Α

QUALITATIVE AND QUANTITATIVE ASSESSMENT OF SEAWEED DECOMPOSITION IN THE STRAIT OF GEORGIA

by

BARRY DOUGLAS SMITH
B.Sc. (Honours), University of New Brunswick, 1974

A THESIS SUBMITTED IN PARTIAL FULFILMENT OF
THE REQUIREMENTS FOR THE DEGREE OF
MASTER OF SCIENCE

in

THE FACULTY OF GRADUATE STUDIES
(Department of Botany)

We accept this thesis as conforming to the required standard

THE UNIVERSITY OF BRITISH COLUMBIA

June, 1979

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Department of <u>Botan</u>

The University of British Columbia 2075 Wesbrook Place Vancouver, Canada V6T 1W5

Date 26 April 1979

ABSTRACT

Appropriate sampling and experimental programs resulted in a qualitative and quantitative assessment of seaweed litter biomasses, decomposition rates and concomitant changes in nitrogen content; detritus biomass and decomposition rates; and faunal distribution patterns for the significant species within a successional seaweed community in the Strait of Georgia, British Columbia, Canada.

A simulation model incorporating suitable data obtained from these sampling and experimental programs facilitated prediction of detritus formation rates, biomass, nitrogen content and the seasonal availability of detritus as a food resource for fauna. Soluble matter release rates from decomposing seaweed litter and its nitrogen content were also determined.

of the ca 43 taxa identified within the seaweed litter collections, Fucus distichus L. (41%), Iridaea cordata (Turner) Bory (26%), Nereocystis lutkeana (Mertens) Postels and Ruprecht (27%), and Laminaria (4%) (L. saccharina (L.) Lamouroux and L. groenlandica Rosenvinge) accounted for more than 97% of total litter deposition. The mean peak summer biomass of all litter was ca 5 g ash-free dry weight (AFDW)/m² with this figure approaching zero during January and February. Litter distribution was patchy and there was sufficient evidence to conclude that most litter was retained, and underwent decomposition, in the immediate vicinity of its place of deposition.

Litter decomposition experiments performed on the 10 most significant contributors to seaweed community structure indicated that decomposition of seaweed litter occurs rapidly compared to vascular plant litter. The time required for seaweed litter to disappear from 2 mm mesh litter bags ranged from . six days, for the lamina of Nereocystis luetkeana, to ca 70 days, for Fucus distichus. Some similarity in decomposition rates was observed amongst species

displaying taxonomic and/or morphologic affinities. Assessment of nitrogen content of decomposing seaweed litter revealed that nine of the 10 species assayed lost nitrogen less rapidly than total litter biomass.

As determined by assaying microbial consumption of particulate material, the time required for detritus (particle size < 1 mm, dry) to fully decompose was short. Of the 10 species tested, Iridaea cordata detritus decomposed most rapidly at a rate of 5.7% per day while rates for Gigartina papillata (C. Agardh) J. Agardh, Laminaria groenlandica, Laminaria saccharina and Nereocystis luetkeana ranged from 2-4% per day. Data for the remaining species were less conclusive although all decomposed at rates less than one percent per day.

Variation in specific decomposition rates was shown to be correlated with the structural composition of the detritus. Those species with a relatively small percentage of crude fibre as a component of their particulate fraction decomposed more rapidly than those species with a higher percentage of crude fibre. For the two most rapidly decomposing species, Iridaea cordata and Nereocystis luetkeana, a trend toward a more rapid decomposition rate as mean particle size decreased was evident.

Natural detritus (particle size < 2 mm, wet) biomass accumulation within the study site peaked at ca 1.4 g AFDW/ m^2 during the latter half of August 1976. This value represents 1-5% of the quantity of detritus predicted to have been formed from seaweed litter alone and a lesser percentage of the total quantity of seaweed detritus formed. Exportation out of the seaweed zone is believed to be responsible for this discrepancy. The predicted rates of detritus formation and soluble matter release from decomposing seaweed litter peaked at ca 0.6 and 0.5 g AFDW/ m^2 per day, respectively, in early September 1976 from a low near zero in February. In total, ca 56% of litter biomass formed detritus, the remainder being released as soluble matter. The mean nitrogen contents of the detritus formed and the soluble matter released were 2.48 \pm 0.03% and 1.36 \pm 0.03%

of their dry weights, respectively. The annual contribution of seaweed litter biomass via detritus and soluble matter to local coastal waters is estimated to be in the range of 70-85 g C/ m^2 .

Detritus formed from seaweed litter was determined to have a C:N ratio of 10-13:1, rendering it suitably nutritious for utilization by fauna as a food resource, however it could not be shown conclusively that the coincidence, en masse, of specific fauna and maximum detritus availability was a response to the availability of detritus as a food resource. The possibility of such a correlation is discussed with reference to two species of caprellids, Caprella alaskana Mayer and Metacaprella anomala Mayer, and the benthic gastropod Lacuna marmorata Dall.

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ACKNOWLE DGEMENTS

Many persons need to be credited for their contribution toward the successful completion of this thesis. I appreciate the supervision of Dr. Ronald E. Foreman who provided research facilities and first hand experience with the study of marine macrophyte systems. Mr. Thomas Nicol was very helpful with computing problems, particularly during development of the simulation model. Perhaps the most important contribution to this work was the effort of my SCUBA partners. I am especially grateful to Mr. Eric L. Cabot who was my diving buddy for most of the field sampling exercises. The staffs of the Woodward Biomedical Library and the U.B.C. Computing Centre provided excellent service. I thank Ms. Nancy A. Smith for her assistance with the typing.

INTRODUCTION

Primary production by terrestrial and aquatic plants is the major source of food energy for consumer organisms. In many cases it has been shown that heterotrophic utilization of primary production involves largely a delayed consumption of detritus. Darnell (1976a) defines detritus as being "all types of biogenic material in various stages of microbial decomposition which represent potential energy sources for consumer species". This definition is appropriate, but includes material that this study interprets as 'litter', defined as larger, less fractured material whose biogenic origin can be easily recognized.

The importance of detritus as a food source for consumers has been demonstrated for several ecosystem types. In an east coast salt marsh studied by Teal (1962) only 7% of the net primary production was utilized in herbivore respiration while 47% was utilized by decomposer organisms associated with detritus derived from Spartina litter. Similarly, data for several terrestrial systems indicate that 62-100% of net primary production enters the litter pool (Rodin and Bazilevich 1967) with future processing forming detritus. An exception to this trend is found in plankton based systems where up to 90% of the primary production may be consumed by zooplankton grazers. In such cases a large portion of the material consumed may pass through the gut of the zooplankters without being assimilated, and enter the decomposer food chain. This is especially true during bloom conditions (Cushing 1964).

To date, studies concerning detritus formation and utilization in coastal marine ecosystems have dealt mainly with aquatic vascular plants such as Zostera marina L. (Harrison and Mann 1975 a&b, Harrison 1977, Tenore et al.1977), Thalassia testudinum Banks ex König (Fenchel 1970, Wolff 1976, Knauer and Ayers 1977), mangroves (Heald 1969) and Spartina alterniflora Loisel as well as other salt marsh plants (Odum and de la Cruz 1967, de la Cruz

and Gabriel 1974, Gosselink and Kirby 1974, de la Cruz 1975, Gallagher et al. 1976, Pickral and Odum 1976, Hanson and Weibe 1977). This work has been reviewed by Fenchel (1972, 1973). The importance of associated microorganisms in this process has been stressed by Johannes (1965), Seki (1972), Fenchel and Harrison (1976), and Heinle et al. (1977). These studies have been largely of a qualitative nature with little attempt to quantify plant detrital contributions to coastal energy flow.

There are but a few studies concerning detritus formation by attached marine macrophytes. Although estimates of primary production for the coastal seaweed zone indicate that these areas are amongst the most highly productive in the world (Clendenning 1971, Mann 1972a) very little is known of the fate of this production. With the macrophytic fringe of the oceans having a productivity that may be up to 40 times that of the ocean (Mann 1972a) and a standing crop exceeding that of phytoplankton by 100 fold (Blinks 1955), the possibility of its having a more than token contribution to the energy flow in near-shore ecosystems of which some commercial fish species may be components becomes a reality. Salmon (Oncorhynchus spp.) and herring (Clupea harengus pallasii Valenciennes), currently the most valuble fish to the British Columbia economy (Statistics Canada 1976) spend critical times of their lives in near-shore waters. Herring are dependent on seaweed as substrate for their spawn (Taylor 1964). Young salmon feed in estuarine waters (Sibert et al. 1977).

Mann (1972b) estimates the yearly productivity of the seaweed zone in St. Margaret's Bay at 1750 g C/m². This makes the seaweed zone the only primary marine resource with a confirmed yearly production greater than 1 kg C/m².

Possible fates of seaweed production are:

1. exudation as soluble matter

- 2. consumption by herbivores
- 3. erosion and fragmentation from lamina tips
- 4. release as reproductive structures
- 5. natural mortality
- 1) The release of soluble organic compounds from marine seaweeds was first demonstrated by Craigie and MacLachlan (1964). Later Sieburth and Jensen (1968) and Sieburth (1969) established that exudation from marine macrophytes is comparable to that of phytoplankton which Fogg (1966) states to lie between 5% and 35% of total carbon fixed within a population. Fucus vesiculosis L. was estimated to lose 30.7% of its total carbon budget as exudate, at an average rate of 41.6 mg $C/100 \, g/hr$. These rates are comparable to those obtained for other Phaeophyta; 44.6, 37.8 and 31.3 for Laminaria digitata (L.) Lamouroux, Laminaria agardhii Kjellman, and Ascophyllum nodosum (L.) Le Jolis, respectively. Chondrus crispus Stackhouse (Rhodophyta) was significantly lower at 4.4 mg C/100 g/hr. Johnston et al. (1977) determined that up to 36% of total carbon fixed by Laminaria saccharina (L.) Lamouroux was released extracellularly. Brylinsky (1977) examined two species each of Rhodophyta, Acanthophora spicifera (Vahl) Borgesen and Chondria dasyphylla (Woodward) C. Agardh, and non-kelp Phaeophyta, Dictyota dichotoma (Hudson) Lamouroux and Sargassum natans (L.) Meyen, and determined physiological release rates of less than 4.0% of total carbon, disclosing an apparent disparity in release rates between kelp-like seaweeds and others.
- 2) Sea urchins are generally recognized as the most significant and prominent grazers in temperate seaweed systems. Miller and Mann (1973) concluded that the green sea urchin Strongylocentrotus droebachiensis Müller, the apparent major herbivore in eastern Canada, consumed only 1-7% of seaweed net production during their period of study. With Strongylocentrotus droebachiensis accounting for 80% of the herbivory in this area (Miller et al. 1971),

consumption of seaweed biomass approached 10% of net production.

On occasion large numbers of sea urchins have severely perturbated the seaweed zone (Leighton et al. 1966, Paine and Vadas 1969, Leighton 1971, Miller and Mann 1973, Breen and Mann 1976, Foreman 1977, Mann 1977). This has sometimes resulted in total denudation of the affected area both by direct grazing and by detaching plants from the substrate. During these periods the detached plants complement dead plant material from other sources in contributing to the pool of marine plant litter.

- 3) Johnston et al. (1977) present quantitative information on erosion from lamina tips. They estimate that for Laminaria saccharina growing in a sheltered location near the head of Loch Creran, Scotland, 40-50% of annual gross production is lost by distal decay, resulting in a contribution to either the detrital or litter pools depending on whether the loss is via erosion or fragmentation, respectively. Plants growing in more exposed locations might be expected to lose a higher percentage of their carbon budget by distal decay. Laycock (1974) demonstrated that large populations of bacteria associated with the lamina tips of Laminaria longicruris de la Pylaie were at least partially responsible for distal decay.
- 4) As release of reproductive structures would be indistinguishable from the exudation of soluble matter or loss of particulate biomass, the need to consider reproductive losses separately is precluded.
- 5) Natural mortality constitutes the final exit pathway.

 The death of the seaweeds initiates their entry into the pool of marine plant litter where they undergo decomposition concomitant with the formation of detritus and detritus processing.

In an attempt to place the various aspects of the seaweed 'biomass budget' into perspective, Khailov and Burlakova (1969) proposed a

quantitative partitioning of the total gross production of seaweeds into suitable compartments. From experiments with five species of Barents Sea macrophytes and 13 species of Black Sea macrophytes they judge loss due to consumption by herbivores to be ca 11.2% and calculate that 37.3% of gross production is represented by living biomass, the major source of detritus, either via erosive or litter pathways.

With the realization that the contribution of seaweed production to the detrital pool may exceed its consumption by herbivores by three to four fold it does not seem unreasonable or premature to suggest that detritus processing is an essential aspect of energy flow in near shore ecosystems. To confirm this hypothesis it is necessary that the dynamics of seaweed litter decomposition along with subsequent detritus formation, processing, and utilization be investigated.

This thesis descriptively and quantitatively assesses the contribution of seaweed litter biomass to the detrital pool. The objectives of the study were:

- to determine the total quantity and seasonal abundance of seaweed litter available as a source of detritus in a defined area
- 2) to determine the formation rate, longevity and decomposition rate of detritus formed from selected seaweed species
- 3) to predict the seasonal rates of detritus formation, its biomass and nitrogen content for a defined area, and assess its importance as a food resource for fauna
- 4) to characterize selected seaweed species in terms of their 'soluble', 'moderately resistant', and 'crude fibre' components and correlate differences in the relative quantities of these components with observed decomposition rates for litter and detritus.

These objectives were realized by conducting specific sampling and experimental programs and by execution of a simulation model of litter and detritus processing based on data acquired from these programs.

METHODS

THE STUDY AREA

adjacent to the southeastern shore of Bath Island, British Columbia, the eastern most of a cluster of small islands known as The Flat Tops. These islands are ca 32 km west of the mouth of the Fraser River, and hug the southeastern extension of Gabriola Island, the northernmost of a group of islands called The Gulf Islands (Figure 1). Bath Island is 3.2 hectares in area, its main geological component being sandstone complemented with minor amounts of shale and conglomerate (Muller 1971). The main research area is a gently sloping one hectare plot well exposed to the southeast. The plot can be appropriately described as a successional kelp bed due particularly to the extensive stand of Nereocystis luetkeana (Mertens) Postels and Ruprecht which does well there (Foreman 1977). This one hectare plot will be known as Site 1. A second location, near Site 1, will be referenced as Site 2.

All laboratory work was performed in the Department of Botany at the University of British Columbia.

SAMPLING

Three sampling programs were implemented:

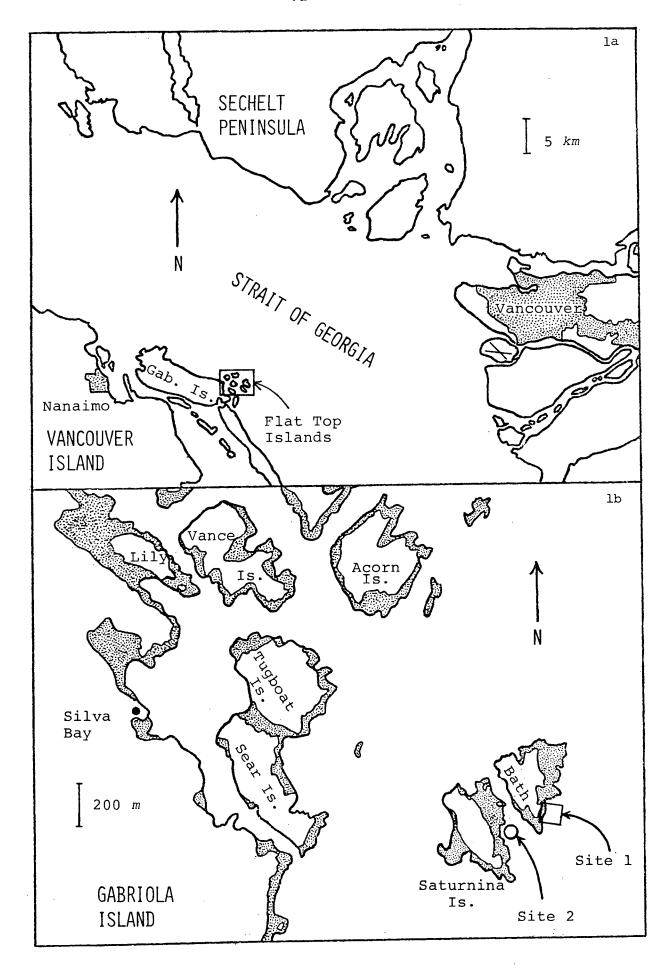
- 1) to determine the seasonal and spatial distribution of seaweed litter biomass within Site 1
- 2) to determine the seasonal distribution of detritus biomass within Site 1
- 3) to determine the seasonal and spatial distribution of invertebrate fauna within Site 1.

Litter Assessment:

The main, permanently marked transect location intersected the shore at 95 m along the 100 m shore front forming the base of Site 1. At times

Figure 1. Locations of field study sites.

- a) Flat Top Islands in relation to the lower mainland of British Columbia.
- b) Site 1 and Site 2 in relation to the Flat Top Islands.



of sampling a line 100 m in length was extended from the high intertidal zone (upper limit of barnacles) to a point beyond the zone of most seaweed No significant accumulations of litter were observed outside of the zone sampled. Two scuba divers then proceeded to collect all seaweed litter that lay within a metre on either side of the transect line. The transect was segmented into ten 20 m^2 quadrats with the collections from each being placed in an appropriately labelled baq. On occasion, when the quantity of litter within a standard 20 m^2 quadrat was more than could be easily collected, the quadrats were subsampled in a representative fashion. Sampling at this site was carried out at ca 3-4 week intervals from August 1975 until October 1976. These data were used to determine the seasonality of the biomass of seaweed litter. On 3 August 1976 similar transects were sampled from 5, 35 and 65 malong the base in order to determine the spatial distribution of litter within Site 1. On one occasion (10 November 1975) a single transect was collected at Site 2, ca 200 m away and less exposed than Site 1, allowing a comparison of the two areas to be made.

When collections were made a seaweed was classified as litter if it could be described by one of the following phrases:

- detached and having settled to the bottom, generally snagged amongst rocks or debris
- 2) attached but apparently dead
- 3) in the case of Nereocystis luetkeana stipes, attached or unattached and lying prone, the pneumatocyst having flooded.

For each site a transect depth profile was recorded and for each quadrat the substrate was described. On 3 August 1976 the number of living

Nereocystis luetkeana plants in each quadrat of the four transects located

within Site 1 was enumerated.

All collections were transported to the laboratory where they were sorted and identified as precisely as possible according to Widdowson (1973, 1974) and Lindstrom et al. (1974). Laminaria saccharina and Laminaria groenlandica were not always distinguishable and so were often recorded only as Laminaria. Nereocystis luetkeana was subscripted as either stipe or lamina litter. For each taxon in every quadrat the wet weight, dry weight (24 hours at 100 C) and ash-free dry weight (12 hours at 425 C) were recorded.

Detritus Assessment:

From May 1976 until October 1976 at ca three week intervals the biomass of detritus within Site 1 was determined. Nine permanent quadrat locations were fixed, roughly corresponding to 20,30...100 m along a transect perpendicular to the shore at 95 m along the base of Site 1. The actual positioning of the quadrat was determined by the availability of relatively flat, continuous substrate extensive enough to accommodate a 0.0625 m^2 quadrat. Each of these quadrat locations was initially scrubbed clean with a wire brush, and again following each sampling period.

Detritus was collected using a hand pump designed for bailing small boats. It was modified by securing an 11 lb plastic bag to the exhaust port. By operating the pump in a normal fashion, passing the intake port over the quadrat, all loose material was sucked into the bag. Control samples were collected by drawing sea water into the bag while the intake port was well above the substrate. Upon returning to shore, the contents of each bag were screened through 2 mm mesh household screening to remove large particles, then passed through preweighed Whatman GF/\mathbb{R} glass fibre filters (2-3 μm pore size) using a Millipore filter apparatus. The residuum was dry weighed (12 hours at 100 C) and ash-free dry weighed (4 hours at 425 C).

Faunal Assessment:

From May until October 1976 at approximately three week intervals, faunal collections were made within Site 1. The sampling procedure involved the collection of $0.0625 m^2$ quadrats at 30,40...100 m along the permanently located transect at 95 m along the base of Site 1. The organisms were collected using an underwater airlift (Foreman 1977) and trapped in a collecting bag made from panty hose. Samples were transported to the laboratory while fresh where they were sorted, identified according to Kozloff (1974), counted, and wet and dry (24 hours at 100 C) weighed.

FIELD EXPERIMENTS

Two field experiments were performed during July and August 1976. The first was designed to obtain in situ rates of decomposition for killed seaweeds, the second to estimate senescence times for those species contributing significantly to the litter within Site 1.

Litter Decomposition Experiments:

Seaweeds were chosen for the litter decomposition experiments on the basis of their contributions to the standing crop of living seaweed biomass within Site 1 (coralline algae excluded). As Site 1 overlaps almost entirely the one hectare plot Foreman (1977) defined for his biomass studies in 1972, his data were used as a criterion for ranking the seaweeds. They are, in decending order of their 'importance values' (Foreman unpub.):

Iridaea cordata (Turner) Bory
Constantinea subulifera Setchell
Laminaria (L. saccharina, L. groenlandica Rosenvinge)
Fucus distichus L.
Odonthalia floccosa (Esper) Falkenberg
Rhodomela larix (Turner) C. Agardh
Plocamium coccineum var. pacificum (Kylin) Dawson
Gigartina papillata (C. Agardh) J. Agardh
Nereocystis luetkeana

The above species accounted for just over 80% of seaweed standing crop biomass, exclusive of coralline algae, as their contribution to litter would be minor.

In the litter bag experiments Laminaria saccharina and Laminaria groenlandica were considered separately as were the stipe and lamina sections of Nereocystis luetkeana, bringing the total count of individual experiments to 11. The appropriate seaweeds were collected live, cut into portions suitable for the litter bags, wet weighed and killed by placing them in a seawater bath at ca 50 C for 10-15 minutes. A separate portion of each seaweed, a control, was wet and dry weighed without undergoing decomposition.

The remaining portions were placed in 15 cm x 15 cm litter bags made from plastic household screening (2 mm mesh). Three litter bags were prepared for each seaweed tested with the exception of Fucus distichus for which four bags were prepared. Each litter bag was placed in a larger (1 cm mesh) bag and suspended from the mesh (5 cm) forming the roof of an aluminum framed cage $(2.0 \text{ m} \times 1.5 \text{ m} \times 0.5 \text{ m})$ constructed as a precaution to reduce the interference of large animals which might graze upon or otherwise interact with the decomposing seaweed. The cage was placed on the bottom at ca 6 m below mean sea level in a relatively sheltered embayment (Site 2). From preliminary experiments it was judged that the breakdown of the seaweeds would be rapid, therefore the litter bags were retrieved based on visual observations of the progression of the decomposition process rather than according to a predetermined schedule. The material which remained in the litter bags at the termination of the incubation period was removed, dry weighed and saved for nitrogen determination. Following completion of all incubations the dry weights were normalized with respect to the control and expressed as a percentage of the original dry weight of the material placed in the litter bags.

Litter Senescence Experiments:

A second experiment was performed to determine the time required for the seaweeds which appeared to be the more significant contributors to the litter within Site 1 to die once having entered the litter pool. Death is considered to be the time when tissue breakdown by autolytic or saprophytic means begins. The species chosen were Nereocystis luetkeana (stipe and lamina sections), Laminaria saccharina, Laminaria groenlandica and Iridaea cordata. Live portions of each of these seaweeds were placed in 1 cm mesh litter bags (not necessarily a single species per bag) and secured to the substrate within Site 1 at ca 3-5 m depth. Some bags were left exposed while others were placed between rocks or within shaded crevices. These bags were observed over five weeks,

noting changes in the condition of their contents.

The time required for a seaweed to die was estimated by assuming that once dead, the number of days required for seaweed biomass to leave a 1 cm mesh litter bag was about one half the number of days required for it to leave a 2 mm mesh bag. The latter data are known from the litter decomposition experiments. By subtracting the latter number of days from the number of days required for the unkilled seaweed to disappear from the 1 cm mesh bags, the length of time required for fresh litter to die was estimated.

LABORATORY EXPERIMENTS

Detritus Decomposition:

Detritus was created from seaweed species which had been collected live, washed, cleaned, dried, crushed by hand and processed in a Wiley mill. Three size fractions of detritus (1000-420 µm, 250-149 µm and 44-0 µm) were then collected by shaking the crushed seaweed through a series of Endicott sieves. The ratio of surface area exposed to microbial attack for the three size categories will be, from the largest to the smallest, ca 1:4:32, when all are present in equal mass. By setting the upper limit of detrital particle size at 1.0 mm (dry) the detritus decomposition experiments can be considered a continuation of the litter decomposition experiments which assessed the formation rate of detrital particles < 2.0 mm (wet). The detritus was derived from the same 10 species used in the litter bag experiments, the stipe and lamina sections of Nereocystis luetkeana being considered separately.

Two experiments were performed to assess the microbial utilization of this detritus, one based on oxygen consumption, the second based on microbial consumption of particulate material. Both experiments were structured around a 3 x 3 x 11 factorial design (Hicks 1973) incorporating three particle sizes, three incubation periods, and 11 experimental sets (10 species).

Experiment 1 (Microbial Oxygen Consumption):

Assessment of oxygen consumption required 12 acid-washed, 300 mL Biochemical Oxygen Demand (BOD) bottles for each incubation set. Oxygen content was assayed by the Winkler method (Strickland and Parsons 1972). Into three of each subset of four bottles, a 1.0 mg plug of detritus of a single size class was placed; the fourth remained a control. This procedure was repeated for the other two size classes. An inoculum of 1.0 mL of fresh seawater was pipetted into each BOD bottle as a source of microbes, following which all bottles were

filled with filtered (0.45 μ m) and aerated seawater. The bottles were capped and incubated in a 15 C water bath and agitated daily. Bottles representing each particle size, and a control (four in total) were removed after each of 5, 10, and 20 days of incubation. They were immediately fixed with the appropriate reagents. Twenty days was sufficient time to allow a significant drop in the oxygen content of the bottles while avoiding depletion. This procedure was repeated for all 11 sets.

Experiment 2 (Microbial Consumption of Particulate Material):

Each incubation set for the experiments to assess loss of particulate matter required eighteen 250 mL Erlenmyer flasks (six flasks per size class) as culture vessels. A 0.1 g plug of detritus representing a single size class was added to each flask. These 18 flasks were divided into two equal sets. To one set, the control, $100 \ mL$ of $0.45 \ \mu m$ filtered, sterile seawater containing KCN at a concentration of 0.1% (Harrison and Mann 1975b) was added. The second set received $100 \ mL$ of the sterile seawater enhanced with $0.15 \ g/L$ of $NaNO_3$ (Gosselink and Kirby 1974) and was inoculated with $1.0 \ mL$ of fresh seawater. Each experimental flask was thus paired with a control flask. All flasks were incubated at $15 \ C$ and agitated regularly. That sterility prevailed in the control flasks was confirmed by the clarity of the control flasks when compared to the experimental flasks.

At 10, 20, and 30 day intervals an experimental flask and a control flask of each particle size (six in total) were retrieved. The contents of each flask were filtered through preweighed Whatman GF/C glass fibre filters. The filters were dried (4 hours at 100 C) and weighed. The loss of particulate material for any treatment group was determined by subtracting the residue weight for each experimental flask from that of the control flask.

Nitrogen Content of Decomposing Litter:

The total nitrogen content of the seaweed material which remained in the litter bags at the time they were retrieved was determined using a macro-Kjeldahl method (Skoog and West 1969). The quantity of nitrogen obtained in each assay was expressed as a percentage of the total dry weight of the material assayed.

Structural Composition of Species Contributing to Litter:

For all 10 seaweed species and the stipe and lamina sections of Nereocystis luetkeana the contribution by each of three basic structural components to living seaweed biomass was determined on a dry weight basis. These components will be referred to as the 'soluble', 'moderately resistant' and 'crude fibre' components.

For experimental purposes material which passed through a filter of 2-3 µm pore size was classified as 'soluble'. 'Moderately resistant' refers to material which is particulate and easily metabolized by microbes, being composed largely of low molecular weight and non-structural polymeric compounds within the cell matrix. 'Crude fibre' consists mainly of cellulosic sugar polymers that are somewhat resistant to the attack of microbes. These polymers are generally responsible for the structural integrity of cell walls (Steward 1974).

Both the soluble and crude fibre components were determined explicitly. The quantity of soluble matter was determined in Experiment 2 of the detritus decomposition experiments. The weight of the residuum obtained from filtering (2-3 µm pore size) the contents of the control flasks at the end of each incubation period was subtracted from the initial weight (0.1 g) of the material in the flasks, this being the quantity of material passed through the filter, i.e. the soluble content. Accepted values for soluble content were obtained by averaging the results of the 10 and 20 day incubation periods since

by day 30 there were indications that some of the control flasks were no longer sterile. An analysis was performed using the method described by Strickland and Parsons (1972) to determine the percentage of crude fibre present in seaweed biomass. The dry weight of the crude fibre fraction was determined following extraction of the alkali/acid-soluble components of 30 mg samples of ground seaweed (0-44 µm particle size). Crude fibre carbohydrate content (expressed as an equivalent amount of glucose) was determined spectrophotometrically. Sample sizes were 1.0 mg.

MODEL DEVELOPMENT AND DATA ANALYSIS

Much of the data required from the previously described sampling and experimental programs were suitable for incorporation into a mathematical model created to simulate the transport of decomposing seaweed biomass through detrital pathways. Most of the data were acquired with this end in mind. The model also incorporated environmental data measured during 1975 and 1976 as a part of an ongoing program by Foreman (unpublished) to describe the meteorological and oceanographic conditions of the area. The model was written in FORTRAN G and debugged and executed by the IBM 370 computer at the University of British Columbia Computing Centre. In addition, numerous support programs and subroutines were used in the analysis of experiments and presentation of results.

RESULTS

Litter Assessment:

Five species (four genera) of seaweeds were responsible for more than 97% of the plant litter collected over the 14 month sampling period from 20 August 1975 until 2 October 1976. These species were Fucus distichus, Iridaea cordata, Nereocystis luetkeana, Laminaria saccharina and Laminaria groenlandica. In all, about 43 taxa were recognized within the litter collections. Table 1 summarizes the distribution of litter biomass collected from the transects at 5, 35 and 65 m within Site 1 on 3 August and at 95 m on 27 July 1976. These transects will be referred to collectively as the midsummer litter collections.

Figure 2 (a-e) presents spatial representations of the distribution of litter at midsummer of 1976, near the time of maximum litter accumulation. The area defined by the abcissa and ordinate represents Site 1 as though it were being observed from above. Note that the litter derived from Fucus distichus and Iridaea cordata, whose normal habitats are the intertidal and upper subtidal zones, respectively (Lindstrom 1973), is retained almost exclusively within the shallow subtidal zone. Nereocystis luetkeana and Laminaria litter is retained in deeper water, in the zone where these plants grow abundantly. Table 2 demonstrates a positive correlation between the number of living Nereocystis luetkeana plants observed during each of the midsummer collections and the quantity of Nereocystis luetkeana litter within these same collections, indicating that litter tends to be retained where it was deposited. From Figure 3 it can be seen that Laminaria litter at Site 2 was collected almost entirely within the outer extent of the transect, in a depth range of 4-5 m below MSL. This range is comparible to the kelp community zone delimited by Lindstrom (1973). Visual examination of the area confirmed a large standing crop biomass of Laminaria in the vicinity of Site 2 and within this depth range.

Table 1. Mean biomass per m^2 of the major contributors to the litter pool within Site 1 based on the collections of 27 July and 3 August 1976.

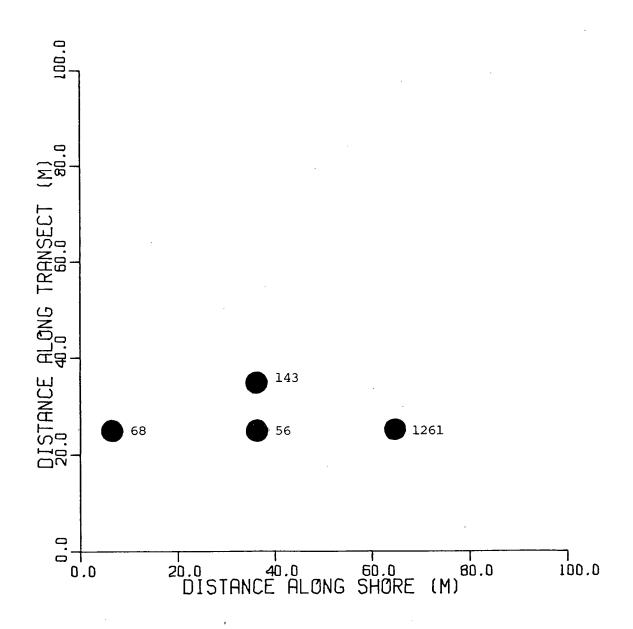
Species	Wet weight	<u>(%)</u>	Dry weight	(%)	Ash-free d	dry weight	(%)
Fucus distichus	27.3	(65.8)	5.40	(70.3)	3.96	(72.0)	
Iridaea cordata	4.6	(11.1)	1.20	(15.6)	0.83	(15.0)	
Nereocystis luetkeana (stipe)	1.2	(2.9)	0.16	(2.1)	0.11	(2.0)	
Nereocystis luetkeana (lamina)	6.3	(15.2)	0.62	(8.1)	0.41	(7.5)	
Laminaria	0.88	(2.1)	0.13	(1.7)	0.09	(1.6)	
All other species	1.18	(2.8)	0.17	(2.2)	0.11	(2.0)	
TOTAL	41.46		7.68		5.51		

Figure 2. Spatial characteristics of litter biomass for the major contributors to the litter pool within Site 1 based on the collections of 27 July and 3 August 1976. Contour intervals are in g ash-free dry weight per 10 m^2 . Solid circles indicate pockets of litter.

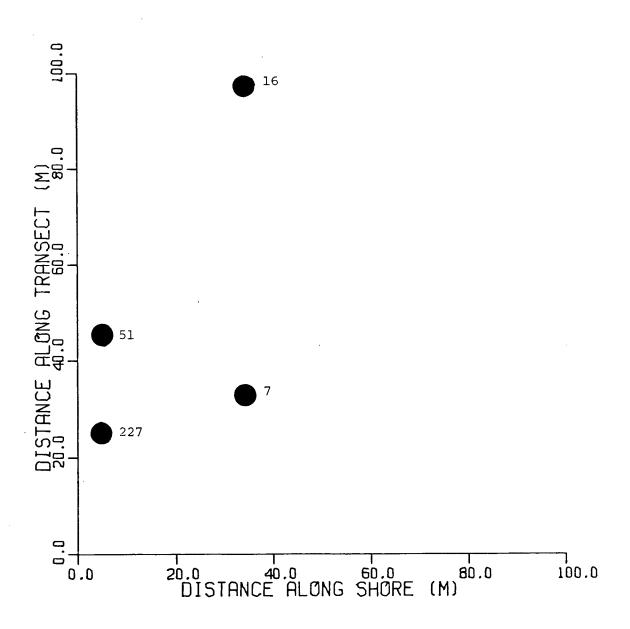
Contour interval

a)	Fucus distichus	as	labelled
b)	Iridaea cordata	as	labelled
c)	Nereocystis luetkeana	(stipe)	1.0
d)	Nereocystis luetkeana	(lamina)	4.0
e)	Laminaria	as	labelled

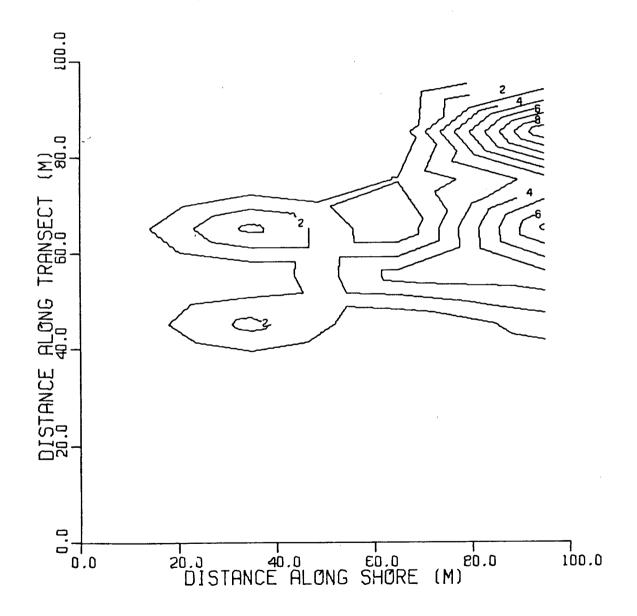
a) Fucus distichus



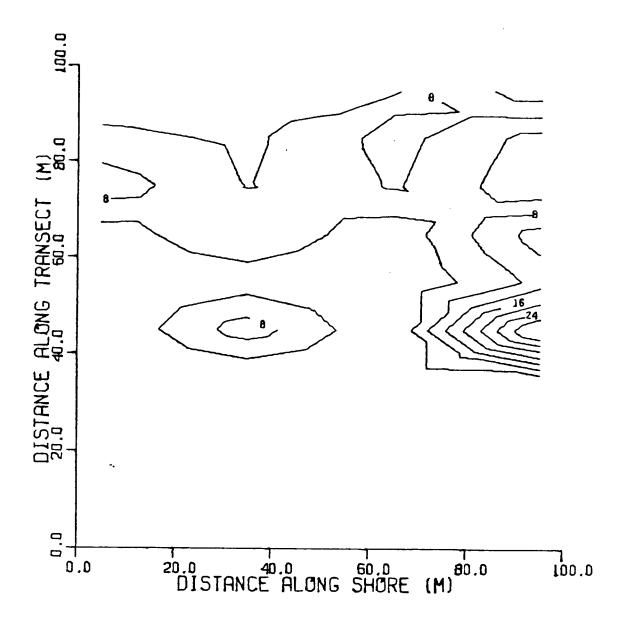
b) Iridaea cordata



c) Nereocystis luetkeana (stipe)



d) Nereocystis luetkeana (lamina)



e) Laminaria

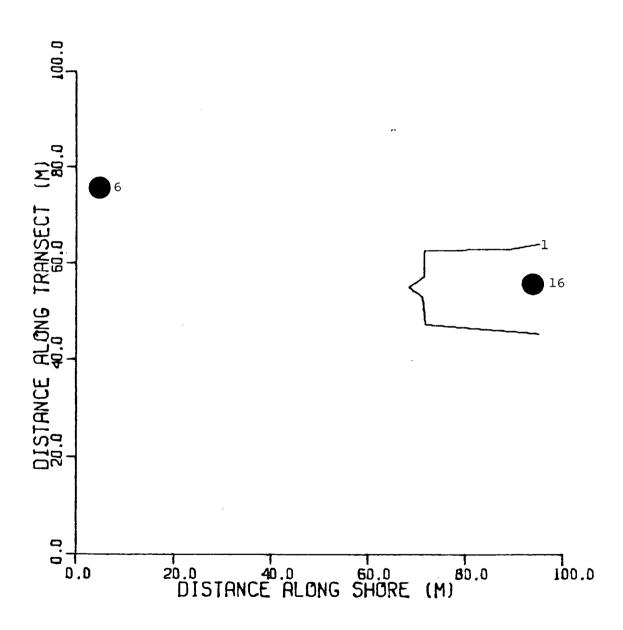


Table 2.

