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The quantitative significance of dissolved and particulate organic matter released during fragmentation of kelp in coastal waters

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Abstract

There are definite differences in the rate of utilisation of the components of the complex substrate represented by kelp debris. The primary photosynthate D-mannitol is used most rapidly, followed by sugars and finally alginates which comprise as much as 45 % of the particulate debris. There are also seasonal differences in the efficiency of conversion of these components into bacterial biomass. During the summer months the gross conversion of carbon to bacterial biomass in the dissolved fraction of detritus is as high as 30 % and may reach 66 % when associated with particles (= carbon: carbon conversion efficiency of 33 %) whilst the value for the particulate fraction is approximately 11 %. Because of the lower conversion efficiencies in the winter, annual conversion of carbon from kelp production to bacterial biomass through the first step in the decomposer food chain is approximately 14 % but this value is as high as 22 % in the summer months (= carbon: carbon conversion efficiency of 11 %). The results suggest that annual bacterial production in the water column based solely on the degradation of kelp is approximately 11.5 g m^{-3} and could rise to as much as 18.1 g m^{-3} during the summer months. These values agree well with estimates of bacterial production based on the biomass of bacteria measured in the water column near to kelp beds.

Introduction

A feature of coastal communities which immediately strikes the biologist is the apparently high production of the coastal vegetation and the fact that there generally seem to be very few herbivores which directly utilise such material. One has only to look at a typical saltmarsh-estuarine ecosystem to see large areas of wetland grasses whose products must drive secondary production in a way which is essentially different from a typical plant-herbivore-carnivore system. Again, in coastal areas, especially where upwelling occurs and in sheltered fjords and sea lochs, dense beds of macrophytes represent zones where primary production vastly exceeds consumption by herbivores.

This excess of primary production which appears to be characteristic of most saltmarshes, swamplands and areas which are dominated by macrophytes has led to the general hypothesis that such organic material may form an important energy input into estuaries and nearshore coastal waters (TEAL 1962; ODUM 1971; for review, NEWELL 1979). Indeed, it seems likely that many of the dense communities of filter-feeding organisms such as oysters, mussels, sponges and tunicates which occur in the vicinity of saltmarshes, estuaries and kelp beds are mainly utilising plant material which has been processed through heterotrophic micro-organisms before being made available as a food resource for larger consumer organisms (DARNELL 1967a, b; RUBLEE et al. 1978; CAMMEN et al. 1978).

Rather surprisingly, despite the pioneering work which has been carried out on the east coast of the United States, until recently (HAINES and HANSON 1979) there has been little information on how much energy is converted through this detritus pathway. How much of the carbon fixed by plants, for example, is 'lost' through metabolic processes and what proportion is converted into microbial biomass? Again, we know rather little about the absorption efficiency of micro-organisms by larger consumer organisms although there is now a good deal of evidence that micro-organisms may be stripped from organic debris which is returned as faeces to the environment for further-colonisation (NEWELL 1965; DARNELL, 1967b; FENCHEL 1972; TENORE et al 1977). The contribution of primary production by saltmarshes and coastal macrophytes and, above all, the efficiency of conversion of this material through microheterotrophs into a form which can be utilised by larger consumer organisms may be a key to our understanding of the high secondary production which is characteristic of coastal waters. It is of the greatest significance both in planning the conservation of wetland areas and in assessment of the carrying capacity of the nearshore waters for shellfish and fisheries resource management.

It is the purpose of this paper to present some recent evidence which suggests that the dissolved and particulate components of the kelp *Laminaria pallida* which, together with *Ecklonia maxima*, forms dense beds off the west coast of the Cape Peninsula, South Africa, may be transformed with a relatively high efficiency into bacterial biomass. Such material then forms a potentially important food resource for the dense communities of deposit- and filter-feeding organisms which occur near to kelp beds (see VELIMIROV et al. 1977; FIELD et al. 1980).

Material and methods

We have recently analysed the chemical composition and rate of degradation of dissolved and particulate components of kelp debris (NEWELL et al. 1980; LUCAS et al. 1981; STUART et al. in press) and have at the same time measured the increase in numbers and biomass of micro-organisms which colonise the debris (LINLEY et al 1981; STUART et al. in press). The succession of micro-organisms which occur under culture conditions are described in a subsequent paper (LINLEY and NEWELL 1981) whilst the increase in numbers and biomass of bacteria which accompanies a known loss of organic carbon allows some estimates to be made of the conversion of algal debris into bacteria.

