	0.17

[a]No sample was taken in September.

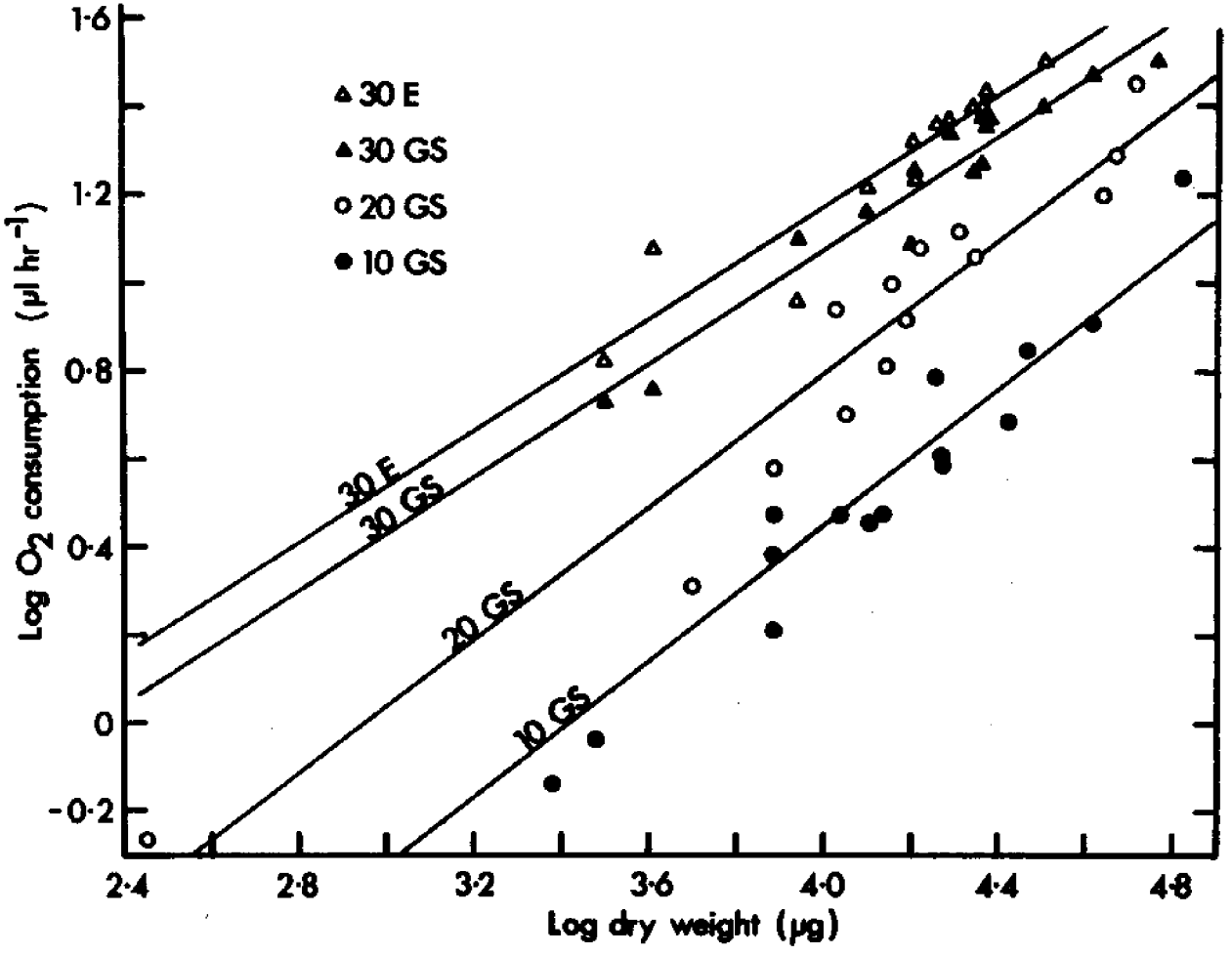

Figure 5. Respiration data for N. succinea. Data were taken at 10, 20, and 30 C in Gulf Stream water (GS) and 30 C in 0.2 µm-filtered estuarine water (E). Regression lines are shown for each temperature.

A multiple regression equation was developed using the data from all four runs:

$$\log R = -4.178 + 0.730 \cdot \log W + 1.373 \cdot \log T \qquad (R^2 = 0.94,\ N = 58)$$

where R is µg carbon released hr^{-1} as CO_2, W is µg dry body weight, and T is temperature in C. The interaction between log W and log T was not significant ($F = 1.45$, $P < 0.23$).

DOC Release

There was no significant release of DOC when N. succinea were first placed into the flasks. The blank flasks contained 7.80 ± 3.42 µg C and the flasks with worms added contained 8.20 ± 3.66 µg C.

During the respiration experiments there was no significant uptake or release of DOC by N. succinea. Since no relation was found with animal weight (Figure 6), mean release (positive values) or uptake (negative values) was calculated for each temperature (µg C hr^{-1} $animal^{-1}$): -0.23 ± 0.59 at 10 C; 0.24 ± 1.19 at 20 C; and -0.07 ± 0.87 at 30 C; the differences between temperatures were not significant. The overall mean for the three temperatures was an uptake of 0.02 ± 0.92 µg C hr^{-1} $animal^{-1}$, but this value was not significantly different from zero. Therefore, release of DOC was considered to be zero in the carbon budget below.

Ingestion

The relation between ingestion (I) in µg dry weight hr^{-1}, peristomial width (PW) in mm, and temperature (T) in C was:

$$\log I = 0.815 + 2.216 \cdot \log PW + 1.274 \cdot \log T \qquad (R^2 = 0.81,\ N = 43)$$

(Section I).

