Marine Biology 68, 223–227 (1982)

MARINE BIOLOGY

Effect of Detrital Nutritional Quality on Population Dynamics of a Marine Nematode (*Diplolaimella chitwoodi*)

S. E. G. Findlay *

Skidaway Institute of Oceanography; P.O. Box 13687, Savannah, Georgia 31406, USA

Abstract

The quantity and nutritional quality of detritus significantly affected the population growth rate (r) and carrying capacity (K) of *Diplolaimella chitwoodi* (Nematoda) in laboratory cultures. The rate of increase (r) was roughly constant for cultures fed *Ulva fasciata*, Pablum, *Gracilaria foliifera* and one *Spartina alterniflora* detritus, but was lower for *Thalassia testudinum* detritus and another *S. alterniflora* detritus. Rate of increase was unaffected by amount of food supplied except for seaweed detritus where r was lower for lower ratios. Carrying capacity (K) was strongly affected by both detrital type and rate of food supply. The best predictor of K was the rate of nitrogen supply to these cultures implying that natural populations may be N-limited. The nitrogen content of detritus appears to be the best measure of its nutritional quality.

Introduction

Marine benthic systems often depend on different types of detritus as energy sources (Mann, 1972). Salt marshes receive large quantities of vascular plant detritus, while other systems receive more macroalgae and phytoplankton detritus. Differences in the nutritional quality of detritus reaching the bottom affect the energetics of the benthos, but the magnitude of this effect is not known.

Macrofauna may incorporate different types of detritus at different rates (Tenore and Hanson, 1980) thus affecting production. These differences in assimilation as a function of food quality probably apply to all components of the benthos. Therefore, detrial type may significantly affect system level processes such as benthic metabolism (O_2 uptake) and trophic efficiency. From these arguments, it is reasonable to expect the food quality of detritus to directly or indirectly affect enery flow between components of the benthos.

Characteristics of detritus affecting its availability and suitability as food for benthic organisms have only recently been examined. Nitrogen content and "available calories" of detritus were good predictors of carrying capacity (K) of the polychaete *Capitella capitata* (Tenore, 1981). Contrarily, growth rate of a chironomid was correlated with ATP content of the food but not with total nitrogen or carbon (Ward and Cummins, 1979). Apparently, food quality can affect the energetics of benthic organisms, but the relative importance of detrital quality compared to predation or competition in regulating benthic population dynamics is unclear. Moreover, the effect of food type has been examined for only a few organisms.

Meiobenthic nematodes are an important component of benthic energy flow (Gerlach, 1978), but little is known about how food quality affects natural populations. The population growth rate of three species of marine nematodes was affected by food type (Alongi and Tietjen, 1980) but the causative factor was not examined. I have used laboratory cultures to examine the effect of food quality on nematode population parameters; the rate of increase (r) and carrying capacity (K). If detrital type does affect these parameters, it is reasonable to ask: (1) what is the limiting factor, or what is the best measure of detrital quality; and (2) does food quality significantly affect natural populations?

Materials and Methods

The nematode *Diplolaimella chitwoodi* (Monhysterida) was established in monoxenic cultures maintained on Gerbers mixed cereal (Pablum). *D. chitwoodi* is a "selective deposit feeder" in the scheme of Wieser (1953). It has a very small ($< 0.5\ \mu m$ diameter) unarmed buccal cavity and probably ingests bacteria or other small particles. Worms to be used in feeding experiments were picked individually from stock cultures and rinsed once with autoclaved sea water.

---

* Present address: Institute of Ecology, University of Georgia; Athens, Georgia 30602, USA

0025-3162/82/0068/0223/$ 01.00

Table 1. Detritus types, rations and nutritional data with resulting values for rate of increase (r d^{-1}) and carrying capacity (K · 10^6 · m^{-2})

