Vol. 3: 151–156, 1980 | MARINE ECOLOGY – PROGRESS SERIES Mar. Ecol. Prog. Ser. | Published August 31

Natural Food Availability and Assimilation in the Bivalve *Choromytilus meridionalis*

R. J. Griffiths

Zoology Department and Institute of Oceanography, University of Cape Town, Rondebosch 7700, South Africa

ABSTRACT: Samples of seawater overlying a bed of the mussel *Choromytilus meridionalis* (Kr.) at Bailey's Cottage, False Bay, South Africa, were analysed for organic and inorganic content in the particle-size ranges 2–100 μm and 100–200 μm diameter. Organic matter comprised 10–30 % of total sample weight, the remainder being predominantly sand. Changes in weight of particulate matter in samples taken throughout the year showed no clear seasonal pattern. Particulate organic material considered available as food to the mussels averaged 2.65 mg l^{-1}. Particulate inorganic matter averaged twice this amount. The energy value of the organic material averaged 6.1 kJ g^{-1}. Phytoplankton was present in 34 % of the samples and is not considered an important constituent in the mussels' diet. The assimilation efficiency of mussels feeding on natural detritus averaged 40 % over the ration levels 3–18 mg l^{-1} dry weight of particulate matter. However, assimilation efficiency on pure *Dunaliella primolecta* culture declined to zero at a ration of 3 mg l^{-1} while pseudofaeces production was initiated at 6 mg l^{-1}. It was concluded that the presence of particulate inorganic matter may be an important dietary requirement, 'diluting' the food and enabling assimilation to continue at the high ration levels experienced in the field.

INTRODUCTION

The employment of algal monocultures has greatly facilitated investigation of the feeding processes of bivalves. Much of this work has centred upon the effects of different ration levels on filtration rates and assimilation efficiencies in *Mytilus edulis*, and has been reviewed by Bayne et al. (1976). However, investigation of food availability in natural seawater has shown that phytoplankton cells are seldom present in sufficient numbers to contribute significantly to the mussels' diet. Authors such as Fox and Coe (1943), Jørgensen (1955) and Widdows et al. (1979) have shown that particulate organic matter is the major food source of many filter-feeding bivalves. Recently, work by Winter (1976) and Widdows et al. (1979) has centred attention on the fact that seawater in the vicinity of mussel beds frequently contains large quantities of particulate inorganic material. They have shown that suspended silt influences feeding and growth in *M. edulis*, and Widdows et al. caution on the extrapolation of laboratory experiments employing dense algal cultures to field conditions.

The filtration rates and assimilation efficiencies of *Choromytilus meridionalis* fed different rations of *Dunaliella primolecta* have been described by Griffiths (1980). In order to test the applicability of these data to field conditions, the levels of naturally available food were examined at the study site. The assimilation efficiencies of mussels feeding on organic detritus in the laboratory and field were then examined and compared with data obtained with the aid of algal cultures.

MATERIALS AND METHODS

Choromytilus meridionalis (Kr.) (45 mm shell length) and seawater were sampled at Bailey's Cottage, False Bay, South Africa (34° 06'S 18° 28'E). A large densely packed mussel bed extends from the surf zone in the sublittoral to an average of 0.5 m above L.W.S. Water for analysis and experiments was collected in seawater 0.5 m deep immediately above the mussel bed. Data on the assimilation efficiencies of 45 mm *C. meridionalis* feeding on *Dunaliella primolecta* culture were obtained from Griffiths (1980). Widdows (1978) has shown a slight increase in assimilation efficiency of *M. edulis* with increasing body size when fed at high algal rations. However, other authors (e. g. Griffiths and King, 1979) have found assimilation efficiency to be independent of size. Although preliminary data on *C. meridionalis* show no marked affect of body size on

0171-8630/80/0003/0151/$ 02.00

assimilation, for comparative purposes only 45-mm mussels were used in experiments presented here.