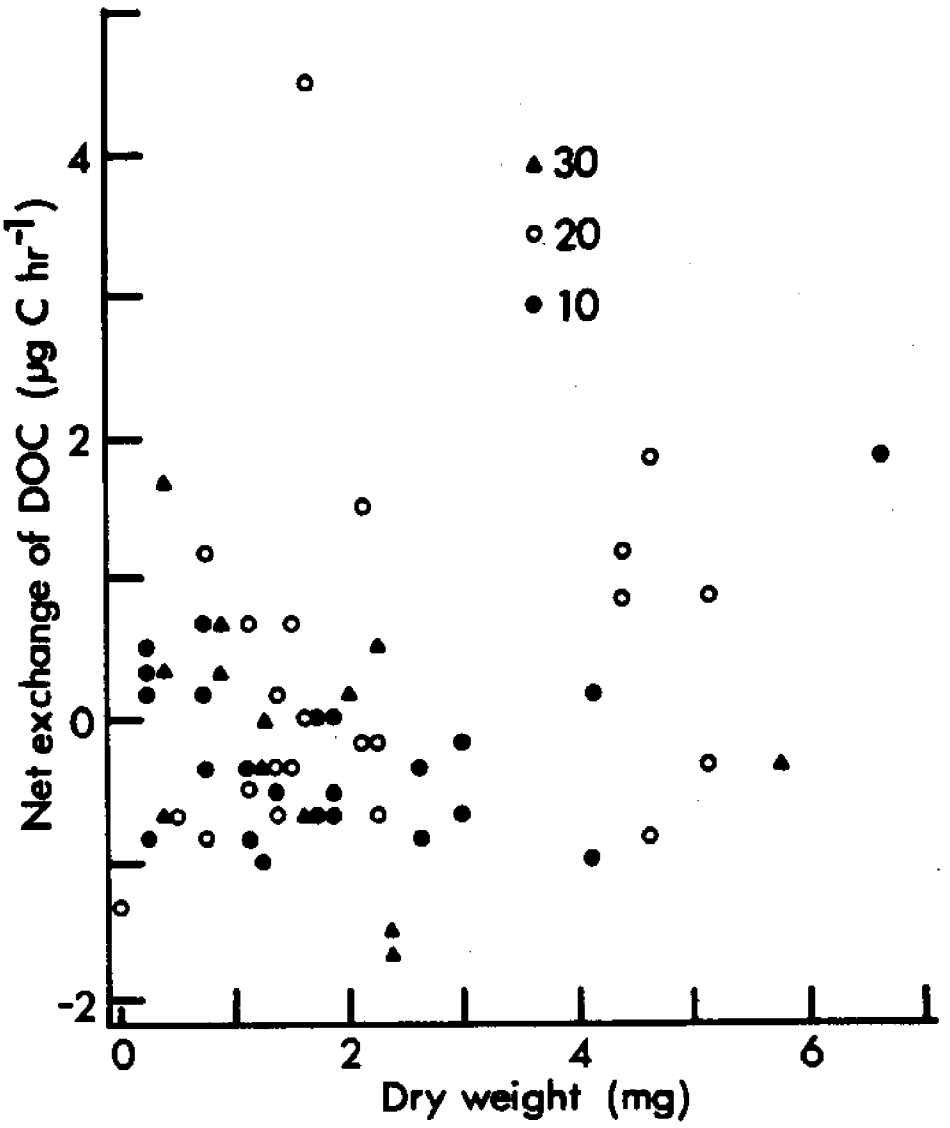

Figure 6. Net exchange of DOC by N. succinea. Data were taken at 10, 20, and 30 C. Positive values represent release of DOC and negative values represent uptake.

Assimilation Efficiency

Digestion of Water-Extracted Spartina and Detritus Microbiota (^{14}C and ^{51}Cr).

N. succinea took up about 7% of the ^{51}Cr as it passed through the gut. The long-term uptake experiment gave a mean uptake of 4.3% (±1.3%) for six worms while the short-term experiment gave a mean uptake of 6.7% (±2.2%) for seven worms. The long-term experiment was considered less reliable than the short-term experiment since it required the assumption that the worms fed at a natural rate on sediment which had been dried and ground; any decrease in feeding rate would have given an apparent assimilation efficiency lower than the actual value. For this reason I assumed a 7% uptake of the ^{51}Cr when correcting the detrital digestion data.

N. succinea digested an average of 57% of the labeled microbial biomass during the two feeding experiments (Table 4). During the 21 hours of experiment I only 12% of the ^{14}C was lost relative to the ^{51}Cr (Table 5) indicating that most of the ^{14}C in the microbial tissue was incorporated into a fairly stable pool of organic compounds; leaching of ^{51}Cr was negligible in sea water. Digestion efficiency of the labeled microbial biomass did not change throughout experiment I (Table 4). Digestion efficiencies for the nonsterile detritus actually were measurements of a combination of digestion of microbes and digestion of $DO^{14}C$ adsorbed to the particles. However, digestion efficiencies of those two components must have been similar since the digestion efficiencies for the sterile and nonsterile detritus were similar (Table 4); therefore, no correction was necessary to estimate the digestion efficiency of the microbes alone.

Table 4. Assimilation of microbial carbon from *Spartina* detritus by *N. succinea*. Assimilation efficiency (AE) was corrected for 7% uptake of ^{51}Cr by *N. succinea* (see text for explanation).

Experiment	Time	Type of food	N	$^{51}Cr:^{14}C$ ratio in food	$^{51}Cr:^{14}C$ ratio in feces	AE (%)
I	6 hr	With microbes	3	0.957±0.019[a]	1.918±0.057	53.6
	21 hr	With microbes	5	1.074±0.026	2.186±0.084	54.3
II	12 hr	With microbes	9	5.886±0.223	15.077±2.183	63.7
	12 hr	Sterile	6	6.853±0.132	15.625±2.317	59.2

[a]Mean ±SE.

Table 5. Relative loss of ^{14}C from the double-labeled detritus during the assimilation efficiency experiment.

