

REVIEW

Energy Balance and Significance of Micro-Organisms in a Kelp Bed Community

R. C. Newell¹, J. G. Field² and C. L. Griffiths²

¹ Institute for Marine Environmental Research, Prospect Place, Plymouth PL1 3DH, United Kingdom

² Department of Zoology, University of Cape Town, Rondebosch 7700, South Africa

ABSTRACT: Primary production by phytoplankton in a Benguela upwelling region off the west coast of the Cape Peninsula, South Africa, is almost equal to that within beds of the kelps *Ecklonia maxima* and *Laminaria pallida*. Total primary production of kelps, understory algae and phytoplankton within an idealised kelp bed of 10 m average depth is $62,190 \text{ kJ m}^{-2} \text{ yr}^{-1}$, as compared to $54,037 \text{ kJ m}^{-2} \text{ yr}^{-1}$ for the phytoplankton community in deeper water nearby. The overall energetic conversion from incident illumination is 1.7% within the kelp bed and 1.5% for phytoplankton in the nearby water column, suggesting that a net production efficiency of 1.5 to 1.7% may approach the maximum attainable by aquatic plants under conditions where nutrients are rarely limiting. The fauna is dominated by filter feeders, which are responsible for 72% of total animal standing stock (B), 77% of total production (P), 94% of respiration (R), 84% of consumption (C) and 89% of faecal production (F). Independent estimates of primary production and energy requirements of consumers balance to within 8%, lending confidence to the calculations. Suspended matter, the food of filter feeders, is comprised of macrophyte particles, animal faeces and phytoplankton in roughly equal proportions. Bacteria which utilise dissolved and particulate components of fragmented macrophytes and faeces may produce up to $6,403 \text{ kJ m}^{-2} \text{ yr}^{-1}$, which is small energetically but belies their importance in protein enrichment of food and in nutrient cycling. The kelp community appears to depend primarily on rapid bacterial mineralisation of fragmented kelp and faeces to recycle the minerals necessary to sustain primary production, supplemented by bouts of upwelling.

INTRODUCTION

The significance of micro-organisms both in the mineralisation of organic debris from a variety of sources and as potential food for consumer organisms has been widely recognised (Darnell, 1967; Mann, 1972; Odum et al., 1973; Odum and Heald, 1975; Cammen et al., 1978; Cammen, 1980a,b). Estimates of the efficiency of assimilation of micro-organisms by consumers, for example, range between 40 and 90% (Zhukhova, 1963; Fenchel, 1970; Hargrave, 1970; Kostalos, 1971; Calow and Fletcher, 1972; Chua and Brinkhurst, 1973; Calow, 1975; Kofoed, 1975a; Wetzel, 1975; Moriarty, 1976; Yingst, 1976; Lopez et al., 1977; Cammen et al., 1978), whilst net assimilation of inert structural components of detritus is commonly less than 10% (Hargrave, 1970; Calow, 1975; Alexander,

1976; Wetzel, 1977; Cammen et al., 1978). Partly for these reasons, it has been generally accepted that plant detritus may be first colonised by microbial decomposer organisms before it becomes suitable as food for consumers. The microbiota may then be stripped from the inert detrital particles, which are subsequently returned to the environment for further microbial colonisation (Newell, 1965; Fenchel, 1970, 1972; Odum and Heald, 1975; Wetzel, 1975; Berrie, 1976; Hargrave, 1976; Yingst, 1976; Lopez et al., 1977; Taghon et al., 1978). Estimates of the amounts of bacterial carbon available to consumer organisms via this decomposer pathway have, however, differed widely and until recently there have been few detailed attempts to determine whether the absorption of microbial carbon could quantitatively match the estimated carbon requirements of consumers.

Most recent studies on the role of bacteria in the nutrition of deposit feeders have reported that the quantity of bacteria consumed is substantially less than the carbon requirements of the organisms (Baker and Bradnam, 1976; Wetzel, 1977; Jensen and Siegmund, 1980). Again, Cammen et al. (1978) and Cammen (1980a, b) have pointed out that bacterial carbon is generally only 1 to 3% of total sediment organic carbon (Dale, 1974; Rublee et al., 1978; Sorokin, 1978; Kepkay and Novitsky, 1980). The annual consumption of microbial carbon by the deposit-feeding polychaete *Nereis succinea* is thus calculated to be 5.2 g m^{-2} whilst the absorption efficiency is 57%; absorbed carbon from the micro-organisms is thus $2.96 \text{ g m}^{-2} \text{ yr}^{-1}$. Carbon incorporation into production plus losses through respiration, however, were $11.59 \text{ g m}^{-2} \text{ yr}^{-1}$. The complete carbon budget for *N. succinea* thus suggests that only $2.96/11.59 = 25.5\%$ of its carbon requirements could be met by utilisation of microbial carbon. Even if absorption of microbial carbon were complete, this resource could only meet 45% of estimated carbon requirements. Cammen et al. (1978) and Cammen (1980b) thus suggested that some of the carbon necessary to balance the budget may come from direct utilisation of plant debris. They cited evidence that some invertebrates have the enzymes necessary to utilise cellulose directly (Yokoe and Yasumasu, 1964; Lewis and Whitney, 1968; Forster and Gabbott, 1971; Elyakova, 1972; Kristensen, 1972) and pointed out that even if absorption efficiency from detritus itself was low, sufficient material may be processed to allow the carbon budget to be balanced.

An alternative method of assessing the trophic significance of micro-organisms is to estimate the microbial production from detrital decomposition and calculate the extent to which the total energy requirements of consumer organisms can be met by utilisation of this food resource (see also Steele, 1974; Mills, 1975; Mills and Fournier, 1979). There is now fairly detailed information on primary production (Field et al., 1977; Dieckmann, 1978, 1980; Mann et al., 1979; Jarman, 1981; summarised in Newell et al., 1980), standing stocks (Velimirov et al., 1977; Field et al., 1980b), and consumption requirements of organisms associated with kelp beds of the west coast of the Cape Peninsula, South Africa. There is also information on microbial carbon conversion of kelp debris in non-enriched local seawater (Linley and Newell, 1981; Linley et al., 1981; Lucas et al., 1981; Newell, 1982; Newell and Lucas, 1981; Stuart et al., 1981, 1982). Comparable results have been obtained in the field in a microcosm experiment (Koop et al., 1982).

It is the purpose of this paper to synthesise the information on both production and population energy requirements for the kelp bed community. The evi-

dence suggests that even though total primary production from macrophytes and nearshore phytoplankton is comparable with phytoplankton production in a nearby upwelling area, the combined microbial and phytoplankton food resources of the kelp bed are insufficient to meet more than 50% of the calculated consumption of the community as a whole. Consumer organisms thus appear to be dependent for about half of their energetic requirements on direct utilisation of detrital material, much as has been reported for individual members of deposit-feeding communities.