Seawater Analysis

Water was sampled between February 1978 and February 1979. The samples included two 21 d series of daily records during summer and winter, and 5 continuous days out of each of the remaining months. On each day 500 ml of seawater was filtered through 200 μm and 100 μm mesh sieves and the fraction caught on the 100 μm sieve, and the filtrate, were filtered through separate pre-ashed, weighed GFC filters (25 mm diameter). Filtered seawater (0.45 μm) was used to wash the particulate matter in the sieve onto the filter. Each filter was flushed with ammonium formate isotonic with seawater, and the dry weight and ash free dry weight (450 °C for 3 h) obtained. An additional 50 ml sample was filtered onto 1 μm Nucleopore filter paper and the residue gently scraped off and concentrated on a glass slide for microscopic examination. An estimate of the presence of phytoplankton in the sample was obtained by subjective assessment of the percentage of the sample volume represented by algal species.

The calorific value of seawater was obtained by filtering the 100 μm fraction of 20 l of seawater collected over the mussel bed, onto a 0.45 μm Millipore filter (142 mm diam.). The residue on the filter was flushed with distilled water to remove salts, gently scraped from the paper with a blunt instrument, washed into a crucible with distilled water and dried at 60 °C for 2 d. The energy value of the particulate matter thus concentrated was measured with a Phillipson microbomb calorimeter. The ash remaining after firing (predominantly sand) was weighed and the energy value of the ash free dry weight of the sample calculated. Grinding the sample to obtain a homogeneous distribution of particulate matter reduced variability in consecutive readings of the same sample. All weighings were done on an electronic microbalance (readability 1 μg).

Assimilation of Detritus in the Field

Samples of 500 ml of seawater collected at Bailey's Cottage were passed through a 100 μm sieve. The particulate matter in the 2–100 μm particle range was then concentrated onto pre-ashed, weighed GFC filters and treated as above. Simulataneous with water collection, 6 mussels were removed from the mussel bed and placed in seawater. All faeces produced within 2 h were concentrated onto weighed GFC filters (pre-ashed) and washed with ammonium formate. Filters were dried at 60 °C, weighed and ashed at 450 °C for 3 h and weighed again. The ratio of the ash-free dry weight to dry weight of the water sample, i. e. food, and the faeces were used to determine the assimilation efficiency according to the method described by Conover (1966).

Assimilation of Detritus in the Laboratory

Mussels were allowed to feed in the laboratory on the detritus in freshly collected seawater to assess whether data comparable with that in the field (above) could be obtained. Large quantities of seawater were collected over the mussel bed each day and filtered through a 100 μm sieve to eliminate large sand particles and debris. Mussels collected the previous day were placed in a recirculating constant flow system which fed water to 4 animal chambers, each of 500 ml capacity. The flow rate exceeded 2 l h^{-1}. Tests using algal culture showed that this rate was sufficiently fast to prevent depletion of food within the animal chambers. The importance of this has been discussed by Hildreth and Crisp (1976). The 20 l of seawater contained within the system was changed at 0.5 h intervals to maintain the food concentration for the 3–4 h duration of the experiment. Replicate 500 ml samples of the water prior to use, and faeces collected immediately as they were produced, were filtered onto separate pre-ashed and weighed GFC filters and analysed as above. Faeces produced during the first hour of the experiment were discarded.

RESULTS

Seawater Analysis

The quantities of particulate organic and inorganic matter in the particle size ranges 2–100 μm and 100–200 μm, measured during one year, are shown in Figure 1. Organic material comprised 10–30 % of the total sample weight, the remainder being predominantly sand. Widdows et al. (1979) found that organic material represented 6–25 % of the particulate matter available to *Mytilus edulis* in the Lynher estuary, and Verwey (1952) an average of 12 % in the Wadden Sea. The organic material in the 2–100 μm range varied from 5–25 % of the total sample weight. Peaks in the amount of inorganic particulate matter generally coincided with rough sea conditions.

Figure 2 shows the variation in the dry weight of particulate organic material in the 2–100 μm and 100–200 μ range during the year. There was no clear

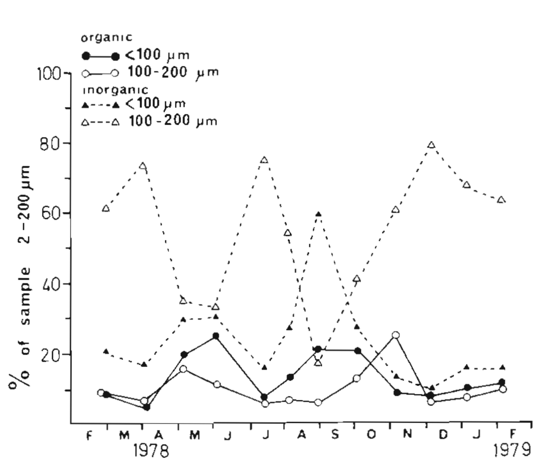

Fig. 1. Distribution of organic and inorganic matter in seawater in the particle diameter ranges 2–100 µm and 100–200 µm; measured as mg dry weight l^{-1} and expressed as a percentage of total sample weight

