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NET PRIMARY PRODUCTIVITY OF INTERTIDAL SYSTEMS: THE DUBLIN BAY EXAMPLE

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ABSTRACT

Reasons for the determining of intertidal primary production are explained, and methods for so doing described. Data are presented for a *Salicornia* bed, a *Zostera* bed, a salt marsh, macroalgae and microphytobenthos from Dublin Bay. *Spartina* production is reviewed. It is concluded that organic production in the intertidal zone is effectively removed, and no sequestration of carbon occurs. However the resources for secondary production may now be readily quantified, and changes in primary production from season to season used in quality monitoring.

INTRODUCTION

Many studies of intertidal primary production in Dublin Bay have been carried out over the last 30 years. These have included substantial investigations of macroalgae regarded as a nuisance, for example Jeffrey *et al.* (1992), curiosity-driven studies of mudflat angiosperms (Madden 1984, Jennings 1991), and ecosystem studies of salt marsh (McNamee 1976). This experience has led us to develop and employ simple methods. We also have a data bank of interest, which is sufficiently robust to be applied to other similar sites in north-western Europe.

Why should efforts be made to determine the primary productivity of intertidal systems? There are five principal reasons:

1. As a fundamental component of the carbon cycle, enabling the estimation of the comparative contribution of species and communities to production (Biomass × 0.45 = C). In the context of global change, C sequestration is an issue and enhanced carbon dioxide concentrations may drive increased primary production.
2. To allow the quantification of all materials cycles, especially major nutrients and pollutants (g biomass m^{-2} × mg g^{-1} of element or substance).

Nitrogen, phosphorus, sulphur, metals, pesticides are all substances of interest both fundamentally and for the biomonitoring of pollutants. Studies of eutrophication are especially important.

3. To determine potential resource levels for secondary production. During the period of growth grazing certainly occurs; and it is also assumed that exudates from living plants enter the environment. After natural senescence of whole annual plants or portions of root and shoot in perennials, dissolved organic matter (DOM) and particulate organic matter (POM) are released. Accumulated biomass disappears rapidly after the summer growing season, and it is assumed that this material subsidises the offshore marine ecosystems.
4. To compare with input of detrital organic matter, and thus determine whether the system is autotrophic or heterotrophic. All estuaries and most other coastal sites receive inputs of organic matter from elsewhere. In urbanised situations sewage is a major contributor to organic loading. It is of interest whether studying the change from autotrophic to heterotrophic state can be an approach to management.
5. To assist management of intertidal environmental quality generally. It has been established that an index based on the ratio of intertidal area occupied by stable communities, opportunist communities, and abiotic areas may be used as a quality indicator (Wilson & Jeffrey 1994)

DEFINITIONS

Concept of net primary production

Net primary production is biomass produced in a season of growth, not correcting for respiratory losses but adding calculated herbivore consumption and other losses from senescence and transfers to non-living litter.

The usual formula for net primary production, as applied to a grassland (Milner & Hughes 1968) is:

$$P_n = \Delta B_{T2-T1} + G + L$$

Where: P_n is net primary production, ΔB_{T2-T1} is change in dry biomass from time 1 to time 2, G is biomass grazed and L is lost biomass.

This means that the *modus operandi* is to determine dry biomass at intervals during the growing season, and to estimate grazing and other losses for similar time periods. This concept is certainly applicable to saltmarsh (Dalby 1987), and has been readily applied to dune systems (Fay & Jeffrey 1995). Whilst measuring biomass is straightforward, the difficult technical problem is estimating grazing and miscellaneous losses. Expression of productivity on a strictly annual basis is often an aspiration, as sample collection is often not possible for a 12 month period. One expedient is to determine biomass at maximal and minimal values.

Organic matter and fixed carbon

The key characteristic of intertidal areas is that, unlike terrestrial grasslands, they are tidally swept. Thus debris, detrital material and planktonic organisms are passively swept in and out of the system. Flux of carbon-containing material, decomposition of organic matter and incorporation of material into sediment are all more difficult to determine.