Comparison between the number of living Nereocystis luetkeana plants within a transect belt and the quantity of Nereocystis luetkeana litter collected within the same belt. Transects at 5, 35, 65 and 95 m along the base of Site 1 were collected either on 27 July or 3 August 1976. The transect at Site 2 was collected on 10 November 1975.

		Number of Nereocystis (per tran	luetkeana	-	Quantity of Nereocystis luetkeana litter collected (g AFDW/transect)			
		(per eru.	3000)	Stipes	Lamina	Total		
Site	1:							
	05	14		4.21	32.04	36.25		
	35	7		6.18	27.47	33.65		
	65	9		4.55	26.17	30.72		
	95	38		27.90	76.57	104.47		
Site	2:	0		2.71	4.09	6.80		

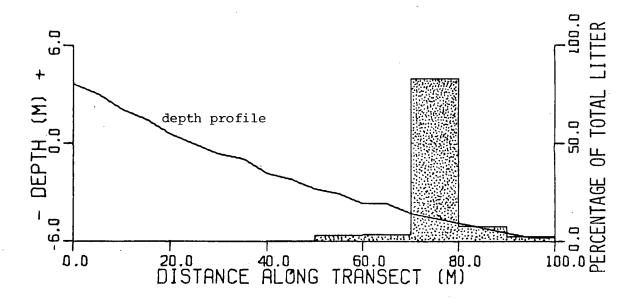


Table 3 indicates that at both Sites 1 and 2 more than 90% of the litter collected was composed of the seaweeds most characteristic of each area, Nereocystis

luetkeana and Laminaria/Agarum for Sites 1 and 2, respectively. The lack of
a significant Nereocystis luetkeana contribution to the litter at Site 2 supports
the interpretation that litter is not transported long distances away from its
place of deposition. The nearest living Nereocystis luetkeana plant to Site 2
was no closer than 100 m. The large accumulation of Laminaria litter at Site 2
may be due to its sheltered location, thereby rendering the area particularly
suitable for retention of litter deposited within the immediate vicinity.

Within Site 1 there was a similar tendency for litter to be retained in shelters or pockets formed by the substrate. All large deposits of litter were found in depressions or where the slope of the substrate was more gradual than usual. This can be confirmed by referring to the depth contours for Site 1 (Figure 4). Comparison of the regions of litter retention (Figure 2) to the contour lines demonstrates that the greatest accumulations of litter are where recognizable depressions in the substrate exist. It is important to note that Iridaea cordata and Fucus distichus litter collected in separate pockets, although the pocket containing Iridaea cordata is only 1.1 m deeper than the pocket containing Fucus distichus. This is further evidence that litter tends to remain in the zone where it was deposited. This effect is less evident in the outer extent of Site 1 where much less litter was collected. Litter entrapment in this region is facilitated by rocks and boulders which provide the topographic relief aiding in the retention of the litter.

The seasonal trend in the biomasses of specific and total litter collected within Site 1 is presented in Figure 5 (a-f). The most important feature of each of these profiles is that a peak period of litter accumulation occurs in August or September in both of 1975 and 1976, with a low near zero in January and February 1976. Figure 5c demonstrates that the presence of Nereocystis luetkeana stipes in the litter is prolonged over the autumn season.

Table 3.

Comparison of the total quantity and specific composition of litter collected within the transect at 95 m within Site 1 on 9 November 1975 and the total quantity and specific composition of litter collected within the transect at Site 2 on 10 November 1975 (g AFDW/transect). Site 1 and Site 2 are separated by ca 200 m, the latter being a less exposed area.

Species	95 <i>m</i> with	in Site l	(%) Site	<u>2</u> (%)
Fucus distichus	0.66	(0.66)	7.81	(0.49)
Iridaea cordata	0.51	(0.51)	16.70	(1.05)
Nereocystis luetkeana (stipe)	90.28	(90.28)	2.71	(0.17)
Nereocystis luetkeana (lamina)	4.79	(4.79)	4.09	(0.26)
Laminaria	1.24	(1.24)	1385.26	(86.77)
Agarum *	1.82	(1.82)	94.39	(5.91)
All other species	0.71	(0.70)	85.81	(5.37)
TOTAL	100.01		1596.47	

^{*} Agarum fimbriatum Harvey & Agarum cribrosum (Mertens) Bory

Figure 4. Depth contours (m below mean sea level) for Site 1. Contour intervals are 0.5 m.

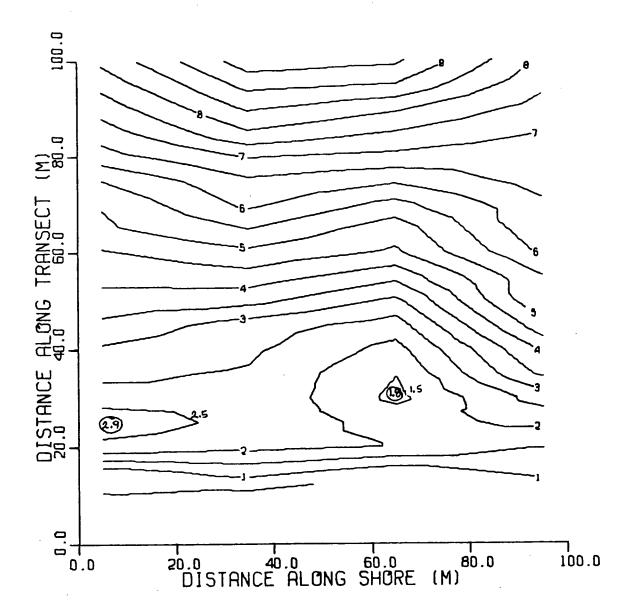
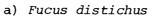
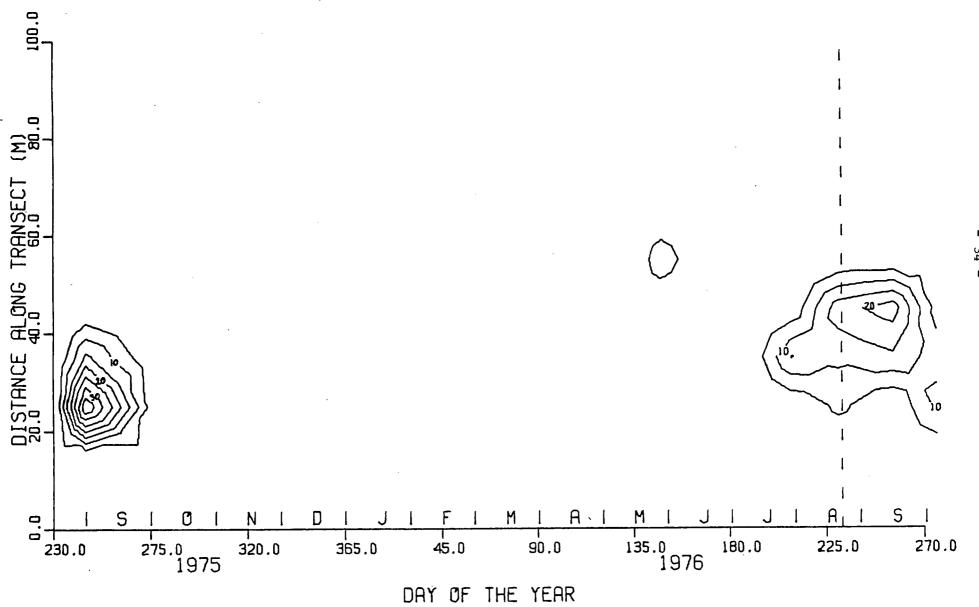


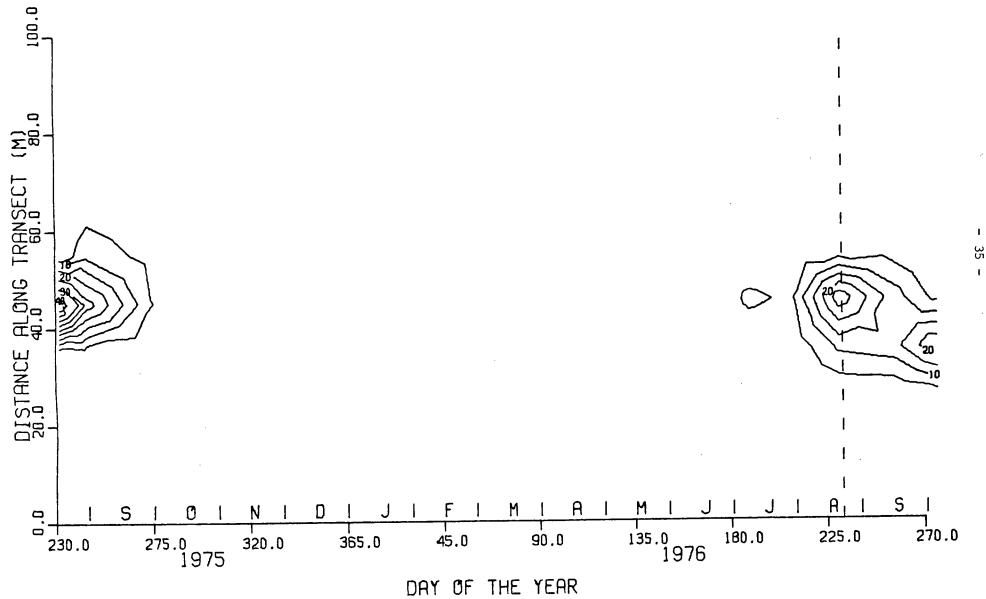
Figure 5. Seasonal distribution of litter biomass for the major contributors to the litter pool within Site 1 based on collections along the 95 m transect location at 3-4 week intervals for the period 20 August 1975 until 2 October 1976. Contour intervals are g ash-free dry weight per 10 m^2 .

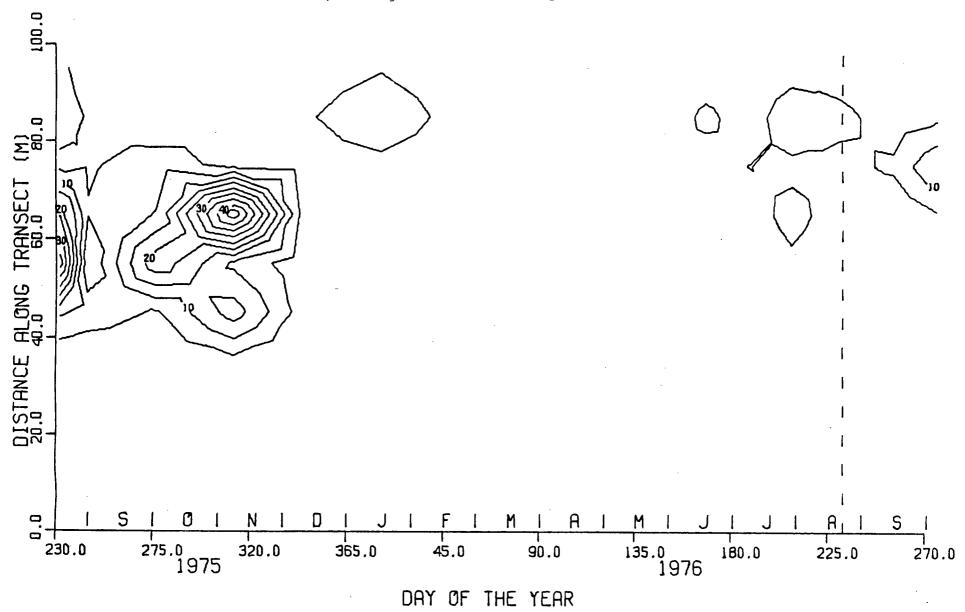
a)	Fucus distic	chus		5.0
b)	Iridaea cord	lata		5.0
c)	Nereocystis	luetkeana	(stipe)	5.0
đ)	Nereocystis	luetkeana	(lamina)	5.0
e)	Laminaria			5.0
f)	Total litter	-		10.0

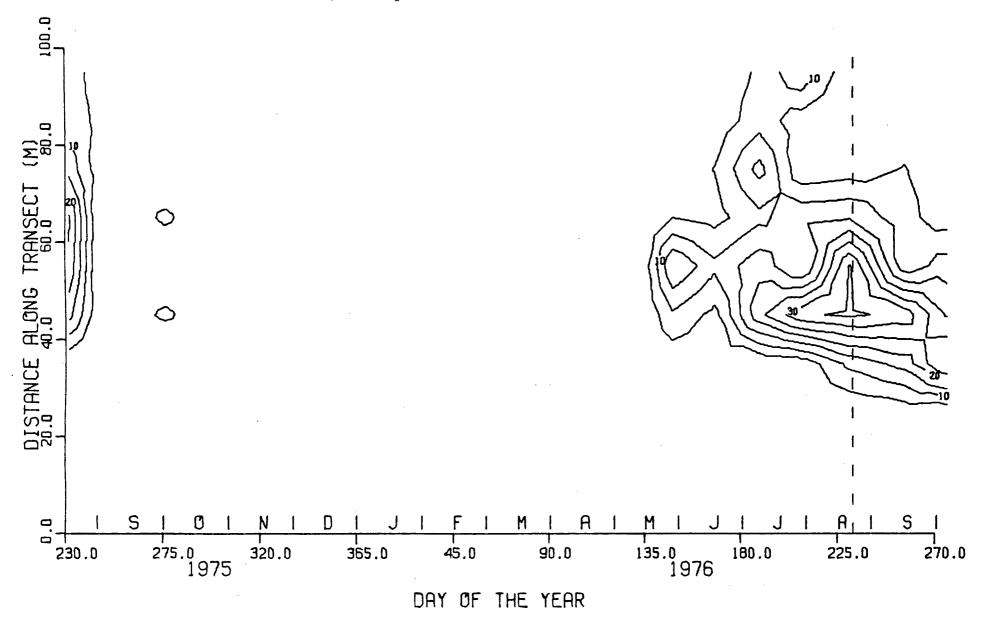
Contour interval

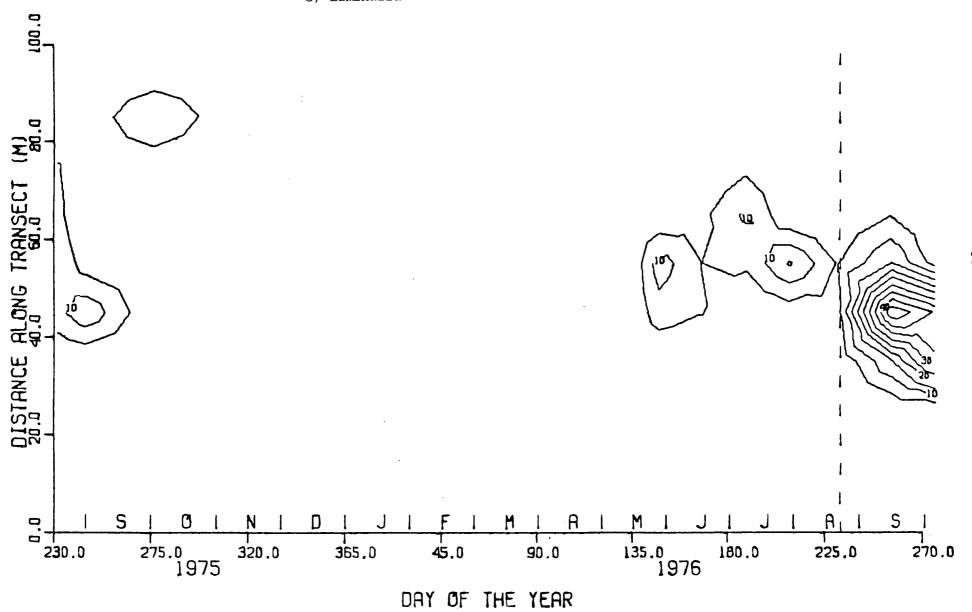


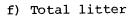


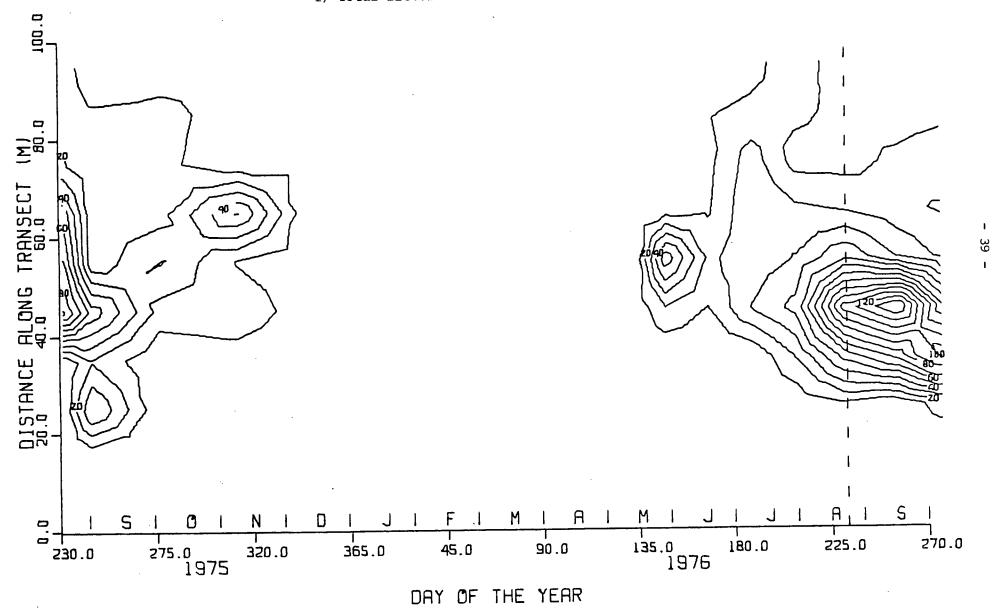












This is expected since Nereocystis luetkeana is the most long-lived of the annual plants which contribute significantly to the litter within Site 1.

The stipes prevail in the litter longer than the lamina of Nereocystis luetkeana as the lamina are more easily detached during rough weather.

Structural Composition of Species contributing to Litter:

The results for all 10 seaweed species are presented in Table

4. There are considerable differences in the percentages of soluble, moderately resistant and crude fibre components in each species, but it is evident that some species having similar percentages of these components also display taxonomic and/or morphological affinities. Both species of Laminaria have similar percentage compositions of these components as have the stipe and lamina of Nereocystis luetkeana. Iridaea cordata and Gigartina papillata are both particularly low in crude fibre content.

Of all the species analysed, Constantinea subulifera has the least percentage of moderately resistant material (29.4%) and the highest percentage of soluble matter (65.6%). It is followed by Fucus distichus in both of these categories, 32.8% and 60.7%, respectively, for moderately resistant and soluble material. Iridaea cordata has both the least percentage of crude fibre (0.86%) and the greatest percentage of moderately resistant material (71.0%).

The variability in the percentages of these components among the various species has facilitated the recognition of correlations between the relative amounts of these components in each species and decomposition parameters of these species. These relationships will be discussed in the context of the appropriate experiments. Of particular consequence is the influence of the percentage content of soluble matter on observed rates of oxygen consumption (Experiment 1) and the influence of the percentage crude fibre content on observed rates of particulate matter consumption (Experiment 2).

Table 4.

The percentages of each of the soluble, moderately resistant and crude fibre components of the significant species within Site 1. Each value is expressed as a percentage of dry weight biomass. Crude fibre glucose refers to the amount of carbohydrate in the crude fibre component expressed as an equivalent amount of glucose. The soluble content and crude fibre components are means of two determinations.

	Galubla	Moderately	Crude Fibre Component		
Species	Soluble Component	Resistant Component	Total	As glucose	
Plocamium coccineum var. pacificum	28.1	59.2	12.70	(3.39)	
Rhodomela larix	30.1	60.0	9.86	(4.28)	
Odonthalia floccosa	40.3	54.7	5.01	(3.44)	
Iridaea cordata	28.1	71.0	0.86	(0.58)	
Gigartina papillata	41.0	57.7	1.30	(1.21)	
Constantinea subulifera	65.6	29.4	4.99	(2.26)	
Fucus distichus	60.7	32.8	6.48	(1.86)	
Nereocystis luetkeana (stipe)	41.1	55.4	3.48	(2.29)	
Nereocystis luetkeana (lamina) 44.7	51.6	3.71	(2.27)	
Laminaria saccharina	41.1	52.6	6.30	(3.14)	
Laminaria groenlandica	36.6	55.7	7.67	(3.37)	
Standard error:	±4.0		±0.62	±0.61	

Litter Decomposition Experiments:

The results for all 11 litter bag experiments are presented in Figure 6 (a-k). As one litter bag from the series of litter bags containing Laminaria saccharina was lost, and there being an apparent similarity between the decomposition rates of both species of Laminaria, the data for these two species were combined.

Five curve models were applied to each data set with the minimal residual error being the criterion for acceptance, provided the curve maintained a smooth, negative slope. For plots where a logarithmic curve was chosen to represent the data, 2.0% of original dry weight was arbitrarily chosen to represent zero percent for graphic purposes, as this curve model approaches the X-axis asymptotically. The five curve models are as follows:

1. Linear: Y = aX + 100.0

2. Quadratic: $Y = aX^2 + bX + 100.0$

3. Logarithmic: lnY = a(lnX) + 100.0

4. Parabolic: $Y = (X - a)^2/4b$; $a^2/4b = 100.0$

5. Hyperbolic: Y = a + (b/(X - c)); a - (b/c) = 100.0

where:

X is the independent variable

Y is the dependent variable

a, b and c are coefficients

In is the natural logarithm

Loss of biomass from the litter bags was rapid but the timing and pattern of decomposition was variable among the species. The lamina of Nereocystis luetkeana decomposed most rapidly, requiring only six days to disappear from the litter bags. The most slowly decomposing species was Fucus distichus, requiring ca 70 days to disappear from the litter bags. Listed in order of decreasing decomposition rates the remaining species are Iridaea cordata (13 days), Laminaria (ca 14 days), Nereocystis luetkeana stipe (ca 18 days), Gigartina papillata (27 days), Rhodomela larix (27 days), Constantinea subulifera (43 days), Odonthalia floccosa (46 days) and Plocamium coccineum var. pacificum (49 days).

Figure 6. Litter decomposition curves (submodels) calculated from data obtained in the litter bag experiments. The curve model (see text), the coefficients (a,b,c) and the coefficient of determination (r^2) are given below for each species.

	Species	<u>Model</u>	<u>a</u>	<u>b</u>	<u>c</u>	r ² (%)
a)	Plocamium coccineum var. pacificum	P	49.40	6.099	_	99.45
b)	Rhodomela larix	L	3.720	100.0	-	98.46
c)	Odonthalia floccosa	P	45.69	5.220	-	97.52
d)	Iridaea cordata	Q	-0.448	-1.978	100.00	99.90
e)	Gigartina papillata	P	27.00	1.823	-	99.94
f)	Constantinea subulifera	P	43.42	4.712	-	97.65
g)	Fucus distichus	LN	-0.059	4.605	_	94.06
h)	Nereocystis luetkeana (stipe)	LN	-0.210	4.605	-	99.90
i)	Nereocystis luetkeana (lamina)	P	6.022	0.907	-	98.56
j)	Laminaria	LN	-0.277	4.605	-	96.80

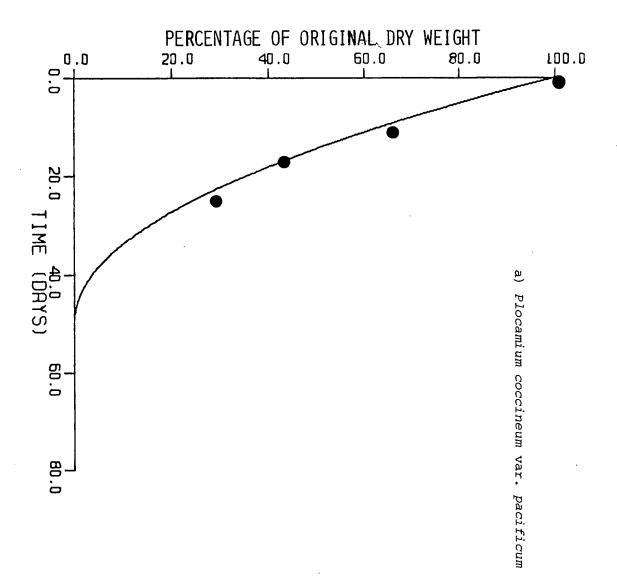
L: linear

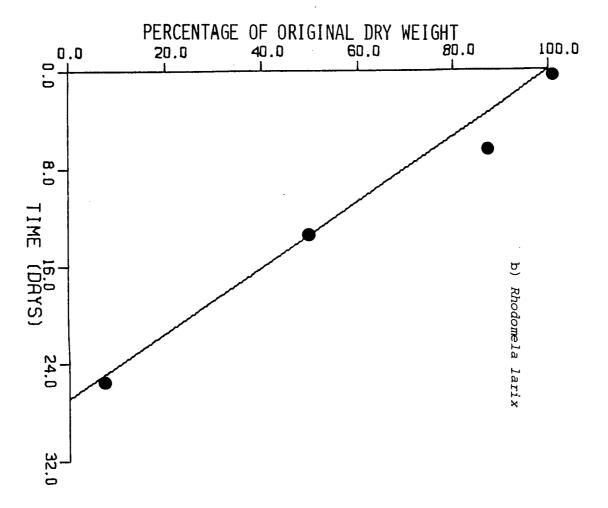
Q: quadratic

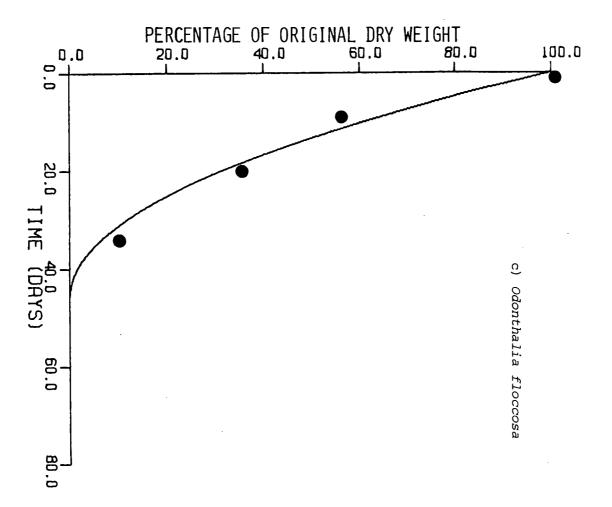
LN: logarithmic

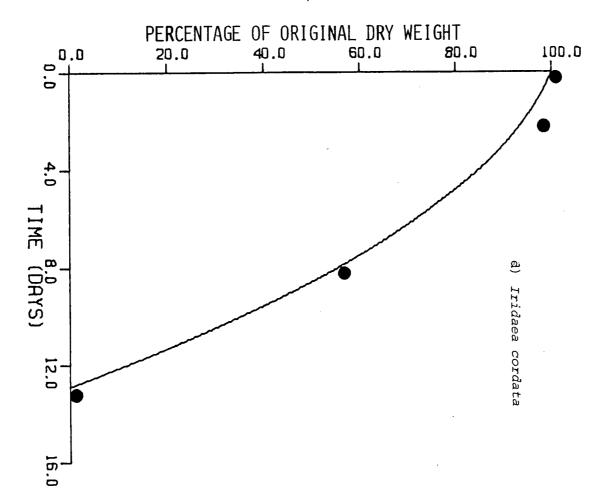
P: parabolic

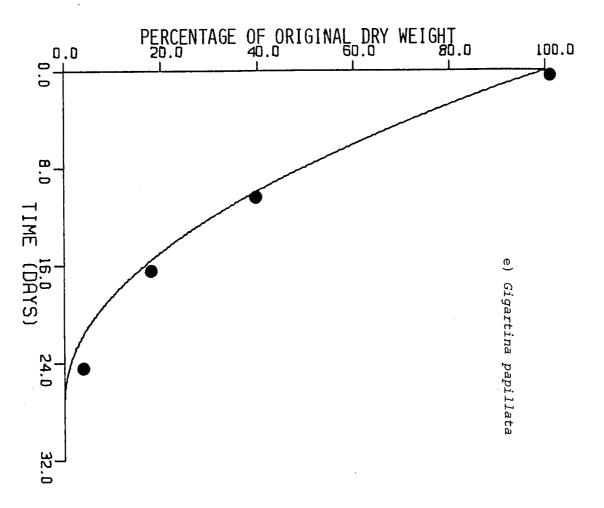
H: hyperbolic

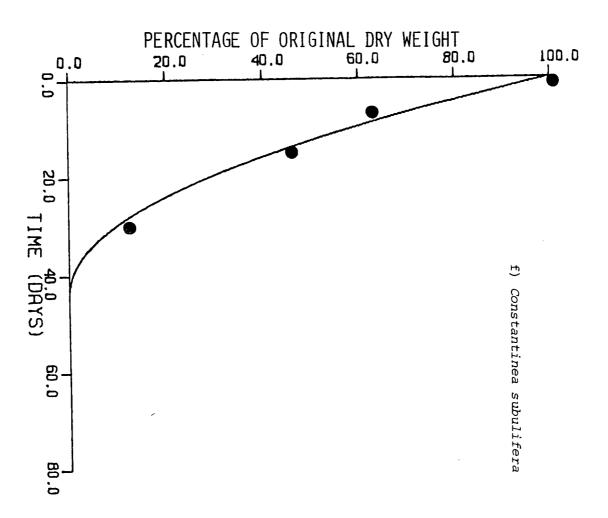


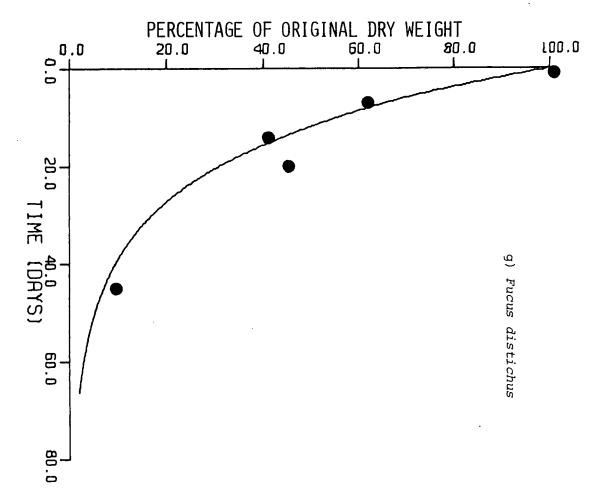


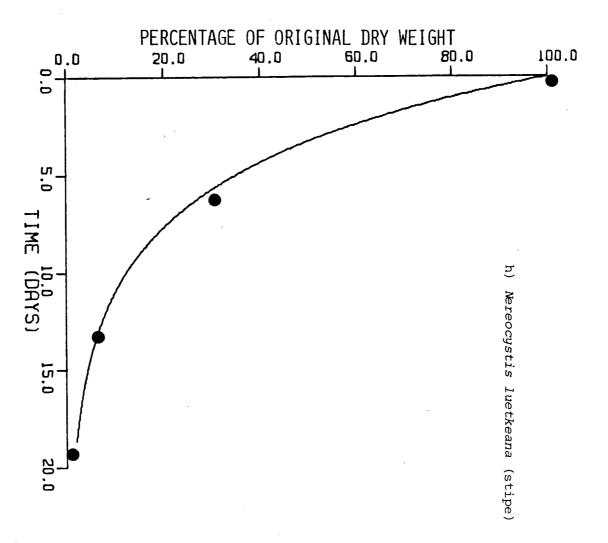


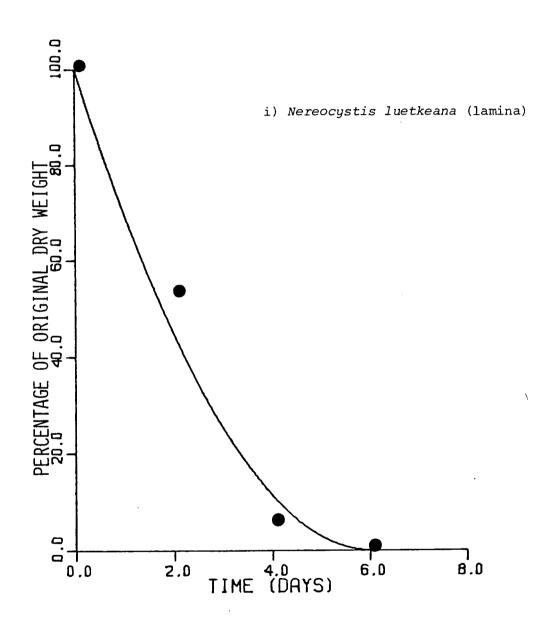












Only Iridaea cordata and Rhodomela larix did not subscribe to a decomposition pattern with a decelerating rate of biomass loss. Iridaea cordata was characterized by an initial lag phase followed by an accelerating rate of biomass loss. Rhodomela larix maintained a linear decomposition rate.

Litter Senescence Experiments:

The experiments to determine the time for the significant contributors to the litter to die were not particularly decisive due to the qualitative nature and infrequency of the observations. The results are presented in Table 5. At the time these experiments were performed the significance of the contribution by *Fucus distichus* was underestimated.

The estimated time for a seaweed to die was determined for the shaded condition only. Continual deposition of new litter upon existing litter probably means that most litter is at least partially shaded; therefore this condition was accepted as giving a more realistic estimate of the time required for the death of the seaweed to occur. These data were obtained in order that the time taken for seaweed litter to form detritus could be more precisely modelled. As the specific litter components tested demonstrated a similarity in their senescence times, six days was accepted as a general estimate for simplicity in modelling. Fucus distichus may have a longer senescence time, but the overall significance of this error is expected to be minor.

Nitrogen Content of Decomposing Litter:

The nitrogen content of seaweed litter at various stages of decomposition is presented in Table 6 for the 10 species assayed. The most notable feature of these results is that all species except *Iridaea* cordata demonstrated an increase in the nitrogen:total biomass ratio of material remaining in the litter bags as decomposition proceeded,

Table 5.

Number of days required for unkilled portions of the major contributors to the litter pool within Site 1 to leave a 1.0 cm mesh litter bag under shaded and exposed conditions. The 'estimated time for senescence' is an estimation of the number of days required for a specific litter component to die once having entered the litter pool. See text for a full explanation.

Species	Exposed	Shaded	Estimated time for senescence
Iridaea cordata	24-30	10-14	5
Nereocystis luetkeana (stipe)	24-30	15-23	9
Nereocystis luetkeana (lamina)	15-23	6-10	6
Laminaria saccharina	24-30	10-14	5
Laminaria groenlandica	24-30	10-14	5

Table 6.