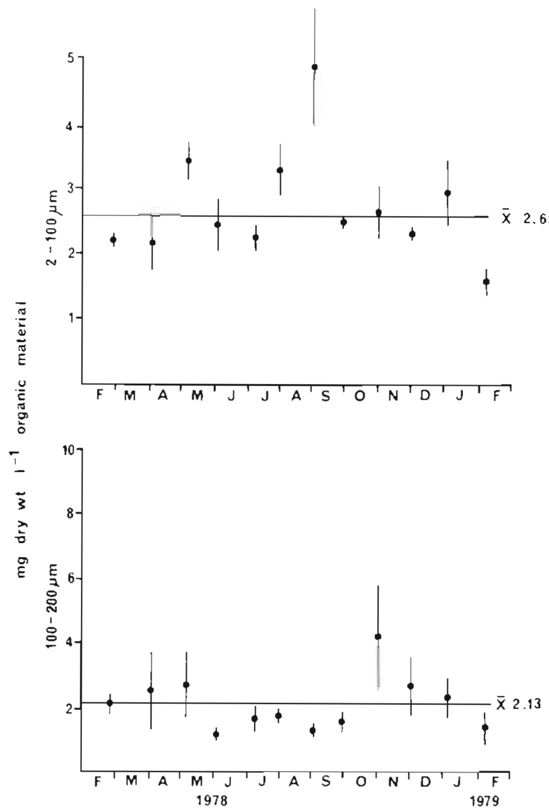

Fig. 2. Changes in weight of particulate organic matter in the diameter ranges 2–100 µm and 100–200 µm in seawater at Bailey's Cottage during one year. Vertical bars: one standard error

seasonal pattern and the data were surprisingly constant at an average of 2.65 mg l^{-1} and 2.13 mg l^{-1}, respectively. Table 1 summarises the data on the distribution of particulate organic and inorganic material. Whereas the 2–100 µm particulate organic material was represented predominantly by free or aggregated particles in the water column, those in the 100–200 µm range were more difficult to assess. During filtering very few free particulates were seen. It was concluded that the greater portion of the organic matter in this size range was attached to the sand grains. This would be rejected in the pseudofaeces.

The origin of the detrital matter at Bailey's Cottage could not be determined. It consisted of brown irregularly shaped particles without cellular structure. From September 1978 to February 1979 the detritus was dominated by uniform particles having the appearance of faecal pellets averaging 20 × 140 µm. Their origin is unknown.

A rough estimate of the presence of phytoplankton is shown in Table 2. The phytoplankters present were predominantly *Nitchia* and *Rhizosolenia* species. The latter was particularly abundant in May 1978 when it formed more than 90 % of the sample. However, phytoplankton was recorded on only 34 % of the days sampled and cannot be considered a major constituent in the diet of filter feeders at Bailey's Cottage.

The energy value of organic material (2–100 µm) in seawater over the mussel bed is shown in Table 3. Each value represents the mean of 2 or 3 readings on one sample. Twenty-five samples were taken on different days, under varying sea conditions, and different states of tide. There was considerable variability in readings on the same sample and between samples. The energy available in seawater averaged 5.74 kJ g^{-1} AFDW (ash-free dry weight) and inorganic material constituted 53 % of the samples. Paine (1966) has shown that endothermy may occur in samples containing $CaCO_3$ and a correction factor of 0.6 J mg^{-1} $CaCO_3$

Table 1. Proportion of organic and inorganic particles in size ranges <100µm and 100–200µm in seawater over a mussel bed at Bailey's Cottage, February 1978 to February 1979 (n = 97)

Amount	Organic		Inorganic	
	<100µm	100–200µm	<100µm	100–200µm
Average mg l^{-1}	2.65	2.13	5.69	15.21
One standard deviation	1.14	1.49	4.47	21.49
Maximum mg l^{-1}	6.95	10.29	25.76	109.12
Minimum mg l^{-1}	1.11	0.39	0.42	0.06
Mean % of sample	13.0	9.3	23.3	54.4

may be applied. Assuming that 50 % of the inorganic matter in Table 3 may represent $CaCO_3$ from exoskeletons or shells of marine organisms, the mean energy value may be increased by 6 % to 6.1 kJ g^{-1} AFDW.