Intertidal

The definition of 'intertidal' used in this paper is the amplitude of highest astronomical tides. This may be found by inspection from the Admiralty Tidal Chart entry for a given port. In Dublin Bay, this is from +4.5m O.D. to +0.4m O.D. The upper boundary includes the slightly saline fore dunes at the front of dune systems, the whole of the rocky shore algal sequence, excluding the spray zone with its lichens, and the upper salt marsh to its abrupt transition to a non-halophytic community.

The lower edge is less ecologically critical, with no abrupt community boundaries between the lowest intertidal and truly benthic communities.

METHODS: COMPARISONS AND SCALING ISSUES

Simple, robust, methods must be used for biomass determination in the intertidal zone. They are derived from terrestrial methods and should ultimately yield data expressed as dry weight yields per metre square per annum ($m^{-2}.y^{-1}$). The intertidal environment is very variable and a range of yield classes will inevitably be encountered. It is necessary to be aware of this and to design a stratified random sampling system, which samples each yield class consistently.

Algal biomass

An individual sample of an *Enteromorpha* mat may be taken using a square quadrat from $0.0625m^2$ to $1m^2$, cutting the mat with a sharp knife and lifting it clear of the substrate. For large quadrats with low cover values, it is worth using a wire rake to gather dispersed filaments. The wet and sediment-contaminated material is weighed in the field using a spring balance. Only a small sub-sample is weighed and transferred to the laboratory. Here it is cleaned, dried and fresh weight:dry weight ratios determined.

Scaling issues arise from the patchiness and pattern of intertidal systems. For example in the 75 ha of the south lagoon of the Bull Island system, the range of biomass presented and the areal extent of each range class are known (Jennings 1996). Another good example is the Narragansett Bay study of Valiela and Teal (1979). Here it is seen that the intensities of production-driven processes in the nitrogen cycle are spatially separated. In order to arrive at a good system analysis, it is vital that a thorough cartographic survey is available. This should have an appropriate level of resolution and accuracy to match that of laboratory-based measurements.

Rooted plants

Examples of intertidal rooted plants include *Salicornia* spp., *Zostera* spp., *Spartina anglica* and saltmarsh vegetation. *Salicornia* and *Zostera* were both sampled using a

10 cm diameter corer. The cores were washed in the lab, and individual components separated where appropriate, e.g. roots, rhizomes, shoots, leaves, flowers, fruits and non-living biomass.

In the case of vegetation samples, aboveground biomass may be harvested and sorted using a quadrat as a guide. Roots can be conveniently sampled with a corer, taking one or more cores per quadrat.

Microphytobenthos

Microalgae, on sediment surfaces, consist mainly of diatoms, with green algae and cyanobacteria also present. Microphytobenthos biomass is estimated using sediment chlorophyll *a* concentrations. Samples are taken using a syringe, modified by cutting off the end of the barrel. It is used as a corer, sampling to a depth greater than 5 mm, in order to protect the top layer of sediment, and returned to the laboratory. The syringe is then cut and the top 5 mm is used for pigment determination. Microphytobenthos can only actively photosynthesise when situated in the photic zone, which is usually less than 2 mm in depth (Paterson *et al.* 1998). Pennate diatoms, the most abundant component of microphytobenthos in intertidal sediment, migrate vertically in and out of the photic zone (Heip *et al.* 1995) linked with both diel and tidal cycles (Underwood and Kromkamp 1999). Although diatoms are present at greater depths they would not be actively photosynthesising and could have been buried for some time. It is for this reason only the top 5 mm is used.