(1) Chemical analysis

The methods used in the chemical analysis of the principal components of dissolved and particulate fractions of kelp debris have been described in some detail by NEWELL et al. (1980), LUCAS et al. (1981) and STUART et al. (in press). Briefly, samples of mucilage or freshly-ground frond debris were freeze dried and analysed for major biochemical components (HOLLAND and GABBOT 1971; HOLLAND and HANNANT 1973), carbon and nitrogen, and for component carbohydrates. Weighed samples of dried mucilage or of particulate material were then incubated in freshly-collected kelp bed seawater at the local temperature of 10°C for up to 30 days and the losses in component carbohydrates synchronised with the increase in bacterial biomass. The data for conversion of kelp material into bacterial biomass were then expressed in terms of dry biomass of bacteria per unit carbon consumed.

(b) Numbers and biomass of Micro-organisms

The numbers of micro-organisms were assessed by acridine orange direct counting (HOBBIE et al. 1977) whilst scanning electron microscopy was used to estimate cell

dimensions which were then converted to microbial biomass from values for the specific gravity of the cells obtained from the literature. Details of the technique used have been given by LINLEY et al. (1981).

Results

Composition of kelp debris

The two kelps which dominate the west coast of the Cape Peninsula, South Africa, are *Laminaria pallida* and *Ecklonia maxima*, both of which grow and at the same time suffer continuous erosion from tips of the fronds. This erosion causes the release of structural particulate matter into the water column as well as a 'dissolved' mucilage component representing non-structural cell contents. There may also be other losses of dissolved organic matter from the surface of the fronds, but the relative significance of 'dissolved' and particulate components released during erosion of the tip can be relatively easily obtained by analysis of the exudates and measurement of the wet weight: dry weight ratio of the fronds (NEWELL et al. 1980). In some cases during the winter, erosion and fragmentation exceed growth and the fronds become shorter; at other times growth can exceed erosion. It is thus obvious that the length of the frond cannot be used to assess growth by these algae. FIELD et al. (1977) and MANN et al. (1979) have punched holes in the frond and used the increasing distance between these and the meristem to assess growth.

By using this method to estimate annual growth of kelp, it has been found that huge quantities of some 3–7 kg m^{-2} y^{-1} dry biomass are produced (for summary, see NEWELL et al. 1980). Of this, 20–30 % is released as 'dissolved' organic matter (see HATCHER et al 1977; JOHNSTON et al. 1977; NEWELL et al. 1980) and the remaining 70–80 % as a particulate fraction during fragmentation. Clearly, the chemical composition of dissolved and particulate components will largely determine their ease of degradation and relative significance as a bacterial substrate. The composition of dried mucilage and dried freshly-ground frond material is summarised from various sources in Table 1.

It can be seen that the dissolved fraction comprises approximately 5 % protein, 0.2 % fat, 6 % polyols (D-mannitol), 2 % sugars plus about 4–5 % each of laminarins and alginates and approximately 70 % ash (NEWELL et al. 1980). Based on the figures shown in Table 1, our analyses yielded a gravimetric recovery of over 92 %. Similar analyses for the composition of fresh fronds are based on data in VON HOLDT et al. (1955) and STUART et al. (in press). Several major differences from the dissolved components are apparent. The proteins are evidently largely bound to the particulate fraction and reach as much as 24 % of the dry weight; the lipids, some of which are essential fatty acids, are higher in the particulate fraction and finally the alginates represent almost 45 % of the dry weight of the frond compared with only 5 % of the dried mucilage fraction. Ash content is only 23 % and as in the case of the mucilage component, a high gravimetric recovery suggests that all major components have been accounted for in our analyses. Estimates for the relative significance of dissolved and particulate organic carbon release vary somewhat but are generally between 65–77 % for the particulate fraction and 23–35 % for the dissolved fraction in *Laminaria*. This agrees well with our estimates of the energetic significance of release of 'dissolved' organic matter during fragmentation in which we calculated that some 33–34 % of the energy production by *Laminaria pallida* was lost as dissolved organic matter during fragmentation (NEWELL et al. 1980).

Table 1

The chemical composition of dried mucilage (DOM) and powdered frond (POM) from the kelp *Laminaria pallida*. Data for mucilage from Newell et al. (1980); source of other data indicated at foot of table.

Component	% of total dry weight	
	DOM	POM
Protein	5.27	23.78[1]
Total Lipid	0.18	0.58[2]
Carbohydrates		
Polyols (Mannitol)	5.86	4.40[3]
Sugars (Fucose)	1.70	1.70[3]
Laminarin	4.59	1.50[1]
Alginate	5.01	44.90[1]
Ash	69.74	22.94[1]
Total Recovery	92.35	99.80
% of Carbon Fixed		
JOHNSTON et al. (1977)	23	77
HATCHER et al. (1977)	35	65
% of Energy Production		
NEWELL et al. (1980)	33–34	66–77

[1] STUART et al. (in prep.)
[2] VELIMIROV (1979)
[3] von HOLDT et al. (1955)
Protein in particulate fraction obtained from nitrogen x 6.25

Clearly, an analogous situation occurs in other macrophytes and in saltmarsh plants although the relative significance of dissolved and particulate fractions, their chemical compositon and ease of degradation are likely to be different from that of kelp. The interesting thing is to see whether for any particular source of organic production, we can follow the conversion of material through the decomposer food web and to assess the probable trophic significance of micro-organisms as a potential food resource for larger consumer organisms.