Percentage nitrogen content of the material remaining within the litter bags at the termination of their incubation period.

	Percentage of	
Species	original dry weight	Percentage nitrogen
Plocamium coccineum var. paci	ficum 100.00	3.74
-	65.26	3.68
	42.50	3.89
	28.22	4.64
Rhodomela larix	100.00	4.24
	86.20	4.43
	48.73	4.74
Odonthalia floccosa	100.00	4.24
	55.35	3.71
	34.51	4.50
Iridaea cordata	100.00	1.94
	97.39	1.94
·	55.66	1.63
Gigartina papillata	100.00	2.54
1	38.50	3.14
	16.79	4.26
	2.72	6.34
Constantinea subulifera	100.00	2.61
	62.30	2.70
	45.20	3.17
Fucus distichus	100.00	1.73
	61.08	2.21
	39.99	2.37
Nereocystis luetkeana (stipe)	100.00	1.50
	29.70	2.16
Nereocystis luetkeana (lamina) 100.00	2.38
	52.80	3.76
Laminaria saccharina	100.00	1.98
	13.70	3.70
Laminaria groenlandica	100.00	2.64
	30.14	4.10
	11.16	5.20

although total nitrogen content decreased. The greatest percentage nitrogen content was observed for Gigartina papillata, most likely because it was the most fully decomposed of all the species when final nitrogen content was analyzed. The nitrogen:total biomass ratio of nearly fully decomposed Gigartina papillata increased over that of undecomposed Gigartina papillata by 250%. Figure 7, which incorporates data from all species assayed, demonstrates that a hyperbolic curve approximates the trend of increasing nitrogen:total biomass ratio very well, indicating an accelerating increase in litter nitrogen content relative to other biomass components as decomposition proceeds.

Detritus Decomposition:

Both experiments tested the following three major effects for their impact on decomposition rates:

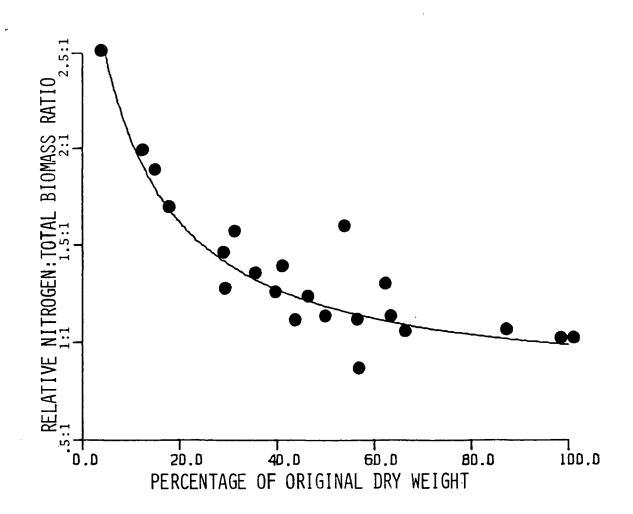
- 1. Length of the incubation period
- Source of the detritus, i.e. the seaweed from which it was created
- 3. Size of the detrital particles

For brevity each of these effects will often be referred to as the 'incubation period', 'detrital species', and 'particle size' effects, respectively.

Experiment 1 (Microbial Oxygen Consumption):

An Analysis of Variance (ANOVA) was performed on the oxygen consumption data obtained in this experiment. The results of the analysis are presented in Table 7. Referring to the three major effects, it can be concluded that only two of them, the detrital species and the length of the incubation period, are significant (p < .05) contributors to the observed differences in the oxygen comsumption rates. In consideration of the latter effect, such a response must be expected since the oxygen within

Figure 7. Plot demonstrating an increase in the ratio of nitrogen:dry weight biomass of decomposing litter expressed relative to a ratio of 1:1 for undecomposed litter. All 10 species assayed are incorporated within the plot. The solid line indicates the best fit through the points.



Analysis of variance table for the results of Experiment 1, demonstrating the effects of particle size, detrital species and length of incubation period on the oxygen consumption by microbes utilizing the detritus as a carbon source.

Source of variance	Degrees of freedom	Sum of squares	Mean sum of squares	Probability
Particle size (PS):	2	0.12379E-02	0.61894E-03	0.63799
Detrital species (DS):	10	0.65865	0.65865E-01	0.0 *
PS - DS interaction:	20	0.18062E-01	0.90311E-03	0.84772
Incubation period (IP)	: 3	5.1409	1.1736	0.17613E-52 *
PS - IP interaction:	6	0.21561E-02	0.35934E-03	0.95198
DS - IP interaction:	30	0.29697	0.98989E-02	0.72414E-10 *
Residual error:	60	0.82011E-01	0.13668E-02	
Total:	131	6.2000		

^{*} significant for $\alpha = 0.05$

the BOD bottle is continually being consumed. That detritus of different biogenic origins contributed significantly to the observed variation in the oxygen consumption rates implies that some species of detritus are more susceptible to breakdown by microbes than others. For the third major effect, particle size, there was no detectable difference among the oxygen consumptions of the three particle sizes. Any response that may have occurred could have been easily attributed to chance.

The second source of significant variation within the experiment can be explained in terms of an interaction between the detrital species and their response over the incubation periods. The essence of the interaction is that utilization of the oxygen in the BOD bottles follows a pattern dependent upon the biogenic origin of the detritus.

By observing Figure 8, which relates the cumulative oxygen consumption to the length of the incubation period for all 10 species, it can be seen that the significance of the interaction term is a result of the relatively steep slope maintained by *Fucus distichus* during the 10-20 day incubation period and to the heterogeneity of the slopes within the 10-15 day incubation period.

Three 'a posteriori' range tests were performed on the data in an attempt to delimit affinities and detect outliers among the responses to the significant major effects. These tests were:

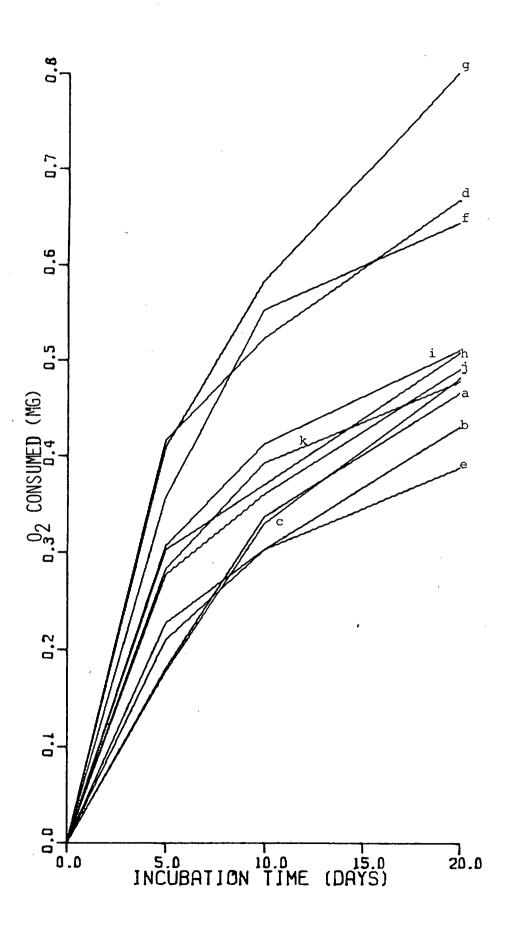
- 1. Duncan's New Multiple Range Test
- 2. Newman Keul's Test
- Tukey's Test

Not unexpectedly, each incubation period (0,5,10, and 20 days) was rendered unique and independent. Only Duncan's Test defined exclusive subsets for the effect of detrital species on oxygen consumption rates.

Both the Newman - Keul's Test and Tukey's Test permitted entities to have

Figure 8. Cumulative oxygen consumption by microbes decomposing the 10 detrital species in Experiment 1. Each data point is the mean result for the three detrital particle sizes.

- a) Plocamium coccineum var. pacificum
- b) Rhodomela larix
- c) Odonthalia floccosa
- d) Iridaea cordata
- e) Gigartina papillata
- f) Constantinea subulifera
- q) Fucus distichus
- h) Nereocystis luetkeana (stipe)
- i) Nereocystis luetkeana (lamina)
- j) Laminaria saccaharina
- k) Laminaria groenlandica



a membership in more than one subset such that affinities were more difficult to detect. The subsets defined by Duncan's Test are presented in Table 8a.

ent on the results obtained, the oxygen consumed by each detrital species after five days of incubation (mean of three particle sizes) was regressed on the percentage soluble content of each species. The result is significant (p < .01) and conclusive if *Iridaea cordata* detritus is excluded from consideration. The relationship between oxygen consumption and soluble content is presented in Figure 9. About 77% of the variation in oxygen consumption can be accounted for by differences in the soluble content of the detrital species. Reference to Table 8b indicates the mean percentage soluble content of the species comprising each subset. The trend of increasingly higher percentage soluble contents for the subsets characterized by the more rapidly decomposing species is evident, with the exception that *Iridaea cordata* decomposes rapidly although containing a relatively small percentage of soluble matter.

Experiment 2 (Microbial Consumption of Particulate Material):

The results of an ANOVA on the decomposition data obtained in this experiment are presented in Table 9. Reference to it shows that there are four significant sources of variation (p < .05). As was the case in Experiment 1, only two major effects were significant, incubation period and detrital species. Two other significant sources of variation were an interaction between incubation period and detrital species and an interaction between particle size and detrital species.

Table 8.

a) Subsets delimited by Duncan's New Multiple Range Test. Each subset contains those detrital species which show a significant (p < .05) degree of affinity with respect to the quantity of oxygen consumed by microbes decomposing the detritus.

Subset 1	Subset 2	Subset 3	Subset 4
Plocamium coccineum var. pacificum	Nereocystis luetkeana (stipe)	Iridaea cordata Constantinea subulifera	Fucus distichus
Gigartina papillata Rhodomela larix	Nereocystis luetkeana (lamina)		
Odonthalia floccosa	Laminaria saccharina Laminaria groenlandica		
•			

b) The average percentage soluble content of the subsets in Table 8a.

Subset 1	Subset 2	Subset 3	Subset 4
34.9 ± 7.2%	40.9 ± 4.1%	C. subulifera 65.6 ± 2.8%	60.7 ± 3.8%
		I. cordata 28.1 ± 0.1%	

Figure 9. Relationship between the percentage soluble contents of the 10 detrital species (exclusive of *Iridaea cordata*) and the quantity of oxygen consumed by microbes decomposing the detritus after five days of incubation, as determined in Experiment 1. The solid line indicates the best fit through the points.

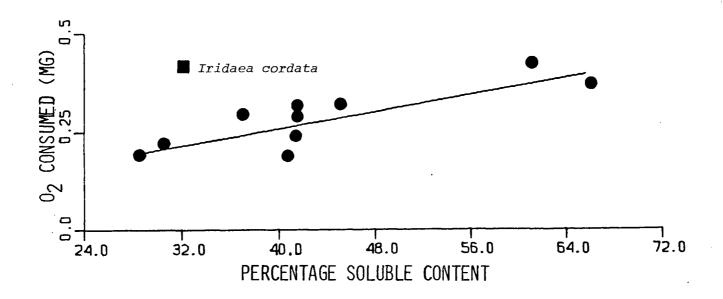


Table 9.

Analysis of variance table for the results of Experiment 2, demonstrating the effects of particle size, detrital species and length of incubation period on the consumption of particulate material by microbes utilizing detritus as a carbon source.

Source of variance	Degrees of freedom	Sum of squares	Mean sum of squares	Probability
Particle size (PS):	2	135.22	67.611	0.27960
Detrital species (DS):	10	41877.0	4187.7	0.0 *
PS - DS interaction:	20	1875.8	93.788	0.40823E-01 *
Incubation period (IP)	: 3	14200.0	4733.4	0.95989E-21 *
PS - IP interaction:	6	363.59	60.599	0.33608
DS - IP interaction:	30	15227.0	507.56	0.15329E-12 *
Residual error:	60	3116.1	51.935	
Total:	131	76795.0		

^{*} significant for $\alpha = 0.05$

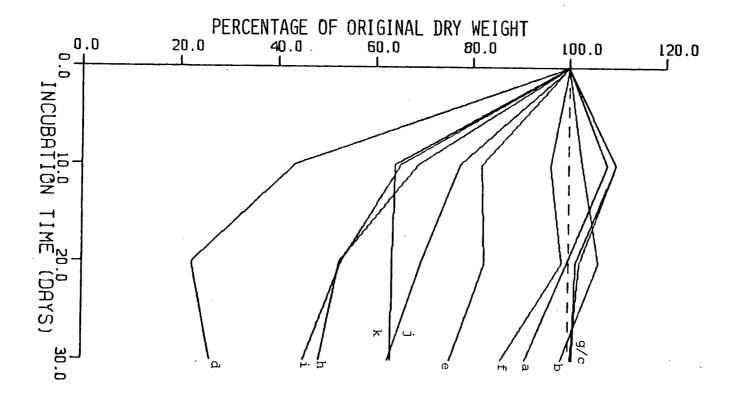
The significant response for the length of the incubation period was expected as the general trend would be a continual loss of particulate material as time proceeds; however, this did not always occur. The second significant response was due to the different decomposition rates of the various detrital species. Figure 10 indicates an initial decay rate for Iridaea cordata which would reduce it to zero in 18 days. In comparison, there appear to be some anomalous results for Plocamium coccineum var. pacificum, Rhodomela larix, Odonthalia flocossa, and Fucus distichus, all of which show an increase in dry weight of particulate matter following 10 days of incubation.

As there was a significant interaction between detrital species and incubation period, range tests were performed to delimit any groupings which might provide insight into the reasons for the interaction. None of the three range tests delimited exclusive subsets. The most definitive was Newman - Keul's Test which delimited five subsets, with Laminaria groenlandica being a member of two of them. As the overall mean for Laminaria groenlandica was closer to that of Laminaria saccharina than of Nereocystis luetkeana (stipe), its nearest neighbours in each of the subsets in which it was placed, it was placed with Laminaria saccharina. This rendered all the subsets unique in composition. The composition of the subsets is presented in Table 10.

There is also a significant interaction between particle size and detrital species. The implication is that there may be some species of detritus whose decomposition rate is dependent upon the size of the detrital particles. Closer inspection of the data revealed that the two most rapidly decomposing species, Iridaea cordata and Nereocystis luetkeana (stipe and lamina sections combined), displayed a trend toward a more rapid decomposition rate as mean particle size decreased. A detectable difference in decomposition rates in response to particle size is most likely for the most rapidly decomposing species since the experimental error would be a smaller proportion of the total variance than

Figure 10. Cumulative loss of particulate material from the 10 detrital species decomposed in Experiment 2. Each data point is the mean result for the three detrital particle sizes.

- a) Plocamium coccineum var. pacificum
- b) Rhodomela larix
- c) Odonthalia floccosa
- d) Iridaea cordata
- e) Gigartina papillata
- f) Constantinea subulifera
- g) Fucus distichus
- h) Nereocystis luetkeana (stipe)
- i) Nereocystis luetkeana (lamina)
- j) Laminaria saccharina
- k) Laminaria groenlandica



Subsets delimited by Newman - Keul's Range Test. Each subset contains those detrital species which show a significant (p < .05) degree of affinity with respect to the quantity of particulate material consumed by microbes decomposing the detritus.

Odonthalia floccosa

Constantinea subulifera

Subset 1	Subset 2	Subset 3	Subset 4	Subset 5
Plocamium coccineum var. pacificum	Gigartina papillata	Laminaria saccharina	Nereocystis luetkeana (stipe)	Iridaea cordata
Fucus distichus		Laminaria groenlandica	Nereocystis luetkeana	
Rhodolema larix			(lamina)	

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for less rapidly decomposing species.

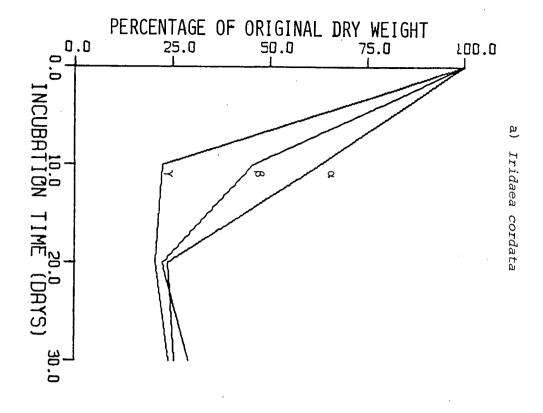
Figure 11 (a,b) graphically presents the results for both of these species. Note in particular that the difference in decomposition rates for the three particle sizes is most evident after only 10 days of incubation, while the conditions within the culture vessels are still sufficiently fresh to maximize the experimental effects. Because of adverse effects caused by the lengthier periods of incubation, the effect of particle size could not be shown to be statistically significant for either species.

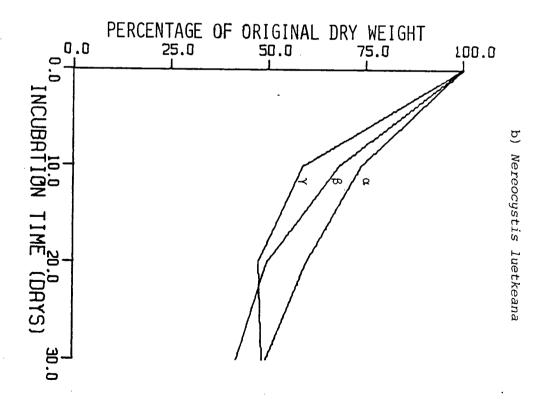
Two regression analyses were performed to test the hypothesis that the decomposition rates of seaweed detritus were at least partially a function of the crude fibre content of the detritus. The dependent variable in both cases was the maximum percentage loss (mean of 3 particle sizes) of particulate material observed for each detrital species in Experiment 2. For the species which showed an initial increase in dry weight as time proceeded, the rate of loss of particulate material was determined in relation to the maximum dry weight attained. The independent variables were crude fibre content and crude fibre carbohydrate expressed in glucose equivalents. Both were expressed as a percentage of the total particulate component (crude fibre plus moderately resistant material).

The results of both regression analyses were significant (p < .05). Figure 12a demonstrates the relationship between maximum percentage loss of particulate material and percentage crude fibre content. Figure 12b presents an equivalent relationship using percent glucose as the independent variable. Since decomposition rates would theoretically never be expected to reach zero, an exponential decay curve was considered the most appropriate model. The regression analyses accounted for 42.8% and 39.9% of the variance observed in Figures 12a and 12b, respectively.

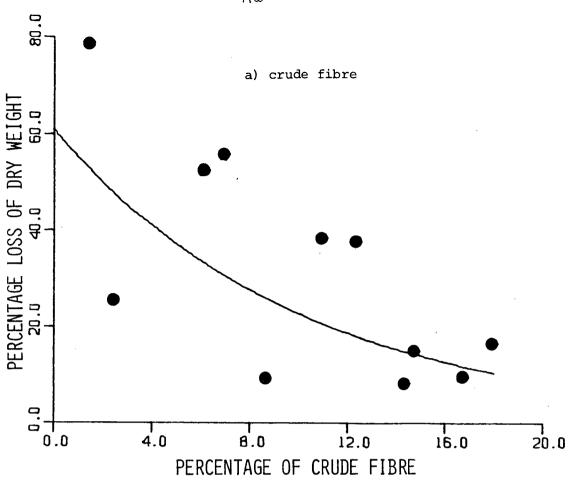
Figure 11. Cumulative loss of particulate material from

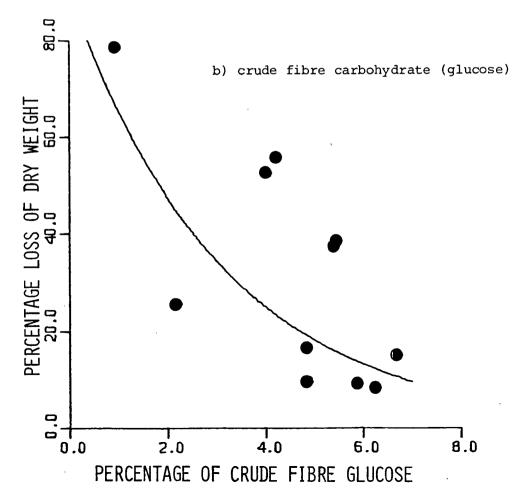
- a) Iridaea cordata
- b) Nereocystis luetkeana (stipe and lamina combined) detritus. For each species the results for the three detrital particle sizes are presented. The three particle sizes are as follows:
 - α) 1000-420 μm
 - β) 250-149 μm
 - γ) 44-0 μ m





- Figure 12. Relationship between the maximum percentage loss of particulate material from the 10 detrital species decomposed in Experiment 2 and the percentage of crude fibre in the particulate material of each detrital species. The solid lines indicate the best fit through the points.
 - a) crude fibre expressed as a percentage of the dry weight of the particulate material.
 - b) crude fibre carbohydrate expressed as an equivalent amount of glucose and as a percentage of the dry weight of the particulate material.





Detritus Assessment:

The biomass of detritus along the permanent transect location within Site 1 is best represented graphically by Figure 13. This three-dimensional representation demonstrates that the availability of detritus reached a maximum of ca 1.4 g AFDW/ m^2 about the middle of August in 1976. The peak occurs near the time of maximum litter biomass and within the central zone of the seaweed bed. The quantity of detritus diminishes towards the inner and outer edges of the bed to 15-30% of the maximum value.

During the summer of 1975 natural detritus was periodically examined microscopically for characteristics which might aid in determination of its origin. Its composition was determined to be amorphous, consisting mostly of variously shaped colourless unidentifiable particles, as well as some diatomaceous material. The latter accounted for ca 10% of the material observed.

Faunal Assessment:

In order to recognize a coincidence of the occurrence of specific fauna and the maximum availability of detritus, the sums, by numbers and dry weights, for each species occurring within the summer faunal collections of 28 July, 18 August and 12 September were expressed as a percentage of the total for the seven collections from May until October. These results are presented in Tables 11a (numbers) and 11b (dry weight). Those species whose occurrence coincides with the maximum availability of detritus were delimited on the basis of the following, somewhat arbitrary, criterion. The qualifying species must have been represented by more than 75% of their total number and dry weight during the summer collections. The three species which met this qualification were:

Cancer oregonensis Dall Metacaprella anomala Mayer Lacuna marmorata Dall

Figure 13. Contour representation of detritus biomass along the 95 m transect location within Site 1 for the period 28 May until 7 October 1976. Contour intervals are 0.2 g ash-free dry weight per m^2 .

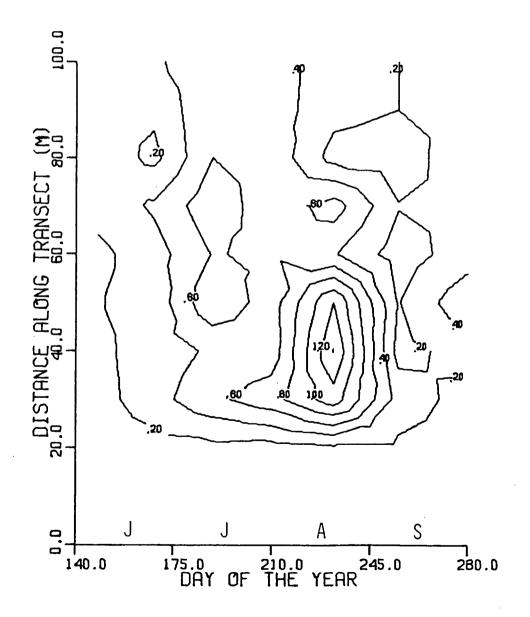


Table lla.

The total number of each faunal species summed over the 28 July, 18 August and 12 September 1976 transect collections. The percentage that this number represents of the total number of occurrences over the entire sampling period is in parentheses. An * denotes those species which are represented by more than 75% of their total number of occurrences within the samples collected on the above three dates.

Species	Number	Percentage of total
Acmaea mitra Rathke	1	(12.5)
Alvinia spp.	119	(16.9)
Amphilochus sp.	11	(44.0)
Amphithoe sp.	1	(1.4)
Balcis micans Carpenter	9	(60.0)
Bittium eschrichtii Middendorff	56	(49.1)
Cancer oregonensis	19	(100.0) *
Chlamys hastatus Sowerby	4	(33.3)
Clinocardium sp.	12	(34.4)
Granulina margaritula	161	(54.9)
Hemigrapsus nudus Dana	3	(50.0)
Hiatella arctica L.	6	(31.6)
Lacuna marmorata	6018	(88.6) *
Lirularia lirulata	66	(57.4)
Margarites pupillus Gould (juvenile)	1111	(37.6)
Margarites pupillus (parental)	449	(39.5)
Metacaprella anomala	9	(100.0) *
Mitrella gouldii Carpenter	109	(46.5)
Mytilus edulis L.	858	(30.6)
Nereis pelagica L.	1	(11.1)
Notoacmea scutum Rathke	8	(40.0)
Ocenebra sp.	25	(48.1)
Odostomia spp.	116	(70.1)
Pagurus kennerlyi Stimpson	1	(8.3)
Pugettia richii Dana	10	(30.4)
Strongylocentrotus droebachiensis	4	(33.3)
Tonicella lineata Wood	53	(31.8)

Table 11b.

The total dry weight of each faunal species summed over the 28 July, 18 August and 12 September 1976 transect collections. The percentage that this figure represents of the total dry weight of individuals collected over the entire sampling period is in parentheses. An * denotes those species which are represented by more than 75% of their total dry weight within the samples collected on the above three dates.

Species	Dry Weight	Percentage of total
Acmaea mitra	2.178	(14.8)
Alvinia spp.	0.1963	(18.6)
Amphilochus sp.	0.0100	(33.6)
Amphithoe sp.	0.0029	(0.7)
Balcis micans	0.0378	(57.7)
Bittium eschrichtii	3.474	(42.1)
Cancer oregonensis	0.1142	(100.0) *
Chlamys hastatus	0.0460	(41.0)
Clinocardium sp.	0.3748	(31.6)
Granulina margaritula	0.4882	(54.3)
Hemigrapsus nudus	1.115	(94.2) *
Hiatella arctica	1.667	(47.1)
Lacuna marmorata	12.23	(75.0) *
Lirularia lirulata	0.6519	(52.1)
Margarites pupillus (juvenile)	3.247	(26.9)
Margarites pupillus (parental)	11.49	(42.7)
Metacaprella anomala	0.0108	(100.0) *
Mitrella gouldii	3.711	(41.5)
Mytilus edulis	62.94	(62.1)
Nereis pelagica	0.0079	(4.5)
Notoacmea scutum	2.163	(42.7)
Ocenebra sp.	1.061	(21.5)
Odostomia spp.	0.3368	(63.3)
Pagurus kennerlyi	0.1475	(55.1)
Pugettia richii	1.942	(27.9)
Strongylocentrotus droebachiensis	0.4500	(6.3)
Tonicella lineata	8.064	(21.0)

For each of these species histograms are presented in Figure 14 (a-c) to describe the temporal distributions of numbers and dry weight over the period sampled, permitting a graphic interpretation of their seasonal abundances. All three species demonstrate a trend of increasing numbers and biomass toward a strong midsummer peak followed by a decrease in these parameters in September and October, implying that the sampling program is a sufficient documentation of their seasonal abundance patterns in 1976.

For Lacuna marmorata, which was particularly abundant throughout the summer months, additional trends were evident. Concomitant with an increase in numbers and dry weight of Lacuna marmorata is a decrease in the mean dry weight per individual. Figure 15 indicates that the greater increase in numbers relative to dry weight appears following the second sampling date (14 June 1976) and is due to the occurrence of a large number of juvenile individuals. Most Lacuna marmorata, and in particular the juveniles, were generally found amongst the detritus and debris accumulated on the bottom and consolidated by the plants comprising the subtidal turf community.

There is evidence that the abundance of juvenile Lacuna marmorata in the detritus and debris is due to their utilizing the detritus as a food resource. Figure 16 demonstrates that 100% of the total number and dry weight of Lacuna marmorata were collected within the quadrats at 30, 40 and 50 m along the transect. Results from the detritus collections of 20 August 1976 determined this to be the area where most detritus retention occurred.

Figure 14. Seasonal distribution histograms of the total number and dry weight (g) of

- a) Cancer oregonensis
 - b) Metacaprella anomala
 - c) Lacuna marmorata

occuring within the seven transect collections from 25 May until 7 October 1976.

Open bars: numbers
Solid bars: biomass

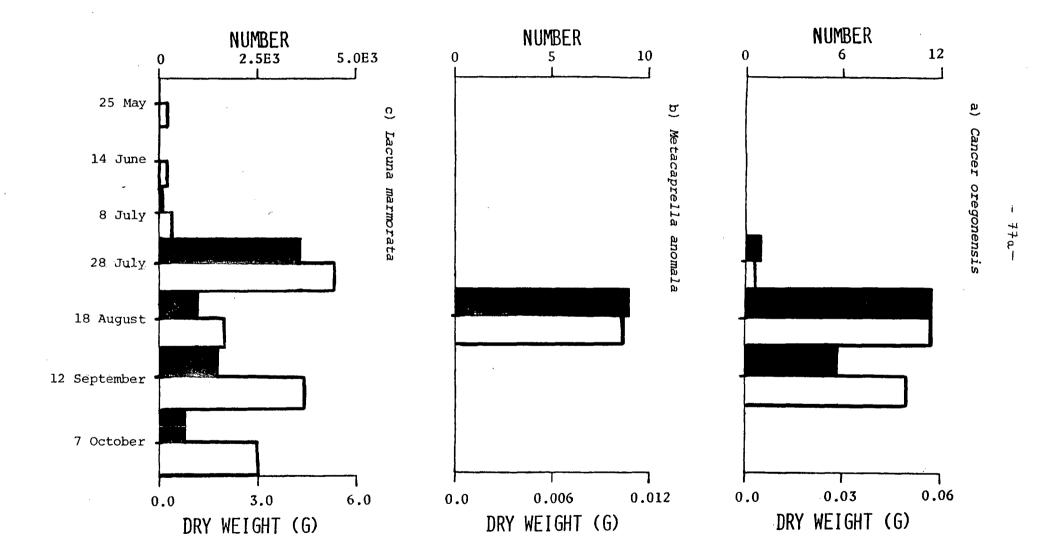


Figure 15. Seasonal trend in the mean dry weight (g) per individual of Lacuna marmorata for the period 25 May until 7 October 1976. The occurrence of juvenile individuals is evidenced by a decrease in the mean dry weight per individual after the second (14 June) sampling date.

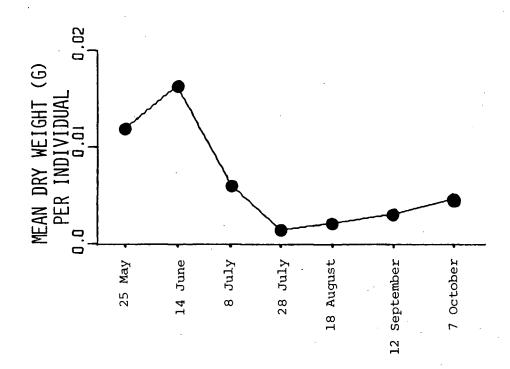
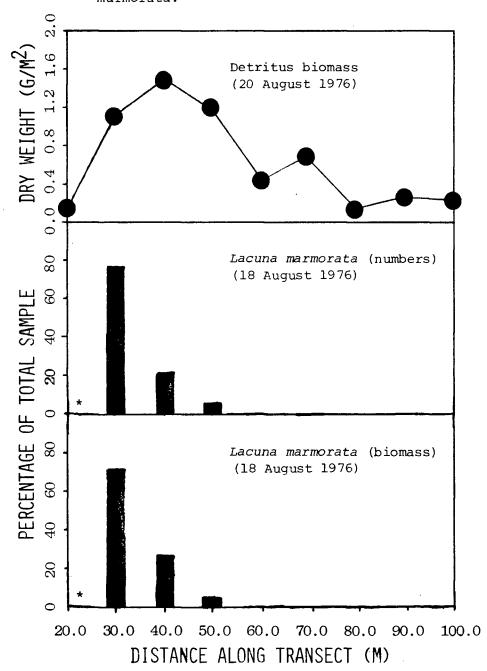


Figure 16. Spatial distribution along the 95 m transect location within Site 1 of Lacuna marmorata (numbers and biomass) and detritus biomass demonstrating a coincidence in the occurrence of their maximum abundances.

* A collection at 20 m on this date contained no Lacuna marmorata.



DISCUSSION

Litter Assessment:

In order to assess detritus formation and subsequent processing within Site 1, it is necessary to know the contributions of significant sources of detritus within the system. In such a coastal area there is potential for input from both terrestrial and marine sources. Bath Island is removed from salt marshes and domestic sewage input, so the potential sources are reduced to plankton, faunal excreta, drift wood and seaweed. Plankton will not be an important contributor, at a biomass call that of seaweed (Blinks 1955). Faunal excreta is not likely to exceed that amount as it is two trophic levels removed from plant production. Perhaps the most significant allochthonous litter source in British Columbia waters is drift wood (Perkins 1974). The seaweed zone of Bath Island is not characterized by a noticeable settlement of wood particles, such that seaweeds can be considered the only important source of litter.

It is difficult to compare litter accumulation at Bath Island to other areas as quantities are a function of the geology and biology of the area being studied. Zobell (1971), in a study of drift seaweeds cast upon San Diego County beaches in California between 1936 and 1954, estimated as much as 184 m³ of seaweeds per 150 m of shoreline on the beach at certain times. In contrast to Zobell's results virtually no litter was collected intertidally or supratidally at Bath Island, and the quantity of litter collected subtidally was very small in comparison to Zobell's intertidal assessment. The difference in the regions of litter deposition is attributable to beaches being accretion areas whereas rocky shores are excretion areas. The only significant comparison that can be made is that the phaeophytes were the dominant contributors to the litter pool in both studies, at 75% and 86% for California and Bath Island, respectively, on a wet weight basis.

The seaweeds contributing the most biomass to the litter in Site 1 are relatively productive species. Both Iridaea cordata and Nereocystis luetkeana grow rapidly during the spring, attaining their maximum standing crop biomasses during the summer. This is followed by a period of increasing litter deposition. At this time the plants have reached a size where they become less able to withstand the onslaught of current and waves, their vulnerability resulting in some plants becoming detached from the subtrate. For Nereocystis luetkeana the lamina are the more significant contributors to the litter. Occasionally healthy plants become detached at their bases and drift subject to the effects of winds and current, due to a pneumatocyst keeping the plants afloat. Neither the fate of these plants nor the number that left Site 1 during the course of this study are known; however it is known that they are not generally cast ashore at either Site 1 or Site 2. Rarely was a Nereocystis luetkeana litter fragment observed upon the shore and only once during the entire study was Nereocystis luetkeana litter collected within an intertidal quadrat. This is not unexpected as rocky shores are areas of excretion. Laminaria and Fucus distichus, although tending to be perennial, contribute significantly to the litter pool after having finished most of their seasonal growth. Slower growing seaweeds are disproportionately represented in the litter collections. Constantinea subulifera, a dominant, long-lived contributor to seaweed standing crop biomass in Site 1 was not collected during the litter sampling program.

By virtue of the sampling scheme undertaken, it has been possible to assess the biomass of seaweed litter within Site 1 in four dimensions. The midsummer collections create an areal profile for the site and delimit the spatial characteristics of litter distribution. The 14-month sampling program at the 95 m transect location within Site 1 contributes a temporal dimension. This

facilitates an extrapolation of the midsummer areal profile over the period of a full year for the five species contributing significantly to the litter.

It will be seen in a later discussion concerning the development of a mathematical model to simulate litter decomposition that the most important observation with respect to the temporal distribution of litter biomass is the similarity of the seasonal patterns of the five major contributors. Although the longevity of Nereocystis luetkeana stipes within the litter exceeds that of other litter, their total contribution is relatively minor. Any loss of information resulting from usage of a single curve model to approximate the seasonal distribution for total litter will be almost negligible.

The quantity of litter available for decomposition is the ultimate driving variable in an attempt to simulate its entry into, and processing within, litter and detrital pathways. Although these collections are most representative of the litter distribution patterns within Site 1, one must be careful not to accept immediately that these data represent the true proportion of each species' contribution to total litter input since neither the decomposition rate for each species nor the residence time for litter in Site 1 have been considered.

Litter Decomposition Experiments:

There are three components of plant litter which are known to influence its decomposition rate. The soluble, moderately resistant and crude fibre components respond differently during the decomposition process. Extrinsic influences must be considered as well. Environmental factors such as temperature, moisture, nutrient availability and microbial composition interactively exert an effect on the decomposition rates and patterns adding to the complexity of the process.