PRIMARY PRODUCTION BY THE KELP BED COMMUNITY

Primary production by marine macrophytes has been compared with that of phytoplankton by Mann (1972, 1973). He found that primary production by the seaweeds in St. Margaret's Bay, Nova Scotia greatly exceeded that of phytoplankton in the open waters of the bay itself, even though the area occupied by phytoplankton greatly exceeded that colonized by macrophytes. From this we might expect the relative contribution by macrophytes to the detrital pool in coastal areas to be high compared with that from phytoplankton. In areas on the western Cape coast, however, upwelling occurs in and immediately outside the kelp beds during much of the year and here the relative contribution by macrophytes and phytoplankton may be very different from that in areas where phytoplankton production is limited by nutrient availability. It is therefore of interest to compare total primary production by all components of the kelp bed system, with that of phytoplankton in the adjacent upwelling area.

The major components of primary production in kelp beds are the kelps and their associated epiphytes, understory algae and phytoplankton. For the purposes of energy-flow calculations, we have taken a typical kelp bed off the southern Cape Peninsula as being represented by 10 km coast \times 500 m width (i.e. to approximately 20 m depth line) of average depth 10 m, derived from data given by Field et al. (1980b).

Macrophyte Production

The dominant macrophytes in South African kelp beds are *Laminaria pallida* and *Ecklonia maxima*, with occasional *Macrocystis angustifolia*. To these should be added the understory algae, comprising mainly *Botryocarpa prolifera*, *Neuroglossum binderianum*, *Pachymenia carnosa*, *Trematocarpus* spp., and *Hymenena venosa*, and kelp epiphytes. The latter occur mainly on *E. maxima* and comprise *Carpob-*

Table 1. Biomass (B, g wet weight m⁻²) frond P/B ratios and production (P) of principal components of a typical kelp bed on the west coast of Cape Peninsula, South Africa. Production values expressed as wet mass, dry mass and carbon (g m⁻² yr⁻¹) and energy equivalents (kJ m⁻² yr⁻¹)

Source	Biomass		Frond P/B	Annual production			
	Total	Frond		Wet	Dry	Carbon	Energy
<i>Ecklonia maxima</i>	3,492	1,746	4	6,983	1,041	306	16,559
Epiphytes	262	262	4	1,047	156	34	2,416
<i>Laminaria pallida</i>	2,307	1,154	4	4,587	573	144	6,273
Understorey	998	998	4.2	4,166	946	255	11,586
Total growth	7,059	4,160	–	16,783	2,716	739	36,834
Kelp mortality in storms (12 % of biomass)	–	–	–	696	97	28	1,370
Total macrophyte production				17,479	2,813	767	38,204

lepharus flaccida, *Carradoria virgata* and *Suhria vitata*, which together add approximately 7.5% to the wet biomass of the host (Allen and Griffiths, 1981). The relative proportions of the standing crop of the 2 major kelp species and of the understorey algae are shown in Table 1 and are based on the mean data for a series of transects on the west coast of South Africa (Field et al., 1980b). Macrophyte biomass values are based on data for Oudekraal and Kommetjie (Field et al., 1980b). Frond production values for the kelp are based on data from Field et al. (1977, 1980b), Dieckmann (1978, 1980), Mann et al. (1979) and Jarman and Carter (1982). For the purposes of calculation, we have assumed the P/B ratio for epiphytes to be the same as that for the frond of their host. Production values for understorey algae were estimated from R. Anderson (University of Cape Town, pers. comm.).

Jarman and Carter (1982) have estimated that approximately 12% of the standing stock of kelp (stipes plus fronds) is lost annually in storms. Mortality thus adds some 1,370 kJ m⁻² yr⁻¹ to the production of the kelp fronds (Table 1).

It is evident that total primary production by the macrophytes amounts to 38,204 kJ m⁻² yr⁻¹, of which the understorey algae contribute $11586/38204 = 30\%$. Frond production by *Ecklonia maxima* plus its epiphytes comprises a further $18975/38204 = 50\%$ of the total, *Laminaria pallida* frond production contributes 16%, with storm mortality of whole kelps making up the remaining 4%. These values have been used to quantify the pathways of energy flow through the kelp bed community as shown in Fig. 1.

Phytoplankton Production

A range of values for phytoplankton production have been summarised in the well known paper by Ryther

(1969), who gives mean production as 50 g carbon m⁻² yr⁻¹ for open ocean, 100 g C m⁻² yr⁻¹ for coastal zones and 300 g C m⁻² yr⁻¹ for upwelling areas. Within a kelp bed itself, primary production per unit area is limited both by depth and the shading effect of macrophytes (Borchers and Field, 1981) and possibly by nutrient availability. Carter* (in press) has recently measured phytoplankton production at the outer edge of a kelp bed at Oudekraal, on the west coast of the Cape Peninsula, and estimated mean annual production at 57 g C m⁻³, a value which coincides with the average for deeper waters outside the kelp bed (Brown, 1981). Using a conversion ratio of 47.82 kJ g carbon⁻¹ (Platt and Irwin, 1973) this yields a phytoplankton production value of 27,257 kJ m⁻² yr⁻¹. Borchers and Field (1981) estimated that the shading effect of kelp reduced phytoplankton by approximately 12% over the whole kelp bed. Primary production by the phytoplankton component in the kelp bed is thus reduced to 23,986 kJ m⁻² yr⁻¹ by the combined effects of shallow depth and shading by macrophytes, a value comparable with the frond production of 25,248 kJ m⁻² yr⁻¹ of the kelp plus epiphytes (Table 1).

In contrast, Brown (1980, 1981), using the oxygen light-dark bottle technique, has shown primary production at an active upwelling site off kelp beds at Oudekraal to be 823 g C m⁻² yr⁻¹, although in an adjacent area at Robben Island, which has a more stable water column influenced by nearby upwelling, primary production reaches a remarkable 1,432 g C

* Carter estimates that the net phytoplankton primary production in a 20 m water column at the edge of the kelp bed is 1.129 kg C m⁻² yr⁻¹ and that most production occurs when the water column is stratified in the top 10 m. Thus our value for the whole kelp bed may appear to be an underestimate. However, Field et al. (1980a) have shown that phytoplankton concentrations in shallow water within the kelp bed are some 50% lower than at the outer edge, justifying our estimate

$\text{m}^{-2} \text{yr}^{-1}$. These estimates were obtained by integrating values down to the 1% light level or the depth of mixing, whichever was the shallower. Her best estimate of primary production in the water column over the Southern Benguela region is given as $1,130 \text{ g C m}^{-2} \text{yr}^{-1}$, or $54,037 \text{ kJ m}^{-2} \text{yr}^{-1}$.

