PRODUCTION BIOLOGY OF AN ESTUARINE POPULATION OF THE GREEN ALGAE, ULVA SPP. IN COOS BAY, OREGON

by

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A DISSERTATION

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The annual cycle of _Ulva_ spp. growth was studied at two intertidal levels in the Coos Bay Estuary, Oregon in 1983 and 1984. The mid intertidal site was an area of rock outcrop and the low intertidal site a bed of _Zostera marina_. _Ulva_ is present at the mid intertidal site throughout the year, but the _Ulva_ population in the low intertidal does not develop until calmer conditions prevail in the estuary, usually in May. Net primary production was estimated by combining measurements of standing stock and growth rates obtained from individually marked plants grown in the field. Growth was relatively constant throughout the growing season which was March to August in the mid intertidal, and May to August in the low intertidal, but growth declined at both levels in September. The amount of biomass transferred to estuarine waters was greatest in July and August. Annual net production was estimated as 798g dry wt m^{-2} in 1983 and 1560g dry wt m^{-2} in 1984; of this 72 - 73% was produced in these two months. The low intertidal site produced the

most *Ulva*; during 1983, 79% of the production was at this level, and in 1984 76% was found here.

Once fixed the carbon is transferred through the estuarine system in a number of ways. The most rapid transfer occurs as the release of dissolved organic carbon during photosynthesis. Carbon 14 tracer techniques were used to estimate that 7.8% of the fixed carbon is lost as dissolved organic carbon during photosynthesis. The majority of the *Ulva* was transferred through the estuarine system as drift material. It was estimated that 70% of net production becomes drift algae. Algae are lost as drift material at a relatively constant rate throughout the growing season. The transfer of carbon by the production and release of gametes or zoospores occurs throughout the year and accounts for 12% of the carbon fixed by the algae. The principal invertebrate grazers of *Ulva* are amphipods and snails; the Brant Goose *Branta bernicla* is the most important vertebrate grazer. Grazing accounts for 10% of net production and is most important at the beginning and at the end of the growing season.

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CHAPTER I

INTRODUCTION

Estuaries are recognised as highly productive systems. Both vascular plants and algae contribute to primary production. In estuaries of the Pacific northwest, such as Coos Bay, Oregon vascular plants are represented by large beds of the eelgrass, *Zostera marina*, and to a lesser degree by the introduced species, *Z. japonica*, marsh vegetation, and input from terrestrial uplands. Algal contributors are phytoplankton, benthic macroalgae and periphyton. The relative contribution of each component to estuarine productivity varies depending on the latitude, size and hydrology of the estuary, but as a generalization phytoplankton are presently considered the most important primary producers in estuaries and submerged vascular plants to play an important but secondary role (Correll 1978). The role of salt marshes is controversial. Teal (1962) and Odum and de La Cruz (1967), suggested that detritus exported from marshes was the cause of high estuarine productivity. Later work however, indicates that in some cases the export of production from salt marshes is very small (Heinle and Flemer 1976; Haines 1977; Nixon 1979); indeed some marshes have been shown to be net importers of carbon (Woodwell et al. 1977). These studies have been conducted on north Atlantic and Gulf coast salt marshes which are extensive and extend well into the mid intertidal. By contrast north Pacific salt marshes occur at higher tidal levels and thus are inundated less frequently. In Coos Bay, as in all estuaries in the northeastern Pacific, extensive filling and diking of salt marshes have further restricted potential production inputs into the estuary.

Comprehensive data on primary production in estuaries of the northeastern Pacific are relatively scarce. Thom (1984b), who extrapolated annual production rates from hourly rates, estimated that the largest contribution of carbon to the Grays Harbor estuary, Washington was made by eelgrass, followed by benthic microalgae, marsh plants, macroalgae and phytoplankton. On a per m^2 basis green algae, Enteromorpha/Blidingia sp. had the highest net productivity, but they were restricted in area so the annual contribution to estuarine production was not large. The presence of any free floating algae associated with the Zostera beds is not mentioned. Naiman and Sibert (1978) suggested that if riverine inputs were retained within the estuary they would contribute the largest portion of organic carbon to the Nanaimo estuary in British Columbia. Of autochthonous sources, marsh plants, particularly Carex, were the most important producers, followed in descending order by eelgrass, benthic microalgae, intertidal phytoplankton and macroalgae. Their results were questioned by Simenstad and Wissmar (1985) who showed that in the Hood Canal, Washington, the carbon input from benthic primary producers was several orders of magnitude greater than total riverine input of dissolved organic carbon, and that on an area basis phytoplankton contributed over half the primary production followed by macroalgae, primarily Ulva and Enteromorpha.