Some authors (Grill and Richards 1964, Minderman 1968, Otsuki and Hanya 1972) chose a 'theoretically preferable' curve model to represent their data on litter decomposition which Olson (1963) introduced as an exponential

decay curve with a constant 'k' related to the half-life of the substance undergoing decomposition. For such a simple model to be satisfactory the process it describes must be simple as well. This is not the case with litter decomposition. Although the curve may adequately describe the individual components of the decomposition process, their combination may defy a simple description.

Hunt (1977) demonstrated this point well and illustrated the unsuitability of applying an exponential decay curve to the decomposition data of Pendleton (1972). The result produced curves which obviously misrepresented the data.

With this in mind it was more suitable to select a curve which extrinsically fit the data well rather than accept an intrinsic model based solely on theoretical considerations. Furthermore, acceptance of an intrinsic model reduces the probability for success of a practical application of such information when compared to efforts based on a more realistic representation of the data.

The most consistent trend observed in the litter bag experiments was the initial rapid loss of material followed by a decrease in this rate as time proceeds. A similar trend is normally observed for terrestrial litter, although over a much longer time period, and is explained as follows. There is an initial rapid loss through leaching of the soluble and more easily metabolised components (Nykvist 1963, Petersen and Cummins 1974, Suberkropp et al. 1976) leaving behind a structural backbone of refractory material which slowly decomposes over a period of months (Lousier and Parkinson 1975, Stachurski and Zimka 1975, 1976 a&b, Gasith and Lawacz 1976). As the refractory material becomes more prevalent its resistance to metabolism by microbes results in the decomposition process slowing down.

Only two species, Rhodomela larix and Iridaea cordata, differed from this trend. Iridaea cordata displayed an accelerating decomposition rate as time proceeded while Rhodomela larix maintained a linear rate of decomposition.

Iridaea cordata is unique by having the lowest observed percentages of soluble and crude fibre components. Having a low soluble content would reduce the

length of an initial period of leaching and the paucity of crude fibre would facilitate a relatively rapid decomposition rate following this period. The initial lag phase may be due to the maintenance of structural integrity during the primary stages of decomposition and the inability of the small amount of soluble matter to mask this effect as it apparently does for other species. The linear decomposition curve for *Rhodomela larix* can perhaps be explained by its having a predominance of short, stubby branches which may become suitably fractured to escape the litter bag before its relatively high crude fibre content limits its decomposition rate in the later stages.

Loss of seaweed biomass from the litter bags was rapid. When compared to terrestrial litter, seaweed litter decomposes at least five times faster. Odum and de la Cruz (1967) and de la Cruz (1975) demonstrated that salt marsh plants decompose at about the same rate as terrestrial plants. Most plants they studied had a considerable amount of their original dry weight remaining after 300 days. Similarly, de la Cruz and Gabriel (1974) determined loss of Juncus roemerianus Scheele from litter bags to be ca 40% per year. Adding aquatic vascular plants to the comparison, Harrison and Mann (1975b) found that Zostera marina lost only 35% of its original dry weight in 100 days, under laboratory conditions. Hunter (1976) studied two freshwater plants, Lemna minor L. and Chara contraria A. Braun ex Kutzing, and found both to retain ca 75% of their original dry weight after ten weeks of submersed incubation in litter bags. That terrestrial, aquatic and marine vascular plants decompose much more slowly than seaweeds, even when submersed, implies that the rapidity of seaweed decomposition is more a function of their composition than of their environment. The influence of the relative quantities of seaweed structural components on decomposition rates is discussed in relation to the detritus decomposition experiments (Experiments 1 and 2).

Nitrogen Content of Decomposing Litter:

The results of this study are particularly significant in that they demonstrate a difference between vascular plant decomposition and seaweed decomposition with respect to nitrogen content. For vascular plant litter there is generally an increase in both the concentration and absolute content of nitrogen following an initial period of leaching during which most of the soluble components escape (Nykvist 1963, Petersen and Cummins 1974, Suberkropp et al. 1976). As most nitrogen escapes as soluble matter it has to be reacquired from the surrounding environment by organisms associated with the litter (Bocock 1964). Alternatively, this study indicates that the relative increase in nitrogen content of decomposing seaweed litter is due to a preferential release of chemical constituents low in nitrogen. That the increase is due to the incorporation of inorganic nitrogen into the litter by the activity of microbes is unlikely as it requires that the microbes have phenomenally rapid growth and nitrogen incorporation rates at a time when inorganic nitrogen in the seawater at Site 1 is at a low concentration (Tully and Dodimead 1957).

This argument is enhanced by demonstrating that C:N ratios of 8:1 or less would be very difficult to attain by metabolic processes. C:N ratios of this order are implied by the data obtained in this study. If the highest percentage nitrogen contents obtained for Laminaria saccharina (3.70%) and Rhodomela larix (4.74%) are related to the percentage carbon contents for Laminaria saccharina (26.76%) and an unspecified Rhodomela (28.32%) (Vinogradov 1953), a C:N ratio of 6-8:1 results. With a value of 6.4% nitrogen content obtained in this study for 97% decomposed Gigartina papillata and a value of 24% carbon content for Gigartina acicularis (Wulfen) Lamouroux (Niell 1976) a C:N ratio of less than 4:1 results, assuming there is a reasonable degree of generic similarity in percentage carbon contents.

The C:N ratio for bacteria is ca 5.7:1 (Spector 1956). To attain

C:N ratios approaching this figure the material in the litter bags would have to be composed almost entirely of microbial biomass, unless a considerable proportion of the nitrogen was a component of the initial seaweed biomass. Whyte and Englar (1975) suggest that a large proportion of the protein in seaweeds, Nereocystis luetkeana in particular, is bonded to the cellulosic fibres of the cell wall. This would prevent the easy release of protein nitrogen since cellulose is a particularly resistant component. The hyperbolic curve presented in Figure 7 is consistent with a protein - cellulose bond hypothesis. An accelerating increase in relative nitrogen content implies the rate of nitrogen loss is independent of the rate of loss of the more abundant biomass components.

Hunter (1976) used litter bags to assess the decomposition rate of Fucus vesiculosus on a rocky shore and within a salt marsh. His results are comparable to those presented in this study with respect to decomposition rates, relative nitrogen content and C:N ratio. Additionally, for the aquatic plants Lemna minor and Chara contraria, he demonstrated no consistent trend for the same parameters, maintaining the uniqueness of seaweeds in this regard.

Detritus Decomposition:

For the subsets delimited in Experiment 1 (Table 8a) the withingroup affinities are somewhat apparent. All groups are composed of species of a single taxonomic class and can be categorized according to the morphology and habit of the seaweeds they contain. Subset 1 contains four species of branched Rhodophyta which are found intertidally or in the shallow subtidal zone. Subset 2 contains three species of subtidal kelp (Laminariales). One other phaeophyte, Fucus distichus, is placed by itself in Subset 4. It resembles the other phaeophytes neither in morphology nor habit, being dichotomously branched and inhabiting the intertidal zone. Subset 3 contains two bladed rhodophytes known to coexist in the shallow subtidal zone (Foreman unpub.).

Similarly, for Experiment 2, the within group affinities can be easily detected. Subset 1 contains all the 'resistant' species, those which did

not exhibit a continual loss of particulate biomass, and Constantinea subulifera. Constantinea subulifera decomposed faster than all other species in Subset 1 and is the only species that did not exhibit an increase in particulate biomass as decomposition proceeded. It is the only bladed seaweed in Subset 1. Although Newman-Keul's Test did not separate Constantinea sublifera from the other species, Duncan's Test delimited an equivalent subset excepting Constantinea subulifera.

The increase in particulate biomass can be explained as a result of increased microbial biomass due to preferential metabolism of soluble matter as demonstrated in Experiment 1. If the growth rate of microbes utilizing the soluble matter exceeds the decomposition rate of the particulate fraction of the detritus a net increase in particulate biomass will result.

Fucus distichus (60.7%) and Constantinea subulifera (65.6%) have soluble contents considerably higher than the eight other species. Although low in soluble content, Rhodomela larix (4.28%), Odonthalia flocossa (3.44%) and Plocamium coccineum var. pacificum (3.39%) have the highest percentages of crude fibre carbohydrate. Experiments 1 and 2, respectively, demonstrated that soluble matter is preferentially metabolized and decomposition is slower for seaweeds with a high crude fibre content.

Laminaria saccharina and Laminaria groenlandica comprise Subset 3. Subset 4 contains the lamina and stipe sections of Nereocystis luet-keana. Kelp being delimited from the other seaweeds indicates taxonomic similarities with regard to decomposition susceptability.

Subsets 2 and 5 contain single species each. Iridaea cordata is isolated because of its rapid decomposition rate. Gigartina papillata is placed between Subset 1 and the subsets containing more easily decomposable species. It is the only intertidal species not contained within Subset 1. It has an affinity with the species in the other three subsets, all of which are bladed seaweeds, in that it has a tendency to be foliose.

There is a basic similarity in the composition of the subsets delimited in Experiment 1 and Experiment 2. Any differences can readily be explained by the influence of detrital soluble matter content on the rates of oxygen consumption obtained in Experiment 1. Referring to Table 8a, the effect of the high soluble contents of Fucus distichus and Constantinea subulifera on their oxygen consumption rates can be negated by placing them in Subset 1 with the other 'resistant' species. All four subsets are now less dissected equivalents of those delimited in Table 10. The inability to dissociate Nereocystis luetkeana from Laminaria saccharina and Laminaria groenlandica, and Gigartina papillata from the other members of the Subset 1 is likely due to the analysis becoming less powerful as a result of the error contributed by the covariance of oxygen consumption with the quantity of soluble matter in the detritus, as demonstrated by Figure 9 and Table 8b.

As a final judgement, three generalizations can be made concerning the decomposition rates observed. Detritus derived from intertidal seaweeds is apparently more resistant to decomposition than detritus derived from subtidal seaweeds. Detritus derived from the faster growing seaweeds decomposes more quickly than detritus derived from the slower growing seaweeds. Seaweed morphology appears to correlate with decomposition susceptibility, the more foliose the seaweed, the more quickly detritus derived from the seaweed decomposes. All three of the above considerations are closely interrelated. Other factors are likely to be involved as well, in particular the resistance of seaweeds to attack by microbes. The presence of antibacterial chemicals in some species is known to enhance resistance (Sieburth 1968).

In Experiment 1 oxygen consumption rates were shown to correlate with the soluble content of specific detritus (Figure 9). Consumption was higher for species having relatively high soluble matter contents. Only *Tridaea cordata* defied this trend. The oxygen consumption rate of microbes decomposing

Iridaea cordata detritus was second only to Fucus distichus, although it has the lowest percentage soluble content (28.1%) observed amongst all species. Its rapid decomposition rate may be partially due to it containing only a very small quantity of crude fibre at 0.86% of its dry weight. This was the lowest quantity observed amongst all the species. This lack of resistant material may render Iridaea cordata more vulnerable to attack by microorganisms such that it decomposes rapidly relative to other species with a similar or greater percentage of soluble matter.

The decomposition rates obtained in Experiments 1 and 2 are complementary. Iridaea cordata provides the best comparison due to its having very little crude fibre, a low soluble matter content, and a rapid decomposition rate. By assuming that the particulate component of detritus is composed mostly of carbohydrate, ca 1.07 mg of oxygen would be required to fully decompose the 1.0 mg plug of detritus introduced into each BOD bottle. At the average oxygen consumption rate of 0.052 mg O2 per day observed for Iridaea cordata over the first 10 days of incubation, 20.5 days would be required to fully decompose the detritus. The rate of loss of particulate matter obtained for Iridaea cordata during the first 10 days of incubation in Experiment 2 was 5.7% per day. At this rate, 18 days would be required to fully decompose the detritus, in close agreement with the 20.5 days estimated by the oxygen consumption method.

Comparing the decomposition rates obtained in Experiments 1 and 2 to those obtained by other persons for vascular plant detritus, the most apparent difference is the relative rapidity of seaweed detritus decomposition.

Odum and de la Cruz (1967) measured oxygen consumption of natural coarse Spartina alterniflora detritus (that which was retained by a 0.239 mm aperture) at ca 1.8 mg O₂/g AFDW/hr at 15 C. This study obtained rates in the range of 2.7-7.0 mg O₂/g AFDW/hr for equivalently sized detritus from Plocamium coccineum var. pacificum and Iridaea cordata, respectively, also at 15 C. The data were

most reliable for these two species since their low soluble contents minimally affected observed oxygen consumption rates.

Differences in decomposition rates for various particle sizes of aquatic vascular plant detritus have been shown for *Phragmites communis* Trinius leaves (Hargrave 1972), *Spartina alterniflora* (Odum and de la Cruz 1967, Gosselink and Kirby 1974) and *Thalassia testudinum* (Fenchel 1970). That a similar response was shown for *Nereocystis luetkeana* and *Iridaea cordata* detritus indicates that decomposition rate may be influenced by the amount of surface area exposed to microbial attack.

Part of the difficulty in determining a relationship between particle size and the parameters tested in Experiments 1 and 2 may be explained by there being only a small amount of crude fibre present in seaweed biomass. Refractory material accounts for a large proportion of vascular plant detritus, and is composed largely of lignins, celluloses and hemicelluloses which slowly decompose over a period of months (Lousier and Parkinson 1975, Stachurski and Zimka 1975, 1976 a&b, Gasith and Lawacz 1976). Lignin is the most resistant of these constituents, having a half-life of about one year at 30 C and under optimal conditions for microbial decomposition (Acharya 1935). The amount of lignin present in leaves was given a range of 16-42% by Jensen (1974), who summarized the work of several authors. With the amount of material lost by leaching ranging from ca 27-40% (Otsuki and Wetzel 1974, Suberkropp et al. 1976), lignin may account for up to 70% of the particulate fraction of the detritus.

In contrast to vascular plants, macrophytic algae contain no lignin, although their cell walls do contain celluloses and hemicelluloses (Steward 1974) which are moderately resistant. The crude fibre content for the 10 species assayed in this study ranged from 1.2-17.7% of the particulate component. As vascular plants contain a much greater amount of crude fibre than seaweeds it is reasonable to conclude that the rapid decomposition rates of seaweed litter and detritus is at least partially due to a paucity of resistant material.

Figures 12a (crude fibre) and 12b (glucose) demonstrate the relationship between decomposition rate and resistant material content; however this parameter was shown to account for only 42.8% of the variance associated with Figure 12a and 39.9% of the variance associated with Figure 12b. Other factors must be involved as well. No doubt some of the variance is due to limitations in the data, but factors determining the resistance and susceptibility of seaweeds to attack by microbes are likely to play important roles.

The three major structural components of seaweeds have been shown to influence the decomposition process independently. In Experiment 1 soluble matter was isolated from the remaining two components as being preferentially metabolized. From the results of Experiment 2 the crude fibre component was identified as an influence on the decomposition rates of the particulate fraction; the greater the quantity of crude fibre, the slower the decomposition rate. The three components can thus be ranked in order of soluble, moderately resistant and crude fibre with respect to the ease with which each is metabolized, as has been previously documented for vascular plant material.

Detritus Assessment:

The accuracy of detritus biomass estimations is questionable. A major criticism is the assumption that the flat, horizontal areas chosen as collecting surfaces are equally as receptive to detritus settlement as uneven surfaces. Such surfaces would be expected to retain a greater proportion of the detritus than the level surfaces. A second criticism is that the biomass data do not take into consideration the decomposition rate of natural detritus. Data in this study indicate that turnover of seaweed detritus is rapid. For Iridaea cordata detritus ca 18-21 days are required, other species requiring a longer turnover time. With sampling intervals of about three weeks, the quantity of detritus deposited on the bottom in Site 1 will potentially be underestimated by 50%, if its biogenic origin is seaweed biomass. As microscopic

examination of the detritus determined it to be composed of ca 10% diatomaceous material, the most significant component of phytoplankton in the Strait of Georgia (Hutchinson and Lucas 1931), seaweed remains the only source abundant enough to account for the remaining 90% of detritus biomass. It is likely that detritus deposition within Site 1 will be underestimated, perhaps by more than 50%; however, this will not preclude the possibility of making judgements regarding the fate of detritus formed from seaweed biomass.

Faunal Assessment:

Vascular plant detritus is a confirmed source of food for fish and invertebrates (Kaushik and Hynes 1968, Iverson 1973, Tenore 1975, Kostalos and Seymour 1976, Sibert et al. 1977). Seaweed detritus derived from the phaeophyte Dictyopteris zonarioides Farlow has been shown to be ingested by the epibenthic deposit-feeding holothurian Parastichopus parvimensis Clark (Yingst 1976). Fucus vesiculosus detritus has been utilized by the brine shrimp Acartia tonsa Dana (Roman 1977) and the molluscs Hydrobia ulvae Pennant and Macoma balthica L. (Newell 1975). In each of these experiments seaweed detritus was the only food source such that no indication of the animals' preference for this food resource was attained. In this study Lacuna marmorata, Metacaprella anomala and Cancer oregonensis were delimited as possible respondents to the availability of natural seaweed detritus as a food resource on the basis of the occurrence of at least 75% of their numbers and biomass during the three midsummer faunal collections. A critical consideration of these species reveals that Cancer oregonensis is an unlikely respondent as its habit is carnivorous and, furthermore, only 19 individuals were collected such that its qualification may be an artifact of inadequate sampling. Cancer oregonessis will not be considered any further.

Inadequate sampling may also be argued as the reason for Meta-caprella anomala qualifying as only nine individuals were collected. Although not abundant during the summer of 1976, Metacaprella anomala has been abundant

at Site 1 in previous years (Foreman unpub.). Circumstantial evidence that Metacaprella anomala is a detritus utilizer was obtained in this study when they were observed attached to the experimental litter bags in numbers from 10-100 individuals about the end of July. This was the only time during the summer of 1976 when their presence was obvious.

Lacuna marmorata was very abundant at Site 1 during the summer of 1976 with about 7400 individuals being collected at densities approaching $70,000/m^2$ (Figure 16). Of particular significance is the more than 10-fold increase in the number and dry weight of juvenile Lacuna marmorata individuals during midsummer.

Preliminary consideration of other species which may have qualified at a lesser percentage indicated they were less likely to be significantly dependent on a summer pulse of detritus. Additional species which would have qualified at a 50% acceptance level are Odostomia spp., Lirularia lirulata Carpenter and Granulina margaritula Carpenter. Odostomia can be removed from consideration as they are generally ectoparasitic in habit (Fretter and Graham 1949). Granulina margaritula and Lirularia lirulata were not particularly abundant in the faunal collections, did not display strong midsummer peaks in numbers or biomass, presented no evidence of the occurrence of juveniles and as their diets are undocumented it is not possible to discuss their occurrence in relation to the availability of detritus from a positive perspective.

An indication that the occurrence of specific marine fauna might be a response to the availability of seaweed detritus as a food source, which was shown in this study to occur about the middle of August, was obtained in the summer of 1975 when an extensive 'bloom' of caprellid amphipods, mainly Caprella alaskana Mayer was observed in Site 1. They were estimated to be present at a density of hundreds per square metre. Also evident at this time was a 'scum' of detritus over the bottom, particularly in the central area of the kelp bed. That

this is at least a periodic phenomenon was confirmed by reference to Foreman's (unpub.) faunal data which contained a record of Caprella alaskana at a density of $520/m^2$ and Metacaprella anomala at $312/m^2$ in 1973 and 1972, respectively, and at lesser densities in other years (Table 12).

Caine (1977) presents evidence that these two species may utilize detritus. Although neither one is represented in his study, he demonstrated (with reference to other authors) that detritus was fed upon by 15 of the 16 species which he investigated. Their mode of feeding was variable, involving various combinations of filter feeding, scavenging and scraping. Food acquisition was determined to be related to the presence or absence of plumose setae on their second antennae, those species with such antennae obtaining a significant amount of their food by scraping and/or filtering particulate matter.

The second antennae of both Metacaprella anomala and Caprella alaskana are characterized by the presence of plumose setae, and since Caine observed that 75% of the stomach contents of caprellids with such setae consisted of diatoms and detritus it is reasonable to conclude that detritus contributes significantly to the diet of these two species. Any argument that Caprella alaskana and Metacaprella anomala are responding to the availability of diatoms is weak. Such a response would have been expected to occur earlier in the year at the time of the spring bloom of diatoms and other phytoplankton in the Strait of Georgia (Hutchinson et al. 1929, Gran and Thompson 1930), not during the summer when nutrient levels in the Strait of Georgia are low (Tully and Dodimead 1957). Diatoms comprised only ca 10% of the biomass of detritus samples collected from the substratum in Site 1 during the summer of 1975.

No 'bloom' of caprellids was detected within Site 1 during the summer of 1976 when this study was conducted. The scarcity of both Caprella alaskana and Metacaprella anomala during the summer of 1976 cannnot be explained with certainty but it is possible that unusual environmental conditions during

Table 12.

History of the occurrence (per m^2) of two species of Caprellidae, Caprella alaskana and Metacaprella anomala, within the summer faunal collections of Dr. R. E. Foreman (unpublished). Foreman's transect units are used, but they are essentially equivalent to the transect units in this study.

Year	Distance along transect (m)	Number C. alaskana	M. anomala
August 1972	75		8
	80		312
July 1973	60	200	
	65	276	28
	70	324	
	75	456	
	80	520	
	85	8	
	95	4	
July 1975	55		4
	60		16
	85		8
	90		4
	95		16
August 1975	50-90	several hundred/m ² *	

^{*} visual estimation of abundance

August, generally the warmest month, were at least partially responsible. The Vancouver Weather Office, ca 35 km from Bath Island at Vancouver International Airport, reported August 1976 to be one of the coldest on record. The mean air temperature for August 1976 was 15.9 C. The normal mean air temperature for August is 17.1 C. On only two occasions since 1937 was a lower mean air temperature recorded during August. Water temperature was similarly influenced. Based on daily readings near Site 1 (Foreman unpub.) the mean water temperature for the first half of August 1976 was 3.64 C below the mean temperature for August 1975 (12.36 C and 16.2 C, respectively) when Caprella alaskana was very abundant.

As metabolism is a function of temperature, persistent cool temperatures could appreciably lower the growth potential of an organism. Microbial decomposition rates of seaweed litter would be similarly affected, reducing the quantity of detritus available. Although based only on a visual interpretation, the quantity of detritus which accumulated on the bottom during August 1976 was observed to be much less than the quantity observed in 1975 when a large bloom of Caprella alaskana was observed. In conclusion, it is reasonable to suggest that the effect of low temperatures on the growth rates of both Caprella alaskana and Metacaprella anomala, coupled with low detritus availability as a food resource, may have been sufficient to prevent a proliferation of these species in 1976.

It has not been shown experimentally that Lacuna marmorata utilizes detritus as a food source, however E. Cabot (pers. comm.) examined the gut contents of individuals collected near Site 1 and found an abundance of diatoms and amorphous material whose biogenic origin could not be identified. He classified this latter material as detritus while conceding it may have been living material rendered unrecognizable due to mastication during and following ingestion. Lacuna are known grazers of seaweeds. Powell (1964) demonstrated that Lacuna fed upon Constantinea subulifera. The author has observed adult Lacuna marmorata grazing upon Nereocystis luetkeana lamina.

These reports refer only to adult snails. Juvenile snails comprised the bulk of the individuals of Lacuna marmorata collected within Site 1 during the period of maximum detritus availability. Figure 16 demonstrates that 100% of the total number and dry weight of Lacuna marmorata were collected in the zone 30-50 m along the permanent transect. Not only is this the turf community zone (Lindstrom 1973), which aids in the retention of the detritus and provides a habitat for Lacuna marmorata, it is also where maximum detritus biomass was observed during the summer (see also Figure 13, page 73). Based on this evidence, and the results from the simulation of litter and detritus processing which indicate seaweed detritus to be suitably nutritious for fauna, it does not seem unreasonable to infer that the success of a midsummer recruitment of juvenile Lacuna marmorata individuals is dependent on the availability of seaweed detritus as a food resource.

SIMULATION MODEL OF LITTER AND DETRITUS PROCESSING

Introduction:

To date decomposition models developed to simulate specific aspects of litter and detritus decomposition have been limited to the terrestrial environment. Boling et al. (1975) were primarily concerned with simulating an aspect of leaf and branch litter decomposition by considering the interaction between fractionation of the material by physical abrasion and microbial conditioning of the resulting particles. Flanagan and Bunnell (1976) developed a model to deal with the influence of moisture, oxygen, temperature and litter composition on the respiration rates of microbes associated with litter, and another to assess the decomposition rates of terrestrial plants under the influence of changing substrate quality.

The need for this degree of resolution becomes more apparent as the complexity of the system increases. Moisture content, temperature and oxygen tension within soil can vary daily and seasonally, greatly influencing the decomposition rates of soil borne litter (Nyhan 1976). This requires that they be incorporated into models simulating terrestrial decomposition processes (Hunt 1977, Reuss and Innis 1977). Decomposition rates are also dependent upon the availability of inorganic nutrients, particularly nitrogen (Kaushik and Hynes 1971, Nichols and Keeney 1973, Howarth and Fisher 1976).

In a marine system many of these complications can be avoided. The buffering quality of seawater helps alleviate the potential variability in many parameters. There are seasonal variations in the contents of inorganic nitrogen and oxygen in the Strait of Georgia, but it is unlikely their concentrations drop to a level limiting the decomposition rates of the species studied. Oxygen concentrations in the upper 10 m of the Strait of Georgia are consistently near 100% saturation (Tully and Dodimead 1957). During litter collections, pockets of litter were occasionally found containing some seaweeds undergoing

anaerobic decomposition, however, the quantity was insignificant compared to the amount of litter undergoing aerobic decomposition. As seaweed litter tends to retain nitrogen preferentially during the decomposition process, the availability of nitrogen is probably not a factor influencing the decomposition rate of most seaweed litter. Substrate quality, temperature, and moisture content remain the major factors to be considered. The effect of substrate quality is accounted for intrinsically within the derived litter decomposition curves leaving temperature the only effect needing to be incorporated into the model. Moisture is obviously not an influential factor.

The numerical objectives of the simulation were:

- 1) to predict the seasonal formation rates, biomass, and longevity of detritus derived from decaying seaweed litter within Site 1
- 2) to predict the seasonal release rates and quantity of soluble matter released from seaweed litter at Site 1
- 3) to estimate the nitrogen contents of the detritus formed and soluble matter released from decomposing seaweed litter.

Determination of these parameters facilitated a comparison between the biomass of detritus predicted to be available as a food resource within Site 1 and the biomass of detritus obtained from the sample collections.

Additionally, an estimate of the seasonal contribution of detritus and soluble matter derived from seaweed litter to the Strait of Georgia was obtained.

Model Development:

Initially, a four dimensional matrix representing the pool of seaweed litter, the driving variable in the model, was created to permit litter to
be referenced in terms of its biogenic origin, the quadrat within the transect
from which it was collected, and the location of the transect. Only Fucus
distichus, Iridaea cordata, Nereocystis luetkeana (stipe and lamina sections considered individually) and Laminaria (L. saccharina and L. groenlandica combined),
the species accounting for more than 97% of the quantity of litter collected,

were incorporated into the model. Extrapolation of the areal profile for each of these species (Figure 2) was facilitated by prorating the 14 month seasonal collections (Figure 5) according to a tenth degree polynomic curve which approximates the seasonal trend in litter biomass. This curve is presented in Figure 17 for total litter biomass.

The litter decomposition curves for these species are presented in Figure 6 (d,g,h,i,j), page 43. For Fucus distichus, Nereocystis luetkeana (stipe) and Laminaria, which decompose exponentially, 1.0% of original dry weight was considered the termination of the decomposition process. The rates were modified by a temperature dependent adjustment factor which accounts for the effect of seasonal temperature differences on decomposition rates. Monthly mean temperatures are presented in Table 13a, based on regular measurements taken at or near Site 1. Temperatures were converted to a decomposition rate adjustment factor (Table 13b) by the following formula, assuming a Q_{10} of 2.0 approximates the effect of temperature on decomposition rates (Boling et al 1975, Reuss and Innis 1977).

where:

 $F = 2 \frac{13.4 - T}{10}$

F is the decomposition rate
 adjustment factor
T is the temperature in C

The mean temperature during the period when the litter bag experiments were performed was 13.4 C.

The adjustment factor was estimated for each day of the year by fitting the following cyclical curve to the adjustment factors determined from the above formula. The formulae for calculation of the following curve are in Croxton et al. (1967).

 $F = 1.375 + (0.20187 \sin(2\pi/366) + 0.29821 \cos(2\pi/366)) \times I$ where:

F is the decomposition rate adjustment factor

I is the day of the year

The model was operated over the time period of 28 February 1976,

Figure 17. Tenth degree polynomic curve fitted to the seasonal biomass data obtained from litter collections along the 95 m transect location within Site 1 from 20 August 1975 until 2 October 1976. Biomass is in g ash-free dry weight per m^2 . The curve model is as follows:

$$PB = \Sigma(p_i DY^{i-1}); i = 1,11$$

where:

PB is the predicted litter biomass DY is the day of the year $\mathbf{p_i}$ are the coefficients

The coefficients are as follows:

- 1) 0.3115825195312500E+01
- 2) -0.1553213977813721E+00
- 3) 0.5167517066001892E-02
- 4) -0.9613301604986191E-04
- 5) 0.1075271284207702E-05
- 6) -0.7727231263743306E-08
- 7) 0.3657364633369298E-10
- 8) -0.1130370536756020E-12
- 9) 0.2186710082213890E-15
- 10) -0.2393779959900677E-18
- 11) 0.1127717301078564E-21

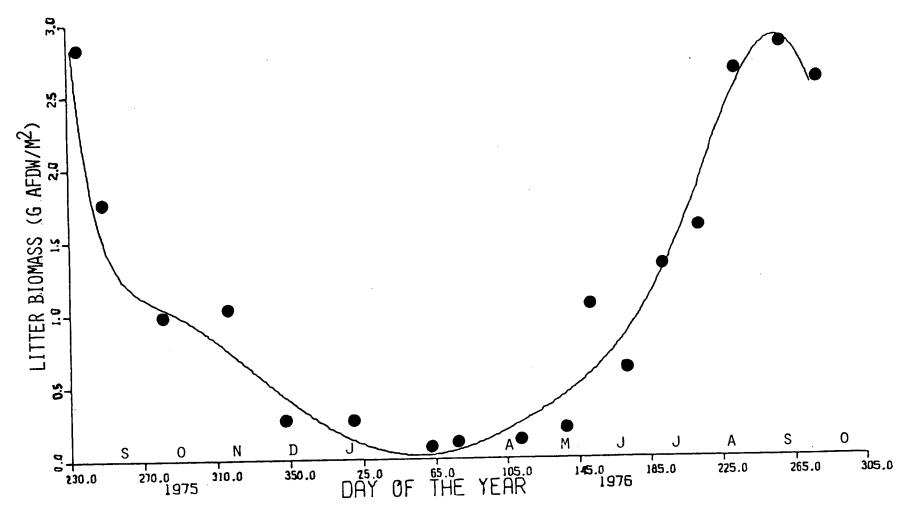


Table 13.

Mean monthly temperatures (a) and the corresponding decomposition rate adjustment factor (b) for the period November 1975 until October 1976. The temperature data are based on periodic readings near Site 1 (Foreman unpub.). See text for an explanation of the adjustment factor.

Month	a) Temperature (C)	b) Adjustment factor
January	5.6	1.717
February	6.1	1.659
March	6.4	1.625
April	7.6	1.495
May	8.4	1.414
June	11.8	1.117
July	13.4	1.000
August	12.5	1.064
September	13.6	0.986
October	9.6	1.301
November	7.7	1.485
December	6.3	1.636

when litter biomass was essentially zero, until 31 December 1976. Since no litter collections were made beyond 2 October 1976, data from the autumn of 1975 were used for the period of October through December 1976. With daily increments beginning on 28 February 1976 litter was mathematically processed according to the temperature corrected specific submodels. Litter biomass available to be decomposed each day was determined by applying the equation for the curve in Figure 17 to the ratio of specific litter:total litter for the most recent sampling date. The onset of decomposition was delayed by an estimated senescence delay of six days (temperature adjusted) as explained on page 54.

Specific litter in each quadrat was processed independently during the simulation. Starting on 28 February 1976, litter which decomposed on this date was subtracted from the litter biomass at the beginning of the day. This calculation was then performed for every subsequent day required to reduce the litter biomass to zero, assuming no further litter deposition. For each of these subsequent days, the remaining litter biomass was subtracted from litter biomass at the beginning of the day to account for daily biomass loss. Remaining litter will be supplemented with freshly deposited litter and undergo decomposition on future days.

Following performance of this cycle for each species in every quadrat, the data were summed to yield the total quantity of detritus formed and soluble matter released on 28 February 1976, with partial sums for the immediately subsequent days. This entire procedure was then repeated, with daily increments, for the duration of the simulation.

During the simulation all soluble matter was released in advance of the particulate material. Until the remaining litter biomass reached the percentage equal to the particulate material content for that species, all exportation was registered as soluble matter. Further decomposition formed detritus.

Concomitant with litter decomposition, the nitrogen content of the detritus formed and the soluble matter released was determined. Unfortun-

ately, due to the rapid decomposition rates of the species involved in the simulation, minimal nitrogen data were obtained for these species. The data are insufficient to support firm conclusions but are suitable for approximating trends for the purpose of modelling. Curve models for estimating litter nitrogen content were selected from those introduced on page 42, with those yielding the best fit being accepted. They are as follows:

```
Fucus distichus Y = -1.09E-02X + 2.83 (L)

Iridaea cordata Y = 7.04E-03X + 1.24 (L)

Nereocystis luetkeana (stipe) Y = -9.33E-03X + 2.44 (L)

Nereocystis luetkeana (lamina) Y = -2.92E-03X + 5.30 (L)

Laminaria Y = 7.85E-05X^2 - 3.39E-02X + 4.92 (Q)
```

where: X is the percentage of litter remaining
 in the litter bag
Y is the percentage nitrogen content of the
 material remaining in the litter bag

The formula derived for calculating the nitrogen content of detritus and soluble matter is as follows:

$$N_{i} = \frac{\text{QL}_{i}(\text{PLU}_{i-1} - \text{PLU}_{i}) (\text{PN}_{i} + \text{PN}_{i-1})}{2} \times \frac{((\text{PN}_{i-1}) (\text{PLU}_{i-1})/\text{PLU}_{i}) - \text{PN}_{i}}{((\text{PN}_{i-1}) (\text{PLU}_{i-1})/\text{PLU}_{i}) - \text{PN}_{i-1}}$$

where:

N is the quantity of nitrogen released as soluble matter or as a component of detritus on day i

QL is the quantity of litter available for decomposition on day i

PLU is the proportion of older litter yet undecomposed (a function of the litter decomposition submodels, Figure 6)

PN is the proportion of nitrogen in the litter (a function of the litter nitrogen content submodels listed above)

i is a counter for the day during the simulation

Detritus decomposition was simulated by usage of the detritus decomposition rates obtained for the initial 0-10 day incubation period in Experiment 2. For Fucus distichus the decomposition rate for 20-30 days was used. All rates were linear and are as follows:

Fucus distichus	0.76%	per	day	
Iridaea cordata	5.65%	per	day	
Nereocystis luetkeana	(stipe)	3.12%	per	day
Nereocystis luetkeana	(lamina)	3.48%	per	day
Laminaria		2.93%	per	day

As the change in nitrogen content of decomposing detritus was not determined, it was modelled as though it decomposed at the same rate as other detritus components. Soluble matter was not decomposed.

To reduce the volume of output produced by the simulation, daily incremental data were summed and averaged over 3-4 week intervals. Greater resolution was superfluous and unmanageable.

A flow chart outlining the major operations involved in the performance of the simulation is presented in Figure 18.

Results:

Operation of the simulation model determined the proportional contributions of Fucus distichus, Iridaea cordata, Nereocystis luetkeana and Laminaria to the litter. Table 14 compares the true proportional contributions of each species to their estimated contributions based on sampled litter biomass alone. As expected, the proportional contribution by Fucus distichus was considerably lower than indicated by the biomass data, due to its particularly slow decomposition rate relative to the other species. The proportional contributions by all other species increased, most dramatically for Nereocystis luetkeana (lamina). The unreliability of litter biomass as an estimator of the true quantity of litter which undergoes decomposition is apparent.

Figure 19 displays the seasonal profile for the rate of detritus formation and release of soluble matter from decomposing seaweed litter within Site 1. Both are seasonal phenomena with peaks occurring during late summer. Maximum observed rates were ca 0.6 and 0.5 g AFDW/ m^2 per day for detritus formation and soluble matter release, respectively. In total, ca 56% of decomposing litter forms detritus, the remainder being released as soluble matter.

Figure 20 displays the predicted detritus biomass formed from litter deposited along the permanent transect location (95 m) in Site 1. Figure 21 presents a similar picture based on total litter deposition within Site 1.

Figure 18. Flow chart outlining the major operations involved in the simulation of litter and detritus processing within Site 1.