	Detritus	*Ulva fasciata*		Pablum			*Gracilaria foliifera*		*Spartina alterniflora* (S-13)	*Spartina alterniflora* (S-1)		*Thalassia testudinum*	
Nutritional data	%N (DW)	5.5		5.0			1.8		0.9	0.9		1.2	
	$\frac{\text{Av. Cal.}}{\text{mg DW}}$	0.89		2.16			1.03		0.43	0.75		0.66	
Experimental rations	$N\left(\frac{\text{mg DW}}{m^2 \cdot \text{day}}\right)$	22.0	7.33	20.2	6.73	2.47	7.04	2.35	3.71	3.56	1.19	4.93	1.64
	$\frac{\text{Av. Cal.}}{m^2 \cdot \text{day}}$	356.0	118.7	864.0	288.0	144.0	410.8	136.9	300.0	299.2	99.7	265.2	88.4
Rate of increase	r (day^{-1}) $\bar{x} \pm$ S.D. (# Reps.)	0.280± 0.010 (2)	0.185± 0.007 (2)	0.230± 0.035 (4)	0.212± 0.003 (2)	0.218± 0.030 (2)	0.280± 0.028 (2)	0.180± 0.020 (2)	0.093± 0.053 (2)	0.260± 0.021 (2)	0.302± 0.110 (2)	0.000± 0.000 (2)	0.000± 0.000 (2)
Carrying Capacity	K($10^6 \cdot m^{-2}$) $\bar{x} \pm$ S.D. (# Reps.)	0.690± 0.028 (2)	0.222± 0.006 (2)	0.510± 0.066 (4)	0.582± 0.218 (2)	0.211± 0.004 (2)	0.256± 0.090 (2)	0.137± 0.060 (2)	0.098± 0.017 (2)	0.064± 0.000 (2)	0.044± 0.016 (2)	0.012± 0.001 (2)	0.005± 0.004 (2)

Plant material for detritus (Table 1) was either collected from the field as standing dead (*Spartina alerniflora* S-1, *Thalassia testudinum*) or grown in culture (*Gracilaria foliifera, S. alterniflora* S-13, *Ulva fasciata*). All detritus was ground to pass a 250 mesh and pre-leached for 3 d in autoclaved seawater (100 ml per g dry wt. detritus) with 1 ml of 3-μm filtered culture medium as a microbial inoculum.

Tissue culture flasks (25 cm^2) were inoculated with 20 similar-sized adult nematodes and 15 ml autoclaved, filtered (1 μm) 25‰ S seawater (AFSW). Various rations of each detritus (Table 1) were split into four equal parts. Ration is defined here as the rate of input to the system. One-quarter of the total ration was added to the flasks at the beginning and then once a week for 3 wk. Two replicates of each treatment were done. Flasks containing only worms and AFSW were set up as controls. Flasks were kept in the dark at 20 °C ± 1 C° except during counting. Worms in the flasks were counted at 120X magnification, daily at first, to note when juveniles appeared, and then twice a week until numbers remained constant for two counting periods.

Initial nitrogen content of each detritus was measured with a Perkin-Elmer Model 240 CHN Analyzer. "Available" calories were defined as those calories lost following 6-h hydrolysis in 1N HCl (Tenore, 1981). Caloric content was measured with a Parr Micro-Bomb Calorimeter.

Upon termination of the experiments, each flask was vortexed and two ml of the seawater detritus suspension were filtered (0.45 μm) to measure the dry weight of food remaining. Worm weight (0.1 μg dry wt individual^{-1}) was negligible. One ml of the suspension from each flask was collected on pre-combusted glass fiber filters for carbon and nitrogen measurements (Perkin-Elmer CHN Analyzer).

Data Analysis. All curves were "time-shifted" so that Day 0 (t_0) for each flask was the day before the first appearance of juveniles. This puts all the flasks on the same relative time scale for computation and reduces variability between replicates.

Based on the shape of the population curves, the logistic equation ($dN/dt = rN\,(K - N/K)$) was accepted as a model of population growth. Carrying capacity (K) was estimated from semi-log plots of N(t) (e.g. Fig. 1). The density at which numbers remained constant for two counting periods was used as the estimate of K. The rate of increase (r) was obtained by iteratively fitting the integrated form of the logistic equation (Hagin, 1975):

$$N(t) = N(0) \cdot r \cdot e^{rt} \Big/ \left[r - \frac{r \cdot N(0)}{K} (1 + e^{rt}) \right]$$

to the population density curves [i.e. actual N(t)].

Two-way ANOVA tested for the effects of detrital type and ration on r and K. Multiple regression examined the dependence of r or K on the independent variables nitrogen and available caloric content of the various rations.