This value may now be compared with the sum of primary production by phytoplankton and macrophytes in the shallow waters of the kelp bed. From p. 105, we obtain a value of $23,986 \text{ kJ m}^{-2} \text{yr}^{-1}$ for kelp bed phytoplankton, $11,586 \text{ kJ m}^{-2} \text{yr}^{-1}$ for understorey algae, and $26,618 \text{ kJ m}^{-2} \text{yr}^{-1}$ for kelp plus epiphytes. This yields a total production of $62,190 \text{ kJ m}^{-2} \text{yr}^{-1}$ for the kelp bed which is similar to the value of $54,037 \text{ kJ m}^{-2} \text{yr}^{-1}$ for phytoplankton production in a deeper water column. This suggests that the high primary production of macrophytes compensates for the reduced phytoplankton production in the shallow waters of the kelp bed, but equally shows that phytoplankton production in upwelling areas, where nutrients are rarely limiting, may approach the value of total primary production in the seaweed zone and considerably exceed that of the macrophytes themselves.

It is also of interest to calculate the net production efficiency of the kelp bed producers compared with the phytoplankton nearby. Professor R. F. Fuggle (School of Environmental Studies, University of Cape Town) has kindly supplied us with data for photosynthetically active radiation (P.A.R.) measured over a 10-yr period near Cape Town and representative of the incident energy on the kelp beds. The data yield an average value of $3,608 \times 10^3 \text{ kJ m}^{-2} \text{yr}^{-1}$ so that net production efficiency for the phytoplankton is $54,037/3,608,000 = 1.5\%$ and for the kelp bed community is $62,190/3,608,000 = 1.7\%$. These values are similar to those obtained by Teal (1962) who found a net production efficiency of 1.3% for a Georgia salt marsh, where the radiation was $2.508 \times 10^3 \text{ kJ m}^{-2} \text{yr}^{-1}$. The similarity of the values for phytoplankton, kelp beds and saltmarshes suggests that a natural net production efficiency of 1.5–1.7% may approach the maximum attainable by plants under aquatic conditions when nutrients are rarely limiting.

SECONDARY PRODUCTION BY THE KELP BED COMMUNITY

The data for standing stock (kJ m^{-1}) of the principal consumer organisms in an idealised kelp bed typical of the west coast of the Cape Peninsula are summarised in Table 2. The standing stock data have been derived from Velimirov et al. (1977); values for Production (P), Respiration (R), Consumption (C) and Faeces (F),

determined for key components of the fauna for each trophic level, have been assumed for the group as a whole.

Grazers

One characteristic feature of the kelp bed community of the Cape Peninsula, is that herbivores directly utilising living kelp as a food resource are scarce. The dominant grazer is the sea urchin *Parechinus angulosus*, which has a mean biomass equivalent to 258 kJ m^{-2} . The gastropods *Haliotis midae* and *Patella* spp. account for 20 and 14 kJ m^{-2} respectively, whilst the remaining herbivores make up only 8 kJ m^{-2} . The standing stock of grazers as a whole is thus 300 kJ m^{-2} , or only 4.17% of that of consumer organisms as a whole.

No information is available on the energetics of *Haliotis midae* or the *Patella* spp. which utilise the kelp, but Greenwood (1980) has derived an energy budget for *Parechinus angulosus*, which comprises 86% of the grazer component. He reported a ratio of P/B of 1.04 and C/B of 15.5; hence grazer production is $312 \text{ kJ m}^{-2} \text{yr}^{-1}$ and consumption $4,650 \text{ kJ m}^{-2} \text{yr}^{-1}$. Respiration (R) and faecal losses (F) are 1,083 and $1,588 \text{ kJ m}^{-2} \text{yr}^{-1}$ respectively. Since Consumption (C) = Production (P) + Respiration (R) + Faeces (F) + Dissolved organic matter (U) the energy budget for the grazers as a whole is:

$$C - (P + R + F) = U$$

$$\text{Or } 4,650 - (2,983) = 1,667 \text{ kJ m}^{-2} \text{yr}^{-1}$$

It is thus evident that the energy budget for herbivores based on data for urchins contains a relatively large component, amounting to as much as 36% of (C) which possibly represents dissolved losses (U). It is also apparent that the grazing component, which is dominated by urchins, has a relatively low P/C ratio of 6.7%, much of the energy consumed being dissipated through respiration (R) faeces (F) and as (U) (see also Table 4).

Filter Feeders

The filter-feeding component dominates the kelp bed fauna with a standing stock equivalent to $5,155 \text{ kJ m}^{-2}$ or 71.8% of the total. The mussel *Aulacomya ater* represents 45.7% of this component, sponges (*Tethya* sp.) 12.5% and ascidians (*Pyura* sp.) 5.7%. The residual 36% comprises a variety of other, smaller filter feeders. A good deal is now known of the filtration rate, absorption efficiency, respiration and production of *A. ater* (Griffiths and King, 1979a, b), both in relation to food availability and body size. It is therefore possible to make some fairly detailed estimates of

Table 2. Standing stock (kJ m^{-2}) and energy budgets ($\text{kJ m}^{-2} \text{yr}^{-1}$) of the fauna of an idealised kelp bed on the west coast of Cape Peninsula, South Africa. Standing stock values derived from Velimirov et al. (1977). Energy budgets for grazers based on data for *Parechinus angulosus* (Greenwood, 1980), for suspension feeders on data for *Aulacomya ater* (Griffiths and King, 1979a, b) and *Pyura stolonifera* (Fitzgerald, 1979), and for carnivores on data for *Jasus lalandii* and *Cirolana imposita* (Humphreys, 1979; Shafir and Field, 1980)

Component	Standing stock (B)	Production (P)	Respiration (R)	Consumption (C)	Faeces (F)
Grazers					
<i>Parechinus angulosus</i>	258				
<i>Haliotis midae</i>	20				
<i>Patella</i> spp.	14				
Others	8				
Sub-total	300	312	1,083	4,650	1,588
Filter feeders					
<i>Aulacomya ater</i>	2,354				
Sponges (<i>Tethya</i> spp.)	648				
<i>Pyura stolonifera</i>	296				
Others	1,857				
Sub-total	5,155	5,825	30,930	62,891	26,033
Large carnivores					
<i>Jasus lalandii</i>	738				
Anemones	199				
<i>Pachymetopon blochii</i>	506				
Others	91				
Sub-total	1,579	632	411	3,160	1,264
Small carnivores					
<i>Cirolana imposita</i>	149	826	648	4,131	289
Total	7,183	7,595	33,072	74,832	29,174

consumption and faecal production by this bivalve, which dominates parts of the kelp bed community. The average natural concentration of suspended particles in the kelp bed is 2.7 mg l^{-1} (Field et al., 1980a). This is equivalent in mass to the optimal ration level of 16×10^6 *Dunaliella* cells l^{-1} and yields a population respiration for *A. ater* of $14,103 \text{ kJ m}^{-2} \text{yr}^{-1}$ from a standing stock of $2,254 \text{ kJ m}^{-2}$ (Table 3). Population respiration for the mussel is thus $6 \times B$. Griffiths and King (1979b) and unpublished population density figures) have also found that production (P) by *A. ater* is $1.13 \times B$.