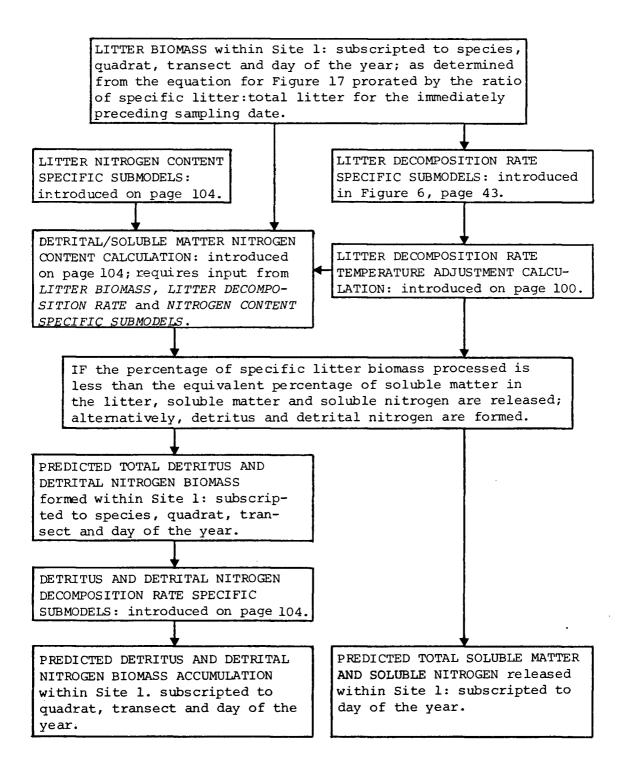


Table 14.

Comparison of the percentage contributions by the major contributors to the litter pool within Site 1 as determined by:

- a) litter biomass alone
- b) application of the decomposition rates of these species to litter biomass data.

These percentages were determined on an ash-free dry weight basis.

Species	Litter biomass	Litter biomass coupled with decomposition rates
Fucus distichus	71.98	40.84
Iridaea cordata	15.07	26.22
Nereocystis luetkeana	(stipe) 1.95	3.57
Nereocystis luetkeana	(lamina) 7.36	23.72
Laminaria	1.69	3.70

Figure 19. Seasonal profiles for the formation rate of detritus and the release rate of soluble matter from decomposing seaweed litter biomass within Site 1. Rates are in g ash-free dry weight per m^2 per day.

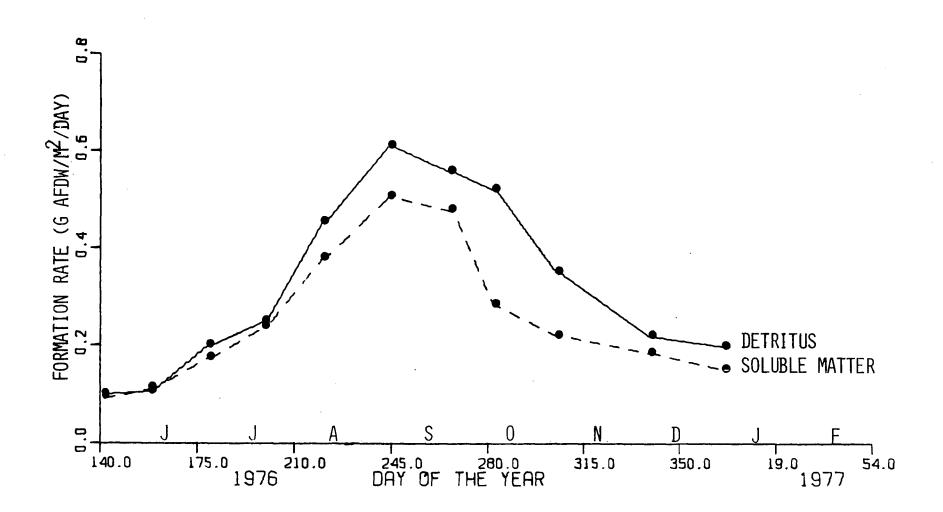


Figure 20. Detritus biomass predicted for the 95 m transect location within Site 1 based on litter collections from that location only. Contour intervals are 2.0 g ash-free dry weight per m.

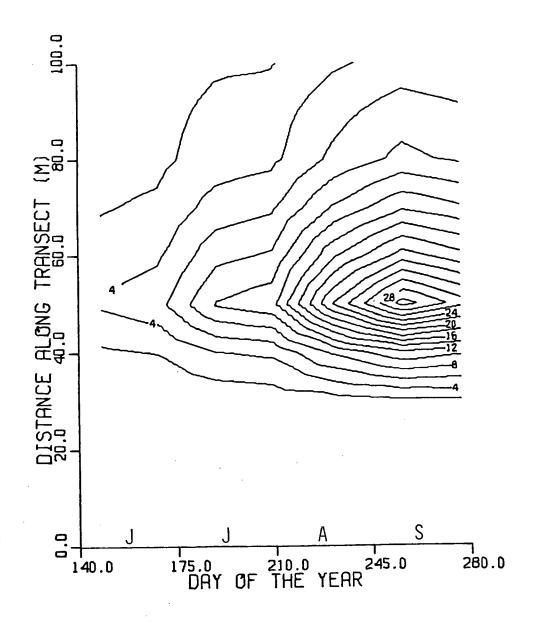
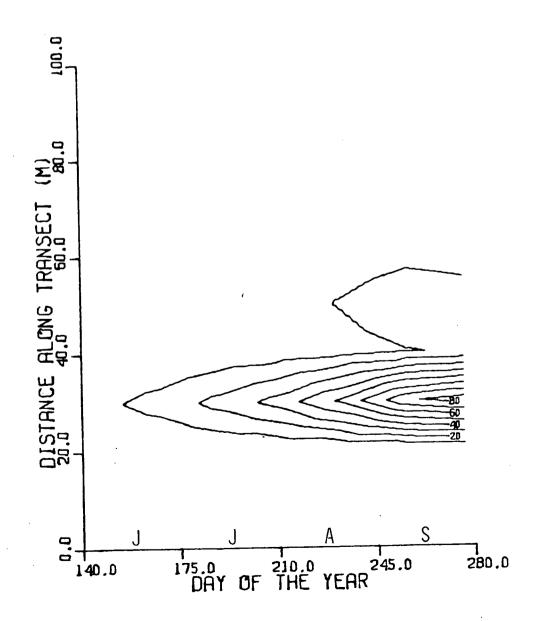


Figure 21. Detritus biomass predicted for Site 1 based on litter collections from all transect locations within Site 1.2 Contour intervals are 10.0 g ash-free dry weight per m.



Reference to Figure 13 (page 73) highlights an obvious discrepancy between predicted and observed detritus biomass. Based on sampling data, detritus biomass along the permanent transect location peaked at $1.4\,g$ AFDW/ m^2 whereas the predicted quantity was ca 30 g AFDW/ m^2 if all detritus was deposited on the substrate. If detritus biomass is more accurately predicted by incorporating all litter data for Site 1, ca 80 g AFDW/ m^2 is estimated. Accepting that the data incorporated into the model are reasonably accurate, the implication is that detritus accumulation in Site 1 amounts to only 1-5% of the quantity of detritus formed from seaweed litter within Site 1, the remainder being exported.

Alternatively, the difference between predicted and observed detritus biomass is a result of litter deposited within Site 1 undergoing decomposition elsewhere, its residence time in Site 1 being very short. Three arguments discount this hypothesis. Most specific litter was collected near stands of the same species. Very little litter was observed outside the seaweed zone. The simulation demonstrated that litter decomposition rates could account for the disappearance of all but 3% of the litter deposited within Site 1.

The mean nitrogen content of detritus at the time of its formation was predicted to be $2.48 \pm 0.03\%$ of its dry weight over the period of the simulation. The quantity of nitrogen released with the soluble matter was a lesser amount at $1.36 \pm 0.03\%$.

Discussion:

Data obtained in this study indicate that ca 80 g AFDW/ m^2 of detritus was formed from seaweed litter during 1976. When soluble matter is added to this figure it is increased to 145 g AFDW/ m^2 . With carbon accounting for 50-60% of the elemental composition of the organic matter (Round 1965), 70-85 g C/ m^2 is the estimate for the amount of carbon leaving seaweed biomass via litter decomposition in Site 1.

This amount accounts for ca 45% of the quantity of seaweed biomass lost from the same area as determined from seasonal differences in standing crop biomass (Foreman unpub.). The remaining biomass must be accounted for by detritus formation directly via lamina tip erosion and by Nereocystis luetkeana leaving Site 1 when detached by winds and waves. Johnston et al. (1977) estimated Laminaria saccharina to lose 40-50% of its gross primary production by lamina tip erosion, a certain percentage of which would be expected to form detritus without being shunted through the litter pool.

It must also be considered that seasonal changes in standing crop biomass may inadequately estimate the total quantity of detritus formed from seaweeds. Mann (1972b) estimates the ratio of yearly production:initial biomass for populations of Laminaria digitata and Laminaria longicruris to be 9.8 and 7.2, respectively. Agarum was less productive at 4.2. Thus, without necessarily constituting a major portion of the standing crop biomass within the seaweed zone, these kelps can account for a large portion of the net production. Such an extensive turnover of biomass results in standing crop biomass underestimating total production and subsequent detritus formation and soluble matter release.

Mann's (1972b) system this consideration is probably appropriate; however, the indications are that Nereocystis luetkeana has the highest biomass turnover of the plants within Site 1 (Foreman unpub.). As Nereocystis luetkeana was ranked tenth in 'importance' of the 'significant' species within Site 1 and third in its contribution to the litter pool, changes in biomass may not severely underestimate total detritus formation and soluble matter release when the entire system is considered. This is supported by Foreman's seasonal biomass data which indicate that 45% of the biomass loss occurred in the depth range 0-3 m below mean sea level. This is the zone dominated by Fucus distichus and Iridaea

cordata, the two dominant contributors to the litter pool. A large biomass turnover has not been shown to be characteristic of these species. The remaining biomass loss is accounted for by the other eight 'significant' species most of which are found in the depth range of 10-30 m below mean sea level. Of these, only Nereocystis luetkeana and possibly Laminaria are characterized by high biomass turnover.

The litter and detritus biomass data (Figures 5, and 20 and 21, respectively) indicate the peak period of detritus formation from seaweed occurs during late summer. This would be consistent with a hypothesis that maximum productivity occurs during the summer months, based on Mann's (1972a) interpretation of the results of Krey (1967) and Sutcliffe (1972) which imply a peak in particulate material biomass derived from seaweed during early spring, at the time of maximum seaweed productivity in St. Margaret's Bay (Mann 1972a).

As only 1-5% of detritus predicted to have been formed from seaweed litter, and a lesser percentage of total detritus formed from seaweed biomass, accumulated within Site 1, the majority of seaweed detritus must be processed elsewhere. Webster et al. (1975) collected an amount of organic matter equivalent to 15% of total plant production in sediment traps placed at deep stations (60 and 65 m) in St. Margaret's Bay, Nova Scotia. Data from shallower stations were less reliable. During the year of their study Laminaria production alone exceeded phytoplankton production by three fold, and with the major settlement peaks occurring when plankton production was low, they conclude seaweed detritus to be the most likely origin of the organic matter collected. Data from this study indicate that < 5% of seaweed detritus is deposited within the seaweed zone, leaving at least 80% to be exported, and subsequently decomposed in coastal waters, along with the soluble matter released.

Lenz (1977) obtained results which may be considered evidence

of the presence of seaweed detritus in coastal water. In an attempt to show a positive correlation between the standing crop biomasses of phytoplankton and/or zooplankton and that of detritus in the Kiel Bight, West Baltic Sea, only data from stations below 15 m depth supported his hypothesis. In water above 15 m depth negative (although nonsignificant) correlations were obtained. The suggestion is that the detritus is of an allochthonous nature, contrary to Lenz's hypothesis that it was formed autochthonously. Sources such as airborne dust, coastal erosion and sediment were discounted but seaweeds were not referenced. Seaweeds are a normal feature of the Western Baltic coastline, and with the Kiel Bight being an enclosed area a possible explanation of his results has been overlooked.

Odum and de la Cruz (1967) determined a maximum rate of 1.4~g $AFDW/m^2$ per day for the exportation of organic matter from an east coast estuarine salt marsh. The average daily rate of detritus formation from seaweed litter is in the range of 0.2-0.4 g AFDW/ m^2 , but the total amount formed may be at least double this figure when complemented by detritus from erosive pathways. If these data are typical, detritus formed from seaweeds should exceed contributions from other plant systems unless such systems are more abundant than the seaweed zone. In the Strait of Georgia, where the seaweed zone is a marked feature of the coastline, this is not the case. There are major estuarine salt marshes at the mouths of the Fraser and Squamish Rivers, but they account for a small proportion of the total coastline. Eelgrass (Zostera marina) meadows are also present in the Strait of Georgia, near Robert's Bank (Forbes 1972, Moody 1978) and Nanaimo (Foreman 1975, Sibert et al. 1977). Rates of formation of Zostera marina detritus are not available for the ecosystem level but there is no evidence to suggest they will be significantly higher than those obtained for the salt marsh systems. It is unlikely that detritus originating from either system will exceed the quantity originating from seaweed biomass other than in the immediate vicinity of the respective systems.

The ecological roles of seaweed detritus and vascular plant detritus will be dissimilar due to the composition of the biomass undergoing decomposition. Seaweed detritus appears to be too short-lived and only seasonally available to provide a long term food resource for fauna. Alternatively, vascular plant detritus has been documented as a long term food resource for fauna during periods when primary production is low (Darnell 1967b).

The predicted nitrogen content of seaweed detritus, determined in this study to be ca 2.48% of its dry weight, is probably underestimated. This is partially due to the specific submodels for the species incorporated into the simulation (page 104) generating less rapid increases in the relative nitrogen content of decomposing litter than indicated by the trend in Figure 7 (page 58). Additionally, the simulation decomposed detrital nitrogen at the same rate as other detrital components. This is probably an underestimation of its true decomposition rate when considering the pattern observed for litter decomposition.

To obtain an indication of the suitability of seaweed detritus as a food resource for fauna a C:N ratio was estimated for the detritus formed. Generic and/or class estimates of the elemental carbon contents, as a percentage of dry weight, for the five species modelled are as follows:

Nereocystis luetkeana ca 20% (J. Whyte pers. comm.)
Fucus spiralis and Fucus vesiculosus 33-36% (Vinogradov 1953, Niell 1976)
Laminaria 12-27% (Vinogradov 1953, Niell 1976)
Rhodophyta (in general) 20-38% (Niell 1976)

These data were prorated according to the percentage contribution by each species to detrital biomass to yield a C:N ratio of 10-13:1. This is less than the value of 17:1 which Russell-Hunter (1970) considers the minimum nitrogen content rendering a food resource suitably nutritious for most fauna. The C:N

ratio of the soluble matter released is in the range of 18-24:1 and must be considered nutritively poor. As the C:N ratio for detritus is probably an overestimation, it follows that the ratio for soluble matter is an underestimation.

In comparison, vascular plant detritus usually undergoes a considerable degree of processing before it attains a nutritive value that renders it suitable for consumption by potential consumers. Harrison and Mann (1975b) found that between 35 and 102 days were required for microbes to reduce the C:N ratio of Zostera marina detritus from an initial value of 20.2:1 to less than 17:1. Iverson (1973) performed preference experiments which demonstrated that decomposing leaves were not fed upon until nitrogen enrichment occurred.

In this study Lacuna marmorata, Caprella alaskana and Metacaprella anomala were delimited as possible utilizers of natural seaweed
detritus, based on their morphology, habit, spatial and/or temporal distribution patterns. The implication was that these species may be responding to a
summer pulse in the availability of sufficiently nutritious seaweed detritus.

It is necessary that experiments be performed to determine these species' food
preference, and their growth and survival while utilizing this resource, in
order to conclude with certainty that they can respond to the availability of
seaweed detritus as a food resource.

SUMMATION

Previous examinations of the role of organic detritus in coastal ecosystems have consistently underplayed the significance of the contribution by detritus originating from seaweed biomass (Darnell 1967b, Fenchel 1972, 1973, Perkins 1974). That detritus derived from seaweed biomass may contribute significantly to coastal energetics was first seriously considered by Mann (1972a). This study supports the interpretation that seaweed detritus biomass exported to coastal waters is likely the major macrophytic source of particulate organic material for the Strait of Georgia, British Columbia, and perhaps exceeds the contribution from planktonic sources during non-bloom periods. It is reasonable to extrapolate that the particulate material content of enclosed areas characterized by a seaweed zone (e.g.St. Margaret's Bay, Kiel Bight) receives a significant contribution from seaweed biomass.

The annual quantity of seaweed detritus formed and soluble matter released from the system studied is estimated to be at least 45% derived from seaweed litter, with a maximum rate of detritus formation being observed during late summer. This amount is complemented by detritus formed directly via erosion of kelp lamina tips.

Decomposition experiments indicated that seaweed litter decomposes very rapidly, seaweed detritus is short-lived, and that this was at least partially due to its paucity of structural material resistant to metabolism by microbes. This has probably been a reason for underestimations of seaweed detritus and soluble matter contributions to total coastal organic material relative to other coastal macrophytes based on sampled biomass alone. The inability to distinguish adequately between organic material originating from phytoplankton and seaweed biomass further complicates this problem (Sutcliffe 1972, Webster et al.1975).

Previous authors' unawareness of the degree to which seaweed detritus biomass contributes to coastal food resources has precluded an interpretation of the importance of this resource to benthic and pelagic faunal distribution patterns. This study has confirmed that seaweed detritus is suitably nutritious for fauna, having a C:N ratio of 10-13:1 or less. Seaweed detritus is thus more acceptable than living seaweed biomass which has C:N ratios ranging from 13.8:1 to 27.2:1 for Laminaria (Mann 1972a) and 40:1 to 80:1 for kelps in general (Russell-Hunter 1970). Although this study could not conclude with certainty that seaweed detritus is a food resource relied upon by specific benthic fauna, there is circumstantial evidence that some species are at least periodically dependent upon its availability. The implication is that the quantity and relatively high nitrogen content of seaweed detritus renders it particularly suitable as a food resource such that one must expect that it has a very significant role in the structure and function of coastal ecosystems.

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APPENDIX I

- A) Numerical species code for litter assessment data in Appendix I (B,C,D).
- B) Litter assessment data for seasonal collections at 95 m within Site 1.
- C) Litter assessment data for collections at 5, 35, 65 and 95 m within Site 1 on either 27 July or 3 August 1976.
- D) litter assessment data for the collection at Site 2 on 10 November 1975.
 - A. 01 Plocamium coccineum var. pacificum
 - 02 Gigartina papillata
 - 03 Fucus distichus
 - 04 Rhodomela larix
 - 05 Odonthalia floccosa
 - 06 Iridaea cordata
 - 07 Nereocystis luetkeana (stipe)
 - 08 Nereocystis luetkeana (lamina)
 - 09 Laminaria saccharina
 - 10 Laminaria groenlandica
 - 11 Constantinea subulifera
 - 12 Ulva spp./Monostroma spp.
 - 13 Prionitis lanceolata Harvey
 - 14 Sargassum muticum (Yendo) Fensholt
 - 15 Agarum spp.
 - 16 Zostera marina
 - 17 Costaria costata (Turner) Saunders
 - 18 Laurencia spectabilis Postels and Ruprecht
 - 19 Laminaria spp.
 - 20 Rhodymenia palmata (L.) Greville
 - 21 Halymenia spp.
 - 22 Analipus japonicus (Harvey) Wynne
 - 23 Gracilariopsis sjoestedtii (Kylin) Dawson
 - 24 Enteromorpha spp.
 - 25 Ceramium spp.
 - 26 Cryptopleura ruprechtiana (J. Agardh) Kylin
 - 27 Gelidium spp.
 - 28 Gigartina spp.
 - 29 Microcladia borealis Ruprecht
 - 30 Rhodymenia pertusa (Postels and Ruprecht) J. Agardh
 - 31 Gymnogrongus linearis (Turner) J. Agardh
 - 32 Alaria spp.
 - 33 Porphyra torta Krishnamurthy
 - 34 Gloiosiphonia capillaris (Hudson) Carmichael
 - 35 Fauchea lanciniata J. Agardh
 - 36 Rhodoptilum plumosum (Harvey and Bailey) Kylin
 - 37 Bossiella spp.
 - 38 Pterosiphonia bipinnata (Postels and Ruprecht) Falkenberg
 - 39 Desmarestia viridis (Müller) Lamouroux
 - 40 Polyneura latissima (Harvey) Kylin
 - 41 Callophyllis flabellulata Harvey
 - 42 Bonnemaisonia nootkana (Esper) Silva
 - 43 Gigartina exasperata Harvey and Bailey
 - 99 Unidentified litter

	В.					WET	DRY	ASH-FREE
	В.	LOC	ATI		PECIE			DRY WEIGHT
_	DATE			QUADRAT		$\frac{(G/10M^2)}{}$	$(G/10M^2)$	$(G/10M^2)$
1	20/08/		95	10-20	03	3.5400	0.6950	0.4650
2 3	20/08/ 20/08/		95 95	20-30 20-30	03 14	24.6050	3.9450	2.8650
4	20/08/		95	20-30	18	0.4400 1.0050	0.0859 0.1616	0.0457
5	20/08/		95	20-30	12	0.1150	0. 0171	0.1052 0.0107
6	20/08/		95	20-30	13	0.2200	0.0691	0.0407
7	20/08/	75 1	95	30-40	07	0.3550	0.0367	0.0252
8	20/08/		95	30-40	14	1.7700	0.2740	0.1593
9	20/08/		95	40-50	07	133.9301	19.6850	10.6700
10	20/08/		95	40-50	80	275.9500	28.1050	16.2350
11 12	20/08/ 20/08/		95 95	40-50 40-50	06	404.7849	84.2100	51.2200
13	20/08/		95	40-50	19 15	110.9500 18.0500	13.0650 2.7100	8.4050
14	20/08/		95	40-50	05	8.0500	1.9150	1.5350 1.0850
15	20/08/		95	40-50	32	3.4400	0.3592	0.2023
16	20/08/		95	40-50	12	10.8050	1.9350	1.2750
17	20/08/		95	40-50	18	6.6650	0.8702	0.4911
18	20/08/		95	40-50	14	0.8100	0.1258	0.0713
19	20/08/		95	40-50	26	0.5200	0.0098	0.0044
20 21	20/08/ 20/08/		95	40-50	44	0.2400	0.0266	0.0155
22	20/08/		95 95	50-60 50-60	08 07	316.0300 489.5400	39.9350	24.0850
23 .	20/03/		9.5	50-60	19	98.3850	60.5550 18.5900	36.9200 9.1000
24	20/08/		95	50-60	06	7.9600	0.9600	0.5501
25	20/08/		95	50-60	13	0.0800	0.0097	0.0049
26	20/08/		95	50-60	18	0.8200	0.0094	0.0060
27	20/08/		95	50-60	15	1.4550	0.2059	0.1107
28	20/08/		95	50-60	17	2.1000	0.2581	0.1491
29 30	20/08/1 20/08/1		95 95	50-60 60-70	21	0.7700	0.0958	0.0583
31	20/08/		95	60-70	07 08	332.5100 342.2148	43.2400 42.5750	24.5650
32	20/08/		95	60-70	19	64.9350	11. 3650	25.8650 6.4200
33	20/08/		95	60-70	21	2.1650	0.2593	0.1608
34	20/08/		95	60-70	32	2.0250	0.3252	0.1973
35	20/08/			60-70	12	7.6100	1.8600	1.0850
36	20/08/			70-80	07	62.1850	6.3400	3.0050
37	20/08/			70-80	08	187.8149	21.0950	13.0900
38 39	20/08/ 20/08/		95 95	70-80	19	68.1050	8.3400	5.3600
40	20/08/		95	70-80 80-90	06 07	0.1250 132.0900	0.0148	0.0091
41	20/08/		95	80-90	08	125.2050	13.6600 12.9400	9.0600 8.0700
42	20/08/		95	80-90	14	0.7400	0.1592	0.0982
43	20/08/			80-90	19	0.3900	0.0446	0.0236
44	20/08/		95	90-100	07	85.6050	12.0700	7.0050
45	20/08/		95	90-100	8 0	133.4850	14.3700	8.8150
46	20/08/			90-100	12	5.5100	0.7350	0.4850
47	20/08/			90-100	19	14.4050	1.9150	1.0850
48 49	02/09/ 02/09/		95 95	00-10 20-30	07 03	10.6000 191.1400	0.9300	0.4620
50	02/09/			20-30	06	6.3200	52.9150 1.0400	39.9000 0.6912
51	02/09/			20-30	12	1.9700	0.3138	0.2020
52	02/09/			20-30	07	0.5800	0.0669	0.0464
53	02/09/			20-30	13	2.1500	0.4837	0.3166
54	02/09/			20-30	04	0.7390	0.1219	0.0788
55	02/09/	/5 1	95	20-30	28	0.3467	0.1017	0.0517

					3.00			
56	02/09/75	1	95	20-30	-129 - 14	0.1428	0.0450	0.0319
5 7		1	95	20 - 30	18	0.0893	0.0225	0.0317
58	• •	1	95	20-30	01	0.1867	0.0435	0.0311
59	•	i	95	30-40	03	86.4250	22.9000	16.4900
60		1	95	30-40	06	6.5150	1.5850	1.0900
61	02/09/75		95	30-40	14	3.2900	0.5950	0.4225
62		1	95	30-40	13	0.9300	0.1849	0.4223
63		1	95	30-40	18	7.3050	0.1843	0.6550
64		i	95	30-40	12	6.2350	1.0300	0.6226
65		1		30-40	07	0.2585	0.0350	0.0212
66		i	95	30-40	08	0.2145	0.0350	0.0199
67		i		30-40	05	0.1892	0.0330	0.0291
68		1	95	40-50	19	163.8250	28.6450	13.9150
69	• •	i	95	40-50	06	177.6851	38.5400	27.0650
70	02/03/75	1	95	40-50	07	406.4399	14.4750	8.1700
71	02/09/75	1	95	40-50	08	124.0600	3.0250	1.8300
72		1	95	40-50	17	8.8750	1.0100	0.4850
73	•	1	95	40-50	18	1.7550	0.2300	0.1521
74		1	95	40-50	16	2.4650	0.2900	0.1872
75		i	95	40-50	12	32.4100	5.3050	3.5800
76		1	95	40-50	18	7.8900	1.3700	0.9050
77		1	95	50-60	07	5.5250	0.7726	0.4500
78		1	95	50-60	08	6.2000	0.8397	0.5051
79	· · · · · · · · · · · · · · · · · · ·	1	95	50-60	28	0.6950	0.2063	0.1006
80	· ·	1	95	50-60	12	7.0000	1.3150	0.8450
81		1	95	50-60	19	7.8300	5.0300	2.5700
82		1	95	50-60	06	85.3900	12.7150	9.0950
83		1	95	60-70	15	49.0550	7.3200	4.0650
84	02/09/75	1	95	60-70	06	17.9800	3.6400	2.5450
85		1	95	60-70	07	99.1050	8.4450	5.3200
86	02/09/75	1	95	60-70	08	26.9900	3.1100	1.7700
87	02/09/75	1	95	60-70	15	8.6150	1.4850	0.8300
88	02/09/75	1	95	60-70	17	2.2300	0.2250	0.1162
89	02/09/75	1	95	60-70	18	0.7417	0.0430	0.2930
90	02/09/75	1	95	60-70	01	0.0437	0.0071	0.0049
91	•	1	95	60-70	12	0.4406	0.0705	0.0459
92	02/09/75			60-70	20	1.1362	0.1256	0.0656
93	02/09/ 7 5			70-80	19	19.9100	2.8450	1.4050
94	02/09/75			70-80	03	10.0000	2.3850	1.8150
95	02/09/75			70-80	07	67.2600	7. 3500	4.3550
96	02/09/75			7 0-80	80	45.6300	4.8150	2.8700
97	02/09/75			70-80	12	12.0400	1.5150	0.9750
98	02/09/75			70-80	21	8.8900	1.3450	0.9350
99	02/09/75			70-80	16	0.2935	0.0271	0.0170
100	02/09/75			80-90	14	0.3370	0.0412	0.0281
101	02/09/75			80-90	07	71.4450	8.0600	4.2500
102	02/09/75			80-90	08	71.0200	6.8750	3.9550
103	02/09/75			80-90	03	6.2100	1.3950	1.0350
104	02/09/75			80-90	12	9.1550	1.3300	0.8700
105	02/09/75			80-90	14	1.3217	0.2309	0.1592
106	02/09/75			80-90	19	23.7550	2.6500	1.3400
107	02/09/75			80-90	21	1.8252	0.2312	0.1610
108	02/09/75			80-90	18	0.3439	0.0392	0.0270
109	02/09/75			90-100	08	43.2150	3.7600	2.1100
110	02/09/75				12	4.1100	0.8450	0.5150
111 112	02/09/ 7 5 02/09/ 7 5			90-100 90-100	06 16	0.0538	0.0040	0.0023
113	02/09/75			90-100	16 23	0.7178 0.2474	0.0626	0.0400
114	04/10/75			10-20	23 07	12.3900	0.0531 1.4100	0.0322 0.8300
115		1		20-30	03	6.1100	1. 3400	1.0200
117	04/10/73	•	, ,	20-30	0.3	0.1100	14 2400	1.0200

				- 130) –		
116	04/10/7	5 1 9	5 20-30		0.8700	0.0950	0.0518
117	04/10/7			12	0.1150	0.0181	0.0119
118	04/10/7				60.9600	7.2450	4.3250
119	04/10/7			08	83.1600	9.6650	5.6300
120							
	04/10/7			06	19.2900	5.1450	3.7150
121	04/10/7			12	10.1500	1.8900	1.2000
122	04/10/7				9.4900	1.3700	0.9450
123	04/10/7	5 1 9	5 50-60	07	262.1899	42.4400	23.5800
124	04/10/7	5 1 9	5 50-60	08	30.9300	3.8550	2.2550
125	04/10/7	5 1 9	5 50-60	19	12.9100	2.6950	1.3600
126	04/10/7	5 1 9	5 50-60		6.5450	1.1450	0.6250
127	04/10/7				13.9450	3.4800	2.4750
128	04/10/7				3.6850	0.5350	0.3291
129	04/10/7			07	114.9350	17.7100	10.2800
130	04/10/7				72.3450	9.2500	5.5300
131	04/10/7			19	1.2200	0.1800	
	-						0.1024
132	04/10/7				2.3250	0.3800	0.2303
133	04/10/7				0.2228	0.0210	0.0127
134	04/10/7				38.9950	4.3850.	
135	04/10/7			07	100.8450	13.0300	7.4350
136	04/10/7				5.9800	1.0500	0.6585
137	04/10/7			21	1.4557	0.1303	0.0910
138	04/10/7	5 1 9	5 70- 80	19	19.4400	2.6600	1.3750
139	04/10/7	5 1 9	5 80-90	19	108.1300	20.2000	10.3550
140	04/10/7	5 1 9	5 80 - 90	07	11.2000	1.3600	0.8350
141	04/10/7		5 80-90	08	23.5900	3.2100	1.8650
142	04/10/7				55.7900	5.1 950	2.7350
143	04/10/7			08	33.8800	3.6400	2.2650
144	04/10/7				0.3900	0.0635	0.0409
145	04/10/7			03	0.7050	0.1465	0.1069
146	04/10/7				0.4450	0.1070	0.0755
147	04/10/7			12			
					0.8600	0.1765	0.1170
148	04/10/7				3.1100	0.4755	0.2560
149	04/10/7			25	0.2549	0.0289	0.0129
150	04/10/7				0.0909	0.0073	0.0035
151	09/11/7			03	5.0100	0.8650	0.6600
1 52	09/11/7			07	34.8600	4 .7 850	3.4300
153	09/11/7				0. 5560	0.0577	0.0351
1 54	09/11/7	5 1 9	5 30-40	1 8	0.8350	0.1046	0.0685
155	09/11/7	5 1 9	5 40-50	06	0.4977	0.0980	0.0682
156	09/11/7	5 1 9	5 40-50	08	4.9605	0.4310	0.2520
157	09/11/7		5 40-50	07	225.6000	32.0000	17.4800
158	09/11/7				0.5860	0.0893	0.0585
159	09/11/7				1.8114	0.2257	0.1201
160	09/11/7				106.3600	15.8550	9.0100
161	09/11/7				1.0163	0.2070	0.1281
162	09/11/7				1.2730	0.3269	0.2370
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163	09/11/7				652.5750	99.5700	48.5550
164	09/11/7	5 1 9			11.9618	1.1097	0.6444
165	09/11/7	5 1 9			8.0589	3.2286	1.8150
166	09/11/7	5 1 9			0.5117	0.0870	0.0606
167	09/11/7				1.8080	0.2693	0.1378
168	09/11/7				17.0100	1.8850	1.1000
169	09/11/7			07	39.0100	6.0 805	3.3594
170	09/11/7	5 1 9	5 70-80	19	1.9064	0.2548	0.1280
171	09/11/7	5 1 9	5 70-80	12	0.5899	0.0915	0.0613
172	09/11/7	5 1 9	5 80-90	08	15.4150	1.3650	0.7821
173	09/11/7			07	78.8750	7.3100	4.4250
174	09/11/7				13.6350	1.7300	0.8524
175			5 90-100		73.4850	7.5550	4.0200
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176	09/11/75	1	95	90-100	08	12.6350	1.0600	2.0150	
177	09/11/75	1	95	90-100	06	0.9593	0.2815	0.2023	
178	09/11/75	1	95	90-100	18	0.4932	0.0752	0.0549	
179	09/11/75	1	95	90-100	26	0.9806	0.2638	0.1701	
180									
	09/11/75	1	95	90-100	16	0.5208	0.1235	0.0784	
181	10/12/75	1	95	30-40	08	2.2775	0.2320	0 .13 59	
182	10/12/75	1	95	30-40	18	0.2334	0. 0265	0.0179	
183	10/12/75	1	95	30-40	16	0.9128	0.0884	0.0556	
184	10/12/75	1	95	30-40	03	1.0582	0.2279	0.1731	•
185		1	95	40-50	07	119.4450	6.4950	3.1250	
186	10/12/75	1	95	40-50	08	4.6847	0.3865	0.2253	
187		1	95	40-50	12	0.6439	0.0971	0.0518	
188	10/12/75	1	95	40-50	03	4.1573	1. 1567	0.7032	
189	10/12/75	1	95	40-50	13	0.0621	0.0062	0.0042	
190		1	95	50-60	07	31.4500	2.8400	1.8400	
191	10/12/75	1	95	50-60	18	0.1078	0.0135	0.0100	
192	10/12/75	1.	95	50-60	0.3	2.8950	0.7572	0.5572	
193	10/12/75	1	95	50-60	12	0.0571	0.0090	0.0590	
194	10/12/75	1	95	50-60	08	7.6800	0.7192	0.4325	
195	10/12/75	1	95	60-70	07	73.3900	6.6200	4.6200	
196	, ,	1	95	60-70	16	0.9771	0.1003	0.0641	
197	10/12/75	i	95	60-70	19	1.0150	0.1175	0.0612	
198	10/12/75	1	95	60-70	80	1.9200	0.1798	0.1039	
199		1	95	70-80	08	25.7900	2.6700	1.5700	
200	10/12/75	1	95	70-80	07	65.5350	4.3500	2.6650	
201	•	1	95	70-80	19	3.8498	0.4575	0.2369	
202	• •	1	95	70-80	06	0.9337	0.1858	0.1405	
203	10/12/75	1	95	70-80	12	0.4138	0.0617	0.0373	
204	10/12/75	1	95	70-80	13	0.0911	0.0288	0.0155	
205	10/12/75	1	95	80-90	07	57. 4550	7. 2650	4.0150	
206	10/12/75	1	95	80-90	08	12.7201	1.3770	0.7991	
207	10/12/75	1	95	80-90	12	1.9476	0.4317	0.2925	
208		1	95	80-90	19	0.2939	0.0455	0.0235	
209	10/12/75	1	95	90-100	08	7.1852	0.7271	0.4500	
210	10/12/75	1		90-100	07	63.8800	3.6650	1.9550	
211	10/12/75	1	95	90-100	12	0.4747	0.0855	0.0549	
212		1		30-40	07	8.2700	1.9150	1.2750	
213	16/01/76			50-60	07	15.5100	2.6900	1.4250	
214	16/01/76			50-60	16	0.5458	0.0633	0.3993	
215	16/01/76			60-70	07	51.9050	6.4650	3.5100	
216	16/01/76			70-80	07	34.8800	5.2800	3.4100	
217			95	80-90	07	79.0 600	11.73 50	9.2850	
218	16/01/76				07	67. 2750	9.1300	4.5800	
219	, ,		95	30-40	32	22.5050	4.0750	2.4500	
220	28/02/76	1	95	50-60	32	12.4850	2.2650	1.4150	
221	28/02/76	1	95	80-90	07	13.7050	2.1550	1.3350	
222	14/03/76	1	.95	20-30	03	17.8300	3.2100	2.3900	
223			95	20-30	12	0.7910	0.1609	0.1086	
224			95	40-50	16	0.2738	0.0473	0.0316	
225			95	40-50	18	0.9937	0.1304	0.0914	
226	-		95	40-50	26	0.5304	0.0924	0.0622	
	•	1		40-50	12		0.2620	0.0022	
227	•					4.3806			
228			95	40-50	33	3.7850	· 0.8650	0.3490	
229		1		40-50	19	5.1550	0.6750	0.3840	
230	14/03/76	1		40-50	03	4.4800	0.8600	0.6249	
231	14/03/76	1	95	40-50	31	0.1194	0.0229	0.0137	
232	14/03/76		95	50-60	19	13.5950	1.9 850	1.0200	
233	14/03/76	1	95	50-60	30	0.1392	0.0298	0.0157	
234	14/03/76	1	95	50-60	12	2.7204	0.4863	0.3219	
235	14/03/76	1	95	50-60	18	0.7566	0.1380	0.0960	
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236	14/03/76	1 95	50-60	33	1.5219	0.3209	0.1363
237	14/03/76	1 95	60-70	19	33.3650	3.4900	1.7900
238	· ·	1 95	60-70	12	4.4150	0.6050	0.4278
239		1 95	60-70	26	0.7586	0.1240	0.0822
240		1 95	60-70	23	0.7683	0.0613	0.0400
241		1 95	70-80	19	3.5262	0.8484	0.4551
242		1 95	10-20	06	33.5350	6.3150	4.6000
243		1 95	10-20	03	3.9550	0.9200	0.7182
244		1 95	10-20	12	1.3579	0.1828	0.1251
245	· .	1 95	10-20	01	0.1107	0.0227	0.0151
246		1 95	10-20	34	0.4318	0.0667	0.0435
247		1 95	20-30	06	0.1964	0.0448	0.0306
248		1 95	30-40	12	0.9776	0.1829	0.1385
249		1 95	30-40	18	0.0486	0.0113	0.1383
250	•	1 95	30-40	35	0.4103	0.0799	0.0545
251		1 95	30-40	36	0.0078	0.0050	0.0038
252	•	1 95	40-50	37	0.6554	0.5100	0.0720
253		1 95	40-50	38	0.2803	0.0421	0.0720
254		1 95	40-50	12	0.3239	0.0622	0.4720
255		1 95	40-50	19	2.2882	0.4315	0.4720
256		1 95	50-60	07	2.8460	0.2307	0.0894
257	•	1 95	50-60	08	3.2728	0.3249	
258		1 95	50-60	12			0.1882
259					3.7472	0.5568	0.3665
	• •	1 95	50-60 50-60	16	0.8896	0.1290	0.0825
260		1 95	50-60	01	0.3636	0.0524	0.0371
261	•	1 95	50-60	06	0.0931	0.0146	0.0102
262	, ,	1 95	60-70	08	0.0709	0.0142	0.0102
263	•	1 95	60-70	12	0.5282	0.0845	0.0610
264		1 95	60-70 70-80	99	0.0509	0.0168	0.0073
265	•	1 95 1 95		08	0.2627	0.0420	0.0252
266	•		70-80	07	0.2610 0.3000	0.0250	0.0109
267		1 95	70-80	16		0.0347	0.0221
268		1 95	80-90	12	2.0972	0.3388	0.2303
269		1 95	80-90	19	1.9176	0.4783	0.2449
270		1 95	90-100	80	0.9496	0.0968	0.0558
271	•	1 95	90-100	03	7.5500	1.3400	0.9851
272	18/04/76			19	6.7250	0.7 950	0.5001
273	13/05/76		20-30	03	33.1000	5.5850	4.0319
274	13/05/76		20-30	12	2.7590	0.3973	0.2761
275	13/05/76		30-40	12	1.0404	0.2515	0.1991
276		1 95	30-40	01	3.9977	0.7109	0.4999
277	13/05/76		40-50	19	9.0550	1.2250	0.7850
278	13/05/76		40-50	05	4.6226	0.6578	0.4434
279	13/05/76		40-50	06	0.6114	0.1356	0.0974
280	13/05/76		40-50	30	0.8033	0.1418	0.0924
281	13/05/76		40-50	39	0.4857	0.0716	0.0488
282	13/05/76		40-50	40	0.4606	0.0773	0.0522
283	13/05/76		40-50	12	2.4051	0.3856	0.2720
284	•	1 95	40-50	01	0.3726	0.0574	0.0360
285	•	1 95	40-50	26	0.3832	0.0831	0.0581
286	•	1 95	40-50	80	0.8949	0.1187	0.0768
287	•	1 95	40-50	03	6.2472	1.4914	1.1313
288	13/05/76		50-60	0.8	15.8850	1.7550	0.8450
289		1 95	50-60	12	1.9601	0.2736	0.1696
290	•	1 95	50-60	06	1.5374	0.3080	0.2148
291		1 95	50-60	01	0.9067	0.1276	0.0756
292		1 95	50-60	17	4.6083	0.4984	0.2685
293	,	1 95	50-60	18	0.7720	0.1075	0.0620
294	, ,	1 95	50-60	32	2.0154	0.4179	0.1991
295	13/05/76	1 95	50-60	36	0.3038	0.0562	0.0242