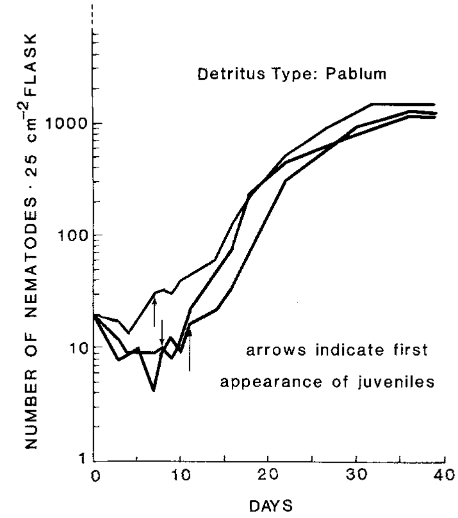

Fig. 1. *Diplolaimella chitwoodi.* Population growth in three replicate flasks cultured on Pablum

Results

Nematode population growth always showed a typical logistic population growth curve (e.g. Fig. 1). Control flasks (worms with AFSW) never reached a density of 40 worms flask^{-1} and generally declined below the inoculum number (20) after the first week (data not shown).

Values of the rate of increase range form 0.0 to 0.38 (Table 1). *Thalassia testudinum* detritus supported very low growth and was not different from control flasks. Rate of increase was affected by detrital type (ANOVA $F=28.92$, 5 df, $P=0.001$) probably due to low values for *Spartina alterniflora* (S-13) and *Thalassia testudinum.* Overall, r was not affected by ration (ANOVA $F=1.93$, 2 df, $P=0.18$), however, the interaction of type × ration (ANOVA $F=2.6$, 4 df, $P=0.08$) indicates r was related to ration for certain types. Specifically, r increased with increasing rations of *Ulva fasciata* and *Gracilaria foliifera* (Table 1).

Carrying capacity, K (number of nematodes · m^{-2}) was significantly affected by both detrital type and ration (e.g. Fig. 2) (type: ANOVA $F=40.8$, 5 df, $P=0.001$; ration: ANOVA $F=19.6$, 2 df, $P=0.001$; interaction: ANOVA $F=9.03$, 4 df, $P=0.001$). For a given ration (30 or 10 mg dry wt. total food) K increased in the order *Thalassia testudinum* < *Spartina alterniflora* (S-1) < (S-13) < *Gracilaria foliifera* < Pablum < *Ulva fasciata* (Table 1). Larger rations of detritus consistently supported a higher density of nematodes.

Multiple regression of r on nitrogen and available caloric rations was not significant ($P=0.25$) (cf. Fig. 3). Multiple regression of K on nitrogen and available calories was significant ($P < 0.0001$) with nitrogen "explaining" 67% and available calories, 2% of the variance of K (cf. Fig. 4).

Two ancillary experiments confirmed that the results were in fact due to detritus type and ration. Worms maintained on *Gracilaria foliifera* prior to use in experimental cultures showed the same results as Pablum-raised nematodes (data not shown), thereby demonstrating that high yields of nematodes fed Pablum was not due to previous acclimation to Pablum in stock cultures. Secondly, adding fresh food to senescent cultures caused renewed exponential growth, whereas changing the water led to no new growth. Therefore, the carrying capacity was probably

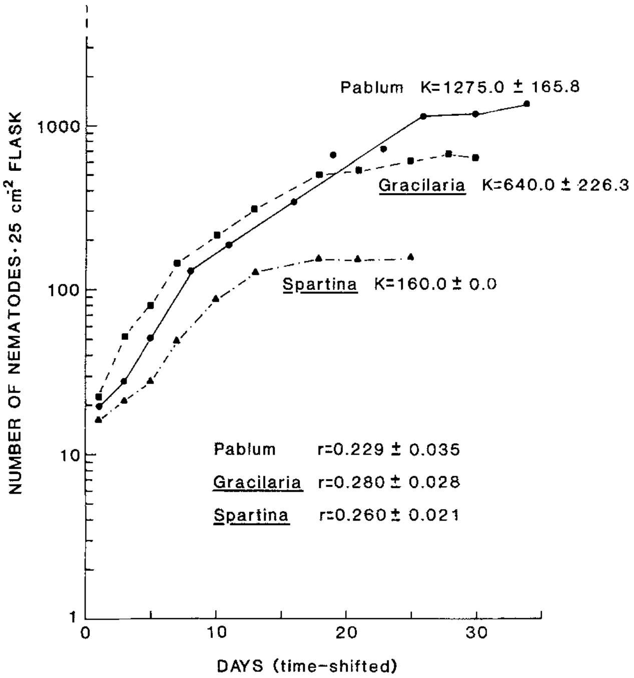

Fig. 2. *Diplolaimella chitwoodi.* Population growth cultured on three detritus types. Each line is the average of two replicates