If these figures for *Aulacomya ater* are also applied to the other members of the filter-feeding component, production (P) for filter feeders in the kelp bed becomes $5,155 \times 1.13 = 5,825 \text{ kJ m}^{-2} \text{yr}^{-1}$ and (R) becomes $30,930 \text{ kJ m}^{-2} \text{yr}^{-1}$. It is now possible to calculate the consumption of the filter-feeding component of the fauna from the sum of respiration ($R = 6 \times B$) and production ($P = 1.13 \times B$), provided that absorption efficiency at the ration level of 2.7 mg l^{-1} , recorded in the kelp bed, is known. Griffiths and King (1979a) found that mussels fed on an optimal ration of *Dunaliella* at 2.7 mg l^{-1} have an absorption efficiency of 20%, although it is well known that absorption

efficiency may increase if mussels are fed on diets including natural particulate debris (see also Kjørboe et al., 1980). With regard to other filter-feeding forms, Fitzgerald (1979) found absorption efficiency of the ascidian *Pyura* to be as high as 90%. Little is, however, known about the absorption efficiency of other forms, particularly the sponges. *A. ater* comprises approximately 45% of the total filter feeders, whereas *Pyura*, sponges and others contribute 55% (Table 2). If the

Table 3. Standing crop and population respiration of different size classes of *Aulacomya ater* in an idealised kelp bed. Based on data from Griffiths and King (1979a) and calculated for an optimal ration of 16×10^6 cells l^{-1} of *Dunaliella* ($= 2.7 \text{ mg l}^{-1}$), which corresponds with the mean concentration of particulate matter reported for the waters of the kelp bed by Field et al., (1980a)

Shell length (mm)	kJ individual $^{-1}$	Standing crop kJ m^{-2}	Population respiration $\text{kJ m}^{-2} \text{yr}^{-1}$
0–40	0.48	43	238
40–60	1.20	313	11,219
60–90	42.0	1,998	2,646
Total		2,354	14,103

value for *Pyura* is taken as typical of non-bivalve filter feeders, the mean absorption efficiency for the group as a whole becomes 58.5%, a value which appears a reasonable one for filter feeders in general and which is similar to the 52% reported for *Mytilus edulis* fed on a diet of 20×10^6 *Phaeodactylum* cells l^{-1} (Kjørboe et al., 1981). Consumption (C) then becomes $100/58.5(6 \times B + 1.13 \times B) = 12.2 \times B = 62,891 \text{ kJ m}^{-2} \text{ yr}^{-1}$ and (F) is $5.05 \times B = 26,033 \text{ kJ m}^{-2} \text{ yr}^{-1}$ (Table 2).

Carnivores

Values for components of the energy budget in carnivores are rather more difficult to calculate since, as recently shown by Shafir and Field (1980), small, relatively inconspicuous carnivores such as the isopod *Cirolana imposita* have a very high Production (P) compared with their biomass, whereas more obvious consumers such as the rock lobster *Jasus lalandii*, have a lower P/B ratio (Table 4). It is therefore convenient to divide the carnivores into 2 categories comprising larger organisms such as the rock lobsters, anemones and fish, and small carnivores such as *Cirolana imposita*.

Production for the large carnivores is estimated at $0.4 \times \text{Biomass}$ (from Shafir and Field, 1980) or $632 \text{ kJ m}^{-2} \text{ yr}^{-1}$. For the purposes of Table 2, a P/C ratio of 20% has been assumed from similar data for *Cirolana*. Consumption thus becomes $632/0.2 = 3,160 \text{ kJ m}^{-2} \text{ yr}^{-1}$ and faecal production (F) = $1,264 \text{ kJ m}^{-2} \text{ yr}^{-1}$, if the absorption efficiency of the large carnivores is 60%. The value of (R) = $411 \text{ kJ m}^{-2} \text{ yr}^{-1}$ for large carnivores has been calculated from data for *Jasus* and yields an R/B ratio of only 0.26 (Humphreys, 1979) compared with 3.6 in grazers and 6 in filter feeders (Table 4). This suggests that at high trophic levels, where the availability of energy is reduced, energy dissipation through respiration may be minimised through the allometric reduction in weight-specific oxygen consumption which occurs in large consumers (see also McNeill and Lawton, 1970).

Data for small carnivores, of which the isopod *Cirolana imposita* is the most common in the kelp bed community, have been assembled from Shafir and Field (1980). They reported the biomass of *C. imposita* within rocky habitats only, so their figures have been adjusted for the whole kelp bed area from data on relative proportions of kelp, rocks and sand given by Velimirov et al. (1977). This yields an estimated standing stock of $149 \text{ kJ m}^{-2} \text{ yr}^{-1}$. The value of P/B = 5.56 so $P = 826 \text{ kJ m}^{-2} \text{ yr}^{-1}$. Population respiration (R) is $648 \text{ kJ m}^{-2} \text{ yr}^{-1}$ based on P/R = 1.02 and consumption (C) $4,131 \text{ kJ m}^{-2} \text{ yr}^{-1}$ based on a P/C ratio of 0.2 (Shafir and Field, 1980). They showed that the absorption

Table 4. Values for production (P), respiration (R), consumption (C) and faecal production (F) as a function of biomass (B) for the major components of a kelp bed community. The ratio of production/consumption is shown. These rates imply linear relationships, but in fact population (P) versus population (R) is a log/log relationship in many organisms (McNeill and Lawton, 1970; Humphreys, 1979). Comparisons between size-dependent ratios for large carnivores such as *Jasus* and small ones such as *Cirolana* are thus likely to be complicated by the allometric effects of body size

Component	P/B	R/B	C/B	F/B	P/C
Grazers	1.04	3.61	15.50	5.29	6.7 %
Filter feeders	1.13	6.00	12.18	5.05	9.3 %
Large carnivores	0.40	0.26	2.0	0.80	20.0 %
Small carnivores	5.56	4.36	27.79	1.95	20.0 %

efficiency is as high as 93% in *C. imposita*, so faecal production (F) is only $289 \text{ kJ m}^{-2} \text{ yr}^{-1}$.

In contrast to the large carnivores, therefore – partly because of their small body size – these predators have a higher R/B ratio of as much as 4.36. But the allometric effects of body size on weight-specific metabolic rate have been compensated by a very high consumption rate (Table 4). Energy dissipation through faeces is reduced by the maintenance of an absorption efficiency of as much as 93%, which results in a high P/R ratio for this animal (see also Shafir and Field, 1980). The values for Production (P), Respiration (R), Consumption (C) and Faecal production (F) as a function of Biomass (B) of each of the major components of the kelp bed community are shown in Table 4.