The role of primary producers depends partially on the physical nature of the estuary (Longhurst 1978). Welsh et al. (1982) found that the best predictor of the importance of a certain type of producer was the area:volume ratio of an estuary. Estuaries with a high proportion of tidelands will thus have a high area:volume ratio, and benthic macrophyte production would be predicted to be important (Welsh et al. 1982). The Coos Bay estuary is approximately 4,400 ha in area and 48% of this area is tidelands (Percy et al. 1974), a portion of these are areas of rock outcropping where sediment deposition is minimal and benthic algae can attach. Salt marshes in the Coos estuary have been reduced to about 10% of their historical extent (Hoffnagle and Olson 1974), which must severely restrict their productivity contributions. Fresh water input is not large as the drainage basin is only 1567 km^2 (Percy et al. 1974).

There are substantial eelgrass beds in Coos Bay which no doubt are important in estuarine productivity. During the summer months much of the macrophyte biomass in these beds consists of associated benthic macroalgae, primarily the green algae Ulva and Enteromorpha spp.(Gonor et al. 1979). The contribution of Enteromorpha spp. to seasonal production in Coos Bay was estimated by Pregnall and Rudy (1985). Species of both Enteromorpha and Ulva have a very wide geographic distribution, occurring in both estuaries and on open coasts from the pole to the equator, and so could be expected to contribute significantly to productivity in certain situations.

Few estuarine animals can feed on living marine macrophyte material; thus most of this plant biomass is utilised by consumers after the plants have died (Kikuchi 1980). This detrital material is rapidly colonized by bacteria and fungi that break down the structural components of the plant's tissue, which many invertebrates cannot do (Hylleberg Kristensen 1972). In turn protozoans, nematodes and harpacticoid copepods feed on the bacteria and fungi on the detrital particles. Larger detritivore animals feed on the organisms on the detritus but pass the detrital particles relatively unchanged through the gut (Newell 1965). Algal detritus is more rapidly colonized and mineralized by microorganisms than vascular plant material (Tenore 1977a). This detrital pathway is of prime importance in estuaries.

Aims of This Study

This study aims to:

1. Quantify the primary production of the green algae, *Ulva* spp. in the Coos estuary.
2. Determine how this production is transferred within the estuary by examining loss of plant tissue due to grazers, reproduction, removal of whole/partial plants from the substrate, and release of dissolved organic material.
3. Construct a production budget for *Ulva* spp. in Coos Bay.

Standing crop is only an approximation of production as it considerably underestimates net production because of unmeasured losses to grazers, plant breakdown and release of reproductive products and the loss of dissolved organic materials during photosynthesis (Mann 1972a; Brinkhuis 1977). High biomass turnover rates have been measured in marine algae (Mann 1972b) and this is one way by which large amounts of organic matter from algae are contributed to estuarine waters. Therefore I measured the growth of Ulva in the field which, when combined with estimates of standing stock, provides a more accurate estimate of net production.

I also estimated in what forms the algal production entered the estuarine system. It is generally assumed that the majority of estuarine macrophyte production becomes available to primary consumers as detrital particles (Odum and de la Cruz 1967), and that direct consumption of plants is negligible (Mann 1972c). In temperate estuaries this is partially true for eelgrass (Kikuchi 1980), and possibly some algae, but Ulva is an attractive food to some invertebrates (Sousa 1979) and to some vertebrates (Einarsen 1965; Sousa 1979), so that the grazing of living algae could be of importance in this estuarine situation. The impact of direct grazing by invertebrates was estimated using counts of animals found attached to plants in the field at low tide and estimates of consumption of algae from laboratory experiments. Black Brant geese (Branta bernicla) are present in the Coos estuary in the spring during their northern migration. They are herbivores, feeding primarily on eelgrass and Ulva (Einarsen 1965). I conducted goose exclosure experiments to determine the impact of their grazing on the *Ulva* standing stocks.

Ulva can be considered an opportunistic species (sensu Connell 1972) as it has the potential for high growth rates (Ohno and Mairh 1982), and high gamete production (Subbaramaiah 1970), and therefore the ability to colonize areas quickly when conditions for growth are favorable. The quantity of material entering the particle pool as a result of the release of gametes or zoospores by *Ulva* was estimated in this study.