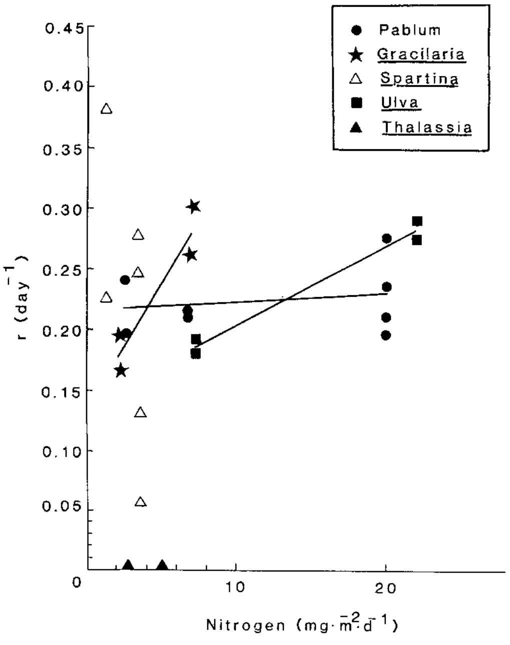

Fig. 3. Relationship of r to nitrogen input to cultures. Lines fit by eye

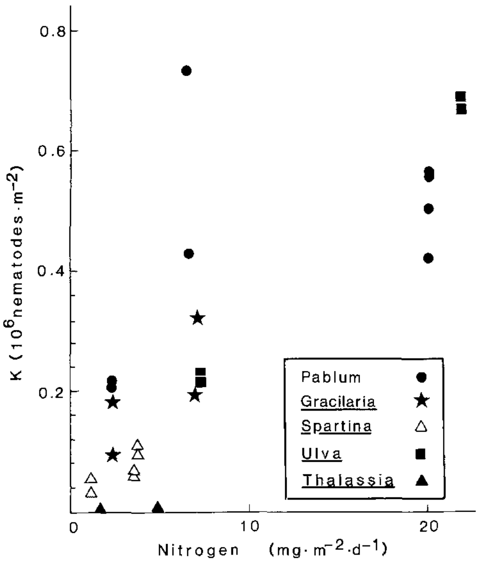

Fig. 4. Relationship of K to nitrogen input to cultures

due to food limitation rather than build-up of metabolites, oxygen depletion, etc.

The initial nitrogen and available caloric content of each detritus are given in Table 1. Dry weight losses (as % initial) ranged from 10 to 80%, with nutritionally "better" foods losing a greater proportion of initial DW. The amount of particulate N remaining in the flasks at the end of the experiments was consistently between 10 and 15% of the total amount added (data not shown) except for *Thalassia testudinum* (~40% remaining). C/N ratios for remaining food were not appreciably different from initial C/N of the detritus.

Discussion

Detrital type affects the rate of increase only for *Spartina alterniflora* S-13 and *Thalassia testudinum* which were apparently very poor foods for *Diplolaimella chitwoodi*. Lack of dependence of r on food quality for other detrital types was probably because food was in excess initially, while nematode densities were below K. At low densities, even a relatively poor food (e.g. *Gracilaria foliifera* vs *Ulva fasciata*) provided sufficient nutrition to enable the population to grow. As the population approached K, food-limitation occurred and the population growth rate declined. Similarly, lower rations did not depress r except for seaweed detritus (*Gracilaria foliifera* and *Ulva fasciata*). Decreasing the amount of food (except seaweeds) still allowed the population to increase at a rate determined by culture conditions. As argued above, food limitation did not occur until densities approached K.

Contrary to other detritus types, r was lower for reduced rations of seaweed detritus (Fig. 3). In light of the possibility that detritivores such as nematodes may directly utilize seaweed detritus (Tenore and Rice, 1980), the situation exists wherein microbes and nematodes may compete for food. Thus, for smaller rations of seaweed detritus, the proportion of food actually available to nematodes may have been reduced by microbial mineralization. Contrarily, *Spartina alterniflora* detritus was probably not directly available to the nematode, therefore competition did not occur and the rate of growth of the population was not depressed until the density approached K.