Table 2. Number of days on which phytoplankters were recorded during the sampling period and an estimate of their abundance (2–100 μm particle size range)

Month	Days sampled	Days algae recorded	Phytoplankters as percentage of sample volume range	mean
Feb./March	21	5	10–60	24
April	5	5	6–30	15
May	5	5	90–98	95
June	5	0	–	–
July	5	1	–	50
July/Aug.	21	8	5–80	28
August	5	0	–	–
September	5	0	–	–
October	5	0	–	–
November	5	0	–	–
December	5	1	–	5
January	5	5	5–50	18
February	5	1	–	2

Table 3. Energy values of organic matter (< 100 μm particle size) in seawater at Bailey's Cottage. AFDW: ash-free dry weight

	kJ g^{-1} dry weight	kJ g^{-1} AFDW	% inorganic
	3.81	7.71*	52.0
	1.70	6.28	73.0
	2.75	10.10*	70.5
	4.00	10.90	53.0
	0.69	1.97	64.2
	2.38	5.74	58.6
	2.48	4.71	52.5
	0.34	1.59	78.4
	0.39	1.71	77.5
	0.79	2.37	66.8
	4.80	10.69	55.1
	2.06	5.21	61.1
	2.34	5.27*	55.5
	1.47	3.27	55.1
	0.37	1.14	67.7
	3.59	4.87	26.0
	4.00	6.27	34.7
	1.79	3.82	53.2
	2.83	3.97	25.9
	3.76	6.72	44.0
	3.61	7.83	54.0
	6.01	10.34	41.9
	2.74	4.64	40.9
	4.63	7.39	37.3
	5.70	9.08*	33.8
Mean	2.76	5.74	53.3

* Sampled during phytoplankton bloom

Assimilation of Natural Detritus

The average ration available as food in seawater falls above the range of positive assimilation efficiency in *Choromytilus meridionalis* when feeding on algal culture. Griffiths (1980) found that the assimilation efficiency fell to zero at a ration of 3 mg l^{-1} *Dunaliella primolecta* and pseudofaeces production was initiated at 6 mg l^{-1} dry weight. The average ration in seawater (< 100 μm particle size range, organic + inorganic) was 8.3 mg l^{-1}.

Figure 3 shows the assimilation efficiency of mussels feeding on natural detritus in the field and in the laboratory. No pseudofaeces production occurred in laboratory experiments. The curve for assimilation efficiency on *Dunaliella primolecta* is given for comparison. The data were plotted in terms of ration dry weight and AFDW. Laboratory measurements showed

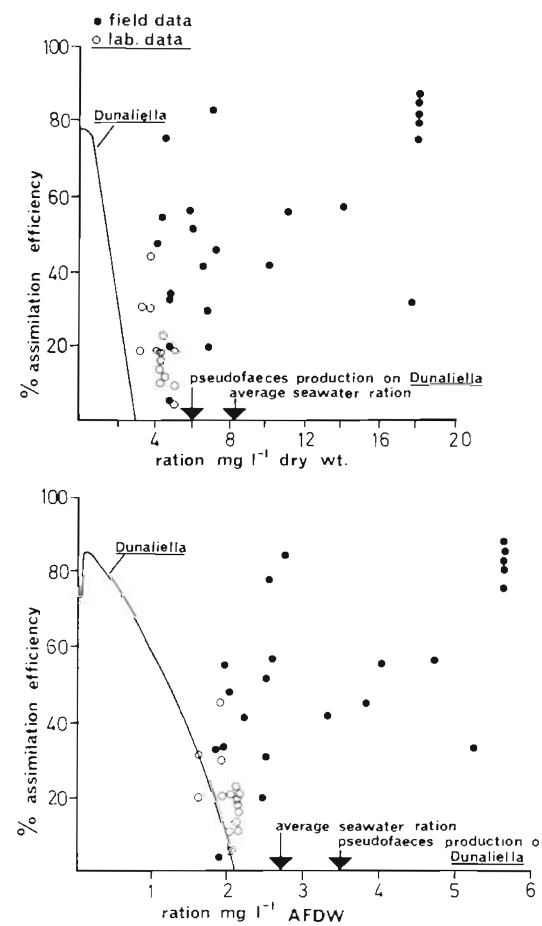

Fig. 3. *Choromytilus meridionalis.* Assimilation efficiency when feeding on natural detritus in field and laboratory. Curve of assimilation efficiency when feeding on pure *Dunaliella primolecta* culture given for comparison. Ration levels expressed as particulate dry weight (includes sand) and ash-free dry weight (AFDW); 2–100 μm particle size range