Time (hr)	$^{51}Cr:^{14}C$ ratio	Cumulative % loss
0	0.945±0.022[a]	--
6	0.957±0.019	1.3
21	1.074±0.026	12.0

[a]Mean ±SE.

The ground labeled Spartina was readily digested by the worms (Table 6). About 22% of the label was lost as the Spartina passed through the worms. Over half this amount was released as DOC, however, yielding a net assimilation of 10.5%. Digestion efficiency remained the same throughout the experiment.

Refractory Detrital Assimilation (^{14}C). Nereis succinea was able to assimilate carbon from the extracted Spartina. The net respired CO_2 (CPM of experimental mean - CPM of control mean) of the worms feeding on extracted Spartina was significantly greater than zero for both runs (Table 7) (one-tailed t-test; experiment I--$P < 0.002$, experiment II--$P < 0.040$); in addition, the net body burden of those worms at the end of experiment I was significantly greater than zero (one-tailed t-test; experiment I--$P < 0.007$). The worms feeding on the nonextracted Spartina also showed significant net respiration of $^{14}CO_2$ for both experiments (one-tailed t-test; experiment I--$P < 0.038$, experiment II--$P < 0.001$) and had a mean body burden significantly greater than zero in experiment I (one-tailed t-test; $P < 0.032$).

The animals appeared to utilize the carbon from the nonextracted Spartina more efficiently than the carbon from the extracted Spartina in experiment I. Since the amount of carbon utilized for growth compared to the amount lost through respiration is a measure of efficiency, I calculated the ratio of CPM ^{14}C respired to DPM ^{14}C retained (body burden) to measure this efficiency; in this case the greater the ratio, the lower the efficiency. Worms feeding on extracted Spartina had significantly higher ratios (t-test; $P < 0.013$) and thus lower efficiencies than those animals feeding on the nonextracted Spartina. In addition, this difference may have extended to the

Table 6. Assimilation of carbon from ^{14}C-labeled ground Spartina by N. succinea. Assimilation efficiency (AE) was calculated both with and without correcting for release of DOC.

Time (hr)	N	$^{51}Cr:^{14}C$ ratio in food	$^{51}Cr:^{14}C$ ratio in feces	$^{51}Cr:^{14}C$ ratio in feces corrected for DOC release	AE (%)	Corrected AE (%)
3	3	0.317±0.020[a]	0.381±0.009	--	22.6	--
12	10	0.310±0.043	0.367±0.013	0.322±0.012	21.4	10.5

[a]Mean ±SE.

Table 7. Assimilation of carbon from extracted ^{14}C-labeled Spartina by N. succinea. Respired CPM were corrected to those of a standard weight worm of 19.0 mg. Body burden was not measured for experiment II.

Experiment	Group	N	Standardized CPM respired	Mean	Net CPM respired	Body burden DPM (mg dry wt)$^{-1}$	Mean	Net body burden DPM (mg dry wt)$^{-1}$	Respired (CPM)/ Body burden (DPM)	Mean
I	Extracted	4	384			195			1.97	
			299	402[a]	347	232	282	245	1.29	1.49
			437	±80	±80	292	±94	±95	1.50	±0.35
			486			409			1.19	
	Control	2	55	55		46	37		1.20	1.55
			55	±0		29	±12		1.90	±0.49
	Nonextracted	4	2544			3244			0.78	
			5656	3390	3128	5382	4091	3701	1.05	0.77
			4877	±2347	±2351	6822	±2578	±2585	0.71	±0.22
			481			914			0.53	
	Control	2	361	262		522	390		0.69	0.66
			162	±141		257	±188		0.63	±0.04
II	Extracted	7		258	164					
				±207	±207					
	Control	2		94						
				±0						
	Nonextracted	7		273	218					
				±117	±118					
	Control	3		55						
				±13						

[a]Mean ±SD.

control animals but there were too few animals in each group to show a significant difference (t-test; $P < 0.125$). Net respiration of $^{14}CO_2$ was greater in the group feeding on nonextracted Spartina (one-tailed t-test; $P < 0.050$) than in the group feeding on extracted Spartina; net body burden (mg dry weight)$^{-1}$ was also significantly greater (one-tailed t-test; $P < 0.038$). There was no significant difference in net CPM respired for the two groups in experiment II.

Digestion of Bacteria (Direct Counting). About 62% of the bacteria entering the gut of N. succinea were digested on the way through the gut (Table 8). It was not possible to tell if bacterial numbers were increasing in the hind gut; animals examined in February and August showed a highly significant increase in bacterial numbers in the hind gut ($P < 0.01$), while those examined in March and May showed no such increase. The mean of the gross digestion, 1 - (minimum count/maximum count), for all worms was 62.3% (±10.8%). The mean of the net digestion, 1 - (final count/maximum count), was 39.9% (±35.5%). Excluding the last worm examined, which gave a negative net digestion, the mean net digestion was 51.8% (±12.2%). The mean bacterial count of the newly ingested material for the five worms taken from within the study area (the second from February and both from March and August) was 2.17 (±0.58) x 10^{10} (g dry weight of gut contents)$^{-1}$.

Carbon Budget

A carbon budget was calculated for N. succinea using the field population estimates and the laboratory and field measurements of carbon flow. The worms were divided into 22 size classes and daily standing stock was estimated for each by linear interpolation between

Table 8. Direct counts of bacteria in the guts of N. succinea. Counts are reported as numbers per g dry weight of gut contents.