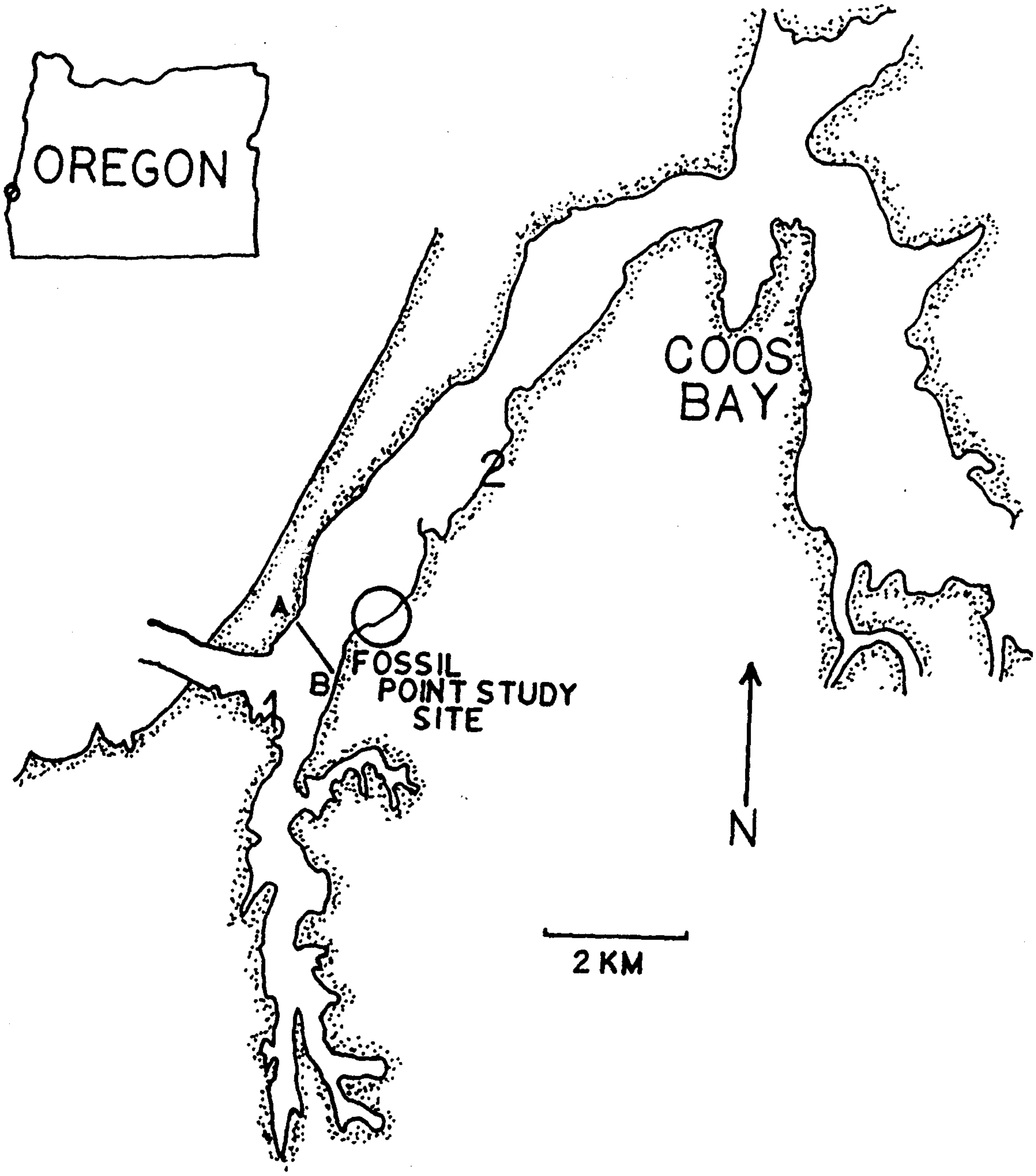
Algal loss from the substrate as a result of wind-induced wave action can be substantial, and in some instances is responsible for the autumn decline in biomass that is characteristic of green algal populations in temperate estuaries (Price and Hylleberg 1982). Algal breakdown is rapid compared to that of vascular plants (Josselyn 1978) and particles of the plant become readily available to detritivores and further decomposition processes. I estimated the export of drift *Ulva* from the study site by capturing it in nets placed downstream from the site. The rate of breakdown of *Ulva* cast up in the strand line was also measured.