no detectable difference in the filtration rate of 45 mm mussels when feeding on detritus or algal culture. An average assimilation efficiency of 40 % (S. E. = 4.1 %, n = 37) was obtained over a wide range of ration levels. Variability in the data (maximum efficiency 87 %, minimum 4.5 %) may be a function of experimental technique. Water sampled at any one instant in the field may not reflect that which had been filtered by the mussel during the hour prior to removal from the bed. Furthermore, Foster-Smith (1975) has shown that some retention of ingested material may occur in *Mytilus edulis* and that this may be mixed with material ingested later and subsequently defaecated. Although the passage of algal cells through the gut of *Choromytilus meridionalis* may take place within 1 h, sand particles may be egested up to 12 h after removal of mussels from the natural habitat.

DISCUSSION

Microscopic examination of the faeces collected from 45 mm *Choromytilus meridionalis* in the field showed that they contained large quantities of sand mixed with detritus. The particulate matter in faeces averaged 50 μm, with particles seldom exceeding 100 μm diameter. Examination of the distribution of particulate matter in seawater showed that 13 % of the organic particulate matter occurred in the 2–100 μm size range. However, more than 50 % of the sample consisted of sand particles in the 100–200 μm size range. Most of the organic material in this range was attached to the sand grains. Mussels filtering on the shore were observed to eject large quantities of sand in the form of pseudofaeces continuously. On the basis of these observations it was concluded that the bulk of food available to the mussels is represented by particles measuring 2–100 μm diameter, and that particles exceeding this size are rejected as pseudofaeces.

Several authors have examined particle size selection in mussels and Bayne et al. (1976) conclude that selective removal does not occur in mussels feeding on natural seawater (2–100 μm particle size range). Although authors such as Vahl (1972, see also review by Bayne et al., 1976) have shown retention of particles below 2 μm by the mussel gill, this size range could not be measured in the present study. In view of the large quantities of organic detritus measured in the 2–100 μm size range, particles below 2 μm are unlikely to form a significant proportion of the diet.

Total organic particulate matter at Bailey's Cottage averaged 5 mg l^{-1}, while an average of 2.65 mg l^{-1} was considered available to the mussels. Armstrong and Atkins (1951) report 1.6–1.8 mg l^{-1} particulate organic material in the English Channel, Widdows et al. (1979) 1.5–1.9 mg l^{-1} in the Lynher estuary, and Verwey 3 mg l^{-1} available to mussels in the Wadden Sea. Other values measured generally average less than 1 mg l^{-1} (Jørgensen, 1955). However, it is doubtful that samples taken in the relative calm of deeper waters may be compared with those from the surf zone. Wave action and continual resuspension of the sandy substrate will enhance degradation of organisms and faeces and maintain high levels of organic detritus in the water column.

The energy value of organic detritus at Bailey's Cottage averaged 6.1 J mg^{-1}. Widdows et al. (1979) obtained a value of 23.5 J mg^{-1} of food available to *Mytilus edulis* by analysing the proportions of carbohydrates, lipids and proteins in seawater. At food suspensions of 1.5–1.9 mg l^{-1} (Widdows et al., 1979) the energy available to *M. edulis* in the Lynher estuary is 35.2–44.7 J l^{-1} of seawater. By comparison, the ration available to *Choromytilus meridionalis* at Bailey's Cottage averages 16.2 J l^{-1}.

The assimilation efficiency on natural detritus proved variable but averaged 40 %. Although the method used may over- or under-estimate the true assimilation efficiency in the field, it is clear that *Choromytilus meridionalis* must be able to maintain a positive energy balance over the normal range of particulate material present in seawater. Experiments using *Dunaliella primolecta* are thus not directly applicable to natural conditions in the field.