Rate of heterotrophic utilisation of organic matter from kelp

The kelp debris which we have supplied both as mucilage and powdered fresh kelp fronds in our incubation media represent a complex substrate whose components have differing rates of decomposition according to their structural complexity (LUCAS et al, 1981; STUART et al. in press). The net loss of the principal carbohydrate components from the media is plotted as a function of incubation time at 10 °C in Figure 1. Losses in particulate matter and sugars from mucilage have been expressed as 'glucose equivalents' since it was not possible to distinguish changes in the relative composition of component hexoses by colorimetric methods during the course of the incubation experiments (see LUCAS et al. 1981). Mannitol, which is a primary photosynthate in kelp, was assayed separately and is also plotted in Figure 1.

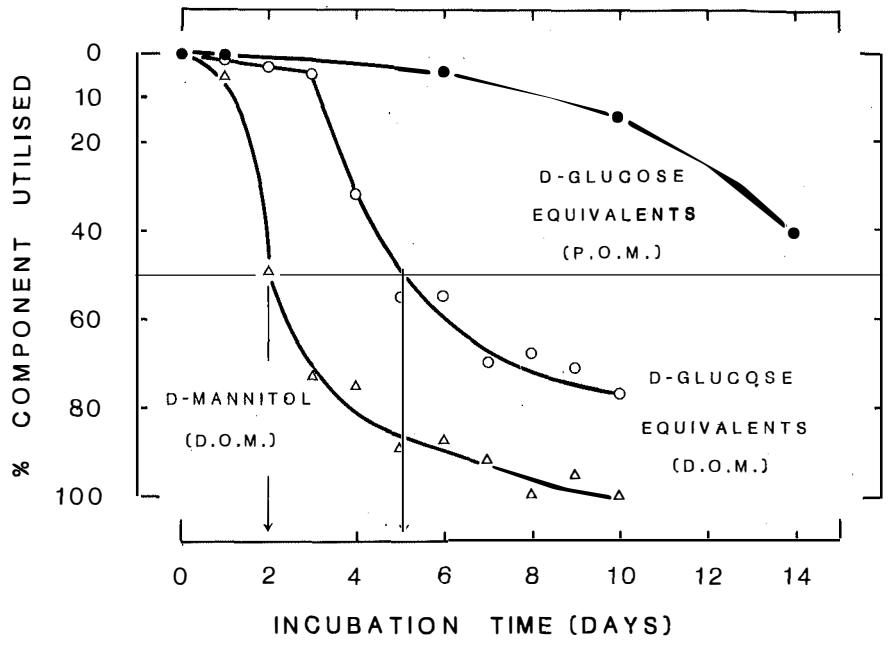


Figure 1

Laminaria pallida D.O.M. & P.O.M.

Non-sterile seawater collected from the kelp bed in summer (February) was incubated at 10°C for up to 14 days with 0.33 g l^{-1} (= 0.254 g l^{-1} organic material) added dry particulate material (43 μm to 64 μm) and separately, with 7.2 g l^{-1} (= 2.18 g l^{-1} organic material) added dry mucilage. The losses of sugars from the media are expressed as glucose equivalents (% loss) against incubation time (days). Losses of the primary photosynthate, Mannitol, from the mucilage incubation media (% loss) are shown also. This component is assayed separately from the sugars and is not reflected in the glucose equivalents losses.

It is evident that mannitol is used rapidly during the course of the incubation period, that sugars are used more slowly, and that the particulate fraction comprising largely alginates (Table 1) is the most slowly utilised of the three major components. The initial concentrations and times for 50% utilisation of total carbon, mannitol, sugars and alginates are summarised in Table 2 which shows that mannitol is rapidly utilised within 48 h whereas the sugars have a 50% utilisation time of 144 h and the alginates in the particulate fraction a value of 432 h. It seems likely, therefore, that mannitol may provide an immediately utilisable substrate for the free-living bacteria which predominate in the water column near to the kelp beds (FIELD et al. 1980) whereas other components such as alginates and particulate matter may be utilised more slowly by attached bacteria and are thus capable of export to peripheral communities some distance from the kelp bed.

Conversion of organic matter into bacterial biomass

The increase in bacterial biomass and simultaneous net utilisation of total organic carbon in media to which known weights of kelp debris have been added allows an estimate of the efficiency of conversion of carbon from kelp debris into bacterial

Table 2

The time taken for 50 % utilisation of the principal components of debris from the kelp *Laminaria pallida* under culture conditions in seawater at 10 °C. Data compiled from LUCAS et al.(1981) and STUART et al. (in press).