RESULTS

Salicornia dolichostachya (Madden 1984)

The data presented relate to a study, undertaken in 1983, of the 24.1 ha *Salicornia dolichostachya* bed to the north of the Bull Island Causeway. Ten replicate samples were collected regularly from a specific 250m^2 area using a PVC corer approximately 10 cm in diameter, and processed as described above. Sampling commenced in April and ended in November and the results are expressed in Figure 1a, b, and c. The number of seedlings germinated by April is in the order of 4000 to 5000.m^{-2} but by July this has declined to about 3000.m^{-2}. Seedling density at the end of the season is approximately one tenth of the initial density (Figure 1a). The constant disappearance between harvests is not easy to explain, but may be attributed to grazing by fish such as the mullet (*Crenimugil labrosus). Salicornia* biomass attained a maximum value in September of approx 400g DW.m^{-2}. This value halved over the next 30 days, suggesting that a pulse of DOM and POM had been released into the intertidal area. In the context of this lagoon, the magnitude of this release is estimated at 241000 m^2 $\times$ 200g.m^{-2} = 48200 kg dry matter.

In the first part of the growing season, production by *Salicornia* was accompanied by green algal growth, with a peak biomass of approximately 100 g DW by day 160 (8th June). This had declined to negligible values in September.

Salient features of this production system are:

- Decreasing density of this intertidal annual, hypothetically attributable to grazing by fish.

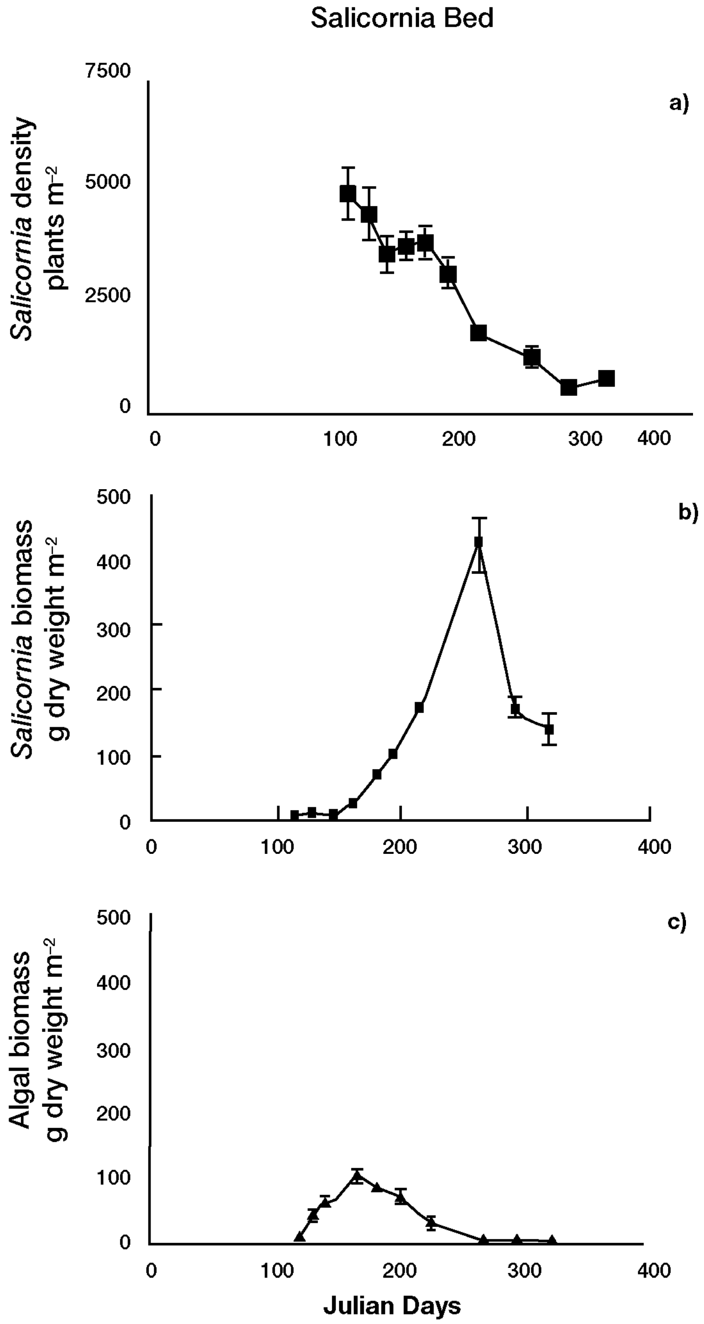

Figure 1. Characteristics (mean, standard deviation) of the North lagoon, Dublin Bay *Salicornia* community: a) *Salicornia dolichostachya* density (number.m^{-2}); b) biomass (gDW.m^{-2}); and c) biomass (gDW.m^{-2}) of *Enteromorpha* spp. in the *Salicornia* bed.