The presence of large quantities of inorganic matter in the bivalve diet appears to be a common phenomenon and Winter (1976) has shown that silt has a beneficial effect on growth in *Mytilus edulis*. However, this is not merely a result of the presence of silt, but an interaction between total particulate concentration and the ratio of food to silt in the water. Widdows et al. (1979) found that increasing particle concentration results in increasing pseudofaeces production in *M. edulis*, and the ingestion ration remains at a constant level. This limits the amount of food entering the gut, enabling digestion to continue at high particulate concentrations. However, the presence of inorganic particles 'dilutes' the available food ration, and increasing inorganic particulate matter in the diet results in a decline in the energy assimilated. The ratio of organic to inorganic matter is thus important in influencing the energy balance.

In *Choromytilus meridionalis* a constant filtration rate is maintained over a wide range of ration levels (Griffiths, 1980) and pseudofaecal production must be important in limiting the ingestion ration at high food levels. When feeding on a concentrated food source such as algal culture, with little particulate inorganic material present, pseudofaecal production is not initiated sufficiently early to limit the ingestion ration before assimilation efficiency falls to zero. Such a concentrated food source would not be experienced in the field. The presence of particulate inorganic matter may prove an important dietary requirement in *C. meridionalis* in 'diluting' the high organic levels in the sea and allowing a positive assimilation efficiency over a wide range of ration levels.

Acknowledgements. This work was supported as part of the Kelp Bed Research Programme by the South African National Committee for Oceanographic Research.

LITERATURE CITED

Armstrong, F. A. J., Atkins W. R. G. (1951). The suspended matter of sea water. J. mar. biol. Ass. U. K. 29: 139–144

Bayne, B. L., Thompson, R. J., Widdows J. (1976). Physiology. In: Bayne, B. L. (ed.) Marine mussels, their ecology and physiology. Cambridge University Press, London, pp. 121–206

Conover, R. J. (1966). Assimilation of organic matter by zooplankton. Limnol. Oceanogr. 11: 328–354

Foster-Smith, R. L. (1975). The effect of concentration of suspension and inert material on the assimilation of algae by three bivalves. J. mar. biol. Ass. U. K. 55: 411–418

Fox, D. L., Coe, W. R. (1943). Biology of the Californian seamussel (*Mytilus californianus*) II. Nutrition, metabolism, growth and calcium depostion. J. exp. Zool. 93: 205–249

Griffiths, C. L., King, J. A. (1979). Some relationships between size, food availability and energy balance in the ribbed mussel *Aulacomya ater*. Mar. Biol. 51: 141–149

Griffiths, R. J. (1980). Filtration, respiration and assimilation in the black mussel *Choromytilus meridionalis*. Mar. Ecol. Prog. Ser. 2: 63–70

Hildreth, D. I., Crisp, D. J. (1976). A corrected formula for calculation of filtration rate of bivalve molluscs in an experimental flowing system. J. mar biol. Ass. U. K. 56: 111–120

Jørgensen, C. B. (1955). Quantitative aspects of filter feeding in invertebrates. Biol. Rev. 30: 391–454

Paine, R. T. (1966). Endothermy in bomb calorimetry. Limnol. Oceanog. 11: 126–129

Vahl, J. (1952). Efficiency of particle retention in *Mytilus edulis* L. Ophelia 10: 17–25

Verwey, J. (1952). On the ecology and distribution of cockle and mussel in the Dutch Waddensea, their role in sedimentation and the source of their food supply. Arch. Néerl. Zool. 10: 171–239

Widdows, J. (1978). Combined effects of body size, food concentration and season on the physiology of *Mytilus edulis*. J. mar. biol. Ass. U. K. 58: 109–124

Widdows, J., Fieth, P., Worral, C. M. (1979). Relationships between seston, available food and feeding activity in the common mussel *Mytilus edulis*. Mar. Biol. 50: 195–207

Winter, J. E. (1976). Feeding experiments with *Mytilus edulis* L. at small laboratory scale II. The influence of suspended silt in addition to algal suspension on growth. In: Persoone, G., Jaspers, E. (eds) Proceedings of 10th European symposium on marine biology, Vol. 1, Ostend, Belgium. Universa Press, Wetteren, pp. 565–581

This paper was presented by Professor R. C. Newell; it was accepted for printing on April 12, 1980