This relationship between K and detrital type/ration may help explain fluctuations in natural populations. Systems receiving pulses of directly available detritus should exhibit population fluctuations closely tied to the rate of food supply. Conversely, systems receiving pulses of detritus which is not directly available should exhibit fewer sporadic fluctuations. Seaweed-based systems should show close temporal correlation between changes in food supply and population size; whereas *Spartina alterniflora*-based populations will "integrate" the rate food supply over longer time spans. The abundance of nematode feeding types does correlate with availability of different food sources (Tietjen, 1969) but the detailed, short-term sampling needed to test these predictions has not been done.

Carrying capacity (K) was a straight-forward function of detrital type and ration. Nitrogen input was obviously a good predictor of K (Fig. 4) demonstrating that, for these culture conditions, these systems were N-limited. Although nitrogen is the most important factor affecting K, differences due to detrital type (vascular vs non-vascular) were also apparent. For roughly equal N inputs, K for *Spartina alterniflora* (two different stocks) and *Thalassia testudinum* fall below those for *Gracilaria foliifera* and *Ulva fasciata* (Fig. 4). Qualitative differences in detritus affect how, and to what degree the overall regulatory factor, nitrogen, influences nematode population dynamics.

Because nitrogen was a good predictor of K, it is important to consider the fate of detrital nitrogen in these systems. Particulate N remaining after K was reached was less than 15% of the N added as food (except *Thalassia testudinum* ~ 40%). This supports the contention that N-limitation has occurred. Nematode nitrogen [assuming nematode dry wt. is 50% protein (Nicholas and Stewart, 1978)] was less than 5% of the particulate N remaining in the flasks. The N lost was probably mineralized to NH_3 by microbes and nematodes. This rather crude budget indicates that nematode incorporation of N is a minor component of the N transformations in these systems. Although nematde-N was a small proportion of system-N, nitrogen was the dominant factor affecting K.

Nitrogen was the best measure of detrital nutritional quality for this nematode. Similarly, N was the prime predictor of carrying capacity of a polychaete over a much wider range of detritus types (Tenore, 1977, 1981). Based on this wide variety of detrital types, although only two organisms were studied, N-content of the detritus *per se* seems to be an excellent indicator of nutritional quality. N-content of material settling to the bottom should be a good indicator of standing stock of the benthos. Obviously, this food quality effect will be modified by temperature, physical disturbance, etc. but other things being equal, nitrogen input is the best measure of the quality of food available to the benthos.

Nematode populations in nature may also exist under N-limiting conditions. Nitrogen limitation occurred in these experimental flasks with N-inputs of 1.2 and 22.0 mg $N \cdot m^{-2} \cdot d^{-1}$ so N-limitation may occur in natural systems where the range is 10 to 100 mg $N \cdot m^{-2} \cdot d^{-1}$ ($\bar{x} = 40.0$, SD=31.5, N=7; references in Zeitschel, 1979). Because natural benthic communities contain a diverse assemblage of organisms, at least some of which are likely to compete with nematodes for nitrogen it is reasonable to assume that the actual amount of N available to nematode populations in the field will be significantly less than the total N sedimenting to the bottom. Therefore, N levels in this experiment may have been close to what is actually available to nematode populations in nature, implying that natural populations are N-limited. Furthermore, the range in experimental densities ($5 \times 10^5 - 7 \times 10^5 \cdot m^{-2}$) of *Diplolaimella chitwoodi* were below the maximum densities reported for other selective deposit-feeding nematode species (Levy and Coull, 1977; Warwick and Price, 1979). If some factor not present in this experiment (e.g. competition or predation) were limiting natural populations, one would expect greater than natural densities in the flasks. These points strongly argue that nematode abundance in nature is, to a large degree, a function of N input. Other factors (e.g. temperature, oxygen) which were "optimum" in the flasks will be more critical to natural populations and may over-ride the effect of food quality. However, except under extreme conditions, it is reasonable to expect food quality to be one of the most significant factors influencing natural populations. Granted the inherent difficulty when extrapolating from laboratory studies to the field, these results demonstrate that food quality (N content) and quantity are important when trying to explain variations in nematode abundance. Large scale abundances are fairly uniform (Coull and Bell, 1979) but small-scale patchiness is well-documented (Findlay, 1981). My results, in conjunction with the small-scale feeding experiments of Lee *et al.* (1977), indicate that food does affect nematode abundance and this probably occurs at small scales.