Substrate	DOM		POM	
	Initial concentration $\mu g\ ml^{-1}$	Time for 50 % utilisation h	Initial concentration $\mu g\ ml^{-1}$	Time for 50 % utilisation h
Total carbon	521	96	78.48	408
D-Mannitol	385	48	—	—
Sugars	118	144	68.92	360
Alginates	—	—	96.28	432

biomass. Figure 2 summarises the results of experiments on 'dissolved' organic matter from kelp by LUCAS et al. (1981) and on dried powdered frond of *Laminaria pallida*, both incubated in seawater freshly collected from the kelp bed during the summer (STUART et al. in press). Unfortunately, strictly quantitative comparisons between the two sets of data are not possible because dissolved organic matter was added to a concentration of 7.2 g dry weight l^{-1} (= 2.18 g l^{-1} organic matter) whereas the powdered frond was incubated at a concentration of only 0.333 g l^{-1} (= 0.254 g l^{-1} organic matter). Nevertheless certain general features are common to both graphs. (a) Once bacteria had colonised the media there is rapid utilisation of carbon from the media which coincides with the increase in biomass of free-living bacterial cocci and rods. (b) The initial rapid utilisation of carbon from the powdered debris declined after approximately 6 days and thereafter the bacteria were attached to the particles. (c) The appearance of flagellates limits the increase in bacterial biomass which usually declines due at least in part, to the grazing activities of the protozoa (see also LINLEY et al. 1981). (d) Finally, the bacterial biomass attained per gram of added substrate is different for dissolved and particulate fractions. The biomass of bacteria per unit added organic matter reaches only 16.5 mg g^{-1} for the particulate fraction whereas it reaches 42 mg g^{-1} dried dissolved organic matter from mucilage, despite the fact that the combined biomass of grazing protozoans per gram of organic matter was similar in both incubation experiments. This is because the initial rapid increase of bacteria in the powdered fresh frond is not sustained and coincides with the utilisation of soluble components of the debris. After these have been used, conversion of the residual alginates and other materials proceeds more slowly and supports a much smaller bacterial biomass per unit carbon used.

The increase of bacteria per unit carbon used from the medium for dried mucilage and for freshly milled particles is shown in Figure 3.

This shows that the increase in bacterial biomass/carbon utilisation x 100 for the initial phase of soluble substrate utilisation is as high as 66 % in the particulate debris and can approach this value in the logistic growth phase of bacteria incubated with mucilage above. Interestingly, we have found that although mannitol is the principal substrate used from mucilage by bacteria in our incubation experiments, the addition of mannitol alone to freshly collected kelp bed seawater fails to promote enhanced bacterial growth. Equally, the overall value for the conversion of carbon in mucilage to