Collected	Bacterial nos. (x 10^{10}) (g dry wt)$^{-1}$			% Gross digestion	% Net digestion
	Maximum	Minimum	Final		
February	7.58±2.02[a]	2.40±0.92	3.90±1.54	68.3	48.5
February	2.72±0.90	0.79±0.27	1.28±0.70	71.0	52.9
March	2.44±0.64	0.99±0.51	0.99±0.51	59.4	59.4
March	1.52±0.50	0.41±0.12	0.41±0.12	73.0	73.0
May	0.99±0.15	0.42±0.13	0.54±0.29	57.6	45.5
May	2.26±0.69	1.14±0.49	1.14±0.49	49.6	49.6
August	2.58±1.13	0.68±0.23	1.71±0.84	73.6	33.7
August	1.57±0.47	0.85±0.18	2.25±0.71	45.9	-43.3

[a]Mean ±SD.

the monthly sample data. Daily water temperature was also estimated by interpolation between sampling dates. Using the estimated standing stocks and water temperatures with the equations derived above, ingestion and respiration were estimated daily for each size class. Ingestion in g dry weight was then converted to consumption of bacterial, algal and total living carbon by using data from Rublee (in preparation), by interpolating between sample dates, and by assuming a dry sediment density of 0.59 g cm^{-3}. Algal carbon was estimated by multiplying chlorophyll a values by 30 (Ferguson and Murdoch, 1975) and total living carbon was estimated by multiplying ATP values by 286 (Holm-Hansen, 1973). Values were summed over all size classes to give total population values and then were summed over each month (Table 9). Production was taken from the monthly values calculated from the smoothed PW-frequency data.

The concentrations of bacterial, algal, and total living carbon were probably higher in the sediment ingested by N. succinea than in the surface sediment measured by Rublee (in preparation). Bacterial counts in the guts of the five worms from the assimilation experiment (Table 8) taken near Rublee's sampling station averaged 30% (±3%) higher than the corresponding counts in the sediment. Rublee's samples were taken by scooping up surface sediment to a depth of approximately 1 cm while the worms appear to ingest only the upper few millimeters of sediment. I scraped sediment gently from the marsh surface in order to simulate worm feeding and compared these samples with samples taken with Rublee's method (Table 10). ATP averaged 31% higher and chlorophyll a averaged 56% higher in the samples scraped from the surface than in the samples which included the entire top centimeter of sediment. Assuming that the increase in bacterial numbers in the worm guts was also due to surface

Table 9. Partial monthly carbon budget for a N. succinea population occupying 1 m^2. Microbial carbon values have been corrected for sampling bias as described in the text. Assimilation efficiency was assumed to be 57% when calculating the percent of respiratory carbon for N. succinea supplied by bacteria and by the total microbial population.

Month	Ingested sediment (g dry wt)	Ingested carbon (g)			Respiration (g C)	% Respired carbon supplied by	
		Bacteria	Micro-algae	Total microbial biomass		Bacteria	Total microbial biomass
August[a]	785	0.209	0.204	0.889	1.457	8.2	34.8
September	568	0.170	0.168	0.828	1.098	8.8	43.0
October	305	0.127	0.084	0.566	0.604	12.0	53.4
November	179	0.075	0.045	0.208	0.346	12.4	34.3
December	113	0.044	0.027	0.071	0.210	11.9	19.2
January	173	0.047	0.012	0.127	0.299	9.0	24.3
February	329	0.111	0.022	0.351	0.586	10.8	34.3
March	424	0.133	0.087	0.420	0.748	10.1	32.0
April	554	0.140	0.148	0.427	1.036	7.7	23.5
May	755	0.165	0.267	0.531	1.443	6.5	20.9
June	523	0.124	0.220	0.406	1.023	6.9	22.7
July	426	0.150	0.187	0.581	0.849	10.0	39.0
August[b]	404	0.131	0.183	0.557	0.832	9.0	38.2
Totals (using August mean)	4944	1.456	1.462	5.241	9.387	8.8	31.8

[a]Extrapolated from last 18 days.

[b]Extrapolated from first 13 days.

Table 10. Comparison of scrapes with scoops of surface salt marsh sediment. Four samples of each kind were taken: light scrapes of the surface sediment; scoops to a depth of approximately 1 cm; and scoops beneath an area just scraped. Samples were analyzed for ATP and Chlorophyll a following Rublee (in preparation).

Date	ATP ($\mu g\ cm^{-3}$)		Chlorophyll a ($\mu g\ cm^{-3}$)		
	Scrape	Scoop	Scrape	Scoop	Scoop beneath scrape
31 August	2.57[a] $\pm$0.16	1.97 $\pm$0.09	--	--	--
1 September	--	--	15.43 $\pm$1.44	9.90 $\pm$0.41	7.18 $\pm$0.29

[a]Mean $\pm$SE.

feeding, I have increased the estimated annual consumption of bacterial carbon by 30%, of algal carbon by 56%, and of total living carbon by 31% to take into account the difference between Rublee's sampling technique and the feeding of N. succinea.

The annual carbon budget of the N. succinea population (Table 11) showed a substantial excess of carbon required over measured carbon intake. If assimilation efficiency for total living carbon was the same as the digestion efficiency for detrital microbes (57%), then only 26% of the carbon requirement could be accounted for; even if 100% of the living carbon that was consumed was assimilated, only 45% of the total carbon requirement could be accounted for.

Discussion

Assimilation of Microbial and Detrital Carbon

Nereis succinea utilized the microbial carbon from the detrital system fairly efficiently. Two independent methods, one measuring bacterial digestion by direct counting and the other measuring microbial digestion by double-labeling with ^{14}C and ^{51}Cr, gave estimates of about 60% digestion of microbes as sediment passed through the gut. Direct counting of sediment bacteria passing through another nereid, N. diversicolor, gave an estimate of 55% for digestion (Zhukhova, 1963). These measures of digestion are not necessarily equivalent to assimilation since any loss of digested cell contents as DOC would reduce the efficiency; therefore, these numbers represent the maximum possible assimilation efficiency. Estimates of bacterial or microbial assimilation for other deposit feeders have ranged from 40% to almost 100% (Fenchel, 1970; Hargrave, 1970; Kostalos, 1971; Calow and Fletcher, 1972; Chua and Brinkhurst, 1973; Calow, 1975; Kofoed, 1975a; Wetzel,

Table 11. Annual carbon budget for a N. succinea population. Carbon input from microbial biomass has been estimated assuming (1) an assimilation efficiency (AE) of 57%, and (2) an assimilation efficiency of 100%. Numbers are g C m^{-2}.