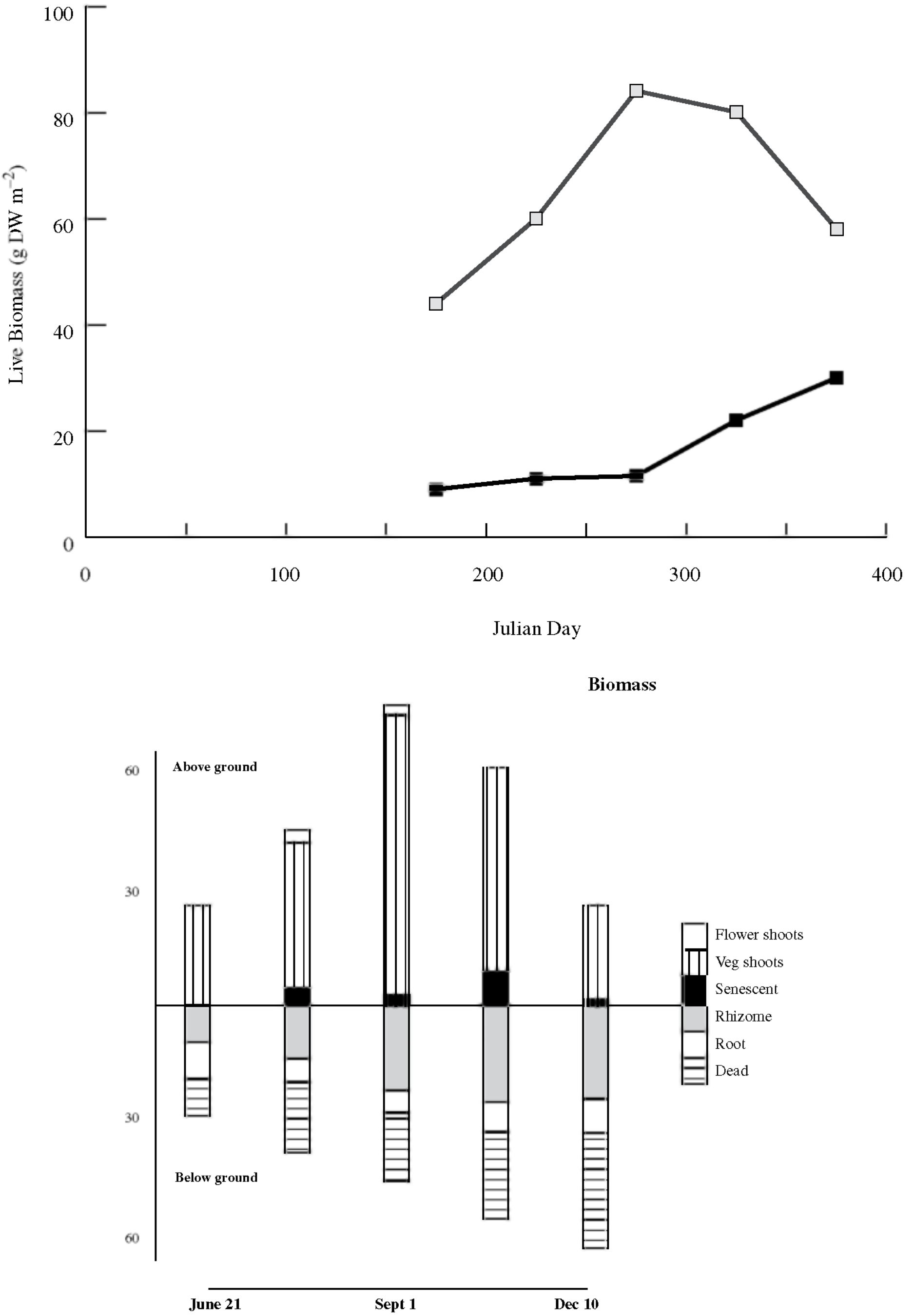

Figure 2. Seasonal (date and Julian day) biomass (gDW.m^{-2}); in the *Zostera noltii* bed; a) live biomass (*Zostera* solid line, algae dotted line); b) partitioning of total *Zostera* biomass among flowering shoots, vegetative shoots, senesced leaf, rhizome, root and dead below-ground material.

- Dual production by *Salicornia* and algae (note that in early June algal biomass is approximately equal to that of *Salicornia*. By September, *Salicornia* has achieved four times this value).
- Rapid disappearance of biomass in autumn.

Zostera noltii **(Jennings 1991)**

This species was investigated in the period June-December 1991, using the *Zostera* bed north of the Merrion Gates. This bed, one of several in the intertidal of south Dublin Bay, has an area of 1.5 ha. A 50m × 20m plot was used to contain the sample collected. At a resolution of $1m^2$, 52% of the squares contained *Zostera* plants.

Sample collection was designed by randomly selecting 10 vegetated squares, and removing cores as above. Sediment was washed away in the laboratory and the vegetation sorted into six components, namely vegetative shoots; generative shoots, senesced leaves, rhizomes, roots and dead below ground material. Dead root and rhizome were grouped.

Data are presented in Fig 2, where a familiar terrestrial pattern of summer biomass being translocated to below ground in the autumn, may be observed. Rhizome tissue is a key reserve for this apparently long lived perennial. A very small investment is made in flowering tissue, and unlike *Salicornia*, seedlings are not observed.

Grazing by Brent Geese in this locality has been investigated by O'Briain (1989, 1991) and Carton (1993). Carton (1993) used an exclosure to determine grazing by Pale-Bellied Brent Geese *(Branta bernicula hrota)* at this site. Her work showed that biomass close to $100gDW.m^{-2}$ in early October was reduced to about $20gDW.m^{-2}$ in December by goose grazing. Leaves were taken first, followed by rhizomes down to 5 cm.