ENERGY BALANCE IN THE KELP BED COMMUNITY

It is now possible to make some general inferences on energy flow through the kelp bed community as a whole. Despite the assumptions required to derive figures for the major trophic categories in Table 2, it seems unlikely that further refinement will substantially alter the following main conclusions:

(1) The overall primary production by kelp, understorey algae and phytoplankton components in a kelp bed community amounts to $62,190 \text{ kJ m}^{-2} \text{ yr}^{-1}$, a value similar to that of $54,037 \text{ kJ m}^{-2} \text{ yr}^{-1}$ produced by phytoplankton alone in a comparable area of deeper water outside the kelp bed. The overall energetic conversion efficiency from incident illumination in both cases is approximately 1.6%.

(2) The consumer community as a whole is dominated by filter feeders, which comprise 72% of the total standing stock and account for 77% of the production (Table 5).

(3) Filter feeders account for 94% of the energy dissipated by the consumers through Respiration (R), compared with less than 4% in each of the other trophic groups (Table 5).

(4) Consumption (C) by the filter feeders amounts to 84% of that of the community as a whole, with only 4–6% in each of the other trophic groups (Table 5).

(5) Filter feeders account for 89% of the faecal production (F) of the community as a whole (Table 5).

It is interesting to compare the estimated total primary production in a kelp bed with the calculated requirements of all primary consumers (detritus and suspension feeders plus grazers). This comparison is presented in Table 6. It is clear that the estimated consumption requirement of primary consumers (mainly filter feeders) is approximately in equilibrium with primary production within the kelp bed; they are estimated to require only 8% more than is produced, while their production efficiency is 10%. Secondary consumers (large and small carnivores) are estimated to require some 16% more than is produced by primary consumers, an imbalance which may be attributed to the errors inherent in laboratory feeding experiments (Shafir and Field, 1980) and to the impossibility of clear trophic demarkation. As might be expected, the carnivores show higher production efficiency of some 24%.

Since the filter-feeding component evidently dominates the fauna, it is of some interest to look at its food supply in more detail. A schematic flow diagram for annual production and consumption in an idealised kelp bed community is shown in Fig. 1. From the total macrophyte production of $38,204 \text{ kJ m}^{-2} \text{ yr}^{-1}$ (Table 1), we estimate that grazers directly crop $4,650 \text{ kJ m}^{-2} \text{ yr}^{-1}$, or 12%. Much of this is 'drift weed' broken free in storms (Greenwood, 1980). Of the remaining $33,554 \text{ kJ m}^{-2} \text{ yr}^{-1}$ some 30% is in the form of dissolved organic matter (DOM) and 70% as particulate matter (POM), (Hatcher et al., 1977; Johnston et al., 1977; Newell et al., 1980) which is released by erosion from the frond tips. Thus filter feeders have available to them phytoplankton and particulate detritus, together comprising some $47,473 \text{ kJ m}^{-2} \text{ yr}^{-1}$

Table 6. Trophic balances and ecological efficiencies in a typical kelp bed community from the west coast of Cape Peninsula. Primary producers include macrophytes and phytoplankton. Primary consumers include suspension and detritus feeders plus grazers; secondary consumers include both large and small carnivores. Compiled from Tables 1 and 2

Component	Consumption ($\text{kJ m}^{-2} \text{ yr}^{-1}$)	Production ($\text{kJ m}^{-2} \text{ yr}^{-1}$)	Net production efficiency (%)
Photosynthetically active radiation	–	3,608,000	–
Primary producers	–	62,190	1.7 %
Primary consumers	67,541	6,137	9.9 %
Secondary consumers	7,291	1,458	23.8 %

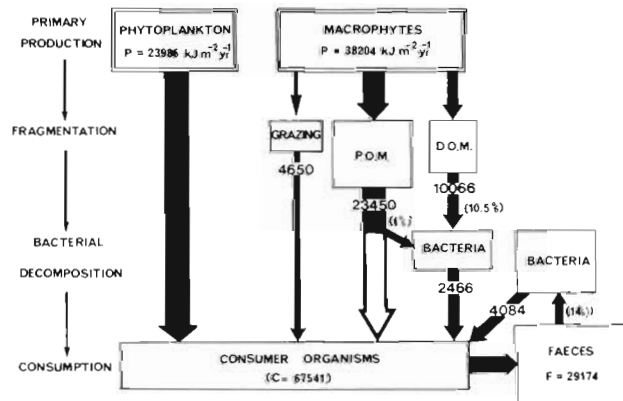


Fig. 1. Simplified energy flow diagram for a kelp bed on the west coast of the Cape Peninsula, South Africa. All values represent flow rates ($\text{kJ m}^{-2} \text{ yr}^{-1}$). Percentages: proportion of energy passed to various categories; these are based on the conversion efficiencies of bacteria on different substrates. Open arrow: inferred flow from particulate organic matter direct to consumer organisms. See text for details

or 75% of their energy requirements. However, while we have some information about the rate and efficiency of conversion of POM and DOM to bacterial biomass in relatively simple experiments using kelp debris incubated in local seawater, we do not know the

Table 5. Percentage composition of the fauna of a typical kelp bed community from the west coast of Cape Peninsula, South Africa, with relative significance (%) of production (P), respiration (R), consumption (C) and faecal production (F) in each trophic category. Compiled from Table 2

Component	Standing stock (B)	Production (P)	Respiration (R)	Consumption (C)	Faeces (F)
Grazers	4.2	4.1	3.3	6.2	5.4
Filter feeders	71.8	76.7	93.5	84.0	89.3
Large carnivores	22.0	8.3	1.2	4.2	4.3
Small carnivores	2.1	10.9	2.0	5.5	1.0

proportion of POM that is converted to bacterial biomass before ingestion. Thus, if all the POM were utilised by bacteria with a carbon:carbon conversion efficiency of 6% (Stuart et al., 1981) and all the DOM were converted at a mean annual efficiency of 10.5% (Lucas et al., 1981) a total energy equivalent of $2,466 \text{ kJ m}^{-2} \text{ yr}^{-1}$ of bacteria would be produced (Fig. 1). The faeces produced by consumers amount to $29,174 \text{ kJ m}^{-2} \text{ yr}^{-1}$ (Table 2) and since this material is converted to bacteria with a mean carbon:carbon efficiency of 14% (Stuart et al., 1982) complete decomposition of faecal matter might yield a further $4,084 \text{ kJ m}^{-2} \text{ yr}^{-1}$ of bacteria. The total energy yield from bacterial degradation of dissolved and particulate components of kelp, and from the decomposition of faeces could thus amount to $6,550 \text{ kJ m}^{-2} \text{ yr}^{-1}$, a value which represents only 9.7% of the energetic requirements of the primary consumers (Table 6).