	100% AE	57% AE
Living carbon consumed:		
Bacterial	1.5	0.9
Algal	1.5	0.9
Total microbial	5.2	3.0
Carbon losses:		
Production	2.1	
Respiration	9.4	
Total	11.5	

Carbon supply - carbon losses =

5.2 - 11.5 = -6.3 g C m^{-2} deficit with AE = 100%, or

3.0 - 11.5 = -8.5 g C m^{-2} deficit with AE = 57%.

1975; Moriarty, 1976; Yingst, 1976; Lopez, 1977). However, digestion rates of bacteria by the gastropod Hydrobia ventrosa varied from as low as -66 to as high as 55% but generally were below 30% (Lopez and Levinton, in press); the authors suggested that a certain number of microorganisms attached to particles could not be digested and that bacteria and microalgae over this amount constituted the available food.

Assimilation of nonliving plant material by N. succinea was low compared to that for microbial biomass. The net assimilation of 10.5% from the ground Spartina represented the maximum possible assimilation efficiency for Spartina, but in this form Spartina would generally be unavailable to N. succinea. Dead Spartina undergoes a significant amount of decomposition while standing and by the time the leaf material falls to the sediment surface, much of the more available material is gone (Odum et al., 1973); only then would it be possible for N. succinea to consume the decaying Spartina. N. succinea was also able to assimilate carbon from the extracted Spartina, which is supposedly representative of the plant substrate of a detrital particle. A larger portion of the assimilated carbon was respired when it came from extracted material than when it came from nonextracted material, as would be expected if much of the more easily utilizeable fraction of the material had been removed by the extraction. Since there was no measure of total consumption, it was not possible to calculate assimilation efficiency of extracted material or even assimilation efficiency relative to the nonextracted material.

The literature on the assimilation of structural components of detritus is contradictory. The amphipod Hyallela azteca, the snail Nassarius obsoletus, and the periwinkle Littorina irrorata were all

unable to assimilate ^{14}C-labeled cellulose or extracted detritus (Hargrave, 1970; Wetzel, 1976; Alexander, 1976) and assimilation efficiency of the snail Planorbis contortus was less than 6% for cellulose and lignin (Calow, 1975). On the other hand, the mysid Mysis stenolepsis and the prawn Palaemon serratus were able to assimilate 50-70% of a cellulose diet (Forster and Gabbot, 1971; Foulds and Mann, in press) and two species of Littorina from the Japan Sea showed high levels of cellulase activity (Elyakova, 1972). A wide variety of invertebrates, including Nereis virens, possess enzymes capable of breaking down cellulose and other structural carbohydrates (Yokoe and Yasumasu, 1964; Lewis and Whitney, 1968; Elyakova, 1972; Kristensen, 1972), but the consensus is that assimilation efficiency of these components is not high. However, it is important to note that by passing large quantities of detrital material through the gut, a detrital feeder may obtain significant quantities of carbon despite a low assimilation efficiency.

Assimilation efficiencies of deposit feeders for total sediment organic matter and detritus vary widely. The range of reported assimilation efficiencies for sediment organic matter by several deposit feeders is from 4 to 41% (Heywood and Edwards, 1962; George, 1964; Gordon, 1966; Hargrave, 1971; Jones, 1973; Yingst, 1976). Assimilation efficiencies as low as 0% and as high as 91% have been reported for detrital material complete with associated microbes (summary tables in Jones, 1973; Ladle, 1974; Berrie, 1976).

Carbon Budget for Nereis succinea

The partial carbon budget for Nereis succinea (Table 11) indicates that survival is not possible using only living carbon. Considering

only losses due to production and respiration and assuming a 57% assimilation for all living carbon, there was an annual net deficit of 8.5 g C m^{-2}.

Since total living carbon was measured indirectly by ATP, some error may have been introduced with the conversion from ATP to carbon. The factor of 286 (C:ATP) used here came from measurements of bacterial, algal, and zooplankton cultures (Holm-Hansen, 1973); however, the relation was similar for natural plankton samples from a variety of lakes (276; Paerl and Williams, 1976). Ausmus (1973) found conversion factors as high as about 500 for terrestrial bacteria, but when some of these bacteria were cultured in soil, the biomass estimated with ATP was more than 50% greater than the biomass observed with direct counting. The ATP in marsh sediments is present mainly in the form of bacteria and microalgae, which were measured independently of ATP by Rublee (in preparation) in the marsh in this study, and in the form of fungi, protozoans, nematodes, and other meiofauna, which were not measured. If microbial ATP is estimated by dividing the values for bacterial and algal carbon (Rublee, in preparation) by 286, then it would account for 52% of the total sediment ATP. Most of the remaining 48% of the sediment ATP was probably due to nematodes (Sikora et al., 1977), which have a C:ATP ratio of about 85:1 (Sikora et al., 1977). Using 286 as the appropriate conversion factor for the microbes and 85 as the appropriate conversion factor for the nematodes, then the overall factor to convert total ATP to total living carbon in this marsh sediment is (0.52 x 286) + (0.48 x 85) or 190. Since I used 286 for the overall conversion, it is not likely that the amount of microbial carbon

consumed by N. succinea was underestimated and, in fact, the quantity consumed may have been overestimated.