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296	13/05/76 1	95	60-70	- 133 12	3.8245	0.4063	0.2288
297	13/05/76 1		60-70	19	6.3100	0.7211	0.4162
298	13/05/76 1		60-70	08	6.3182	0.6107	0.2747
299	13/05/76 1		70-80	19	60.1800	6.8250	3.9050
300	13/05/76 1		70-80	08	14.5000	1.6200	0.8800
301	13/05/76 1		70-80	21	0.9292	0.2889	0.2023
302	13/05/76 1	95	70-80	12	8.3423	0.9848	0.5673
303	13/05/76 1	95	80-90	32	4.8430	0.7709	0.5019
304	13/05/76 1	95	80-90	08	2.2702	0.2221	0.1154
305	13/05/76 1		80-90	07	0.7471	0.0873	0.0455
306	13/05/76 1		80-90	17	0.9479	0.0558	0.0300
307	13/05/76 1		90-100	08	5.9302	0.5884	0.2707
308	27/05/76 1		20-30	0.3	23.2200	3.7100	2.2250
309	27/05/76 1		30-40	08	16.6071	3.0046	1.0604
310	27/05/76 1		30-40	06	1.1753	0.2220	0.1148
311	27/05/76 1		30-40	12	0.9594	0.2078	0.1218
312 313	27/05/76 1 27/05/76 1		40-50 40-50	12 0 7	2.0550	0.2802	0.1687
314	27/05/76 1 27/05/76 1		40-50	08	0.7146 166.0100	0.0560 19.3800	0.0258
315	27/05/76 1		40-50	21	0.2598	0.0269	9.1350 0.0142
316	27/05/76 1		40-50	39	2.2138	0.0209	0.0142
317	27/05/76 1		40-50	05	3.0646	0.5944	0.3627
318	27/05/76 1		40-50	06	7.2250	1.5250	0.6750
319	27/05/76 1		40-50	30	2.6233	0.4636	0.2867
320	27/05/76 1		40-50	18	4.1712	0.6603	0.3398
321	27/05/76 1		40-50	99	8.8300	1.6100	0.7250
3 22	27/05/76 1	_	40-50	28	2.2480	0.1582	0.0773
323	27/05/76 1		40-50	19	97.6350	13.7150	7.7100
324	27/05/76 1	95	50-60	08	394.7700	41.5150	20.1500
325	27/05/76 1	95	50-60	0.3	53.4600	11.2350	8.3050
326	27/05/76 1		50-60	17	26.5650	2.9600	1.72.00
327	27/05/76 1		50-60	26	2.6600	0.5650	0.4100
328	27/05/76 1		50-60	12	18.5000	2.2850	1.5350
329	27/05/76 1		50-60	19	162.4150	19.9450	12.6600
330	27/05/76 1		50-60	06	32.9950	6.1750	4.2350
331	27/05/76 1		50-60	13	8.3400	1.2650	0.8400
332	27/05/76 1		50-60	21	4.3400	0.8400	0.6500
333 334	27/05/76 1 27/05/76 1		50-60	05 28	14.2650	2.6250	1.4150
335 335	27/05/76 1		50-60 50-60	18	4.8000 13.2500	1.0700 1.9300	0.8050 1.0800
33 5	27/05/76 1		50-60	41	1.5500	0.2700	0.1750
337	27/05/76 1		50-60	99	15.5350	2.9000	1.3300
33 7	27/05/76 1		60-70	19	6.3724	0.7580	0.4949
339	27/05/76 1		60-70	12	1.3167	0.1621	0.0983
340	27/05/76 1		60-70	05	0.0697	0.0120	0.0080
341	27/05/76 1		60-70	08	109.5050	10.1850	4.9050
342	27/05/76 1		60-70	. 07	0.2621	0.0214	0.0111
343	27/05/76 1		70-80	07	40.3400	5.3600	3.5550
344		95	70-80	80	56.5000	5.7350	3.1100
345	27/05/76 1	95	70- 80	12	5.1486	0.6758	0.4133
346	27/05/76 1	95	70-80	3 9	1.4528	0.1386	0.0738
347	27/05/76 1		70-80	16	0.6961	0.0794	0.0521
348	27/05/76 1		80-90	08	61.9600	5.8150	3.0450
349	27/05/76 1		80-90	07	3.0702	0.4064	0.2312
350	27/05/76 1		80-90	12	50.0400	5.1600	3.4700
351	27/05/76 1	95	80-90	19	3.6000	0.5200	0.3500
352	27/05/76 1	95	50-60	17	1.7334	0.1906	0.1218
3 53	27/05/76 1	95	50-60	15	3.6784	0.5265	0.3591
3 54	27/05/76 1		50-60	26	0.1844	0.0317	0.0214
35 5	27/05/76 1	95	50-60	39	0.5353	0.0530	0.0273

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356	27/05/76 1 9	5 50-60	42	24.7700	1.5900	0.8600
357		5 90-100	08	61.2000	5. 1950	2.3750
358		5 90-100	12	2.3793	0.2678	0.1590
359		5 90-100	18	1.3191	0.1743	0.0634
360	27/05/76 1 9	5 90-100	19	0.5567	0.0558	0.0389
361	16/06/76 1 9	5 20-30	03	8.0000	1.6600	1.2350
362		5 20-30	28	0.2831	0.0804	0.0602
363		5 20-30	14	2.8084	0.4003	0.2846
364	•	5 20-30	18	2.0012	0.2546	0.1596
365	•	5 20-30	08	1.8125	0.2145	0.1251
366	•	5 20-30	12	0.4779	0.0594	0.0373
367	•	5 30-40	80	8.7181	0.8376	0.5146
368		5 30-40	07	0.3423	0.0450	0.0311
369		30-40 5 30-40	19	4.8449	0.5625	0.3795
370 371		5 30-40 5 30-40	04 16	0.2732 0.3695	0.0381 0.0387	0.0262 0.0235
372		5 30-40	18	1.3930	0.0387	0.0233
373		5 30-40	42	0.9429	0.0774	0.0420
374		5 40-50	08	53.0450	6.1950	3.4950
375		5 40-50	07	1.7719	0.3196	0.1513
376		5 40-50	21	1.7369	0.1940	0.0923
377	16/06/76 1 9	5 40-50	18	1.0026	0.1224	0.0621
378	16/06/76 1 9	5 40-50	12	6.1983	0.9872	0.6219
379	· · · · · · · · · · · · · · · · · · ·	5 40-50	19	71.0250	9.0350	5.2500
380		5 50-60	07	1.3119	0.1964	0.1209
381		50-60	08	132.6150	18.4750	11.3200
382		5 50-60	12	1.6852	0.4256	0.2531
383	* *	5 50-60	18	1.2169	0.2002	0.1140
384		5 50-60	39	1.8834	0.3029	0.1953
385 386		5 50-60 5 50-60	06 1 9	8.0944 48.3250	1.9966 7.5250	1.3814 4.9750
387		5 50-60	31	0.7347	0.1765	0.0745
388		5 50-60	99	0.6639	0.1714	0.0679
389		5 60-70	19	43.4150	5.5450	3.3850
390		5 60-70	30	5.0800	0.7635	0.4141
391		5 60-70	80	36.5900	4.2300	3.1650
392	16/06/76 1 9		07	11.0400	1.5600	0.9700
393	16/06/76 1 9	5 60-70	12	0.9285	0.1136	0.0677
394	16/06/76 1 9		06	2.3621	0.4602	0.2811
395	16/06/76 1 9		80	52.6150	6.0200	5.1000
396	16/06/76 1 9		07	14.4000	2.1950	1.47 50
397		5 70-80	19	2.9389	0.3173	0.1807
398	16/06/76 1 9	5 80-90	07	78.7900	10.6300	6.5700
399	•	5 80-90	08	26.8700	2.9200	1.8650
400		5 80-90	12	0.2207	0.0640	0.0423
401 402	• • • • • • • • • • • • • • • • • • • •	80-90 80-90	26 21	1.5169	0.2424	0.1331
402		15 80-90 15 80-90	32	0.6624 1.5529	0.0974 0.2156	0.0629 0.1379
404	•	5 80-90	39	2.9886	0.4057	0.1379
405		95 90-100	07	20.5400	2.0950	1.3450
406		5 90-100	08	24.9850	2.3850	1.3650
407		95 9 0- 10 0	03	4.8500	0.9800	0.4450
408	•	5 20-30	19	4.3446	0.7538	0.5292
409	•	5 20-30	08	0.3828	0.0511	0.0335
410		5 30-40	06	10.5881	1.7868	1.2479
411		30-40	26	1.9508	0.2813	0.2076
412	, , ,	5 30-40	12	0.2424	0.0299	0.0215
413		5 40-50	80	313.4749	36.9900	23.4950
11 1 11	07/07/76 1 0	15 110-50	Λ6	5/1 0 25/	9 9000	6 0650

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416	07/07/76 1	95	40-50	18	1.2201	0.1341	0.0806
417	07/07/76 1	95	40-50	12	7.1478	0.9584	0.7075
418	07/07/76 1	95	50-60	0.8	224.8300	27.1650	18.2450
419	07/07/76 1	95	50-60	19	94.0550	11.5650	5.9450
420	07/07/76 1	95	60-70	12	86.6050	10.9550	6.9950
421	07/07/76 1	95	60-70	08	130.9150	13.4500	8.5750
422	07/07/76 1	95	60-70	07	71.7900	4.1100	2.2350
423	07/07/76 1	95	60-70	19	153.0950	17.9750	10.9100
424	07/07/76 1	95	70-80	07	114.4100	8 .71 50	5.1250
425	07/07/76 1	95	70-80	19	56.6400	6.4400	3.4350
426	07/07/76 1	95	70-80	18	0.3661	0.0470	0.0273
427	07/07/76 1	95	70-80	08	253.8101	26.3700	16.6950
428	07/07/76 1	95	80-90	19	28.7000	1.8350	1.2050
429	07/07/76 1	95	80-90	17	13.1600	2.9150	1.6350
430	07/07/76 1	95	80-90	06	0.8025	0.1617	0.1129
431	07/07/76 1	95	80-90	07	20.3550	2.6550	1.6500
432	07/07/76 1	95	80-90	08	114.0950	12.1100	7.6300
433	07/07/76 1	95	90-100	19	1.0981	0.1423	0.0700
434	07/07/76 1	95	90-100	07	3.4135	0.3415	0.2058
435	07/07/76 1	95	90-100	08	91.0650	9.4400	5.7500
436		95	20-30		5.5710		
	• •			03		1. 1911	0.8128
437	27/07/76 1	95	20-30	19	5.1550	0.6734	0.4718
438	27/07/76 1	95	20-30	12	2.8377	0.3288	0.1991
439	27/07/76 1		20-30	08	6.4184	0.6869	0.4476
440	27/07/76 1	95	20-30	18	5.1469	0.5 896	0.3410
441	27/07/76 1	95	30-40	03	101.5150	18.87 00	15.2200
442	27/07/76 1		30-40	06	7.71 50	1.3300	0.9150
443	27/07/76 1	95	30-40	18	12.1050	1.1250	0.7 850
444	27/07/76 1	95	30-40	80	25.7850	2.1600	1.4800
445	27/07/76 1	95	30-40	19	8.2500	1.3100	1. 0850
446	27/07/76 1	95	30-40	12	16.7500	1.9050	1.5950
447	27/07/76 1	95	40-50	80	570.7849	47.2100	33.8850
448	27/07/76 1	95	40-50	07	26.5200	2.0750	1.5.150
449	27/07/76 1	95	40-50	19	25.8300	3.1900	1.8350
450	27/07/76 1	95	40-50	06	37.8100	5.3700	4.0650
451	27/07/76 1	95	40-50	01	2.6062	0.3195	0.1724
452		95	40-50	18	1.5821	0.1304	0.0890
453	27/07/76 1	95	40-50	21	2.1989	0.1304	
454		95	40-50				0.1563
	27/07/76 1			12	11.4400	1.2000	1.0050
455	27/07/76 1		40-50	03	7.6900	1.2900	1.0150
456	27/07/76 1	95	50-60	08	108.6100	13.7900	9.1550
45 7	27/07/76 1		50-60	07	31.0800	5.5550	3.6750
458	27/07/76 1	95	50-60	19	52.5500	18.77 00	15.6050
459	27/07/76 1		50-60	12	8.5800	1.5450	1.2200
460	27/07/76 1		50-60	21	9.0000	1.1600	0.9600
461	27/07/76 1	95	50-60	16	0.9015	0.1039	0.0568
462	27/07/76 1	95	60-70	8 0	205.9950	2 1. 1850	13.9 850
463	27/07/76 1	95	60-70	07	71.4000	10.3550	7.21 00
464	27/07/76 1	95	60-70	12	23.3565	0.3875	0.2426
465	27/07/76 1	95	60-70	19	9.5694	1.0723	0.5183
466	•	95	70-80	08	8.4700	0.9550	0.7700
467	27/07/76 1	95	70-80	07	34.9300	5.2000	3. 4250
468	27/07/76 1		70-80	32	14.1950	2.1800	1.5650
469	27/07/76 1	95	80-90	03	5.2741		
	• •					1.0257	0.7345
470	27/07/76 1	95	80-90	19	1.7023	0.2125	
471	27/07/76 1	95	80-90	08	29.2250	3. 1600	2.2800
472	27/07/76 1		80-90	07	108.9700	15.7850	9.9700
473	27/07/76 1	95	90-100	80	146.2150	20.2550	14.5650
474	27/07/76 1	95	90-100	07	32.4750	2.8300	2.1000
475	18/08/76 1	95	20-30	03	38.1450	8.0950	6.3150

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					1.26			
476	18/08/76	1	95	20-30	- 136 05	11.6100	2.0200	1.5200
477		1	95	20-30	18	1.5821	0.1717	0.1033
478		1	95	20-30	12	1.8356	0.1718	0.1192
479	•	1	95	20-30	0 1	1.0314	0.0882	0.0478
480	18/08/76	1	95	20-30	26	6.2800	1.1698	0.8461
48 1	18/08/76	1	95	30-40	03	108.9950	16.7100	11.1500
482	• •	1	95	30-40	80	142.3800	16.6500	11.2500
483	18/08/76	1	95	30-40	12	163.6450	20.4550	14.4650
484	18/08/76	1	95	30-40	41	5.3937	0.6902	0.4241
485	18/08/76		95	30-40	18	28.4650	3.0950	1.8600
486	18/08/76	1	95	30-40	06	103.9550	15.4400	11.2000
487	18/08/76	1	95	30-40	26	26.6850	3.9900	2.5300
488	18/08/76	1	95	30-40	05	15.2850	2.2650	1.3950
489	18/08/76	1	95	30-40	01	0.2523	0.0313	0.0185
490 491	18/08/76	1	95 95	40-50	08	502.6599	55.1850	36.1600
491	18/08/76 18/08/76	1	95	40-50 40-50	12 19	220.1250	29.3550 4.3900	20.1850 2.7400
493	18/08/76	1	95	40-50	06	32.6950 215.9700	40.8100	28.3000
494	18/08/76	1	95	40-50	03	135.1050	24.2950	17.9800
495	18/08/76	1	95	40-50	18	27.5050	5.4500	3.6150
496	18/08/76	1	95	40-50	05	8.1789	1.0795	0.7041
497	18/08/76	1	95	40-50	26	39.5900	5.4500	3.6150
498	18/08/76	1	95	40-50	21	8.4910	1.0280	0.7041
499	18/08/76	1	95	40-50	28	1.5597	0.3126	0.2304
500	18/08/76	1	95	50-60	08	485.7649	51.4300	35.4600
50 1	18/08/76	1	95	50-60	17	38.6100	4.0050	3.1850
502	18/08/76	1	95	50-60	12	21.2300	2.2950	1.5 850
503	18/08/76	1	95	50-60	21	23.8450	3.0150	2.1250
504	18/08/76	1	95	50-60	19	63.3800	6.9200	4.7250
505	18/08/76	1	95	50-60	0 1	3.9344	0.6301	0.3080
506	18/08/76	1	95	50-60	26	28.3250	3.0300	1.7850
507	18/08/76	1	95	50-60	07	1.3701	0.1348	0.0914
508 509	18/08/76 18/08/76	1	95 95	60-70 60-70	08 0 7	191.6700 17.0700	21.4300 2.7150	14.6600 1.7600
510	18/08/76	1	95	60-70	12	2.3436	0.2711	0.1897
511		1	95	60-70	17	14.2900	5.7050	2.3450
512			95	70-80	07	34.6350	5.0950	3.2250
513	18/08/76			70-80	08	35.1150	4. 1850	2.1400
514			95	70-80	12	0.7280	0.1040	0.0832
515			95	70-80	19	2.0366	0.2761	0.1289
516	, ,	1		70-80	18	0.1193	0.0152	0.0097
517	18/08/76	1	95	80-90	07	64.4550	10.0350	6.5900
518	•	1	95	80-90	80	2.427.8	0.3023	0.1847
519		1		80-90	19	5.9 485	0.7 400	0.4008
520				90-100	07	23.0500	3.6700	2.5250
521		1		90-100	08	6.3524	0.7209	0.4139
522				90-100	21	0.3461	0.0468	0.0307
523				90-100	17	16.9200	2.8200	1.5300
524	12/09/76			20-30	08	23.2000	2.4700	1.4400
525			95	20-30	14	10.6000	1.8350	0.9850
526	12/09/76			30-40	14	69.6250	10.0350	5.7150
527 528	12/09/76 12/09/76			30-40 30-40	03 06	94.9050 93.5450	19.6250 19.3950	14.1200 13.2500
529	12/09/76			30-40	19	106.8550	19.3930	14.6200
530		1		30-40	08	242.0400	27.2200	16.9900
531		i		30-40	12	49.2850	7.6000	5.0550
		1		30-40	41	21.3200	2.0650	1.7150
533	•	1		30-40	18	37.2750	5.8450	2.7900
534	12/09/76	1	95	30-40	26	11.6500	2.2050	1.1950
535		1		40-50	80	494.0750	53.0150	33.1850
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536	12/09/76	1	95	40-50	07	6.7943	0.7635	0.4728	
537	12/09/76	1	95	40-50	12	110.7150	16.3100	11.2500	
538	12/09/76		95	40-50	26	16.8000	2.8600	1.7800	
539		1	95	40-50	19	424.7200	70.0050	49.4300	
540		1	95	40-50	03	167.2500	30.9400	22.5900	
541	•	1	95	40-50	18	35.0950			
							4.8500	2.5200	
542	12/09/76		95	40-50	43	26.4500	4.0750	2.7300	
543	•	1	95	40-50	06	94.0550	18.1000	12.4500	
544	12/09/76		95	40-50	21	45.6350	6.4750	4.3200	
545	12/09/76		95	40-50	14	2.5160	0.3758	0.2594	
546		1	95	40-50	01	3.0232	0.3604	0.1587	
547	12/09/76	1	95	40-50	41	7.0569	0.8647	0.4507	
548	12/09/76	1	95	50-60	19	163.5000	23.5150	15.1800	
549	12/09/76	1	95	50-60	08	100.5550	10.8800	6.7650	
550	•	1	95	50-60	12	24.4950	4.0650	2.6050	
551		1	95	50-60	06	12.2150	2.7050	1.8050	
552	· ·	1		50-60	05	0.9159	0.2738	0.1134	
553	•	i		50-60	13	0.2111	0.0845	0.0482	
554	12/09/76			50-60	26	7.1013	1.3148	0.8489	
555									
	•	1	95	50-60	07	7.0305	0.8064	0.4694	
556	, ,	1	95	50-60	18	5.1796	0.8388	0.3636	
557	12/09/76		95	50-60	41	8.9100	1.2250	0.4850	
558		1	95	50-60	01	4.6600	0.6750	0.4600	
559		1	95	50-60	03	5.7300	1. 3850	0.3000	
560	12/09/76	1	95	60-70	80	94.4600	10.7150	6.6150	
561	12/09/76	1	95	60-70	07	1.8890	0.2702	0.1686	
562	12/09/76	1	95	60-70	19	50.1850	7. 2950	4.8100	
563	12/09/76	1	95	60-70	12	14.5500	2.0600	1.2700	
564	·	1	95	70-80	07	49.1700	9.1950	5.8850	
565		1	95	70-80	08	70.5900	8.1500	5.2500	
566	12/09/76		95	70-80	32	3.1765	0.5835	0.3575	
567		i	95	70-80	12	3.4576	0.4796	0.3367	
568		i	95	70-80	01	0.4577	0.0929	0.0407	
569	•	1	95	70-80	18		0.1059		
570	•					0.6422		0.0579	
	, ,	1	95	70-80	03	1.2381	0.2448	0.1720	
571	-, ,	1	95	70-80	16	1.2396	0.1758	0.1249	
572	12/09/76			70-80	19	0.3588	0.0595	0.0338	
573	12/09/76	1	95	80-90	80	29.1750	2.9950	1.7300	
574	12/09/76	1	95	80-90	12	0.7766	0.1930	0.1180	
575	12/09/76	1	95	80-90	07	29.2950	4.2350	2.5950	
576	12/09/76	1	95	80-90	16	0.4123	0.0803	0.0479	
577	12/09/76	1	95	80-90	13	0.6259	0.1630	0.0806	
578	12/09/76	1	95	80-90	17	1.7170	0.2763	0.1578	
579	12/09/76	1	95	80-90	19	2.8581	0.4127	0.2221	
580	12/09/76	1	95	90-100	17	5.0999	0.6413	0.3992	
581	12/09/76	i	95	90-100	- 08	3.9500	0.4527	0.2720	
582	12/09/76	i	95	90-100	07	6.5977	1.0538	0.7129	
583	12/09/76	1	95						
				90-100	12	0.0684	0.0172	0.0126	
584	02/10/76	1	95	20-30	03	77.0000	17.8100	12.1050	
585	02/10/76	1	95	20-30	12	2.9621	0.6880	0.5202	
586	02/10/76	1	95	20-30	06	8.2050	2.5350	1.8100	
587	02/10/76	1	95	20-30	14	3.6172	0.8046	0.4312	
588	02/10/76	1	95	20-30	1 8	1.4642	0.3212	0.1420	
589	02/10/76	1	95	20-30	05	0.2628	0.1382	0.0954	
590	02/10/76	1	95	30-40	19	250.6851	47.4450	33.9450	
591	02/10/76	1	95	30-40	08	547.3850	52.4300	31.7250	
592	02/10/76	1	95	30-40	06	133.7350	35.0600	24.8400	
593	02/10/76	1	95	30-40	26	36.4550	7.8300	4.5650	
594	02/10/76	1	95	30-40	28	12.1550	2.5100	1.3950	
595	02/10/76	1	95	30-40	03	48.5350	10.4250	7.5450	
J	02/10/10	•	<i>,</i>	J 0- 40	UJ	40.737U	10.4230	1.5430	

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596	02/10/76 1	95	30-40	05	11.8950	3.8100	2.4800	
597	02/10/76 1	95	30-40	18	51.2050	8.0500	3.7950	
598	02/10/76 1		30-40	12	56.9850	8.3750	5.6400	
599	02/10/76 1		40-50	19	271.4250	53.1700	39.3750	
600	02/10/76 1		40-50	08	356.4199	32.8100	19.4250	
601	02/10/76 1		40-50	12	32,4350	5.1750	3.5450	
602	02/10/76 1		40-50	03	15.6200	4.4700	2.9450	
603	02/10/76 1		40-50	14	10.4550	1.8350	1.0950	
604	02/10/76 1		40-50	26	13.4150	2,9800	1.8500	
605	02/10/76 1		40-50	18	1.9460	0.3532	0.1775	
606	02/10/76 1		40-50	06	17.5400	4.6700	3.0650	
607	02/10/76 1		50-60	08	248.4351	22.0700	12.5000	
608	02/10/76 1		50-60	07	64.6100	4.9000	2.5300	
609	02/10/76 1		50-60	12	0.6199	0.1287	0.0917	
610	02/10/76 1	95	50-60	03	3.6947	0.7197	0.5092	
611	02/10/76 1	95	50-60	19	34.4100	4.2600	2.6100	
612	02/10/76 1	95	60-70	07	85.7700	7.7900	4.2400	
6 1 3	02/10/76 1	95	60-70	80	29.2000	4.2600	2.4050	
614	02/10/76 1	95	60-70	03	12.1650	2.3900	1.7200	•
6 15	02/10/76 1		60-70	19	2.7120	0.2795	0.1468	
6 16	02/10/76 1		60-70	12	2.2073	0.5147	0.2864	
6 17	02/10/76 1		70-80	07	135.8199	27.4400	14.8400	
618	02/10/76 1		70-80	80	42.5650	4.4700	2.4300	
6 19	02/10/76 1		70-80	32	10.5100	0.5750	0.3700	
620	02/10/76 1		70-80	19	7.6931	0.9847	0.4548	
621	02/10/76 1		80-90	08	17.4650	1.9950	0.9450	
622	02/10/76 1		80-90	07	43.5850	7. 6800	4.3200	
623	02/10/76 1		80-90	19	7.2600	0.9400	0.4650	
624	02/10/76 1		90-100	80	6.0332	0.5654	0.2909	
625	02/10/76 1	95	90-100	07	26.5850	4.3300	2.3450	
							a.	
		•						

	c.							WET	DRY	ASH-FREE
	С.	LC	OCI	TIC	on si	PECI	ES	WEIGHT	WEIGHT	
	DATE				QUADRAT			$(G/10M^2)$	$(G/10M^2)$	$(G/10M^2)$
1	03/08/	76	1	05	20-30	03	4	84.6650	88.6950	68.0250
2	03/08/	76	1	05	20-30	06	11	40.0000	338.5798	
3	03/08/		1	05	20-30	26		16.4550	2.7000	
4	03/08/		1	05	20-30	08		7.6588	0.8080	
5	03/08/		1	05	20-30	18		12.6600	1.4950	
6	03/08/		1	05	20-30	14		2.7200	0.3694	
7	03/08/		1	05	20-30 20-30	28 05		2.1704	0.5108 4.9250	
8 9	03/08/ 03/08/		1	05 05	20-30	19		28.5400 15.7750	2.4950	
10	03/08/		i	05	20-30	04		21.5350	3.5000	
11	03/08/		1	05	20-30	12		44.2800	5.7100	
12	03/08/		1	05	30-40	06		7.1800	1.5450	
13	03/08/		1	05	30-40	12		9.2500	1.9250	1.1050
14	03/08/	76	1	05	30-40	13		3.2001	0.5774	
15	03/08/		1	05	40-50	06		20.5850	69.7750	
16	03/08/		1	05	40-50	0.3	1	04.6800	20.8350	
17	03/08/		1	05	40-50	26		8.4350	1.8100	
18	03/08/		1	05	40-50	28		0.9000	0.2450	
19	03/08/		1	05	40-50	12		13.8050	2.3150	
20 21	03/08/ 03/08/		1	05 05	40-50 40-50	05 01		12.3300 10.1650	2.2100 1.4200	
22	03/08/		1	05	40-50	17		2.5400	0.3200	
23	03/08/		1	05	40-50	04		0.0933	0.020	
24	03/08/		1	05	40-50	18		1.2958	0.164	
25	03/08/		1	05	40-50	13		3.9750	0.9650	
26	03/08/		1	05	40-50	19		1.9421	0.3449	0.2367
27	03/08/		1	05	40-50	21		0.2569	0.0330	0.0177
28	03/08/		1	05	50-60	06		81.3450	15.0000	
29	03/08/		1	05	50-60	12		16.5950	2.540(
30	03/08/		1	05	50-60	80		25.5950	2.3450	
31	03/08/		1	05	50-60	07		4.6602	0.7386	
32 33	03/08/		1	05 05	50-60 50-60	03 21		12.7750 2.5422	2.8100 0.2946	
34	03/08/ 03/08/		1	05	50-60	18		1.3132	0.1538	
35	03/08/			05	50-60	26		0.0822	0.0118	
36	03/08/	76	1	05	50-60	19		35.7500	0.046	
37	03/08/		1	05	60-70	08		35.6100	3.595	
38	03/08/	76	1	05	60-70	19		6.2579	0.8419	
39	03/08/	76	1	05	60-70	14		6.2900	0.9050	0.6400
40	03/08/	76	1	05	60-70	21		1.9572	0.237	
41	03/08/		1	05	60-70	06		1.1912	0.188	
42	03/08/		1	05	70-80	17	_	36.7900	4.285	
43	03/08/		1	05	70-80	08		52.0551	16.5450	
44	03/08/	16 76	1	05	70-80	19		73.9400	10.015	
45 46	03/08/ 03/08/			05 05	70-80 70-80	03 04		8.8400 0.0239	1.5800 0.0080	
47	03/08/		1	05	70-80	12		0.0239	0.0419	
48	03/08/		1	05	80-90	08		85.1200	8.500	
49	03/08/		i	05	80-90	06		4.5886	0.863	
50	03/08/		1	05	80-90	19		75.2100	7.660	
51	03/08/		1	05	80-90	03		1.2371	0.248	
52	03/08/		1	05	90-100	19		16.5350	2.610	
53	03/08/		1	05	90-100	06		16.5450		
54	03/08/		1	05	90-100	08		88.2300		
55	03/08/	76	1	05	90-100	07		53.6950	6.200	3.6750

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56	03/08/76	1 35	20-30	03	373.0649	76.5350	56.0650
57	03/08/76	1 35	20-30	80	17.8650	1.7500	1.2850
58	03/08/76	1 35		06	49.2500	10.5650	7.6650
59	03/08/76	1 35	20-30	05	11.3616		
						2.0021	1.1739
60	03/08/76	1 35	20-30	12	2.7305	0.4110	0.2495
61	03/08/76	1 35	20-30	28	1.8208	0.4086	0.2102
62	03/08/76	1 35	20-30	18	12.0039	1.5051	0.7785
63	03/08/76	1 35	20-30	01	0.6768	0.0846	0.0421
64	03/08/76	1 35	30-40	03	1036.5000	203.9650	143.2050
65		1 35	30-40	06	39.7750	7.9550	5.7700
66	03/08/76	1 35	30-40	28	3.9950	1.0200	0.7950
67	03/08/76	1 35	30-40	05	2.6954	0.5430	0.3551
68	03/08/ 7 6	1 35	30-40	18	0.3607	0.0508	0.0310
69	03/08/76	1 35	30-40	26	2.3150	0.5050	0.3650
70	03/08/76	1 35	30-40	29	1.8300	0.2352	0.1520
71	03/08/76	1 35	30-40	12	1.5361	0.1964	0.1146
72	03/08/76	1 35	30-40	14	14.0000	1.9850	1.3550
73	03/08/76	1 35	40-50	07	21.7600		
						3.3450	2.3150
74	03/08/76	1 35	40-50	08	154.9600	15.2900	10.1100
75		1 35	40-50	06	34.9750	6.3100	3.1750
76	03/08/76	1 35	40-50	19	1.2517	0.1280	0.0739
77	03/08/76	1 35	50-60	29	3.3673	0.4505	0.2928
78	03/08/76	1 35	50-60	19	1.4928	0.1998	0.1199
79	03/08/76	1 35	50-60	08	18.5050	2.1300	1.9300
80	03/08/76	1 35	60-70	08	102.9800	11. 1450	7.1450
81	03/08/76	1 35	60-70	07	35.4350	4.8450	3.2800
82	03/08/76	1 35	60-70	12	1.1846	0.1553	0.0865
83	03/08/76	1 35	60-70	19	3.7344	0.4829	0.2993
84	03/08/76	1 35	70-80	08	52.79 50	5.8350	3.8250
85	03/08/76	1 35	70-80	12	2.1478	0.2111	0.1122
86	03/08/76	1 35	80-90	03	12.6550	1.9700	0.6700
87	03/08/76	1 35	80-90	19	1.8483	0.2728	0.1511
88	03/08/76	1 35	80-90	08	177.6650	6.3100	3.1750
89			80-90		12.9500		
	03/08/76			07		1.0600	0.5850
90	03/08/76	1 35	90-100	06	104.7050	20.5750	16.0650
91	03/08/76	1 35	90-100	03	66.6900	15.4900	9.4050
92	03/08/76	1 65	20 - 25	03	8607.0000	1708.7400	1261.3799
93	03/08/76	1 65	20-25	12	10.4262	1.2318	0.6441
94	03/08/76	1 65	20-25	18	2.1294	0.2808	
95	03/08/76		20-25	01	5.9601	0.8388	0.4581
96		1 65		26	2.1747	0.5115	0.3060
97	03/08/76		20-25	28			
	•	1 65			8.9331	2.0253	1.2237
98	•	1 65		03	78.3000	15.0300	11.2250
99	, ,	1 65		12	7.2684	0.7425	0.4899
100	03/08/76	1 65	50 - 60	19	2.3463	0.4283	0.3075
101	03/08/76	1 65	50-60	08	0.4096	. 0.0615	0.0410
102	03/08/76	1 65	50-60	07	37.5000	5.1500	3.3800
103	, ,	1 65		18	0.1538	0.0265	0.0132
104	•	1 65		08	15.4350	1.7950	1.2950
	•						
105	03/08/76	1 65		19	2.9700	0.4900	0.2500
106	03/08/76	1 65		06	4.1600	0.8750	0.5600
107	03/08/76	1 65		19	13.2450	1. 8850	1.1050
108	03/08/76	1 65	7 0-80	80	119.1200	12.8800	8.4250
109	03/08/76	1 65	70-80	07	13.3850	1.5500	1.0450
110	03/08/76	1 65	70-80	03	0.2005	0.0993	0.0765
111	03/08/76	1 65	70-80	26	0.0841	0.0299	0.0157
112	03/08/76	1 65	70-80	18	1.2598	0.1914	0.0651
	03/00/10						
113		1 65	70-80	12	1.7927	0.2972	0.1431
114	03/08/76	1 65		80	159.4600	16.6100	9.4350
115	03/08/76	1 65	80-90	07	0.9458	0.1760	0.1261