Saltmarsh (Hayes 1999)

Bull Island saltmarsh was sampled in August 1998 and early January 1999, to determine the biomass at the end and start of the growing season. Five transects were taken along the saltmarsh, two between Bull Bridge and the causeway and three from the causeway to the end of the island. All transects were divided into three zones according to saltmarsh vegetation types, the lower, middle and upper zones defined by McNamee (1976) (see also Jeffrey 1977). A vertical distance of just over 1 metre separated the lowest from the highest zones. At each sampling station three replicate 0.0625 m^2 quadrats were taken of the above ground vegetation and three cores of below ground vegetation were taken per quadrat and processed as described above.

The average above ground biomass of the saltmarsh as a whole in summer was 0.7 $kg.m^{-2}$ while below ground it was 6.1 $kg.m^{-2}$. By January the biomass had fallen by more than half to 0.38 $kg.m^{-2}$ above ground and to 2.91 kg m^{-2} below ground. The fate of the below ground biomass lost from the system is unclear but loss of large amounts of below ground production has been noted elsewhere (Schubauer & Hopkinson 1984). The most probable explanation of winter disappearance in this case is root respiration, combined with decomposition. The total net productivity of Bull Island saltmarsh was 3.5 $kg.m^{-2}.y^{-1}$ of which the below ground portions contributed 3.2 $kg.m^{-2}.y^{-1}$. This high proportion of underground production is within the range of below ground productivity estimates for saltmarsh species (0.3–7.6 kg.m^{-2}.y^{-1}) compiled by Good *et al.* (1982).