The estimates of carbon required by the N. succinea population are not excessive when compared to other studies. Annual production for N. succinea was estimated as 2.1 g C or 4.1 g AFDW m^{-2}. This value is within the range of annual production estimates for other polychaetes: Nepthys incisa, 9.3 g dry weight m^{-2} (Sanders, 1956); Nereis virens, 8.4 g dry weight m^{-2} [calculated using 5383 kcal/(g dry weight); Kay and Brafield, 1973]; Ampharete acutifrons, 2.3 g dry weight m^{-2} (Warwick and Price, 1975); Nephthys hombergi, 7.3 g dry weight m^{-2} (Warwick and Price, 1975); Arenicola marina, 3.3-6.3 g AFDW m^{-2} (Wolff and de Wolf, 1977). Annual respiration was estimated as 9.4 g C or approximately 94 kcal m^{-2}. The only comparable value is that for Nereis virens of 16.7 kcal m^{-2} yr^{-1} (Kay and Brafield, 1973); the authors suggested that their value for annual respiration may have been an underestimate. In addition, the calculated respiration rate for N. succinea agreed closely with respiration rates of eight other deposit feeders (Section I).

There is a fairly consistent relation between annual production (P) and annual respiration (R) in kilocalories for a variety of poikilotherms (McNeill and Lawton, 1970) which may be expressed as

$$\log R = 1.0733 \cdot \log P + 0.3757.$$

If production of N. succinea is converted from g C to kcal m^{-2} using 5383 kcal/g dry weight (calculated from data for Nereis virens in Kay and Brafield, 1973), then annual production in this study was 25 kcal. For this production the equation predicts an annual respiration of 75 kcal, while the estimated value was actually 94 kcal. Thus, neither the

production nor the respiration values estimated for N. succinea are unreasonable; this implies that the worms have some way of obtaining carbon in addition to that taken up from living microbial biomass.

There are three possible sources of carbon for N. succinea which were not considered in the carbon budget: (1) uptake of DOC; (2) selective predation on meiofauna and other macrofauna, and (3) uptake of non-living carbon from the plant detritus.

The significance of uptake of DOC by marine invertebrates has been a subject of controversy for many years (Jorgensen, 1976). Interpretation of experimental evidence for net influx or efflux of DOC based on ^{14}C-labeled compounds is difficult due to substantial differences in the internal and external pools of these compounds (Johannes et al., 1969). However, recent measurements of absolute amounts of primary amines with the use of fluorescamine showed a substantial net uptake of these compounds from interstitial water by another nereid polychaete, N. diversicolor, and the polychaete Capitella capitata (Stephens, 1975); this uptake was of the same magnitude as the animals' requirements for reduced carbon as estimated from oxygen consumption.

Although N. diversicolor was able to take up a substantial amount of dissolved primary amines under laboratory conditions, the importance of this uptake in nature has not been proven. Uptake of DOC is highly dependent upon ambient concentration and appears to follow Michaelis-Menten kinetics for selected compounds (Stephens, 1972; Jorgensen, 1976). Thus, experimental conditions are extremely important when uptake rates are measured and interpreted. Stephens (1975) used amino acid concentrations of 50 μM, approximating that of the concentration of primary amines of the interstitial water where N. diversicolor are

found. However, the critical concentration is that of the water within the worm burrow and this concentration may be quite different from that of the interstitial water for two reasons. First, the worms are constantly removing primary amines from the water. For example, consider a 300 mg N. diversicolor living in a burrow with a volume of 3 cm^3, approximately 10 times that of the worm. The 3 ml of water in the burrow will contain 0.15 μmoles of primary amines if the concentration is the same as for interstitial water, 50 μM. Using Stephens' uptake rate, a 300 mg N. diversicolor will take up 0.23 μmoles hr^{-1} of primary amines from this concentration, giving a turnover time of about 40 min for the primary amines in the burrow water. Therefore, the rate of supply of primary amines from the surrounding sediment into the burrow water will be important in determining the concentration. Second, N. diversicolor irrigate their burrows (Lindroth, 1941, as cited in Stephens, 1975) and replace the burrow water with water from above the sediment surface. Total dissolved amino acids usually are less than 0.5 μM in unpolluted sea water (Jorgensen, 1976) and uptake of primary amines from that concentration would be insignificant, assuming Michaelis-Menten kinetics. The primary amine concentration in the burrow water will be determined by three factors: (1) removal by the worms; (2) supply from the surrounding sediment; and (3) dilution with water from above the sediment surface. Measurements of the actual concentration of primary amines in burrow water must be made before the true significance of their uptake to nereid polychaetes can be determined.

Predation of meiofauna may also provide N. succinea with a significant amount of carbon. Nonselective consumption of meiofauna has already been included in the carbon budget since about 44% of the total

living carbon ingested by the worms (as measured by ATP) was not accounted for by bacteria or algae; much of this excess "microbial" carbon may have actually been in the form of meiofauna or larger microfauna (e.g., ciliates). Nematodes dominate the meiofauna of salt marshes both in numbers and biomass (Rogers, 1969; Brickman, 1972). Average sizes reported for salt marsh nematodes have varied by almost two orders of magnitude: Georgia, 0.12-0.47 µg wet weight (Teal and Wieser, 1966); South Carolina, 2.83 µg dry weight (Sikora et al., 1977); and New Jersey, 1.60 µg dry weight (Brickman, 1972). Converted to µg C by assuming a 4:1 wet to dry weight ratio (Wieser, 1960) and a carbon content of 33% of the dry weight (Sikora et al., 1977), these values range from 0.01 to 0.94 µg C animal^{-1}. In order to obtain the 8.5 g C needed to satisfy their requirements, the N. succinea population in 1 m^2 would need to consume from 9.0 x 10^6 to 1.1 x 10^9 nematodes each year, depending on the size of the nematodes. This is equivalent to a consumption of 25-2940 nematodes day^{-1} worm^{-1}. For comparison, an individual grass shrimp Palaemonetes pugio was able to consume 20-64 nematodes day^{-1} and 24-90 total meiofauna day^{-1} in a simulated salt marsh ecosystem (Susan Bell, personal communication); since these feeding rates represent only differences in standing stocks of the meiofauna and do not allow for reproduction during the time intervals, they probably are underestimates. The polychaete Nephthys incisa doubled its net incorporation of 5-month-old detritus when meiofauna were added to the experimental system (Tenore et al., 1976).