In reality, a major proportion of the particulate matter must enter the filter feeders directly, with undigested material entering the 'faecal loop' shown in Fig. 1. Refractory material may then be defaecated, resuspended by wave action and re-filtered, and may do this several times before being completely utilised thus accounting for the difference between the consumption requirements of the filter feeders and that actually available from absorption of the phytoplankton plus particulate debris in the water column. The rate at which faeces are colonised and converted into suitable food for filter feeders by bacteria is therefore likely to be a key process in the dynamics of the kelp bed community. In this regard, it is interesting to note that annual production of particulate matter is comprised in almost equal proportions of phytoplankton, macrophyte fragments and faecal matter (Fig. 1).

The processes of production and consumption within the kelp bed community should also be viewed in relation to the kelp bed and neighbouring ecosystems, as has been illustrated in Fig. 2. Jarman and Carter (1982) estimate that 12% of kelp biomass or 6% of kelp production is broken free in storms and it is reasonable to apply this figure to all macrophytes, 2.5% being stranded annually (Koop et al., 1982) while 3.5% is 'drift weed' which is consumed or degraded in shallow water. The upper part of the flow diagram in Fig. 2 is based on Koop et al. (1982) and Griffiths and Stenton-Dozey (1981); it shows energy flow through a beach whose main energy input is stranded kelp. Probably, nutrient regeneration from the kelp on the strandline is fast, but bacteria themselves seem of little energetic significance as food for the subtidal kelp bed community.

This highlights the twin roles of bacteria in the system. In degrading detritus the bacteria themselves become available as food to consumers, but because of

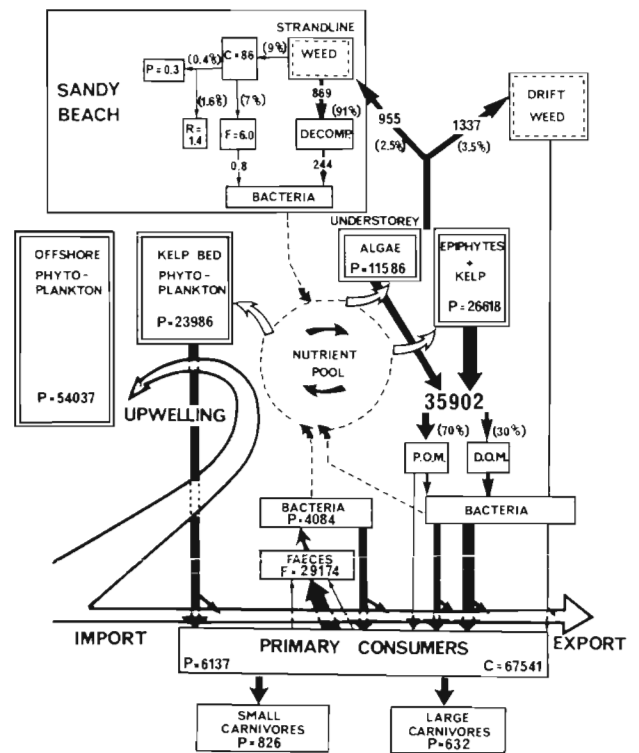


Fig. 2. Energy flow and nutrient cycling in a kelp bed and adjacent ecosystems on the west coast of the Cape Peninsula, South Africa. Primary producers inside the kelp bed are kelps and their epiphytes, phytoplankton and understorey macrophytes, with greater primary production by phytoplankton in deeper water beyond the kelp beds. Energy flow is indicated by solid arrows, nutrients by broken arrows and upwelling currents by shaded arrows. All values are energy flow rates ($\text{kJ m}^{-2} \text{ yr}^{-1}$), with some values of production (P), consumption (C), respiration (R), and faeces (F). Percentages: proportion of energy passed from one compartment to another. The nutrient pool is replenished by bacterial activity and by upwelling. See text for details.

the losses incurred at 6 to 14% efficiencies, their energetic value is small even though their protein, and consequently their nutritional value, may be high compared with that of seaweeds (Mann, 1972). Concurrently with degradation of detritus, nutrients are released by the activity of bacteria (indicated by broken lines in Fig. 2). The energetics of the kelp bed thus appear to be dependent primarily on rapid mineralisation of the fragmentation products of seaweed and of faeces by bacteria which are responsible for recycling nutrients necessary to sustain primary production. The nutrient pool is also supplemented by upwelling.

The movement of water during upwelling will also result in export of suspended and dissolved material from the kelp bed to areas offshore. This is likely to be most marked during heavy wave action when detritus is resuspended and most fragmentation occurs (Field et al., 1980a). Relaxation of upwelling, or downwelling

with onshore winds, however, results in transport of offshore plankton blooms into the kelp bed and since offshore primary production is of the same order as occurs in kelp beds (Fig. 2), it is likely that imports and exports are balanced.

Acknowledgements. We thank our colleagues at the University of Cape Town and the Sea Fisheries Institute, upon whose research (cited herein) this synthesis is based. We are grateful to K. Koop for commenting on the manuscript and to S. Tolosana for help in preparing it. Our thanks are also due to K. H. Mann who helped initiate the research programme and criticised the manuscript. The work was supported by the South African National Committee for Oceanographic Research.