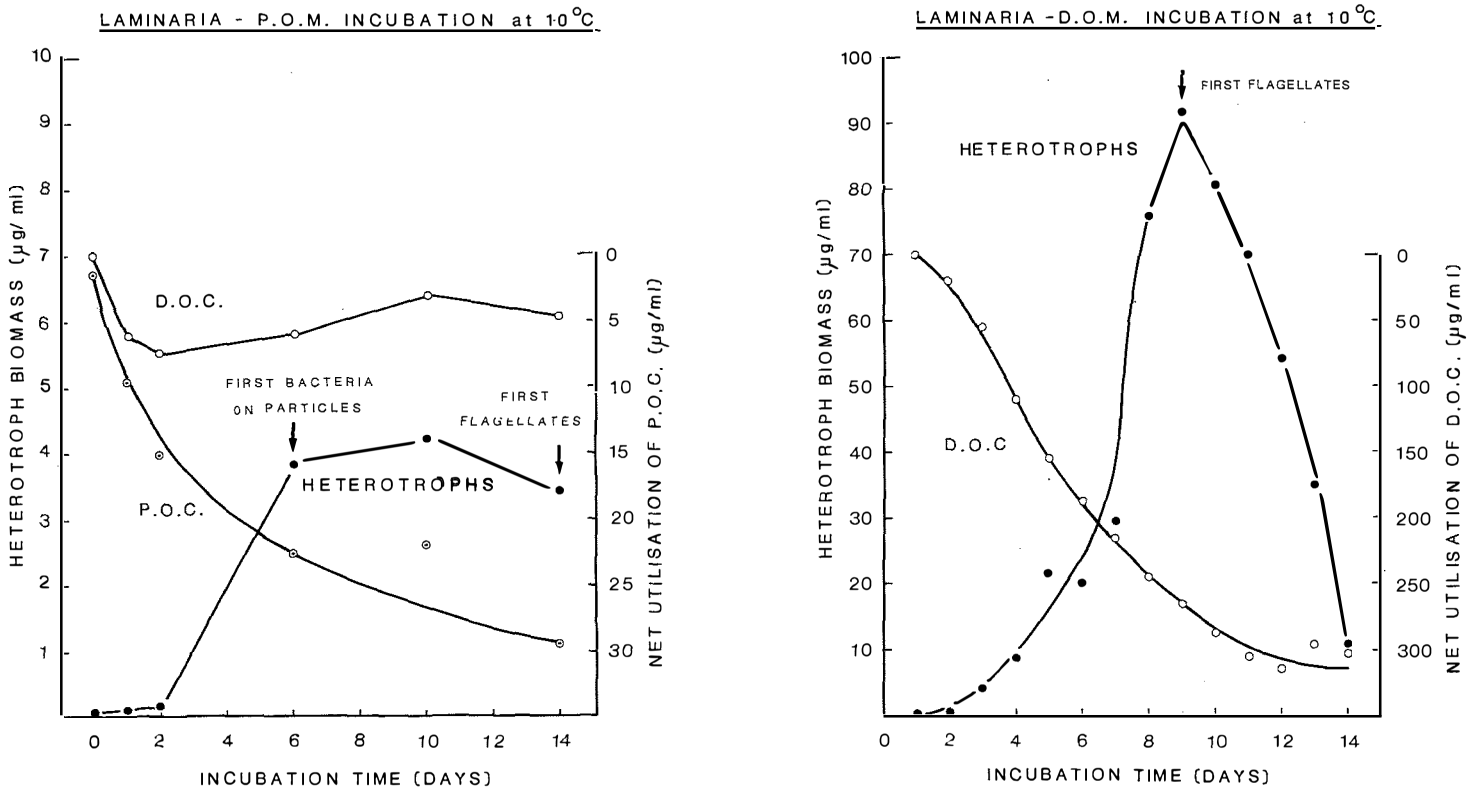
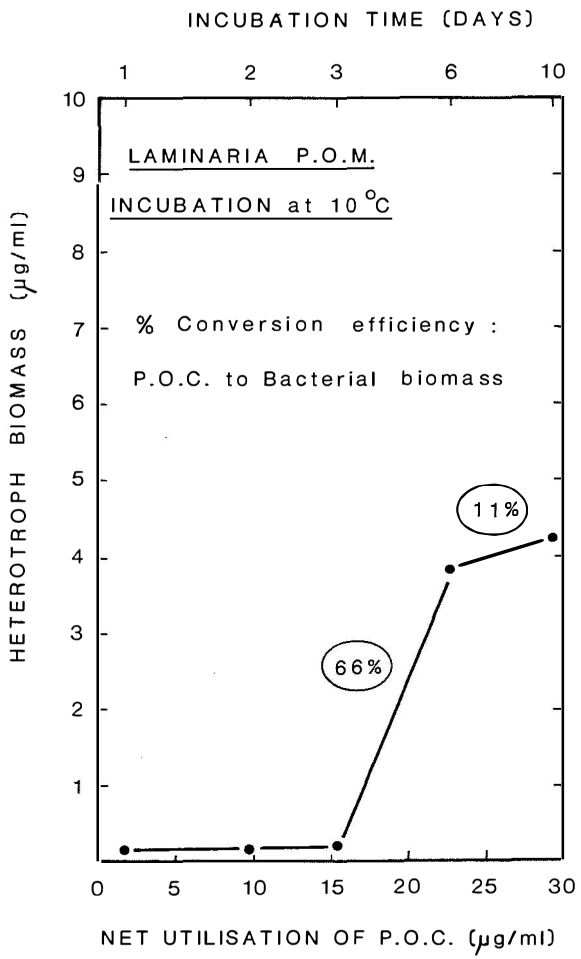


Figure 2
Laminaria pallida D.O.M. & P.O.M.

The net utilisation of dissolved and particulate organic carbon ($\mu g\ ml^{-1}$) and corresponding increase in heterotroph biomass ($\mu g\ ml^{-1}$) in seawater to which 0.33 g l^{-1} (= 0.254 g l^{-1} organic matter) dry particulate material (43 μm to 64 μm) and 7.2 g l^{-1} (= 2.18 g l^{-1}) dry mucilage from *Laminaria pallida* had been added and incubated separately for up to 14 days at 10°C. For the particulate incubation experiment, organic carbon losses are expressed as P.O.C. and D.O.C. leachate from P.O.M. which if summed, gives total organic carbon loss.