Predation on other macrofauna probably is not important in supplying carbon to N. succinea. The average standing stock of N. succinea was 1.1 g C m^{-2}, but only 0.5 g C m^{-2} for all the other

macro-infauna (Cammen, in preparation). In order to supply the 8.5 g C m^{-2} needed by N. succinea, the other infauna would need an annual turnover of about 17 times, even assuming a 100% assimilation efficiency by N. succinea. However, there is no reason to assume that annual production is more than the typical one to six times the average standing stock (Waters, 1969; Burke and Mann, 1974) for these animals.

Ingestion and assimilation of the detrital substrate material (considered apart from the accompanying microbiota) potentially represents a significant carbon source for N. succinea. Apparently N. succinea was able to assimilate about 10% of the carbon from ground fresh Spartina and the feeding experiments on the extracted, refractory Spartina showed that some uptake was present. The N. succinea population in 1 m^2 ingests about 4950 g dry weight of sediment and detritus each year with an organic content of about 6.8%; this gives a yearly ingestion of 337 g organic matter m^{-2}. If organic carbon is 53% of this organic matter (Bader, 1954), then annual consumption of organic carbon is 177 g m^{-2}; of this amount about 5.2 g is living carbon. In order to make up the deficit of 8.5 g C m^{-2}, the N. succinea population needs to assimilate only 4.9% of the nonliving organic matter ingested.

It is likely, then, that N. succinea was able to balance its carbon budget with some combination of uptake from DOC, selective predation on meiofauna, and assimilation of dead plant material. Additional evidence would be required in order to assess the relative importance of these sources of carbon. However, microbial biomass probably does not represent a major source of carbon to N. succinea.

Importance of Living Carbon to Aquatic Deposit Feeders or Detritovores

Many aquatic deposit feeders and detritovores function similarly despite wide taxonomic differences. The relation between consumption of organic matter at 15 C and body weight was the same for 16 species including polychaetes, amphipods, gastropods, stonefly nymphs, decapods, crabs, and oligochaetes (Section I):

$$(1)\quad \log OM = -0.451 + 0.729 \cdot \log W \qquad (r^2 = 0.93),$$

where OM is mg organic matter consumed day^{-1} and W is mg dry body weight. Assuming sediment organic matter is 53% organic carbon (Bader, 1954), the equation becomes

$$(2)\quad \log C = -0.727 + 0.729 \cdot \log W$$

where C is mg organic carbon consumed day^{-1} and W is mg dry body weight. In addition, the seven species for which respiration data were available had the same relation between respiration and body weight (Section I):

$$(3)\quad \log R = 0.043 + 0.727 \cdot \log W \qquad (r^2 = 0.98)$$

where R is µl O_2 consumed $animal^{-1}$ hr^{-1} and W is mg dry body weight. If O_2 consumed is converted to carbon lost (as was done above for N. succinea) and expressed on a daily basis, the equation becomes

$$(4)\quad \log RC = -1.894 + 0.727 \cdot \log W$$

where RC is mg carbon released day^{-1} as CO_2 and W is mg dry body weight. It is now possible to combine Equations 2 and 4 to express the amount of carbon lost as CO_2 as a function of organic carbon consumption:

(5) $\log RC = -1.169 + 0.997 \cdot \log C$.

This equation can be simplified to

(6) $RC \cong 0.07 \cdot C$.

Thus, for these deposit feeders about 7% of the organic carbon consumed each day is lost as respired CO_2. It follows that at least 7% of the organic carbon consumed must be assimilated. If these animals are to survive utilizing only living microbial carbon, and if their assimilation efficiency for living carbon is about 60%, then about 11-12% of the organic carbon consumed must be living carbon. If other carbon losses such as growth, mortality, and DOC release are considered, this figure will be even greater.

However, the systems for which we have reliable data suggest that only 1-3% of the total sediment organic carbon is living carbon. The percentage of living microbial carbon to total organic carbon averaged about 1.5% in this marsh (Rublee, in preparation), less than 1% in a Georgia Spartina marsh (Christian et al., 1975), between 0.06 and 3% in the Newport River estuary in North Carolina (Ferguson and Murdoch, 1975), and 0.1-3.0% (mean of 1.0%) for nine Wisconsin lakes (Lee et al., 1971); values were occasionally higher in a South Carolina salt marsh with station means of 0.8-7.6%, but the overall mean value was only 2.7% (Simons, 1976). In a variety of intertidal surface sediments from Nova Scotia, bacteria averaged less than 1% of the total carbon (Dale, 1974), assuming carbon is 34.4% of the dry weight of bacteria (Ferguson, unpublished data). In all of these systems deposit feeders apparently cannot use living microbial carbon as their major source of carbon.

Some published data does show a much higher living carbon to non-living carbon ratio. Most of these data come from the muramic acid technique of estimating microbial biomass (Moriarty, 1975, 1976, 1977a, 1977b; King and White, 1977). According to Moriarty (1977b), bacterial carbon can make up as much as 30% of total sediment carbon, but his technique probably overestimates muramic acid by 10-20 times (King and White, 1977). Even using the more conservative technique of King and White (1977), Morrison et al. (1977) found dry weights of bacteria on decaying leaf material were approximately 15-20 times greater when calculated with muramic acid than when calculated with ATP, although they indicated their ATP conversion might have resulted in an underestimate of dry weight. The muramic acid method uses a component dependent to a large extent on the surface area of the cell (muramic acid) to predict a component dependent on the volume of the cell (carbon) and this makes the conversion factor dependent on cell size. The conversion factors which have been calculated (Millar and Casida, 1970; Moriarty, 1975, 1977a) are for cultured cells which are generally larger than those from natural samples. For example, bacterial cell sizes in the marsh investigated in this study averaged about 0.2 μm^3 (Rublee, in preparation) as compared with the commonly cited value of 1 μm^3 for an average bacterium (Luria, 1960). As the volume is decreased by a factor of 5, the volume:surface area ratio decreases by only 1.7 times. Thus, if cell carbon were estimated in this system using conversion factors derived from cultured cells, an overestimate of about 70% would result. This error will vary depending on the relative sizes of the bacteria. With the uncertainty surrounding the use of this method and the possible overestimates resulting, the high estimates of microbial