LITERATURE CITED

- Alexander, S. K. (1976). Relationship of macrophyte detritus to the salt marsh periwinkle, *Littorina irrorata* Say. Ph. D. thesis, Louisiana State University, Baton Rouge
- Allen, J. C., Griffiths, C. L. (1981). The fauna and flora of a kelp bed canopy. S. Afr. J. Zool. 16: 80–84
- Baker, J. H., Bradnam, L. A. (1976). The role of bacteria in the nutrition of aquatic detritivores. Oecologia (Berl.) 24: 95–104
- Berrie, A. D. (1976). Detritus, micro-organisms and animals in fresh water. In: Anderson, J. M., Macfadyen, A. (eds.) The role of terrestrial and aquatic organisms in decomposition processes. Blackwell Scientific Publications, Oxford, pp. 323–338
- Borchers, P., Field, J. G. (1981). The effect of kelp shading on phytoplankton production. Botanica Marina 24: 89–91
- Brown, P. C. (1980). Phytoplankton production studies in the coastal waters off the Cape Peninsula, South Africa. M. Sc. thesis, University Cape Town (1981)
- Brown, P. C. (1981). Pelagic phytoplankton, primary production and nutrient supply in the southern Benguela region. OTrans. R. Soc. S. Afr., in press
- Calow, P. (1975). The feeding strategies of two freshwater gastropods, *Ancylus fluviatilis* Mull and *Planorbis contortus* Linn. (Pulmonata) in terms of ingestion rates and absorption efficiencies. Oecologia (Berl.) 20: 33–49
- Calow, P., Fletcher, C. R. (1972). A new radiotracer technique involving ^{14}C and ^{51}Cr , for estimating the assimilation efficiencies of aquatic, primary consumers. Oecologia (Berl.) 9: 155–170
- Cammen, L. M. (1980a). Ingestion rate: an empirical model for aquatic deposit feeders and detritivores. Oecologia (Berl.) 44: 303–310
- Cammen, L. M. (1980b). The significance of microbial carbon in the nutrition of the deposit feeding polychaete *Nereis succinea*. Mar. Biol. 61: 9–20
- Cammen, L. M., Rublee, P., Hobbie, J. E. (1978). The significance of microbial carbon in the nutrition of the polychaete *Nereis succinea* and other aquatic deposit feeders. Sea Grant Pub. UNC-SG-78-12, North Carolina State University, Raleigh
- Carter, R. (1982). Phytoplankton biomass and production in a southern Benguela kelp bed system. Mar. Ecol. Prog. Ser. 8: 9–14
- Chua, K. E., Brinkhurst, R. O. (1973). Bacteria as potential nutritional resources for three sympatric species of tubificid oligochaetes. In: Stevenson, L. H., Colwell, R. R. (eds.) Estuarine microbial ecology. University South Carolina Press, pp. 513–517
- Dale, N. G. (1972). Bacteria in intertidal sediments: factors related to their distribution. Limnol. Oceanogr. 19: 509–518
- Darnell, R. M. (1967). Organic detritus in relation to the estuarine ecosystem. In: Lauff, G. H. (ed.) Estuaries. Publ. Am. Ass. Advant Sci, pp. 374–375
- Dieckmann, G. S. (1978). Aspects of growth and production of *Laminaria pallida* (Grev.) J. Ag. off the Cape Peninsula. M. Sc. thesis, University Cape Town
- Dieckmann, G. S. (1980). Aspects of the ecology of *Laminaria pallida* (Grev.) J. Ag. off the Cape Peninsula (South Africa). I. Seasonal growth. Botanica Mar. 23: 579–585
- Elakova, L. A. (1972). Distribution of cellulases and chitinases in marine invertebrates. Comp. Biochem. Physiol. 43: 67–70
- Fenchel, T. (1970). Studies on the decomposition of organic detritus derived from the turtle grass *Thalassia testudinum*. Limnol. Oceanogr. 15: 14–20
- Fenchel, T. (1972). Aspects of decomposer food chains in marine benthos. Verh. dt. zool. Ges. 65: 14–22
- Field, J. G., Jarman, N. G., Dieckmann, G. S., Griffiths, C. L., Velimirov, B., Zoutendyk, P. (1977). Sun, waves, seaweed and lobsters: the dynamics of a west coast kelp bed. S. Afr. J. Sci. 73: 7–10
- Field, J. G., Griffiths, C. L., Linley, E. A., Carter, R. A., Zoutendyk, P. (1980a). Upwelling in a nearshore marine ecosystem and its biological implications. Estuar. coast. mar. Sci. 11: 133–150
- Field, J. G., Griffiths, C. L., Griffiths, R. J., Jarman, N., Zoutendyk, P., Velimirov, B., Bowes, A. (1980b). Variation in structure and biomass of kelp communities along the south west Cape coast. Trans. R. Soc. S. Afr. 44: 145–203
- Fitzgerald, B. (1979). A preliminary investigation of the filtration rates of *Pyura stolonifera* (Heller) under laboratory conditions. Unpubl. B. Sc. (Hons) project, Zoology Dept., University Cape Town
- Foster, J. R. M., Gabbott, P. A. (1971). The assimilation of nutrient from compound diets by the prawns *Palaemon serratus* and *Pandalus platyceros*. J. mar. biol. Ass. U.K. 51: 943–961
- Greenwood, P. J. (1980). Growth, respiration and tentative energy budgets for two populations of the sea urchin *Parechinus angulosus* (Leske). Estuar. coast. mar. Sci. 10: 347–367
- Griffiths, C. L., King, J. A. (1979a). Some relationships between size, food availability and energy balance in the ribbed mussel *Aulacomya ater*. Mar. Biol. 51: 141–149
- Griffiths, C. L., King, J. A. (1979b). Energy expended on growth and gonad output in the ribbed mussel *Aulacomya ater*. Mar. Biol. 53: 217–222
- Griffiths, C. L., Stenton-Dozey, J. (1981). The fauna and rate of degradation of stranded kelp. Estuar. Coast. Shelf Sci. 12: 645–655
- Hargrave, B. T. (1970). The utilisation of benthic microflora by *Hyalella azteca* (Amphipoda). J. Anim. Ecol. 39: 427–437
- Hargrave, B. T. (1976). The central role of invertebrate faeces in sediment decomposition. In: Anderson, J. M., Macfadyen, A. (ed.) The role of terrestrial and aquatic organisms in decomposition processes. Blackwell, Oxford, pp. 301–321
- Hatcher, B. G., Chapman, A. R. O., Mann, K. H. (1977). An annual carbon budget for the kelp *Laminaria longicruris*. Mar. Biol. 44: 85–96
- Humphreys, W. F. (1979). Production and respiration in animal populations. J. Anim. Ecol. 48: 427–454