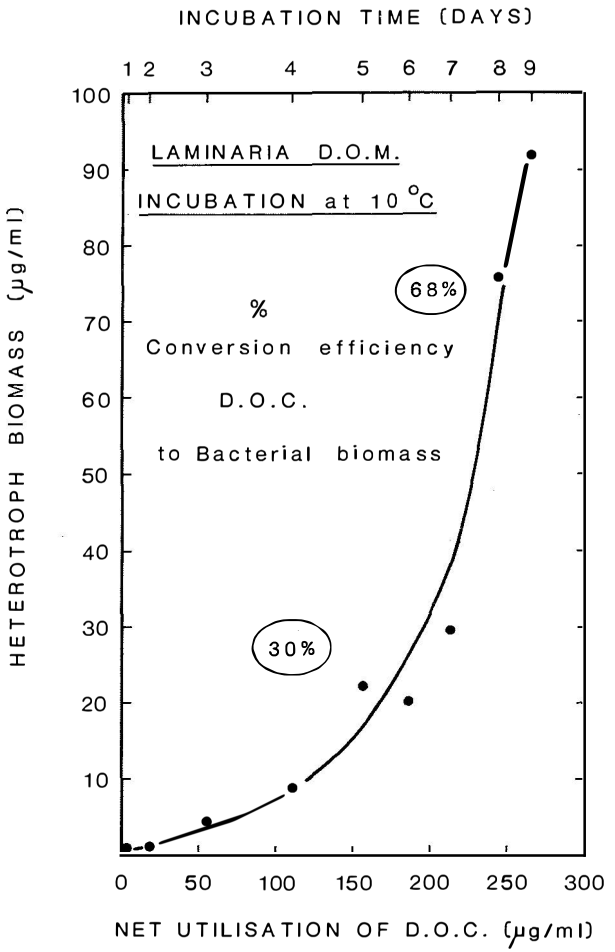


Figure 3

Laminaria pallida D.O.M. & P.O.M.

The relationship between biomass of heterotrophs ($\mu g\ ml^{-1}$) and net organic carbon loss ($\mu g\ ml^{-1}$) in seawater to which 0.33 $g\ l^{-1}$ (= 0.254 $g\ l^{-1}$ organic matter) dry particulate material (43 μm to 64 μm) and 7.2 $g\ l^{-1}$ (= 2.18 $g\ l^{-1}$) dry mucilage from *Laminaria pallida* had been added and incubated separately for up to 14 days at 10°C.

bacterial biomass is generally 30 % in the summer and may fall to 12 % in the winter (LUCAS et al. 1981). Evidently, the complex substrates releases by kelp are utilised much more efficiently in seawater than would be predicted from kinetic studies on single substrates, and the presence of additional nitrogen sources and other components in the particulate debris may further enhance bacterial growth. It is noteworthy that HAINES and HANSON (1979) have recently obtained high conversion efficiencies of saltmarsh plant material into microbial biomass on an ash-free basis of 19.4 % for *Salicornia*, 55.6 % for *Juncus* and 64.3 % for *Spartina* in nitrogen-enriched cultures. The corresponding value for the initial phase of degradation of powdered kelp debris would be 33 % on a carbon:carbon basis since carbon is ~50 % of the dry biomass of bacteria.

The bacterial biomass which can be supported from carbon sources in mucilage is also affected by seasonal factors including the nature of the bacterial assemblage in the seawater available to colonise the substrates. LUCAS et al. (1981) have found that the increase in biomass of bacteria per unit carbon loss was approximately 12 % in the winter but increased to as much as 29.4 % in the summer due to the development of a population of large bacterial rods in the media (see also LINLEY et al. 1981). A bacterial biomass : carbon utilisation conversion efficiency of some 12 % in the winter to 29 % in the summer can therefore be assumed for the freely-dispersed dissolved organic matter whilst a value of as much as 66 % may be charcteristic of soluble matter retained within particulate debris after fragmentation. In contrast, similar measurements on particulate debris suggest that the increase in bacterial biomass per unit carbon utilised from the particulate fraction is only 11 % (STUART et al. in press).

These values may now be used to calculate a budget for the heterotophic fate of organic production by kelp and to estimate the annual biomass of bacteria which can be sustained by kelp production.

Discussion: Carbon flow into the first step of the decomposer food web

The basic conversion of carbon from primary production by kelp into bacterial biomass can thus be summarised as follows. Some 70 % of carbon production is released as particulate organic matter (HATCHER et al. 1977; JOHNSTON et al. 1977; NEWELL et al. 1980) and this is converted to bacterial biomass with an efficiency of approximately 11 %. That is, carbon production from kelp is tranformed to bacterial biomass with an overall efficiency of 7.7 % (this is equivalent to a primary carbon production : bacterial carbon conversion of approximately 3.9 % since bacteria contain approximately 50 % carbon). The remaining 30 % released as dissolved organic matter could have an average annual conversion of 21 % (12 % in winter and 29 % in summer). That is, conversion of carbon production to dry bacterial biomass via the dissolved pathway may have an overall efficiency of 6.3 %. This would give a combined dry biomass from both particulate and dissolved pathways of 7.7 + 6.3 = 14.0 % of primary production of carbon by kelp.