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116	03/08/76	1	65	90-100	08	102.8700	10.6850	6.6050
117	03/08/76	1	65	90-100	05	0.0289	0.0115	0.0072
118	27/07/76	1	95	20-30	03	5.5710	1.1911	0.8128
119	27/07/76	1	95	20-30	19	5.1550	0.6734	0.4718
120	27/07/76	1	95	20-30	12	2.8377	0.3288	0.1991
121	27/07/76	1	95	20-30	08	6.4184	0.6869	0.4476
122	27/07/76	1	95	20-30	18	5.1469	0.5896	0.3410
123	27/07/76	1	95	30-40	03	101.5150	18.8700	15.2200
124	27/07/76	1	95	30-40	06	7.7150	1.3300	0.9150
125	27/07/76	1	95	30-40	18	12.1050	1.1250	0.7850
126	27/07/76		95	30-40	08	25.7850	2.1600	1.4800
127	27/07/76	1	95	30-40	19	8.2500	1.3100	1.0850
128	27/07/76	1	95	30-40	12	16.7500	1.9050	1.5950
129	27/07/76		95	40-50	80	570.7849	47.2100	33.8850
130	27/07/76		95	40-50	07	26.5200	2.0750	1.5150
131	27/07/76		95	40-50	19	25.8300	3.1900	1.8350
132	27/07/76		95	40-50	06	37.8100	5.3700	4.0650
133	27/07/76		95	40-50	01	2.6062	0.3195	0.1724
134	27/07/76		95	40-50	18	1.5821	0.1304	0.0890
135	27/07/76		95	40-50	21	2.1989	0.2472	0.1563
136	27/07/76			40-50	12	11.4400	1.2000	1.0050
137	27/07/76		95	40-50	03	7.6900	1.2900	1.0150
138	27/07/76		95	50-60	80	108.6100	13.7900	9.1550
139	27/07/76		95	50-60	07	31.0800	5.5550	3.6750
140	27/07/76		95	50-60	19	52.5500	18.7700	15.6050
141	27/07/76		95	50-60	12	8.5800	1.5450	1.2200
142	27/07/76		95	50-60	21	9.0000		0.9600
143	27/07/76		95	50-60	16	0.9015	0.1039	0.0568
144	27/07/76		95	60-70	08	205.9950	21. 1850	13.9850
145	27/07/76		95	60-70	07	71.4000	10.3550	7.2100
146	27/07/76		95	60-70	12	23.3565	0.3875	0.2426
147	27/07/76		95	60-70	19	9.5694	1.0723	0.5183
148	27/07/76		95	70-80	08	8.4700	0.9550	0.7700
149 150	27/07/76		95	70-80	07	34.9300	5.2000	3.4250
	27/07/76		95	70-80	32	14.1950	2.1800	1.5650
151	27/07/76		95	80-90	03	5.2741	1.0257	0.7345
152 153	27/07/76		95	80-90	19	1.7023	0.2125	0.1396
154	27/07/76		95	80-90	08	29.2250	3.1600	2.2800
155	27/07/76		95	80-90	07	108.9700	15.7850	9.9700
156	27/07/76		95 95	90-100	08	146.2150	20.2550	14.5650
סכו	27/07/76	1	30	90-100	07	32.4750	2.8300	2.1000

	D.						ASH-FREE
		LOCATIO		PECI			DRY WEIGHT
	DATE		QUADRAT	4 5	$\frac{(G/10M^2)}{(G/10M^2)}$	$\frac{(G/10M^2)}{437000000000000000000000000000000000000$	$(G/10M^2)$
1 2	10/11/		40 - 50 40 - 50	15 19	80.3100 26.1500	13.0600 3.5400	8.6900 1.7950
3	10/11/ 10/11/		40-50	21	1.8549	0.2727	0.1930
4	10/11/		40-50	27	0.6478	0.1043	0.0568
5	10/11/		40-50	16	0.5302	0.0886	0.0579
6	10/11/		40-50	12	9.1300	1.5100	1.1500
7	10/11/	75 2 00	50-60	19	590.7000	81.6200	43.2650
8	10/11/		50-60	28	33.1100	6.4100	3.2950
9	10/11/		50-60	15	90.9900	11.4200	6.9050
10	10/11/		50-60	11	166.4399	26.8500	14.2150
11 12	10/11/ 10/11/		50-60 50-60	26 23	29.7000 11.0400	4.0100 1.2938	2.7850 0.8025
13	10/11/		50-60	03	34.9100	8.5600	6.5050
14	10/11/		50-60	13	9.0900	2.0218	1.3464
15	10/11/		50-60	08	19.1500	2.1899	1.3032
16	10/11/	75 2 00	50-60	12	9.8900	1.1897	0.8325
17	10/11/		50-60	21	18.0400	2.1508	1.5943
18	10/11/		50-60	01	0.0839	0.0108	0.0071
19	10/11/		50-60	16	0.5793	0.0702	0.0450
20	10/11/		50-60 50-60	18	2.3471	0.2741	0.1905
21 22	10/11/ 10/11/		50-60	05 0 7	0.3337 10.0801	0.0666 1.9792	0.0414 0.9223
23	10/11/		50-60	06	0.5205	0.1276	0.0918
24	10/11/		60-70	27	0.1726	0.0654	0.0313
25	10/11/		60-70	19	616.5100	92.7200	48.9200
26	10/11/		60-70	15	302.3599	41.3500	24.7450
27	10/11/		60-70	06	58.1200	12.8300	9.3200
28	10/11/		60-70	26	22.5000	4.2200	2.7400
29 30	10/11/		60 -7 0	12	5.9400 60.5000	1.0600	0.7250
31	10/11/ 10/11/		60-70 60-70	11 08	31.9000	20.3900 2.7600	11.9400 1.6600
32	10/11/		60-70	05	3.2400	0.8537	0.5842
33	10/11/		60-70	18	3.3416	0.4581	0.3434
34	10/11/		60-70	23	0.6200	0.1018	0.0639
35	10/11/		70-80	19	15020.6500		1151.5050
36	10/11/		70-80	15	781.5999	87.1000	49.5400
37	10/11/		70-80	12	111.5000	18.7000	12.5550
38	10/11/		70-80	13	10.8000	3.7795	2.6450
39 40	10/11/ 10/11/		70-80 70-80	26 05	37.7500 5.3965	5.2895 1.1315	3.8552 0.8472
41	10/11/		70-80	01	1.6910	0.2190	0.1560
42	10/11/		70-80	28	29.6500	8.1000	4.1550
43	10/11/		70-80	18	1.7778	0.2200	0.1478
44	10/11/	75 2 00	70-80	27	8.1455	1.4740	0.8067
45	10/11/		70-80	17	57.3500	7.6000	4.3700
46	10/11/		70-80	29	21.3720	2.2630	1.5358
47	10/11/		70-80	30	9.1785	1.5230	0.9002
48 49	10/11/		80-90	15	46.8200	7. 1 250	4.1800
49 50	10/11/ 10/11/		80 - 90 80-90	19 06	1306.7649 26.3450	200.6600 9.6150	104.2400 7.2650
51	10/11/		80-90	11	24.4850	5.0300	3.2100
52	10/11/		80-90	07	41.5800	2.7650	1.6550
53	10/11/			. 08	16.2400	1.8950	1.1250
54	10/11/	75 2 00	80-90	12	31.9700	5.8300	3.9100
55	10/11/	75 2 00	80-90	03	2.5750	0.6550	0.5300

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56	10/11/75 2	00	80-90	26	15.1850	2.9150	1.8100	
57	10/11/75 2	00	80-90	27	0.2763	0.0824	0.4553	
58	10/11/75 2	00	80-90	23	0.7448	0.1144	0.0730	
59	10/11/75 2	00	80-90	16	2.9408	0.4470	0.2853	
60	10/11/75 2	00	80-90	01	0.1499	0.0324	0.0215	
61	10/11/75 2	00	90-100	19	400.4800	64.5100	35.5350	
62	10/11/75 2	00	90-100	03	3.8900	1.0567	0.7789	
63	10/11/75 2	00	90-100	15	4.1800	0.5678	0.3295	
64	10/11/75 2	00	90-100	18	1.3172	0.1758	0.0668	
65	10/11/75 2	00	90-100	01	0.0603	0.0095	0.0069	
66	10/11/75 2	00	90-100	06	0.2573	0.0366	0.0263	
67	10/11/75 2	00	90-100	16	0.4718	0.0538	0.0344	
68	10/11/75 2	00	90-100	17	7.3291	0.6472	0.3303	
69	10/11/75 2	00	90-100	11	0.3866	0.1014	0.0587	
70	10/11/75 2	00	90-100	21	1.6267	0.2121	0.1379	
71	10/11/75 2			31	0.2648	0.0762	0.0388	
72	10/11/75 2	00	90-100	07	1.9939	0.2807	0.1322	
73	10/11/75 2	00	90-100	12	0.6059	0.0777	0.0549	
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APPENDIX II

- A) Numerical species code for faunal assessment data in Appendix II (B).
- B) Faunal assessment data for seasonal collections at 95 m within Site 1.

- A. 01 Mytilus edulis
 - 02 Amphithoe sp.
 - 03 Notoacmea scutum
 - 04 Margarites pupillus (parental)
 - 05 Margarites pupillus (juvenile)
 - 06 Strongylocentrotus droebachiensis
 - 07 Lacuna marmorata
 - 08 Mitrella gouldii
 - 09 Tonicella liniata
 - 10 Gnorimosphaeroma oregonense Dana
 - 11 Idotea wosnesenskii Brandt
 - 12 Unidentified polycheate
 - 13 Pugettia richii
 - 14 Amphilochus sp.
 - 15 Metacaprella anomala
 - 16 Alvinia spp.
 - 17 Pandora sp.
 - 18 Strongylocentrotus purpuratus Stimpson
 - 19 Disporella sp.
 - 20 Ocenebra sp.
 - 21 Acmaea mitra
 - 22 Cancer oregonensis
 - 23 Odostomia spp.
 - 24 Hiatella arctica
 - 25 Granulina margaritula
 - 26 Balcis micans
 - 27 Bittium eschrichtii
 - 28 Lirularia lirulata
 - 29 Chlamys hastatus
 - 30 Cancer branneri Rathbun
 - 31 Nereis pelagica
 - 32 Pagurus kennerlyi
 - 33 Hemigrapsus nudus
 - 34 Clinocardium sp.
 - 35 Anatanias normani Richardson
 - 36 Crepipatella lingulata Gould
 - 37 Leptosynapta clarki Heding
 - 38 Searlesia dira Reeve
 - 39 Hyas lyratus Dana

	В.				WET	DRY
		_	PECI		WEIGHT	WEIGHT
_		DUADR		N/M	(G/M^2)	(G/M^2)
1	25/05/76	30	04	1744	74.7920	48.5392
2	25/05/76	30	06	32	50.3296	21.2704
3	25/05/76	30	01	48	0.3216	0.2912
4 5	25/05/76	30	07	336 128	5.0624	4.0352
6	25/05/76 25/05/76	30 30	08 09	16	8.7632	6.7760
7	25/05/76	30	02	384	15.0528 11.3696	9.0064 1.9808
8	25/05/76	30	10	64	0.6432	0.2448
9	25/05/76	30	11	16	0.5712	0.2448
10	25/05/76	30	12	16	0.3072	0.1424
11	25/05/76	30	13	32	6.0544	1.6736
12	25/05/76	40	04	736	8.7520	4.1920
13	25/05/76	40	09	144	9.8592	3.3936
14	25/05/76	40	02	16	0.9824	0.1456
15	25/05/76	40	07	16	0.3008	0.1872
16	25/05/76	40	80	32	2.2448	1.3536
17	25/05/ 7 6	40	01	48	1.2480	0.4576
18	25/05/76	40	14	48	0.2416	0.0400
, 19	25/05/76	40	27	16	0.7040	0.5408
20	25/05/76	40	16	64	0.2592	0.2384
21	25/05/76	40	17	32	1.3008	0.6880
22	25/05/76	50	04	640	23.0720	13.8928
23	25/05/76	50	06	16	51.5792	16.3488
24 25	25/05/76 25/05/76	50 50	01 09	16 96	0.1760	0. 1744
26	25/05/76 25/05/76	50	08	48	3.8592 1.9360	2.4976 1.4672
2 7	25/05/76	50	07	16	0.2640	0. 1808
28	25/05/76	50	18	16	15.2992	8.0816
29	25/05/76	50	19	32	2.6224	0.5712
30	25/05/76	50	20	48	1.0960	0.6368
31	25/05/76	60	21	16	108.5984	81.1376
32	25/05/76	60	17	16	1.2720	0.7936
33	25/05/76	60	03	1 6	0.5952	0.3296
34	25/05/76	60	16	16	0.0208	0.0064
35	25/05/76	70	01	608	4.7440	2.3152
36	25/05/ 7 6	70	07	16	0.3136	0 . 1 376
37	25/05/76	70	09	64	10.0368	4.2112
38	25/05/76	70	04	64	0.4912	0.3040
39	25/05/76	70	16	32	0.1104	0.0768
40	25/05/76	70	23	32	0.2688	0.0912
41	25/05/76	70	03	16	1.0912	0.4656
42 43	25/05/76	70	24	16	0.4080	0.1408
44	25/05/76	80	13	16 16	0.8288	0.3328
45	25/05/76 25/05/76	80 80	17 03	16 48	0.7472	0.5712
46	25/05/76	80	09	16	7.1456 16.5360	3.4768 8.7424
47	25/05/76	80	04	48	2.1504	0.7872
48	25/05/76	80	23	16	0.0752	0.7672
49	25/05/76	80	16	32	0.0784	0.0544
50	25/05/76	80	25	16	0.0656	0.0464
51	25/05/76	80	26	16	0.0896	0.0560
52	25/05/76	90	09	192	95.3872	41.3648
53	25/05/76	90	01	848	15.4192	4.2960
54	25/05/76	90	24	16	0.8448	0.3232
55	25/05/ 7 6	100	09	64	34.8784	18.5936

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56	25/05/76	100	01	128	2.4640	1.2656
57	25/05/76	100	28	16	0.4208	0.2144
58	25/05/ 7 6	100	23	32	0.0960	0.0560
59	25/05/76	100	26	16	0.1536	0.1280
60	14/06/76	30	13	96	46.2352	16.4960
61	14/06/76	30	08	400	20.4720	14.2064
62	14/06/76	30	27	192	19.4672	16.2656
63	14/06/76	30	19	64	20.3312	8.0240
64	14/06/76	30	01	64	0.4560	0.4400
65	14/06/76	30	20	80	13.5344	10.6256
66	14/06/76	30	17	16	0.4640	0.4592
67	14/06/76	30	09	32	4.9920	3.6784
68	14/06/76	30	07	96	1.7424	1.3664
69	14/06/76	30	25	192	0.6784	0.5392
70	14/06/76	30	29	32	0.6304	0.2768
71	14/06/76	30	04	2112	49.9344	26 .07 52
72	14/06/76	30	16	112	0.0496	0.0464
73	14/06/76	30	31	16	1.0048	0.0608
74	14/06/76	30	02	256	0.6064	0.1456
75	14/06/76	30	14	48	0.4960	0.1024
76	14/06/76	30	32	48	1.8624	0.3712
77 77	14/06/76	30	23	80	0.2304	0.2016
7 8	14/06/76	40	04	1264	53.1856	34.3632
7 9	14/06/76	40	06	64	87.1632	52.2160
80	14/06/76	40	13	96	58.1264	18.9584
81	14/06/76	40	27	64	5.2336	4.4192
82	14/06/76	40	02	240	11.2000	2.8640
83	14/06/76	40	31	32	8.3056	2.1440
84	14/06/76	40	01	96	3.0976	1.9424
85	14/06/76	40	09	48	8.9104	6.0048
86	14/06/76	40	07	144	3 .1 280	2.1504
87	14/06/76	40	08	96	6.4160	4.6064
88	14/06/76	40	29	32	0.5360	0.4784
89	14/06/76	40	33	16	2 .7 008	0.1952
90	14/06/76	40	34	48	8.0576	4.5248
91	14/06/76	50	01	1728	45.4352	15.4976
92	14/06/76	50	04	432	16.1040	27.7840
93	14/06/76	50	02	48	1.7104	0.4032
94	14/06/76	50	14	32	0.2496	0.0400
95	14/06/76	50	09	80	11.8240	6.1936
				48		
96	14/06/76	50	27		1.5856	1.3024
97	14/06/76	50	24	96	2.2208	0.9856
98	14/06/76	50	20	16	0.9648	0.7664
99	14/06/76	50	03	16	2.8400	1.7 952
100	14/06/76	50	25	16	0.0784	0.0560
101	14/06/76	50	31	48	2.2560	0.2832
102	14/06/76	60	09	160	20.7024	10.2160
103	14/06/76	60	17	16	8.5616	5.0768
104	14/06/76	60	04	48	1.1328	0.7376
105	14/06/76	60	24	32	0.8640	0.4016
106	14/06/76	60	32	16	1.0064	0.1 360
107	14/06/76	60	16	16	0.0352	0.0224
108	14/06/76	60	07	16	0.9856	0.6656
109	14/06/76	60	25	32	0.1568	0.0832
110	14/06/76	60	01	15968	1047.8113	313.5952
111	14/06/76	60	26	32	0.1920	0.0528
112	14/06/76	60	03	16	0.6736	0.3280
113	14/06/76	70	01	5648	293.9121	129.1760
114	14/06/76	70	21	16	18.5600	12.6832
115	14/06/76	70	09	64	71. 2096	39. 268 8

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116	14/06/76	70	25	16	0.0608	0.0240
117	14/06/76	70	03	16	34.8112	23.1152
118	14/06/76	80	01	112	1.7824	0.9040
119	14/06/76	80	09	32	3.4384	2.2128
120	14/06/76	80	08	16	0.8400	0.6336
121	14/06/76	80	16	32	0.0752	0.0528
122	14/06/76	80	28	80	0.6256	0.3872
123	14/06/76	90	09	128	49.4336	26.8400
124	14/06/76	90	01	2832	84.0800	33.0752
125	14/06/76	90	20	32	35.3648	25.7392
126	14/06/76	90	03	48	16.2544	9.6464
127	14/06/76	90	25	256	0.9808	0.6704
128	14/06/76	90	28	16	0.0656	0.0400
129	14/06/76	90	35	48	0.1952	0.0608
130	14/06/76	100	31	16	1.3696	0.0688
131	14/06/76	100	-14	32	0.0512	0.0368
132	14/06/76	100	02	48	0.1072	0.0336
133	14/06/76	100	01	16	0.0800	0.0352
134	14/06/76	100	18	16	3.0864	2.1232
135	14/06/76	100	20	32	8.0512	5.9120
136	14/06/76	100	09	48	6.8960	3.0128
137	14/06/76	100	08	64	2.1040	1.4880
138	14/06/76	100	36	16	1.4592	0.9072
139	08/07/76	30	09	112	65.0576	36.7824
140	08/07/76	30	08	96	6.9744	5.1392
141	08/07/76	30	04	2048	86.1360	53.0400
142	08/07/76	30	21	16	0.3680	0.3232
143	08/07/76	30	25	80	0.3616	0.2496
144	08/07/76	30	14	32	0.1792	0.0432
145	08/07/76	30	23	16	0.0736	0.0560
146	08/07/76	30	26	16	0.0208	0.0112
147	08/07/76	30	13	16	1.8592	0.3696
148	08/07/76	30	02	32	0.4896	0.1072
149	08/07/76	30	27	16	1.0416	0.8528
150	08/07/76	30	31	16	0.2512	0.1296
151	08/07/76	30	07	544	3.8736	2.5424
152	08/07/76	30	01	32	8.4880	4.7728
153	08/07/76	30	34	16	0.5328	0.3984
154	08/07/76	40	37	16	126.2608	7.9184
155	08/07/76	40	13	48	85.2464	18.0976
156	08/07/76	40	01	16	18.9696	9.0544
157	08/07/76	40	24	32	1.2384	0.7296
1 58	08/07/76	40	34	48	1.2448	0.9312
159	08/07/76	40	07	288	3.116 8	1.8688
160	08/07/76	40	20	32	4.8912	3.7920
161	08/07/76	40	25	32	0.1376	0.0784
1 62	08/07/76	40	04	7 68	26.5008	14.5776
163	08/07/76	40	27	304	39.3072	31.0624
164	08/07/76	40	08	416	25.4128	17.1744
165	08/07/76	40	32	64	3.5104	1.1184
166	08/07/76	40	29	32	0.4688	0.3024
167	08/07/76	40	02	16	0.5136	0.1440
168	08/07/76	50	25	16	0.1056	0.0640
169	08/07/76	50	23	32	0.1072	0.0720
170	08/07/76	50	02	16	0.1184	0.0288
171	08/07/76	50	14	32	0.2224	0.0544
172	08/07/76	50	09	32	3.2336	1.6320
173	08/07/76	50	07	176	1.8496	0.9504
174	08/07/76	50	04	496	23.6528	12.6944
175	08/07/76	50	28	112	5.2784	2.8544
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176	08/07/76	50	13	32	50.4272	11.5120	
177	08/07/76	50	33	16	5.6192	1.2320	
178	08/07/76	50	01	48	0.7936	0.3664	
179	08/07/76	50	19	48	11.9664	3.1264	
180	08/07/76	50	08	16	0.8400	0.5888	
181	08/07/76	60	09	96	67.9712	35.3216	
182	08/07/76	60	07	80	1.5200	0.8352	
183	08/07/76	60	21	32	20.5600	15.0272	
184	08/07/76	60	25	16	0.0976	0.0608	
185	08/07/76	60	08	16	0.7200	0.5632	
186	08/07/76	60	01	32	0.8272		
187	08/07/76	60	28	16	0.7776	0.5968	
188	08/07/76	60	20	16		0.5024	
					0.4112	0.3360	
189	08/07/76	70	09	32	289.1968	133.9840	
190	08/07/76	70	01	1296	93.9984	41.6960	
191	08/07/76	70	25	48	0.2608	0.1760	
192	08/07/76	70	08	64	2.7376	1.8864	
193	08/07/76	70	28	32	0.3536	0.2176	
194	08/07/76	80	09	32	62.1408	32.3648	
195	08/07/76	80	12	16	33.2800	0.2720	
196	08/07/76	80	21	16	112.5360	79.9024	
197	08/07/76	80	25	16	0.0912	0.0736	
198	08/07/76	80	01	112	2.5792	1.5712	
199	08/07/76	80	07	16	1.5536	0.4720	
200	08/07/76	90	01	512	25.7472	12.8496	
201	08/07/76	90	09	96	39.6304	21.7296	
202	08/07/76	90	21	16	16.6560	11.5264	
203	08/07/76	90	25	32	0.2352	0.1760	
204	08/07/76	90	20	48	2.3056	1. 8544	
205	08/07/76	90	33	16	0.2592	0.1200	
206	08/07/76	100	28	32	0.2032	0.1504	
207	08/07/76	100	02	48	0.1792	0.0560	
208	08/07/76	100	09	80	19.3760	10.0704	
209	08/07/76	100	25	272	1.1824	0.7488	
210	28/07/76	30	07	57088	175.6880	86.3280	
211	28/07/76	30	04	640	32.8736	18.2752	
212	28/07/76	30	08	176	12.9984	8.7072	
213	28/07/76	30	13	16	29.8256	6.9984	
214	28/07/76	30	09	48	13.5872	6.8544	
215	28/07/76	30	01	32	3.3152	1. 6688	
216	28/07/76	30	29	16	0.6176	0.3 008	
217	28/07/ 7 6	30	34	16	2.1728	1.3 952	
218	28/07/76	30	27	32	4.3168	3. 3664	
219	28/07/76	40	25	32	0.2032	0.147 2	
220	28/07/76	40	27	176	22.4224	17.3 808	•
221	28/07/76	40	0 1	16	2.4400	0. 9456	
222	28/07/76	40	09	80	13.4672	6.61 60	
223	28/07/76	40	08	112	7.4816	4.9728	
224	28/07/76	40	02	16	0.1776	0.0432	
225	28/07/76	40	14	16	0.0896	0.0576	
226	28/07/76	40	29	32	0.7 056	0.4352	
227	28/07/ 7 6	40	07	256	2.5216	1. 5376	
228	28/07/76	40	13	32	41.3696	13.1232	
229	28/07/76	40	39	16	9.0400	1.9120	
230	28/07/76	40	04	2064	89.1056	48.8448	
231	28/07/76	50	01	128	3.8032	. 0.9872	
232	28/07/76	50	24	48	1.3872	0. 5600	
233	28/07/76	50	13	32	8.3280	2.4432	
234	28/07/76	50	27	16	0.7456	0.5536	
235	28/07/76	50	14	16	0.0384	0.0176	
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236 237 238 239 240 241 242	28/07/76 28/07/76 28/07/76 28/07/76 28/07/76 28/07/76	50 50 50 50 50 50	08 28 05 09 16 23	16 96 80 32 32 16	0.9472 3.4016 0.4448 1.3008 0.0800 0.0368	0.6272 1.8768 0.2256 0.6736 0.0368 0.0192	
243 244 245 246 247	28/07/76 28/07/76 28/07/76 28/07/76 28/07/76 28/07/76	50 60 60 60	07 26 01 20 09 03	48 16 624 48 32 32	0.6432 0.0912 60.5008 2.4768 16.1616 11.8912	0.3936 0.0496 19.4144 1.2976 5.5120 5.2208	
248 249 250 251 252 253 254	28/07/76 28/07/76 28/07/76 28/07/76 28/07/76 28/07/76	60 70 70 70 70 70 70	08 01 09 25 07 08 26	80 3984 32 64 16 32	5.3120 680.6001 8.0448 0.3760 0.7680 2.2256 0.0912	3. 1232 312. 9919 3. 2096 0. 2128 0. 5248 1. 4352	
255 256 257 258 259 260	28/07/76 28/07/76 28/07/76 28/07/76 28/07/76 28/07/76	80 80 80 80 90	21 09 25 16 01	16 16 16 16 16 5888 48	55.1056 24.7504 0.1024 0.0336 951.0400 6.6208	0.0272 34.8400 10.0736 0.0640 0.0272 433.9199 2.5856	
261 262 263 264 265 266	28/07/76 28/07/76 28/07/76 28/07/76 28/07/76 28/07/76	90 90 90 100 100	20 24 25 09 33 22	48 16 32 48 16	4.8304 0.6192 0.2144 9.4768 0.2240 36.9072	3. 2272 0. 2736 0. 1184 3. 9680 0. 0480 12. 7424	
267 268 269 270 271 272	28/07/76 28/07/76	100 100 100 100 30	16 25 08 20 23	16 16 16 32	0.0256 0.1040 0.9200 6.3760 0.0848 65.5968	0.0080 0.0656 0.5888 4.0384 0.0656 24.6576	
273 274 275 276 277 278	18/08/76 18/08/76 18/08/76 18/08/76 18/08/76 18/08/76	30 30 30 30 30 30	05 04 34 08 09 13	2048 1168 112 64 16	4.5472 62.0896 5.2224 4.2688 3.2416 4.8176	2.6832 35.0544 3.3408 2.9536 1.8192 1.4304	
279 280 281 282 283	18/08/76 18/08/76 18/08/76 18/08/76 18/08/76	30 30 30 40 40	24 27 25 25 04	16 32 32 320 896	3.2352 4.1568 0.1776 1.6000 28.0512	1.4384 3.2576 0.1104 1.0112 15.5920	
284 285 286 287 288 289	18/08/76 18/08/76 18/08/76 18/08/76 18/08/76 18/08/76	40 40 40 40	05 15 07 16 23 08	2208 32 3008 80 160	9.2720 0.1008 15.7056 0.1616 0.4032 1.2432	4.3888 0.0423 7.5888 0.0816 0.1872 C.9200	
290 291 292 293 294 295	18/08/76 18/03/76 18/08/76 18/08/76 18/08/76 18/08/76	40 40 40 50	13 22 09 27 05 07	16 32 32 16 5920 368	0.3120 0.4208 3.3232 0.2608 37.5568 1.2928	0.2416 0.1536 1.4880 0.2032 19.7600 0.8320	

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296	18/08/76	50	23	928	3 .7 280	2.6880	
297	18/08/76	50	16	688	1.8960	1.2128	
298	18/08/76	50	15	32	0.1216	0.0304	
299	18/08/76	50	25	288	1.0528	0.6560	
300	18/08/76	50					
	•		06	32	0.6912	0.3872	
301	18/08/76	50	04	176	6.9392	4.0704	
302	18/08/76	50	28	528	7.1216	4.0272	
303	18/08/76	50	27	448	17.2064	13.7136	
304	18/08/76	50	34	3 2	0.4432	0.3424	
305	18/08/76	50	20	80	2.1872	1.6208	
306	18/08/76	50	09	16	0.9040	0.5648	
307	18/08/76	50	08	496	10.6928	5.8048	
308	18/08/76	60	01	560	57.0384	39.0960	
309	18/08/76	60	09	48			
					30.5504	15.1232	
310	18/08/76	60	03	16	0.3088	0.3008	
311	18/08/76	60	25	16	0.0640	0.0384	
312	18/08/76	60	23	32	0.1552	0.1056	
313	18/08/76	60	16	16	0.0304	0.0144	
314	18/08/76	70	01	912	193.1456	103.9456	•
315	18/08/76	70	09	32	7.2976	3.7664	
316	18/08/76	70	33	16	8.9952	4.3280	
317	18/08/76	70	15	48	0.1712	0.0720	
318	18/08/76	70	25	64	0.3312	0.2160	
319	18/08/76	70	23	16	0.0656	0.0288	
320	18/08/76	70	08	112	6.7600		
		70				4.8432	
321	18/08/76		16	16	0.0272	0.0176	
322	18/08/76	80	09	48	46.9456	22.8896	
323	18/08/76	80	03	16	0.6192	0.3872	
324	18/08/76	80	80	48	1.8448	1.3008	
325	18/08/76	80	20	32	1.0048	0.7840	
326	18/08/76	80	25	48	0.2784	0.1936	
327	18/08/76	80	28	32	0.4112	0.2464	
328	18/08/76	90	0 1	256	10.7168	6.5168	
329	18/08/76	90	0.3	32	18.4032	11.77 28	
330	18/08/76	90	09	32	8.3744	5.0496	
331	18/08/76	90	20	48	0.9872	0.7824	
332	18/08/76	90	25	64	0.2912	0.2192	
333	18/08/76	90	20	16	1.8368	1.3920	
334	18/08/76	90	28	16	0.2768	0.2032	
335	18/08/76	100	28	128	2.0704	1. 3728	
336	18/08/76	100	15	32	0.0816	0.0272	•
337	18/08/76	100	08	144	7.1424	4.9152	
338	18/08/76	100	22	160	2.3824	0.7984	
339	18/08/76	100	25	272	1.3600	0. 9056	
340	18/08/76	100	09	112	11.6592	6.4352	
341	18/08/76	100	20	48	1. 9680	1. 4816	
342	1 8/08/76	100	13	1 6	2.5888	0. 8160	
343	18/08/76	100	14	64	0.0976	0.0352	
344	12/09/76	30	05	1648	5.9104	3.7936	
345	12/09/76	30	07	11760	62.9824	33.37 92	
346	12/09/76	30	23	96	0.5104	0.3200	
347	12/09/76	30	16	176	0.5376	0.2832	
348	12/09/76	30	13	16	14.5312	3.6832	
3 49	12/09/76	30	06	16	14.4016	6.6304	
	-	30					
3 50	12/09/76		34	16	0.8496	0.5552	
351 350	12/09/76	30	24	16	1.0144	0.3952	
352 353	12/09/76	30	04	672	37.5696	22.0496	
3 53	12/09/76	30	0.8	160	9.8400	7.0640	
354	12/09/76	40	05	5440	22.1040	16.0640	
355	12/09/76	40	07	9840	50.6720	33.7200	

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356	12/09/76	40	25	800	151 - 3.0080	2.3120	
357	12/09/76	40	23	480	1.8560	1.6160	
358	12/09/76	40	16	560	1.0240	0.8880	
359	12/09/76	40	04	1568	70.8944	39.9840	
360	12/09/76	40	12	16	2.4160	0.4336	
361	12/09/76	40	27	128	18.5264	14.9632	
362	12/09/76	40	08	240	15.6912	10.5376	
363	12/09/76	40	32	16	4.9376	2.3600	
364	12/09/76	40	13	16	9.8672	2.7264	
365	12/09/76	40	20	16	0.5728	0.4976	
366	12/09/76	40	28	112	1.4336	0.9824	
367	12/09/76	50	27	48	2.5504	2.1616	
368	12/09/76	50	08	16	1.1360	0.9072	
369	12/09/76	50	33	16	0.3520	0.2656	
370	12/09/76	50	05	5472	29.5776	20.1536	
371	12/09/76	50	07	2192	8.2304	6.2720	
372	12/09/76	50	23	64	0.4272	0.2816	
373	12/09/76	50	16	272	0.5856	0.5040	
374	12/09/76	50	28	96	1.1488	0.8368	
375	12/09/76	60	09	16	1.6224	1.3680	
376	12/09/76	60	01	352	50.8896	29.9392	
377	12/09/76	60	22	32	0.5088	0.3872	
378	12/09/76	60	07	32	0.7232	0.4128	
379	12/09/76	60	05	320	0.9552	0.7312	
380	12/09/76	60	06	16	0.1984	0.1824	
381	12/09/76	60	28	16	0.4144	0.3008	
382	12/09/76	60	08	16	0.9088	0.6848	
383	12/09/76	60	26	16	0.0848	0.0576	
384	12/09/76	60	16	32	0.0896	0.0672	
385	12/09/76	60	23	48	0.1088	0.0848	
386	12/09/76	70	01	608	85.0928	34.4528	
387	12/09/76	70	09	16	3 .1 792	2.0640	
38 8	12/09/76	7 0	05	80	0.2768	0.2192	
389	12/09/76	70	22	3 2	0.2736	0.2080	
390	12/09/76	70	34	16	0.4096	0.3632	
391	12/09/76	70	20	16	0.1776	0.1264	
392	12/09/76	70	28	16	0.4832	0.3248	
393	12/09/76	70	25	160	0.7664	0.6096	
394	12/09/76	7 0	26	96	0.6128	0.4704	
3 95	12/09/76	70	31	16	0.2048	0.1264	
396	12/09/76	80	09	16	19.5952	12.9728	
397	12/09/76	90	09	80	14.5488	10.4736	
398	12/09/76	90	01	368	32.1 248	23.2128	
399	12/09/76	90	03	32	25.2224	16.9328	
400	12/09/76	90	25	80	0.3408	0.2624	
401	12/09/76	100	22	32	0.2784	0.2320	
402	12/09/76	100	09	48	7. 8256	5. 5 1 36	
403	12/09/76	100	25	. 176	0.7904	0.6384	
404	12/0,9/76	100	1.3	16	0.5328	0.4336	
405	12/09/76	100	28	1 6	0.3552	0.2592	
406	12/09/76	100	14	80	0.0800	0.0496	
407	12/09/76	100	20	16	2.0464	1.7 200	
408	07/10/76	30	05	1488	11.2128	7.41 60	
409	07/10/76	30	07	3072	35.5760	21.0624	
4 10	07/10/76	30	30	16	2.2464	0.8032	
411	07/10/76	30	34	32	0.7920	0.6544	
412	07/10/76	30	20	16	11.1072	8.9712	
413	07/10/76	30	08	112	7. 9808	6.0048	
414	07/10/76	30	25	144	0.6432	0.4544	
4 15	07/10/76	40	13	16	38.8848	12.0320	

				-]	LJ2 -			
416	07/10/76	40	30	48	18.9936	7.5088		
417	07/10/76	40	06	1 6	34.2896	17.3856		
418	07/10/76	40	09	16	0.9008	0.6960		
	•							
419	07/10/76	40	34	160	7.1328	5. 5264		
420	07/10/76	40	27	128	17.2544	14.6784		
421	07/10/76	40	80	320	21.2240	16.2288		
422	07/10/76	40	01	32	0.7584	0.4400		
423	07/10/76	40	25	144	0.5744	0.4256		
424	07/10/76	40	07	1648	20.5664	13.3760		
425	07/10/76	40	05	2480	25.8608	16.1504		
426	07/10/76	40	04	176	8.2272	5.7280		
427	07/10/76	40	23	32	0.1344	0.0928		
428	07/10/76	40	16	16	0.0624	0.0224		
429	07/10/76	50	25	464	2.3104	1.2464		
430	07/10/76	50	28	304	5.0768	3.2384		
431	07/10/76	50	05	20064	174.7696	100.8064		
432	07/10/76	50	07	5776	22.9680	15.2000		
433	07/10/76	50	23	464	2.85 7 6	2 .1 888		
434	07/10/76	50	16	8976	18.6352	13.0112		
435	07/10/76	50	04	80	5.6576	3.4848		
	•							
436	07/10/76	50	27	160	9.1904	7.4688		
437	07/10/76	50	20	32	2.1152	1.6080		
438	07/10/76	50	34	16	1.2976	0.9056		
439	07/10/76	50	30	16	1.0704	0.3648		
				16				
440	07/10/76	50	09		5.5120	2.9552		
441	07/10/76	50	32	16	0.2448	0.1 088		
442	07/10/76	60	32	16	0.1248	0.0912		
443	07/10/76	60	05	64	0.3120	0.2256		
444	07/10/76	60	01	112	0.5376	0.3584		
	•						1	
445	07/10/76	60	07	48	0.4640	0.3088	,	
446	07/10/76	70	09	16	13.9712	8 .71 20	•	
447	07/10/76	70	80	80	4.5664	3.4224		
448	07/10/76	70	28	48	0.6208	0.5088		
	07/10/76	70		704	53.5872			
449			01			36.8704		
450	07/10/76	70	20	1 6	0.7312	0.5312		
451	07/10/76	70	30	32	0.8192	0.5712		
452	07/10/76	80	01	16	0.2208	0.0992	•	
453	07/10/76	80	05	64	1.4656	0.9264		
454	07/10/76	80	09	16	2.4128	1. 1328		
455	07/10/76	80	20	3 2	0.6960	0.4992		
456	07/10/76	80	32	1 6	0.1600	0.0944		
457	07/10/76	80	25	3 2	0.1712	0.0992		
458	07/10/76	80		16	0.7424	0.5088		
			80					
459	07/10/76	80	28	112	1. 9696	1.2480		
460	07/10/76	80	16	128	0.2352	0 . 1664		
461	07/10/76	80	23	64	0.3856	0.2960		
462	07/10/76	90	09	64	16.5152	10.0528		
463	07/10/76	90	0 1	112	0.7088	0.6144		
464	07/10/76	90	12	16	0.5856	0.5040		
465	07/10/76	90	03	16	11.556 8	7.3088		
466	07/10/76	90	02	32	0.0352	0.0160		
		100	09	3 2				
467	07/10/76				7.1264	3.0128		
468	07/10/76	100	38	64	49.2656	34.3504		
469	07/10/76	100	20	3 2	1.1936	0.9504		
470	07/10/76	100	08	80	2 .7 808	2.0432		
471	07/10/76	100	24	16	0.4592	0.4192		
472	07/10/76	100	25	384	2.0944	1.3008		
473	07/10/76	100	07	64	0.2288	0.1920		
474	07/10/76	100	26	16	0.2480	0.1952		
475	07/10/76	100	28	16	0.3200	0.2368		
, , ,	5., .9, .0		_ ~	• •	3.0200	J. 239 J		

APPENDIX III

Detritus assessment data for seasonal collections at 95 m within Site 1.