to total carbon cannot be considered reliable. Tunnicliffe and Risk (1977) estimated bacteria made up from 33 to 100% of the sediment organic carbon in the Minas Basin. However, bacteria numbers were converted to carbon using 1 μm^3 as the cell volume and apparently assuming that all the cell dry weight was carbon. If the data are recalculated with the conversion factors from Ferguson and Rublee (1976) and with cell size assumed to be 0.2 μm^3, then bacterial carbon is only 2.5% of the total sediment carbon.

Deposit feeders do not appear to be able to increase their ingestion of living carbon relative to total organic carbon by selecting detrital particles from the sediment. The amount of bacterial carbon growing on Spartina decaying in the field reached a peak of only 0.3% of the total carbon after 184 days (Rublee, in preparation). Microbes on decaying oak leaves in Florida made up from 0.1 to 0.8% of the dry weight (Morrison et al., 1977), although their biomass may have been underestimated. Gosselink and Kirby (1974) reported that microbes incubated with decomposing Spartina accounted for one-fourth to three times the AFDW of the remaining Spartina after only 30 days but there were three problems with their experimental design as applied to this question. First, they added nitrogen to a nitrogen-limited system, possibly increasing the decomposition rate; second, their system was incubated only with organisms able to pass an 0.45-μm filter or survive oven-drying at 60 C and the lack of grazers may have resulted in an artificially high biomass of microbes; third, they were unable to differentiate the microbes actually attached to the decaying Spartina particles from those suspended in the water. The most applicable data indicate a relatively low standing stock of living microbial carbon associated with detrital particles.

Zooplankton may also need to consume detritus in order to satisfy their carbon requirement. Detritus is abundant in the seston and this results in significant ingestion by zooplankton (Poulet, 1976; Lenz, 1977); this detritus can be utilized as a carbon source by the zooplankton although it appears that algae or protozoans must also be ingested as a supplement (Heinle et al., 1977; Roman, 1977). A carbon budget calculated for the copepod Eurytemora affinis showed that the population was unable to satisfy its carbon requirement by consumption of phytoplankton during several months in the Patuxent River (Heinle and Flemer, 1975) and the authors hypothesized that detritus was consumed to help meet this requirement.

Wetzel (1975, 1976) calculated that assimilation of microbial carbon by the snail Nassarius obsoletus was sufficient to satisfy its daily carbon requirement and allow for some growth, but the uptake rates for microbial carbon may have been overestimated. The carbon retained by snails feeding on sediment cores with either the microbes or the benthic algae labeled with ^{14}C was measured over time and a retention rate calculated for each time interval; this rate was a function of the amount of unassimilated material in the gut as well as the true retention rate. Thus, the measured retention rate would always be greater than the true retention rate with the difference diminishing over time as the total carbon retained increased relative to the amount in the gut; however, the feeding experiments lasted only 3-6 hours, a short enough time so that the gut contents would still have significantly influenced calculation of the retention rate. In addition, with this type of experimental design the total ^{14}C in the snails (gut contents plus retained ^{14}C) should have increased continuously throughout the

experiments; in fact, the total ^{14}C in the snails decreased after the initial high value, which represented ingestion, making interpretation of the data difficult. Finally, the rates of ingestion of microbial carbon by the snails were estimated by the maximum retention rates of ^{14}C when feeding on labeled bacteria or benthic algae and were about 100 and 300 $\mu g\ C\ hr^{-1}$ $(mg\ snail\ C)^{-1}$, respectively. These rates may be compared with estimates I have made from fecal production [2 $\mu g\ C\ hr^{-1}$ $(mg\ snail\ C)^{-1}$, Wetzel, 1975] for microbial ingestion by the snails by assuming that all ingested carbon was in the form of microbes assimilated with a 50% efficiency; this estimate was much less, only 4 $\mu g\ C\ hr^{-1}$ $(mg\ snail\ C)^{-1}$. The discrepancy between these two estimates of ingestion rate was actually greater since microbial carbon was probably only a small fraction of the total ingested carbon; in the natural sediment the microbes made up only 0.7% of the total carbon (Christian et al., 1975). Either the ingestion rate based on fecal production was underestimated or the retention rate was overestimated. The ingestion rate estimated from fecal production was somewhat greater than the ingestion rate that would have been predicted with Equation 2 (above), but the difference was not large. This suggests that the retention rates were overestimated and that it is unlikely that N. obsoletus can balance its carbon budget with only microbial carbon.

Even though living microbial carbon may provide only a minor portion of the total carbon required by detritovores, consumption of microbes may still be essential. Vital micronutrients such as vitamin B_{12} may be available to deposit feeders only in the form of microbial biomass. In addition, the quality of the carbon compounds consumed must be considered. It is possible that detrital carbon may be used to

satisfy metabolic requirements of the animals while the microbial carbon might be incorporated into tissue, resulting in growth. For example, the snail Hydrobia ventrosa retained over twice as much assimilated carbon 24 hours after feeding on bacteria and barley hay colonized with bacteria than after feeding on sterile hay (Kofoed, 1975b); most of the respiratory loss of carbon occurred within 2 to 3 hours following the meal on sterile hay. Further investigation is needed into the quality of the carbon consumed by detritovores as well as the quantity.

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