Now at first sight it might seem that a conversion of only some 14 % of kelp carbon production into bacterial biomass would mean that only small quantities of bacteria are available as a potential food resource for filter- and deposit-feeding organisms. Studies by FIELD et al. (1977), DIECKMANN (1978) and MANN et al. (1979), however, have shown that production by kelp beds is very high indeed. This means that large populations of microheterotrophs may be supported through primary production by the kelp, even though the gross conversion efficiency may be only some 14 % of primary carbon production. NEWELL et al. (1980) have summarised the data for kelp

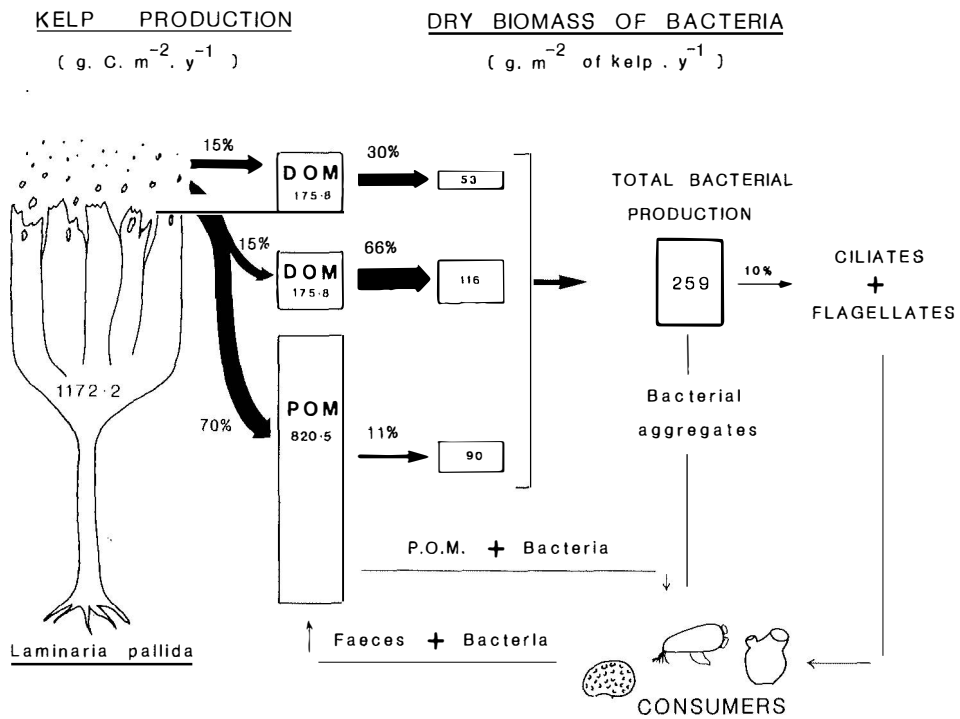


Figure 4

Laminaria pallida D.O.M. & P.O.M.

Generalised carbon budget for *Laminaria pallida* and its subsequent conversion during the summer into bacterial biomass. The 15% : 15% : 70% split of *Laminaria* production (1172 g C m^{-2} y^{-1}) into "free" D.O.M. (eg. cell contents); D.O.M. associated with P.O.M. (eg. less soluble hexoses) and more refractory insoluble P.O.M. (eg. alginates & celluloses) is based on proportions given by JOHNSTON et al. (1977), HATCHER et al. (1977), and NEWELL et al. (1980). The thickness of the arrows denotes the relative percentages of the D.O.M. & P.O.M. proportions (g C m^{-2} y08) and their conversion (% efficiency) into bacterial dry biomass (g m^{-2} of kelp y^{-1}) associated with each of these component pathways. The sum of these components gives total bacterial production which may be grazed by micro-zooplankton or become available to benthic consumer organisms.

production from a variety of sources. An average figure of 1172.2 g carbon.$m^{-2}.y^{-1}$ is obtained for mixed kelp beds of *Laminaria* and *Ecklonia* on the west coast of the Cape Peninsula. Annual dry bacterial biomass supported per m^{-2} of kelp bed would thus be 164.1 grams.

Clearly, the values are likely to be rather lower in winter than in summer because the biomass which develops on kelp debris is lower (LINLEY et al. 1981; LUCAS et al. 1981) and there may be seasonal differences in the relative proportions of dissolved and particulate debris released into the water column. A generalised carbon budget for *Laminaria* and its subsequent conversion during the summer into bacterial biomass through dissolved and particulate pathways is shown in Figure 4. This illustrates conditions when macrophyte growth, fragmentation and subsequent conversion into bacteria is at its maximum.