Acknowledgements. This work was supported by an NSF Grant (OCE 7825862) to Dr. K. Tenore. Thanks are due to Dr. K. Tenore for serving as my thesis advisor and to B. Dornseif for technical assistance. Drs. R. Hanson, D. Menzel, N. Phillips, J. Porter, K. Porter, J. Tietjen and R. Wiegert reviewed and improved the manuscript. B. Hopper identified the nematode.

Literature Cited

Alongi, D. M. and J. H. Tietjen: Population growth and trophic interactions among free-living marine nematodes. *In:* Marine benthic dynamics, pp 151–166. Ed. by K. R. Tenore and B. C. Coull. Columbia: University of South Carolina Press 1980

Coull, B. C. and S. S. Bell: Perspectives of marine meiofaunal ecology. *In:* Ecological processes in coastal and marine systems, pp 189–216. Ed. by R. J. Livingston. New York: Plenum Press 1979

Findlay, S. E. G.: Small-scale spatial distribution of meiofauna on a mud- and sand flat. Estuar. coast. Shelf Sci. *12,* 471–484

Gerlach, S. A.: Food-chain relationships in subtidal silty sand marine sediments and the role of meiofauna in stimulating bacterial productivity. Oecologia *33,* 55–69 (1978)

Hagin, F. G.: A first course in differential equations, 342 pp. New Jersey: Prentice-Hall, Inc. 1975

Lee, J. J., J. H. Tietjen, C. Mastropaolo and H. Rubin: Food quality and heterogeneous spatial distribution of meiofauna. Helgol. wiss. Meeresunters. *30,* 272–282 (1977)

Levy, R. V. and B. C. Coull: Feeding groups and size analysis of marine meiobenthic nematodes from South Carolina, U.S.A. Vie Milieu *27,* 1–12 (1977)

Mann, K. H.: Macrophyte production and detritus food chains in coastal waters. Mem. Ist. Ital. Hydrobiol. *29* (Suppl.), 353–382 (1972)

Nicholas, W. L. and A. C. Stewart: The calorific value of *Caenorhabditis elegans* (Rhabditidae). Nematologica *24,* 45–50 (1978)

Tenore, K. R.: Utilization of aged detritus derived from different sources by the polychaete, *Capitella capitata.* Mar. Biol. *44,* 51–55 (1977)

Tenore, K. R.: The effect of organic nitrogen and caloric content on detrital utilization by the deposit-feeding polychaete, *Capitella capitata.* Estuar. coast. Shelf Sci. *12,* 39–47 (1981)

Tenore, K. R. and R. B. Hanson: Availability of detritus of different types and ages to a polychaete macroconsumer, *Capitella capitata.* Limnol. Oceanogr. *25,* 553–558 (1980)

Tenore, K. R. and D. L. Rice: A review of trophic factors affecting secondary production of deposit feeders. *In:* Marine benthic dynamics, pp 325–340. Ed. by K. R. Tenore and B. C. Coull. Columbia: University of South Carolina Press 1980

Tietjen, J. H.: The ecology of shallow water meiofauna in two New England estuaries. Oecologia *2,* 251–291 (1969)

Ward, G. M. and K. W. Cummins: Effects of food quality on growth of a stream detritivore, *Paratendipes albimanus* (Meigen) (Diptera: Chironomidae). Ecology *60,* 57–64 (1979)

Warwick, R. M. and R. Price: Ecological and metabolic studies on free-living nematodes from an estuarine mud-flat. Estuar. coast. mar. Sci. *9,* 257–271 (1979)

Wieser, W.: Die Beziehung zwischen Mundhöhlengestalt, Ernährungsweise und Verkommen bei freilebenden marinen Nematoden. Eine ökologisch-morphologische Studie. Ark. Zool. ser. II *4(26),* 439–484 (1953)

Zeitzschel, B.: Sediment-water interactions in nutrient dynamics. *In:* Marine benthic dynamics, pp 195–218. Ed. by K. R. Tenore and B. C. Coull. Columbia: University of South Carolina (1979)

Date of final manuscript acceptance: March 18, 1982.
Communicated by S. K. Pierce, College Park