Macroalgae (Jeffrey *et. al.*, 1992)

An extensive survey of intertidal macroalgal biomass in Dublin Bay was undertaken in 1989 and 1990. Eleven sampling stations were investigated to represent the main sub-environments in Dublin Bay. *Enteromorpha* spp. were found to be the most dominant group of green algae. Green algae were more extensive in North Dublin Bay with over 95% of the intertidal green algae occurring in these more sedimentary areas. Details are given in Jeffrey *et al.* (1992). The value quoted in Table 1 represents the total mean algal biomass in late June 1989 for the South Lagoon, over an area of 46.4 ha of cover, out of a total of 75ha (61.8% cover).

In Dublin Bay, green algal cover was closely related to sediment containing particulate organic matter, and mineralising nitrogen, expressed as an ammonium flux (Jeffrey *et.al.* 1995).

Coverage of brown fucoid algae was very heterogenous at most stations and biomass was higher in South Dublin Bay. Fucoid distribution was more localised than green algae but had a higher standing biomass. Yearly intertidal macroalgal dry weight biomass for the Bay as a whole was 185000 kg, with green algae contributing 69000 kg and fucoid algae 116000 kg. Green algal production ranged from 0.06–0.4 kg.m^{-2}.y^{-1}, and fucoid algae from 0.2–0.3 kg.m^{-2}.y^{-1}.

In Nauset Marsh, New England, maximum annual macroalgal biomass occurs in summer with *Fucus* producing 0.4 kg.m^{-2}.y^{-1} and *Ascophyllum* producing 1.2 kg.m^{-2}.y^{-1}

Table 1. Comparison of green algal biomass data. A: Estimates of mean maximum biomass (g DW. m^{-2}); B: Biomass (g DW. m^{-2}) calculated for larger system

A	**Site Location**	**Mean Max. Biomass (g DW. m^{-2})**	**Author**
	North Bull Lagoon	404	Walsh (1988)
	Lynher Estuary	196	Joint (1978)
	Two Indian Estuaries	540	Pandey & Masao (1986)
B	**Site Location**	**Mean Overall Biomass (g DW. m^{-2})**	**Author**
	North Bull Island	147	Walsh (1988)
	North Bull Island	84.5	Jeffrey *et al.* (1992)
	Langstone Harbour	39	Lowthion *et al.* (1983)
	Eden Estuary	34	Owens & Stewart (1983)

(Roman, *et al.* 1990). In the west coast estuaries of North America estimates of macroalgal productivity range from 0.2–1.3 kg.m^{-2}.y^{-1} (Emmett *et al.* 2000).

Microphytobenthos (Hayes, unpublished)

The microphytobenthos inhabit the intertidal and subtidal sediments of estuarine and shallow coastal systems and are a primary source of fixed carbon in estuarine food webs and of special importance in unvegetated areas. Microphytobenthos biomass was sampled every two weeks between April 2000 and September 2001 at two intertidal sites, the mudflat in the South Bull Island Lagoon on the Northside of the Bay and a sandflat at Blackrock strand on the southside. Productivity was higher at Bull Island than Blackrock, as expected, as this site is not as exposed. Production was calculated as 0.03–0.1 kg.m^{-2}.y^{-1} at Bull Island and 0.02–0.04 kg.m^{-2}.y^{-1} at Blackrock (Hayes, unpublished), using the model of Colijn and de Jonge (1984). These values are within the range of productivity estimates reported for estuarine flats but most other sites have higher production, (MacIntyre *et al.* 1996; Underwood and Kromkamp 1999; Emmett *et al.* 2000).

Spartina

The most important difference between North American and European saltmarshes is the dominance in the lower marsh zone of *Spartina alterniflora* along with other *Spartina* species such as *Spartina patens* in North America. *Spartina* is well known for its ability to filter out waterborne particles, so in Europe was used in extensive planting programmes for land reclamation (Hemminga *et al.*, 1998). Many European saltmarshes contain *Spartina anglica* and it has been identified in most saltmarsh sites in Ireland (Curtis and Sheehy-Skeffington 1998). To the best of our knowledge, no production estimates have been undertaken in Ireland.