			DRY	ASH-FREE
			WEIGHT	DRY WEIGHT
	DATE Q	UADRAT	(G/M^2)	(G/M^2)
1	28/05/76	20	0.13	0.07
2	28/05/76	30	0.62	0.12
3	28/05/ 7 6	40	1.15	0 . 1 5
4	28/05/76	50	1.01	0.19
5	28/05/76	60	0.60	0.15
6	28/05/76	70	1.39	0.28
7	28/05/76	80	1.61	0.33
8	28/05/76	90	1.75	0.27
9	28/05/76	100	1.54	0.27
10	17/06/76	20	0.25	0.11
11	17/06/76	30	1.19	0.32
12	17/06/76	40	0.87	0.30
13	17/06/76	5 0	0.86	0.27
14	17/06/76	60	1.01	0.32
15	17/06/76	70	1.17	0.43
16	17/06/76	80	0.76	0.15
17	17/06/76	90	1.23	0.24
18	17/06/76	100	1.48	0.37
19	08/07/76	20	0.32	0.14
20	08/07/76	30	2.20	0.55
21	08/07/76	40	4.46	0.43
22	08/07/76	50	4.13	0.76
23	08/07/76	60	2.11	0.61
24	08/07/76	70	3.97	0.74
25		80	2.52	
	08/07/76			0.60
26 27	08/07/76	90	3.63	0.58
27	08/07/76	100	2.98	0.54
28	29/07/76	20	0.28	0.12
29	29/07/76	30	2.99	0.72
30	29/07/76	40	2.87	0.48
31	29/07/76	50	1.98	0.50
32	29/07/76	60	2.06	0.57
33	29/07/76	70	1.66	0.46
34	29/07/76	80	2. 19	0.54
35	29/07/76	90	2.17	0.50
36	29/07/76	100	2.24	0.54
37	20/08/76	20	0.31	0.16
3 8	20/08/76	30	5.38	1. 11
39	20/08/76	40	6.60	1.39
40	20/08/76	50	6.00	1. 20
41	20/08/76	60	1.57	0.42
42	20/08/76	70	3.35	0.69
43	20/08/76	80	0.58	0.13
44	20/08/76	90	1.17	0. 26
45	20/08/76	100	1.05	0.23
46	12/09/76	20	0.45	0.16
47	12/09/76	30	1.48	0.32
48	12/09/76	40	0.61	0.13
49	12/09/76	50	1.02	0.19
50	12/09/76	60	0.61	0.10
51	12/09/76	70	0.78	0.21
52	12/09/76	80	0.49	0.09
53	12/09/76	90	0.99	0.20
54	12/09/76	100	0.82	0.20
55	07/10/76	20	0.29	0.10
70	5., 10, 10	_ 0		

			-	155 -
56	07/10/76	30	0.52	0.12
57	07/10/76	40	0.97	0.28
58	07/10/76	50	1.91	0.55
59	07/10/76	60	0.93	0.30
60	07/10/76	70	0.72	0.23
61	07/10/76	80	0.78	0.34
62	07/10/76	90	0.61	0.22
63	07/10/76	100	1.75	0.45

APPENDIX IV

Depth data (m below mean sea level) for the transects at 5, 35, 65 and 95 m within Site 1.

		Transect	location	
Distance along transect (m)	<u>05 m</u>	<u>35 m</u>	65 m	95 m
00	-1.4	-1.2	-1.1	-0.9
05	-0.6	-0.6	-0.8	-0.3
10	0.5	0.3	-0.2	0.6
15	0.8	1.2	0.8	1.2
20	2.3	2.1	2.0	1.5
25	2.9	2.3	1.8	2.1
30	2.3	2.4	1.3	2.7
35	2.6	2.4	1.5	3.7
40	2.9	2.6	1.8	4.1
45	3.4	2.7	2.3	4.9
50	3.8	3.7	2.9	5.5
55	4.1	4.3	3.7	5.5
. 60	4.4	4.9	4.4	6.1
65	4.9	5.5	4.7	6.4
70	5.0	6.1	5.3	6.4
75	5.5	6.4	6.1	6.7
80	6.3	7.0	6.9	6.7
85	6.7	7.9	7.5	7.0
90	7.2	8.5	8.1	7.3
95	7.6	9.1	9.0	7.6
100	8.1	9.8	9.6	7.9

APPENDIX V

Litter decomposition experimental data.

Species	Length of incubation period		
		100.00	
Plocamium coccineum var.		100.00	
	10	65.26	
	16	42.50	
	24	28.22	
Rhodomela larix	. 0	100.00	
	6	86.20	
	13	48.73	
	25	6.48	
Odonthalia floccosa	0	100.00	
	8	55.35	
	19	34.51	
	33	9.23	
	33	3.23	
Iridaea cordata	0	100.00	
	2	97.39	
	8	55.66	
	13	0.13	
Gigartina papillata	0	100.00	
Gigartina papiliata	10	38.50	
	16	16.79	
	24	2.72	
	24	2.72	
Constantinea subulifera	0	100.00	
	6	62.30	
	14	45.20	
	29	11.57	
	0	100.00	
Fucus distichus	0	61.08	
	6		
	13	39.99	
	19	44.38	
	44	8.67	
Nereocystis luetkeana (s	tipe) 0	100.00	
-	6	29.70	
	13	5.38	
	19	0.01	
Nereocystis luetkeana (la	amina) 0	100.00	
Mereocystrs Idetheama (16	2	52.80	
·	4	5.49	
	6	0.08	
	Ū	*****	

Appendix V (continued)

Laminaria saccharina	0 8 9	100.00 13.70 11.30
Laminaria groenlandica	0 3 8 9	100.00 30.14 11.16
	9	10.1

APPENDIX VI

Oxygen consumed (mg) by microbes decomposing three particle sizes of the 10 detrital species in Experiment 1 following three periods of incubation.

•	Inc	ubation p	eriod			
Species	5 days					
					、	
Plocamium coccineum var. pacificum		0.32	0.49	44-0	•	particle
	0.20	0.36			- 1	size
	0.17	0.33	0.47	1000-420	μm_J	5126
Rhodomela larix	0.22	0.31	0.42			
	0.16	0.29				
	0.25	0.31	0.42			
	0.23	0.51	0.42			
Odonthalia floccosa	0.19	0.37	0.46			
	0.15	0.28	0.49			
	0.19	0.34	0.49			
	0.13	0.51	0.45			
Iridaea cordata	0.50	0.57	0.65			
	0.42	0.45	0.64			
	0.33	0.55	0.71			
·						
Gigartina papillata	0.26	0.28	0.38			
	0.20	0.33				
•	0.22	0.30	0.36			
Constantinea subulifera	0.35	0.60	0.62			
	0.37	0.54	0.67			
	0.35	0.52	0.64			
Fucus distichus	0.38	0.57	0.84			
	0.46	0.55	0.71			
	0.39	0.63	0.85			
Nereocystis luetkeana (stipe)	0.28	0.36	0.52			
	0.29	0.35	0.50			
	0.34	0.40	0.50			
Nereocystis luetkeana (lamina)	0.29	0.36	0.57			
	0.36	0.47	0.47			
	0.27	0.41	0.49			
Laminaria saccharina	0.25	0.39	0.54			
	0.29	0.37	0.46			
	0.29	0.32	0.47			
Laminaria groenlandica	0.31	0.35	0.45			
	0.25	0.38	0.50			
	0.29	0.45	0.48			

APPENDIX VII

Percentage of particulate material remaining following three periods of incubation for three particle sizes of the 10 detrital species decomposed in Experiment 2.

Species	10 days	20 days	30 days			
Plocamium coccineum var. pacificum	100.0	101.4	95.6	44-0	μm	
_	114.8	86.7	77.3	250-149	um	particle
	94.9	109.5	94.5	1000-420		size
Rhodomela larix	98.1	102.0	95.0			
	102.6	110.0	96.7			
	107.7	106.6	103.5			
Odonthalia floccosa	111.3	101.3	100.0			
	123.3	110.7	104.6			
	95.0	92.4	97.7			
Iridaea cordata	22.4	20.7	24.2			
	45.4	22.5	29.5			
	62.8	24.0	25.8			
Gigartina papillata	74.1	70.0	77.3			
	101.1	99.6	97.2			
	89.1	89.4	63.1			
Constantinea subulifera	100.7	97.1	88.1			
	94.9	109.5	94.5			
	93.3	89.3	75.5			
Fucus distichus	123.7	100.9	96.0			
	101.1	99.6	97.2			
	104.8	106.4	103.5			
Nereocystis luetkeana (stipe)	54.2	44.4	48.2			
	70.9	52.2	35.0			
	81.2	60.6	62.2			
Nereocystis luetkeana (lamina)	63.9	51.2	49.2			
·	65.0	47.4	49.1			
	66.7	59.6	37.1			
Laminaria saccharina	73.6	71.1	72.3			
	77.2	70.1	45.1			
	81.4	67.2	70.6			
Laminaria groenlandica	60.4	67.1	72.5			
	62.8	59.6	55.1			
•	68.6	63.6	61.8			

APPENDIX VIII

FORTRAN G computer program for the simulation model of litter and detritus processing within Site 1.

Main program: Accepts parameters determining the data to be processed, *i.e.* wet, dry or ash-free dry weight; sets the significance level of the chi-square test for patchiness in litter distribution; calls subroutines M1, M2, M3 and M4.

- M1: Creates a three dimensional matrix (species, quadrat, transect) of litter biomass data defining the areal distribution of litter within Site 1. The matrix is based on data from the transect collections at 5, 35, 65 m within Site 1 on 3 August and at 95 m on 27 July 1976.
- M2: Tests (chi-square) for patchiness in the distribution of specific litter within equivalent quadrats of the four transects defining the areal distribution of litter within Site 1. If the result is non-significant, the data are averaged to reduce the influence of sampling variability.
- M3: Calculates the equation (Figure 17) for the seasonal distribution of total litter biomass within Site 1.
- ${\tt M4:}$ Performs the operations outlined in the flow chart in Figure 18.

```
INTEGER WTPAR
 2
       COMMON WTPAR /AREA1/ WTDAS(5,4,10) /AREA2/ DAY1(17), P(11), REGWT(
      +17)
       COMMON /AREA3/ WT(4,5,17,10), SDET(4,5,17,10), SSOMP(4,5,17,10), S
 3
      +PROD(4,5,17,10), SPRODP(4,5,17,10), SPROSP(4,5,17,10), SDETP(4,5,1
      +7,10)
   15 WRITE(6,1)
 4
     1 FORMAT(' ','ENTER: WTPAR(I1)'/'WET WT=1'/'DRY WT=2'/'AFDW=3')
 6
       READ(5,2) WTPAR
 7
     2 FORMAT(I1)
 8
       IF((WTPAR.GT.3).OR.(WTPAR.EQ.0)) GO TO 15
9
   16 WRITE(6,3)
10
     3 FORMAT(' ','ENTER: PROB-LEVEL(F4.0) @ .01,.05 OR .10')
11
       READ(5,4) PROB
12
     4 FORMAT(F4.0)
13
       X2=0.
14
       IF(ABS(PROB-.01).LT..0001) X2=11.341
15
       IF(ABS(PROB-.05).LT..0001) X2=7.815
       IF(ABS(PROB-.10).LT..0001) X2=6.251
16
17
       IF(X2.EQ.O.) GO TO 16
18
       WRITE(6.14) PROB, X2
   14 FORMAT('-', 'PROB LEVEL=', F4.2, 3X, 'X2=', F6.3)
19
20
       CALL Ml
21
       CALL M2
22
       CALL M3
23
       CALL M4
24
       STOP
25
       END
26
       BLOCK DATA
27
       COMMON /AREA1/ WTDAS(5,4,10)
28
       DATA WTDAS/200*0./
29
       END
30
       SUBROUTINE M1
31
       INTEGER SP, WTPAR, DAS2, DATE, DAS, TX
32
       DIMENSION DAS1(4)
33
       COMMON WTPAR /AREAl/ WTDAS (5,4,10)
34
       DAS=2
35
       DO 2 N=1,156
36
       READ(2,4) DAS2,SP
37
     4 FORMAT(7X,13,6X,12)
38
       IF(N.EQ.1) DAS1(1)=DAS2
39
       IF((SP.NE.3).AND.(SP.NE.6).AND.(SP.NE.7).AND.(SP.NE.8).AND.(SP.NE.
      +19)) GO TO 2
40
       BACKSPACE2
41
       IF(WTPAR.EQ.1) READ(2,5) TXDX1, DATA
42
       IF(WTPAR.EQ.2) READ(2,5) TXDX1,B1,DATA
43
       IF(WTPAR.EQ.3) READ(2,5) TXDX1,B1,B2,DATA
44
     5 FORMAT(10X,F3.0,6X,3F10.0)
45
       IF(SP.EQ.3) SP=1
46
       IF(SP.EQ.6) SP=2
47
       IF(SP.EQ.7) SP=3
48
       IF(SP.EQ.8) SP=4
49
       IF(SP.EO.19) SP=5
50
       IF(DAS2.EQ.DAS1(DAS-1)) GO TO 6
```

```
51
        DAS1(DAS)=DAS2
52
        DAS=DAS+1
53
      6 DO 7 TX=1,10
      7 IF((TXDX1.EQ.(TX*10.)-10.).AND.(SP.LE.5)) WTDAS(SP.DAS-1,TX)=DATA+
54
       +WTDAS(SP,DAS-1,TX)
55
      2 CONTINUE
        RETURN
56
57
        END
58
        SUBROUTINE M2
59
        COMMON WTPAR /AREA2/ WTDAS (5,4,10)
60
        COMMON /AREA3/ WT(4,5,17,10), SDET(4,5,17,10), SSOMP(4,5,17,10), S
       +PROD(4,5,17,10), SPRODP(4,5,17,10), SPROSP(4,5,17,10), SDETP(4,5,1
61
        INTEGER SP, TXDX1, TX, WTPAR, DATE, DAS
        DIMENSION SUM1(5), SUM2(5), WT(5,10), FREO(5,10), CHISO(5,10), CHI
62
       +WT(5,4,10), STAND(5,10)
63
        DATA SUM1/5*0./, SUM2/5*0./, WT/50*0./
64
        DO 1 N=1.625
65
        IF(WTPAR.EQ.1) READ(1,2) TXTX1,SP,DATA
        IF(WTPAR.EQ.2) READ(1,2) TXDX1,SP,B1,DATA
66
        IF (WTPAR.EO.3) READ(1,2) TXDX1,SP,B1,B2,DATA
67
68
      2 FORMAT(10X,13,3X,12,1X,3F10.0)
69
        IF((SP.NE.3).AND.(SP.NE.6).AND.(SP.NE.7).AND.(SP.NE.8).AND.(SP.NE.
       +19)) GO TO 1
70
        IF(SP.EQ.3) SP=1
71
        IF(SP.EO.6) SP=2
72
        IF(SP.EQ.7) SP=3
73
        IF(SP.EQ.8) SP=4
74
        IF(SP.EO.19) SP=5
75
        TX = (TXDX1/10)
76
        WT(SP,TX+1)=WT(SP,TX+1)+DATA
77
        SUM1(SP) = SUM1(SP) + DATA
78
      1 CONTINUE
79
        DO 3 SP=1,5
80
        DO 3 TX=1,10
81
        FREO(SP,TX) = WT(SP,TX)/SUMl(SP)
      3 \text{ SUM2}(SP) = SUM2(SP) + WTDAS(SP, 1, TX)
82
83C ** CORRECTIVE ADJUSTMENT FOR AN UNREPRESENTATIVE DATUM FOR 'IRIDAEA
84C ** CORDATA' OBTAINED FOR THE 27 JULY 1976 COLLECTION AT 95 M.
85
        SUM2(2) = SUM2(2) + 20.
86
        DO 4 SP=1.5
87
        DO 4 TX=1,10
88
      4 STAND(SP,TX)=FREQ(SP,TX)*SUM2(SP)
89
        DO 5 SP=1.5
90
        DO 5 TX=1,10
91
        UNIT=WTDAS (SP, 1, TX)
92
        CHIWT(SP, 1, TX) = STAND(SP, TX)
93
        DO 12 DAS=2,4
94
        CHIWT(SP, DAS, TX) = WTDAS(SP, DAS, TX)
95
     12 IF ((WTDAS(SP,DAS,TX).LT.UNIT).AND.(WTDAS(SP,DAS,TX).NE.O.)) UNIT=W
       +TDAS (SP, DAS, TX)
96
        IF(UNIT.EQ.0) GO TO 5
97
        IF((WTPAR.EO.1).AND.(UNIT.GT.10.)) UNIT=10.
98
        IF((WTPAR.EQ.2).AND.(UNIT.GT.2.)) UNIT=2.
99
        IF((WTPAR.EO.3).AND.(UNIT.GT.1.)) UNIT=1.
```

```
100
         SUM1=0.
101
         SUM1=SUM1+(STAND(SP,TX)/UNIT)
102
         IF(SUM1.EQ.O.) GO TO 5
103
         DO 6 DAS=2,4
104
       6 SUM1=SUM1+(WTDAS(SP,DAS,TX)/UNIT)
105
         EXP=SUM1/4.
106
         SUM2=0.
107
         SUM2=SUM2+((STAND(SP,TX)/UNIT) **2)
108
         DO 7 DAS=2.4
109
       7 SUM2=SUM2+((WTDAS(SP,DAS,TX)/UNIT)**2)
110
         CHISO(SP,TX) = (SUM2/EXP) - SUM1
111
         IF(CHISQ(SP,TX).GE.X2) GO TO 5
112
         DO 8 DAS=1,4
113
       8 CHIWT(SP, DAS, TX) = EXP*UNIT
114
       5 CONTINUE
115
         DO 11 DAS=1,4
         DO 11 SP=1,5
116
         WRITE(7,13) DAS, SP
117
118
      13 FORMAT('-',3X,'DAS=',12,3X,'SP=',12)
119
         DO 11 DATE=1,17
120
         DO 10 TX=1,10
121
      10 WT(DAS,SP,DATE,TX) = (REGWT(DATE)/REGWT(14)) *CHIWT(SP,DAS,TX)
122
      11 WRITE (7,9) DATE, (WT(DAS, SP, DATE, TX), TX=1,10)
123
       9 FORMAT(' ','DATE=',12,2X,10F10.4)
124
         RETURN
125
         END
126
         SUBROUTINE M3
127
         COMMON WTPAR /AREA2/ DAY1(17), P(11), REGWT(17)
128
         DIMENSION YRES (17), WT(17), SPRYY (411)
129
         DIMENSION S(11), SIGMA(10), A(10), B(10), DATEWT(17)
130
         DOUBLE PRECISION YY (411), EXPO, RDATE
131
         LOGICAL LK, ANSWER
132
         INTEGER WTPAR, D, Y, DATE, DAS, TX
       ' DATE=1
133
134
         SUM1=0
135
         REWIND1
136
         DO 10 N=1,625
137
         IF(WTPAR.EQ.1) READ(1,12) D,M,Y,DATA
138
         IF (WTPAR.EQ.2) READ(1,12) D, M, Y, B1, DATA
139
         IF(WTPAR.EQ.3) READ(1,12) D,M,Y,B1,B2,DATA
140
      12 FORMAT(3I2,13X3F10.0)
141
         DAY2=JULDAY (M, D, Y+1900) - JULDAY (8, 18, 1975)
142.
         IF(N.EQ.1) DAY1(1)=DAY2
         IF(DAY2.NE.DAY1(DATE)) GO TO 11
143
144
         SUM1=SUM1+DATA/100.
145
         IF(N.NE.625) GO TO 10
146
      11 DATEWT(DATE) = SUM1
147
         DATE=DATE+1
148
         DAY1(DATE) = DAY2
149
         IF(DATE.EQ.18) GO TO 10
150
         SUM1=DATA
151
      10 CONTINUE
152
         NWT=0
153
         K=10
154
       N=17
155
         LK=.TRUE.
```

```
156
         CALL OLOF (K.N. DAY1, DATEWT, REGWT, YRES, WT, NWT, S, SIGMA, A, B, SS, LK, P)
157
         MAX=K+1
158
         WRITE (7,2) (J, P(J), J=1,MAX)
       2 FORMAT(' ',3('P(',I2,')',E20.12,2X))
159
160
         WRITE(7,3) K, SS
       3 FORMAT(' ','K= ',I2,2X,'SS= ',F10.4/)
161
162
         WRITE (7,4) (L, DATEWT(L), REGWT(L), YRES(L), L=1, N)
       4 FORMAT(' ',2('DAY=',I2,' DATEWT= ',F6.2,' REGWT= ',F6.2,' YRES= ',
163
        +F6.2,5X))
164
         WRITE (6, 13)
      13 FORMAT(' ','IS A PLOT OF ''TOTAL LITTER VS TIME'' DESIRED? (T OR F
165
166
         READ(5,14) ANSWER
      14 FORMAT(L1)
167
         IF(.NOT.ANSWER) GO TO 15
168
169
         DO 5 DATE=1,411
170
         YY(DATE)=0.
171
         RDATE=DATE
172
         DO 5 J=1, MAX
173
         EXPO=J-1
174
       5 YY(DATE) = YY(DATE) + (P(J) * (RDATE * *EXPO))
175
         DO 9 DATE=1,411
176
       9 SPRYY (DATE) = YY (DATE)
177
         CALL SCALE (SPRYY, 411, 6., YMIN, DY, 1)
         CALL AXIS(0.,0.,'1975',-4,3.,0.,230.,40.)
178
179
         CALL PLOT(3.,0.,3)
180
         CALL PLOT(4.,0.,2)
         CALL AXIS(4.,0.,'1976',-4,7.,0.,25.,40.)
181
         CALL AXIS(0.,0., 'LITTER BIOMASS (G/M2:AFDW)',26,6.,90.,YMIN,DY)
182
         CALL PLOT(0.05, SPRYY(2), 3)
183
184
         DO 7 DATE=3,411
185
         W=DATE*0.025
186
       7 CALL PLOT(W, SPRYY(DATE), 2)
187
         DO 8 DATE=1,17
188
         V=DAY1(DATE) *0.025
         U=DATEWT(DATE) *0.02
189
       8 CALL SYMBOL(V, U, 0.28, 30, 0., -1)
190
191
         CALL SYMBOL(3.7,-.5,.2,'DAY OF THE YEAR',0.,15)
192
         CALL SYMBOL(4.,5.,.2, TOTAL LITTER',0.,12)
193
         CALL PLOTND
194
      15 RETURN
195
         END
196
         SUBROUTINE M4
197
         COMMON /AREA2/ DAY1(17), P(11), REGWT(17)
         COMMON /AREA3/ WT(4,5,17,10), SDET(4,5,17,10), SSOMP(4,5,17,10), S
198
        +PROD(4,5,17,10), SPRODP(4,5,17,10), SPROSP(4,5,17,10), SDETP(4,5,1
        +7,10)
         INTEGER DATE1, DATE2, DATE3, DATE4, DATE5, DATE6, DATE7, DATE8, DA
199
        +TE9, DATEll, DATEll, SP, DAS, TX
200
         DIMENSION DETP(523), SOMP(523), PROD(523), PRODP(523), PROSP(523),
        +DRATE(5), DET(523), DOM(5), YPROI(5), TEMFAC(523), SQLX(17)
201
         DOUBLE PRECISION SUM1, SUM2, RATIO, PRATIO(11), EXPO, DATE10
         DOUBLE PRECISION QL, QLR(523), YWT(5,80), YWTI, YWTP, YWTC, YPRO(5
202
        +,80), YPROP, YPROC, QLX(523)
         DATA DRATE/.00760,.05651,.03123,.03479,.02934/, DOM/.393,.717,.589
203
        +,.553,.611/, QLX/523*0./
```

```
204
         DATA YPROI/.10892347,.12155714,.09405,.14905,.14466232/
205
         DO 13 DATE12=1.80
206
         YWT(1, DATE12) = EXP((-.059039*DATE12) + 4.60517)
207
         YWT(2,DATE12) = (-.448099*DATE12**2) - (1.97802*DATE12) + 100.
         YWT(3, DATE12) = EXP((-.209873*DATE12) + 4.60517)
208
209
         YWT(4, DATE12) = ((DATE12-6.022245)**2)/(4*.0906686)
         YWT(5,DATE12) = EXP((-.277057*DATE12)+4.60517
210
211
         YPRO(1,DATE12) = (-.067956*YWT(1,DATE12))+17.688
212
         YPRO(2,DATE12) = (.0440286*YWT(2,DATE12)) + 7.75285
213
         YPRO(3,DATE12) = (-.058322*YWT(3,DATE12))+15.2371
214
         YPRO(4,DATE12) = (-.182204*YWT(4,DATE12)) + 33.1254
215
         YPRO(5, DATE12) = (.490395E - 03*YWT(5, DATE12)**2) - (.21176*YWT(5, DATE12)**2)
        +)) + 30.7386
216
      13 CONTINUE
217
         A=0.20187
218
         B=0.29821
219
         DO 8 DATE11=1,523
220
       8 TEMFAC(DATE11)=1.375+A*SIN((8.*ATAN(1.)/366.)*(DATE11+231))+B*COS(
        +(8.*ATAN(1.)/366.)*(DATE11+231))
221
         DO 1 DAS=1.4
222
       DO 1 SP=1.5
223
         DO 1 TX=1,10
224
         RATIO=WT(DAS,SP,1,TX)/(REGWT(1)*10.)
225
         DO 5 I=1,11
226
         EXPO=I
227
       5 PRATIO(I)=(P(I)*RATIO)/EXPO
228
         DO 12 DATE11=1,523
229
         DETP(DATE11)=0.
230
         SOMP (DATE11) = 0.
231
         PROD(DATEll) = 0.
232
         PRODP (DATE11) =0.
233
         PROSP(DATE11)=0.
234
         DET(DATE11)=0.
235
         QLR(DATE11)=0.
236
      12 CONTINUE
237
         DO 16 DATE11=194,522
238
         DATE1=DATE11
239
         IF(DATEll.GT.410) DATEl=DATEll-407
240
         DATE10=DATE1
241
         SUM1=0.
242
         SUM2=0.
         DO 2 I=1,11
243
244
         EXPO=I
245
         SUM1=SUM1+(PRATIO(I)*(DATE10**EXPO))
       2 SUM2=SUM2+(PRATIO(I)*(DATE10+1.D0)**EXPO)
246
247
         QL=SUM2-SUM1-QLR(DATE11)
248
         IF(QL.LT.0.) QLX(DATE11+1)=QLX(DATE11+1)-QL
249
         IF(OL.LE.O.) GO TO 16
250
         IF(DATE11.LE.201) QLR(DATE11+1)=QL+QLR(DATE11)
251
         YWPT=1.D0
252
         YPROP=YPROI(SP)
253
         DO 3 DATE2=1,80
254
         DATE3=DATE2+DATE11+(6*TEMFAC(DATE11))
255
         IF(DATE3.GT.523) GO TO 16
256
         DATE 3= (TEMFAC (DATE 3) *DATE 2) +DATE 11+ (6*TEMFAC (DATE 11))
```

```
257
          YPROC=YPRO(SP, DATE2)/100.
258
         YWTC=YWT(SP,DATE2)/100.
259
          IF((DATE3.GT.523).OR.(YWTC.LT..01)) GO TO 16
260
          OLR(DATE3) = OL*YWTC+OLR(DATE3)
261
         YWTI=YWTP-YWTC
262
          IF(YWTC.GE.DOM(SP)) GO TO 4
          DETP (DATE 3) = DETP (DATE 3) + (YWTI *QL)
263
264
         PRODP(DATE 3) = PRODP(DATE 3) + YWTI *QL*((YPROC+YPROP)/2.)*(((YPROP*YWTP
        +)/YWTC-YPROC)/((YPROP*YWTP)/YWTC-YPROP
265
          GO TO 10
266
       4 SOMP (DATE 3) = SOMP (DATE 3) + (YWTI *QL)
267
         PROSP(DATE3)=PROSP(DATE3)+YWTI*QL*((YPROC+YPROP)/2.)*(((YPROP*YWTP
        +)/YWTC-YPROC)/((YPROP*YWTP)/YWTC-YPROP
268
      10 YPROP=YPROC
269
         YWTP=YWTC
270
       3 CONTINUE
      16 CONTINUE
271
272
          DO 15 DATE 7=194,523
273
          DO 11 DATE8=1,80
274
          DATE9=DATE7+DATE8-1
275
          IF(DATE9.GT.523) GO TO 15
276
          DATE9=TEMFAC(DATE9) * (DATE8-1))+DATE7
277
          IF(DRATE(SP)*(DATE8-1).GT.1.).OR.(DATE9.GT.523)) GO TO 15
278
          DET(DATE9) = DETP(DATE7) *(1.-(DRATE(SP)*(DATE8-1)))+DET(DATE9)
279
      11 PROD(DATE9) = PRODP(DATE7) * (1.-(DRATE(SP) * (DATE8-1))) + PROD(DATE9)
280
      15 CONTINUE
          DO 6 DATE11=412,523
281
282
          QXL(DATE11-409)=QLX(DATE11)
283
          DETP(DATE11-409) = DETP(DATE11)
284
          DET(DATE11-409)=DET(DATE11)
285
          PRODP(DATE11-409)=PRODP(DATE11)
286
          PROD(DATE11-409) = PROD(DATE11)
287
          SOMP (DATELL-409) = SOMP (DATELL)
288
       6 PROSP(DATELL-409)=PROSP(DATELL)
289
          SDET(DAS, SP, 1, TX) = 0.
290
          SSOMP (DAS, SP, 1, TX) =0.
291
          SPRODP(DAS, SP, 1, TX) = 0.
292
          SPROSP(DAS, SP, 1, TX) = 0.
293
          SDETP(DAS, SP, 1, TX) =0.
294
          SPROD(DAS, SP, 1, TX) = 0.
295
          SUM3=0.
296
          SUM4=0.
297
          SUM5=0.
298
          SUM6=0.
299
          SUM7=0.
300
          DATE5=1.
301
          DO 14 DATE4=2,411
302
          SUM3=SOMP (DATE4) +SUM3
303
          SUM4=PRODP (DATE4) +SUM4
304
          SUM5=PROSP(DATE4)+SUM5
305
          SUM6=DETP(DATE4)+SUM6
306
          SUM7+OLX(DATE4)+SUM7
307
          IF (ABS (DAY1 (DATE5) - DATE4) .GT..001) GO TO 14
308
          SDET (DAS, SP, DATE5, TX) = DET (DATE4)
309
          SSOMP (DAS, SP, DATE5, TX) = SUM3
310
          SPRODP(DAS, SP, DATE5, TX) = SUM4
```

```
SPROSP (DAS, SP, DATE5, TX) = SUM5
311
312
          SDETP (DAS, SP, DATE5, TX) = SUM6
313
          SPROD (DAS, SP, DATE5, TX) = PROD (DATE4)
314
          SQLX(DATE5)=SUM7
315
          SUM3=0.
316
          SUM4=0.
317
          SUM5=0.
318
          SUM6=0.
319
          SUM7=0.
320
          DATE5=DATE5+1
321
      14 CONTINUE
322
       1 CONTINUE
323
          DO 7 DAS=1,4
324
          DO 7 SP=1,5
325
          DO 7 DATE6=1,17
          WRITE(8,9) DAS, SP, DATE6, (SDET(DAS, SP, DATE6, TX), TX=1,10)
326
327
          WRITE(10,9) DAS, SP, DATE6, (SSOMP(DAS, SP, DATE6, TX), TX=1,10)
          WRITE(11,9) DAS, SP, DATE6, (SPRODP(DAS, SP, DATE6, TX), TX=1,10)
328
329
          WRITE(12,9) DAS, SP, DATE6, (SPROSP(DAS, SP, DATE6, TX), TX=1,10)
330
         WRITE (13,9) DAS, SP, DATE6, (SDETP (DAS, SP, DATE6, TX), TX=1,10)
       7 WRITE(14,9) DAS, SP, DATE6, (SPROD(DAS, SP, DATE6, TX), TX=1,10)
331
       9 FORMAT(I1,I1,I2,1X,10Ell.4)
332
333
          DO 18 DATE6=1,17
334
      18 WRITE(6,17) DATE6, SQLX(DATE6)
      17 FORMAT(' ', I2, 2X, E11.4)
335
336
          RETURN
337
          END
```