- Jarman, N. G., Carter, R. A. (1982). The primary producers of the inshore regions of the Benguela. *Trans. R. Soc. S. Afr.*, in press
- Jensen, K. T., Siegismund, M. R. (1980). The importance of diatoms and bacteria in the diet of *Hydrobia* species. *Ophelia* 19 (Suppl.): 193–199
- Johnson, C. S., Jones, R. G., Hunt, R. D. (1977). A seasonal carbon budget for a laminarian population in a Scottish sea loch. *Helgoländer wiss. Meeresunters.* 30: 527–545
- Kepkay, P. E., Novitsky, J. A. (1980). Microbial control of organic carbon in marine sediments: coupled chemoautotrophy and heterotrophy. *Mar. Biol.* 55: 261–286
- Kjørboe, T., Møhlenberg, F., Nøhr, O. (1980). Feeding, particle selection and carbon absorption in *Mytilus edulis* in different mixtures of algae and resuspended bottom material. *Ophelia* 19: 193–205
- Kjørboe, T., Møhlenberg, F., Nøhr, O. (1981). Effect of suspended bottom material on growth and energetics in *Mytilus edulis*. *Mar. Biol.* 61: 283–288
- Kofoed, L. H. (1975a). The feeding biology of *Hydrobia ventrosa* (Montagu) 1. The assimilation of different components of the food. *J. exp. mar. Biol. Ecol.* 19: 233–241
- Koop, K., Newell, R. C., Lucas, M. I. (1982). Biodegradation and carbon flow based on kelp (*Ecklonia maxima*) debris in a sandy beach microcosm. *Mar. Ecol. Prog. Ser.* 7: 315–326
- Kostallos, M. S. (1971). A study of the detritus pathway: the role of detritus and the associated microbiota in the nutrition of *Gammarus minus* Say (Amphipoda Gammaridae). Ph. D. thesis, University of Pittsburgh
- Kristensen, J. H. (1972). Carbohydrases of some marine invertebrates with notes on their food and on the natural occurrence of the carbohydrates studied. *Mar. Biol.* 14: 130–142
- Lewis, D. B., Whitney, P. J. (1968). Cellulase in *Nereis virens*. *Nature, Lond.* 220: 603–604
- Linley, E. A. S., Newell, R. C. (1981). Microheterotrophic communities associated with the degradation of kelp debris. *Proc. 15th Europ. Mar. Biol. Symp. Kieler Meeresforsch.* 5: 345–355
- Linley, E. A. S., Newell, R. C., Bosma, S. A. (1981). Heterotrophic utilisation of mucilage released during fragmentation of kelp (*Ecklonia maxima* and *Laminaria pallida*). I. Development of microbial communities associated with the degradation of kelp mucilage. *Mar. Ecol. Prog. Ser.* 4: 31–41
- Lopez, G. R., Levinton, J. S., Slobodkin, L. B. (1977). The effect of grazing by the detritivore *Orchestia grillus* on *Spartina* litter and its associated microbial community. *Oecologia (Berl.)* 30: 111–127
- Lucas, M. I., Newell, R. C., Velimirov, B. (1981). Heterotrophic utilisation of mucilage released during fragmentation of kelp (*Ecklonia maxima* and *Laminaria pallida*). II. Differential utilisation of dissolved organic components from kelp mucilage. *Mar. Ecol. Prog. Ser.* 4: 43–55
- Mann, K. H. (1972). Macrophyte production and detritus food chains in coastal waters. *Mem. 1st. Ital. Idrobiol.* 29 (Suppl.): 353–383
- Mann, K. H. (1973). Seaweeds: their productivity and strategy for growth. *Science, N.Y.* 182: 975–981
- Mann, K. H., Jarman, N. G., Dieckmann, G. S. (1979). Development of a method for measuring the productivity of *Ecklonia maxima* (Osbeck) Papenf. *Trans. R. Soc. S. Afr.* 44: 27–42
- McNeill, S., Lawton, J. M. (1970). Annual production and respiration in animal populations. *Nature, Lond.* 225: 472–474
- Mills, E. L. (1975). Benthic organisms and the structure of marine ecosystems. *J. Fish. Res. Bd Can.* 32: 1657–1663
- Mills, E. L., Fournier, R. O. (1979). Fish production and the marine ecosystems of the Scotian Shelf, Eastern Canada. *Mar. Biol.* 54: 101–108
- Moriarty, D. J. W. (1976). Quantitative studies on bacteria and algae in the food of the mullet *Mugil cephalus* L. and the prawn *Metapenaeus bennettiae* (Racek and Dall). *J. exp. mar. Biol. Ecol.* 22: 131–143
- Newell, R. C. (1965). The role of detritus in the nutrition of two marine deposit feeders, the prosobranch *Hydrobia ulvae* and the bivalve *Macoma balthica*. *Proc. zool. Soc. Lond.* 144: 25–45
- Newell, R. C. (1982). The role of decomposers in the near-shore region of the west coast. *Trans. R. Soc. S. Afr.* (in press)
- Newell, R. C., Lucas, M. I. (1981). The quantitative significance of dissolved and particulate organic matter released during fragmentation of kelp in coastal waters. *Proc. 15th Europ. Mar. Biol. Symp. Kieler Meeresforsch.* 5: 356–369
- Newell, R. C., Lucas, M. I., Velimirov, B., Seiderer, L. J. (1980). Quantitative significance of dissolved organic losses following fragmentation of kelp (*Ecklonia maxima* and *Laminaria pallida*). *Mar. Ecol. Prog. Ser.* 2: 45–59
- Odum, W. E., Heald, E. J. (1973). The detritus-based food web on an estuarine mangrove community. In: Cronin, L. E. (ed.) *Estuarine research*, Vol. 1. Academic Press, New York, pp. 265–286
- Odum, W. E., Zieman, J. C., Heald, E. J. (1973). The importance of vascular plant detritus to estuaries. In: Chabreck, R. H. (ed.) *Proceedings of the coastal marsh and estuary symposium*. Louisiana State University, Div. of Continuing Education
- Platt, T., Irwin, B. (1973). Caloric content of phytoplankton. *Limnol. Oceanogr.* 18: 306–309
- Ryther, J. H. (1969). Photosynthesis and fish production in the sea. *Science, N.Y.* 166: 72–76
- Shafir, A., Field, J. G. (1980). Importance of a small carnivorous isopod in energy transfer. *Mar. Ecol. Prog. Ser.* 3: 203–215
- Sorokin, Y. I. (1978). Microbial production in the coral-reef community. *Arch. Hydrobiol.* 83: 281–323
- Steele, J. H. (1974). The structure of marine ecosystems, Harvard University Press, Cambridge, Mass.
- Stuart, V., Lucas, M. I., Newell, R. C. (1981). Heterotrophic utilisation of particulate matter from the kelp *Laminaria pallida*. *Mar. Ecol. Prog. Ser.* 4: 337–348
- Stuart, V., Newell, R. C., Lucas, M. I. (1982). Conversion of kelp debris and faecal material from the mussel *Aulacomya ater* by marine micro-organisms. *Mar. Ecol. Prog. Ser.* 7: 47–57
- Taghon, C. L., Self, R. F. L., Jumars, P. A. (1978). Predicting particle selection by deposit feeders: a model and its implications. *Limnol. Oceanogr.* 23: 752–759
- Teal, J. M. (1962). Energy flow in the salt marsh ecosystem of Georgia. *Ecology* 43: 614–624
- Velimirov, B., Field, J., Griffiths, C. L., Zoutendyk, P. (1977). The ecology of kelp bed communities in the Benguela upwelling system. Analysis of biomass and spatial distribution. *Helgoländer wiss. Meeresunters.* 30: 495–518
- Wetzel, R. L. (1975). An experimental-radiotracer study of detrital carbon utilisation in a Georgia salt marsh. Ph. D. thesis, University of Georgia
- Wetzel, R. L. (1977). Carbon resources of a benthic salt marsh invertebrate *Nassarius obsoletus* Say (Mollusca: Nassariidae). In: Wiley, M. (ed.) *Estuarine processes*, Vol. 2. Academic Press, New York, pp. 293–308

Yingst, J. Y. (1976). The utilisation of organic matter in shallow marine sediments by an epibenthic deposit-feeding holothurian. *J. exp. mar. Biol. Ecol.* 23: 55-69

Yokoe, Y., Yasamasu, I. (1964). The distribution of cellulase in invertebrates. *Comp. Biochem. Physiol.* 13: 323-338

Zhukhova, A. I. (1963). On the quantitative significance of micro-organisms in the nutrition of aquatic invertebrates. In: Oppenheimer, C. H. (ed.) *Marine microbiology*. Thomas, Springfield, Ill., pp. 699-710

This review was submitted to the editor; it was accepted for printing on December 12, 1981