The Flax Pond ecosystem study, an extensive project undertaken in the US in the late 1970s, showed production of *Spartina* was 1.1 kg.m^{-2}.y^{-1} including roots and shoots (Woodwell *et al.* 1979). In a 1979 review of *Spartina,* estimates of net annual primary production for *S. alterniflora* were shown to range from 0.2–6.0 kg.m^{-2}.y^{-1} (Long and Woolhouse 1979). Since then, the most productive *Spartina* marsh recorded was in Georgia, US with *S. alterniflora* producing 7.6 kg.m^{-2}.y^{-1} and *S. cynosuroides* 7.7 kg.m^{-2}.y^{-1} and below ground biomass contributing 68% and 60% respectively (Schubauer and Hopkinson 1984). More recent studies in Brazil, (da Cunha Lana *et al.* 1991) and The Netherlands (Hemminga *et al.* 1996) gave productivity values of 1.6 kg.m^{-2}.y^{-1} and 1.7 kg.m^{-2}.y^{-1}, respectively.

Fate of fixed carbon

- Senescence

The natural death of plant tissue is readily observable in intertidal angiosperms. In the annual *Salicornia* the plant population senesces simultaneously, loses biomass, but continues standing. The seeds remain embedded in the standing lignified tissue. The fate of the green tissue may be autolysis and presumably microbial consumption.

- Grazing

Grazing (*Zostera; Enteromorpha*) by birds has already been referred to, but the taking of nutrient rich *Salicornia* seed by Teal, Mallard and Pintail is also well known (Ferns 1992). There are no quantitative studies to indicate carbon balance or protein nitrogen contribution to diet for this specialised form of grazing. The postulated grazing of *Salicornia* seedlings by mullet is another topic worth study.

- Decomposition

We assume that microbial decomposition is a continuous process that rapidly reduces biomass of non-living plant tissue. It would be worth making estimates of microbial biomass to judge the season of most activity, which we assume is early autumn, following plant senescence. Partial decomposition is probably a prerequisite to removal by the tide.

- Tidal dispersal

In the Flax Pond study, tidal dispersal was seen to be a major fate for biomass. (Woodwell *et al.* 1979). The marsh complex makes a significant particulate carbon contribution to near-shore coastal ecosystems. We assume that this is a generally applicable observation.

- Sequestration

There is no evidence of long term carbon sequestration by burial of estuarine primary production.

COMPARISONS AND CONCLUSIONS

The estimates for intertidal net primary production, expressed in summary in Table 2, bear comparison with the well-known table for the world (Lieth 1975). The range for saltmarsh is as high as that cited for many terrestrial communities, including cultivated land. Algal production is at most a tenth of the saltmarsh value.

The intertidal system serves as an energy source for inshore and offshore secondary production. Virtually all production is consumed and standing crop of perennial angiosperm communities is close to constant. In the whole intertidal area,

Table 2. Synopsis of intertidal primary production for communities in Dublin Bay. Values are expressed in kg dry weight.m^{-2}.y^{-1}

Compartment	**Production kg DW m^{-2} y^{-1}**
Mudflat Fucoid algae	0.2–0.3
Green Algae	0.07–0.4
Microphytobenthos	0.03–0.1
Salicornia	0.5
Spartina[1]	1.0
Zostera	0.1
Saltmarsh	3.0–4.0

[1] Extrapolated value

dynamic changes in the area a community occupies are well known. These changes may be systematic and seral, as in the formation of salt marsh, and must entail sediment accumulation. Alternatively, explosive invasion by *Spartina* spp., especially *S. anglica*, has transformed some intertidal areas in production terms. In the case of saltmarsh development the escalation of production is from the 0.5 kg.m^{-2}.y^{-1} of the *Salicornia* bed to the 3.0–4.0 kg.m^{-2}.y^{-1} of the Saltmarsh (Table 2). In the case of *Spartina*, the change is a gain in the order of 0.5 kg.m^{-2}.y^{-1} in production, with a consequent increase in sediment accumulation. Vegetation changes of this kind are readily determined by aerial survey and may be translated into system production values. This kind of management tool will be useful in managing all anticipated scenarios of intertidal change.

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