These data are also summarised in Table 3 which shows figures for the relative significance of dissolved and particulate organic matter based on HATCHER et al (1977), JOHNSTON et al. (1977) and NEWELL et al. (1980) and also shows the estimated conversion into bacterial biomass based on the results of our summer series of incubation experiments. A release of 70% of the 1171.2 g carbon m^{-2} y^{-1} as a particulate fraction during fragmentation and converted with an efficiency on 11% during the summer months would yield 90.18 g dry biomass of bacteria m^{-2} of kelp bed y^{-1}. JOHNSTON et al. (1977) estimated that about half the remaining dissolved fraction in *Laminaria saccharina* is released as extracellular products and half as leakage during fragmentation. Of the 30% of carbon production released as a dissolved organic fraction, it is therefore likely that half will be converted with an efficiency of 29% as freely-dispersed dissolved organic matter released into the water column. The other half remaining associated with particles during fragmentation may be converted into bacterial biomass with an efficiency of 66%. Carbon production by the kelp will therefore support a dry bacterial biomass during the summer equivalent to 258.9 g m^{-2} of kelp y^{-1}. This is equal to a gross conversion of kelp carbon to bacterial biomass of 22.09% during the summer months compared with the annual average of approximately 14% ($\simeq$ a kelp carbon: bacterial carbon conversion efficiency of 11% in summer and an annual value of 7%).

It is also possible to arrive at some estimates of the annual production of bacteria which could be supported in the water column via carbon production from a mixed kelp bed of 700 hectares. An annual dry bacterial biomass of 164.1 grams m^{-2} of kelp bed based on an overall annual conversion efficiency of 14% of algal production would yield 114.8×10^4 kg dry biomass of bacteria per year from a kelp bed of 700 ha. The relatively restricted receiving waters are likely to be of the order of 1000 hectares at an average depth of 10 metres, or 1000×10^5 m^3. Thus the annual dry biomass of bacteria released from the kelp bed and based on conversion of dissolved and particulate fractions from the fragmenting kelp is likely to be approximately 11.48 g m^{-1} but could rise to as much as 18.13 g m^{-3} during the summer months (see Table 3).

Interestingly, FIELD et al. (1980) have published figures for the standing stock of bacteria in the water column in an upwelling area near to the kelp beds off the Cape Peninsula. They obtained a standing stock equivalent to 24.7 g carbon m^{-3} y^{-1} which yields an annual production of 7.41 g carbon m^{-3} y^{-1} based on a P:B ratio of 0.3 (see SOROKIN and MIKHEEV 1979) Since dry bacterial material comprises approximately 50% carbon, the estimated annual produktion for bacteria based on their figures is 14.82 g dry biomass m^{-3} y^{-1}. Again, LINLEY (in prep.) has studied the seasonal variations in bacterial biomass in the kelp beds themselves and has estimated a bacterial production value of 7.76 g dry biomass m^{-3} y^{-1} using a P:B ratio of 0.3.

Table 3

The production from a mixed kelp bed and its subsequent heterotrophic conversion into bacterial biomass through dissolved and particulate pathways. Data for production based on figures summarised by NEWELL et al. (1980); conversion values based on summer incubation experiments. A mean value of 70 % of carbon production has been used for particulate matter (see also HATCHER et al. 1977; JOHNSTON et al. 1977). Note that a lower conversion into bacterial biomass will be attained during the winter months.

Average carbon production of kelp bed	1172.2 g m^{-2} y^{-1}
A *Particulate Organic Matter* at 70 % of carbon production	820.54 g carbon m^{-2} y^{-1}
Bacterial Biomass based on conversion efficiency of 11 % of particulate carbon production	**90.18 g dry biomass m^{-2} kelp**
B *Dissolved Organic Matter* at 30 % of carbon production	351.66 g carbon m^{-2} y^{-1}
(a) 15 % DOM directly released and converted with 30 % efficiency in summer. Bacterial biomass	52.75 g dry weight m^{-2} kelp y^{-1}
(b) 15 % DOM released with particulate fraction and converted with 66 % efficiency in summer. Bacterial biomass	116.05 g dry weight.m^{-2} kelp y^{-1}
Total Dry Bacterial Biomass from DOM	**168.80 g m^{-2} of kelp**
Total Annual summer equivalent of Bacterial Biomass.m^{-2} of kelp bed	258.98 g
Annual conversion efficiency from carbon production by kelp to bacterial biomass	22.09 %
Annual equivalent of Bacterial Biomass supported by 700 ha kelp bed	181.29 x 10^4 kg dry mass y^{-1}
Estimated volume of water into which bacteria are liberated	1000 x 10^5 m^3
Annual summer equivalent of bacterial production supported from kelp production	18.13 g m^{-3}

That is, the estimated bacterial production figures based on measurements of the standing stocks of bacteria in the water column near to the sites of 'excess' primary production adjacent to the kelp bed are very close to those which we have predicted

could be supported from degradation of dissolved and particulate components of kelp above. Provided the conversion efficiency into larger consumer organisms is known, it thus becomes possible to estimate the carrying capacity of the inshore environment via the detritus food web from estimates of primary production by the macrophytes.

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