Primary production is transferred through the estuary via the release of dissolved organic materials from plants. The amount of material released in this manner during algal growth has been estimated for a number of species (Khailov and Burlakova 1969; Moebus and Johnson 1974; Brylinsky 1977; Pregnall 1983b) and varies depending on conditions such as degree of desiccation, the amount of rainfall, and salinity

(Pregnall 1983b). Laboratory experiments were undertaken to quantify the amount of dissolved organic materials released by Ulva during photosynthesis.

The study was conducted in the Coos Bay estuary in the area between Fossil Point and Pigeon Point (Figure I-1), hereafter referred to as Fossil Point. This site was chosen for its close proximity to the Oregon Institute of Marine Biology and because there are large outcroppings of rock with substantial benthic algae and eelgrass beds within the area. Additionally this area of the bay is traditionally used by Black Brant during their spring migration. No attempts were made to identify the species of Ulva collected during this study. This genus exhibits extreme environmental polymorphism (Chihara 1968; Mshigeni and Kajumulo 1979; Provasoli and Pintner 1980), particularly under estuarine conditions (Steffensen 1976a; Wilkinson 1980; Oza et al. 1985).

FIGURE I-1. Location of study site within Coos Bay, Oregon. 1: Point Adams; 2: Empire Boat Landing; A - B: Transect line for drift algal studies.


OREGON
COOS BAY
2
A
B
1
FOSSIL POINT STUDY SITE
N
2 KM

CHAPTER II

GROWTH AND STANDING STOCK OF ULVA SPP.

Introduction

Estuarine macroalgae rarely attain the high standing stocks characteristic of seagrasses (M^c Roy and M^c Millan 1977) or salt marshes (Hoffnagle 1980). However, macroalgae have a high biomass turnover rate and consequently the potential for high levels of production (Mann 1972b). This production can be measured in a number of ways (Ryther 1956; Brinkhuis 1977; Bach and Josselyn 1979). Estimations of maximum standing stocks can be used in species in which one assumes there is no loss of living material during the growing season. Changes in standing stocks over a period of time can also be used. However, these methods do not take into account losses to grazers, removal of plants from the substrate, the production and release of gametes, or the release of dissolved organic materials, and can severely underestimate net production (Mann 1972a).

Other commonly used methods for estimating production of macroalgae are the measurement of oxygen production (e.g. Littler and Murray 1974;

Heine 1983) or the incorporation of radioactive carbon into plant tissue during photosynthesis (e.g. Wassman and Ramus 1973; Bach and Josselyn 1979; Hall and Fisher 1985). Normally these methods involve the enclosure of whole or partial plants in a chamber for a short period of time which may not be representative of the growing period as a whole (Brinkhuis 1977). Ulva shows a circadian rhythm in photosynthetic activity (Mishkind et al. 1979) which means that rates taken at different times of the day, or from algae that have been held in the lab for differing periods will vary. The oxygen evolution method can also be subject to considerable errors in both sampling and interpretation (Littler and Arnold 1980). A fourth way in which production can be measured involves observing the growth of known individuals, either in laboratory situations or in situ, over a period of time and extrapolating the rate obtained to the population as a whole (Mann 1972b). This method is particularly suited to flat bladed species of algae which are relatively easy to mark in some fashion. Ulva is such a species: it has a relatively flat blade, no structural differentiation, and it grows in a diffuse manner with no specialized area of meristematic tissue; the entire plant is capable of photosynthesis.

Providing realistic field conditions in a laboratory setting can be difficult and laboratory artifacts can lead to results that have little relevance to field situations. Rhyne (1973) showed that measuring the growth of Ulva curvata in the laboratory under simulated field conditions could produce much higher, and thus probably unrealistic growth rates than those measured in the field. To give an estimate of net production of *Ulva* I combined monthly measurements of standing stock with the monthly growth rates of marked field individuals. Net production is a measure of gross production minus respiration. Field measurements such as those in this study do not take into account the loss of dissolved organic carbon (DOC) during photosynthesis, thus true net production is not being measured. The significance of DOC release is discussed in Chapter III.

Physical conditions have also been shown to control seasonal algal biomass (Horn et al. 1983). The most important physical factors are rainfall, water temperature, solar insolation and nutrient levels, the role of each varies depending on the season and location. Semi-natural studies of the growth of *Ulva fasciata* in outdoor continuous culture by Lapointe and Tenore (1981) indicated that high algal densities caused shading of plants which resulted in a reduction of growth rates. They predicted that growth rates in the field would be greatest during the early part of the growing season when algal densities were low. Solar input is of obvious importance, especially to annual algae such as *Ulva* which have high light saturation intensities (Lapointe and Tenore 1981), but probably a variable combination of physical factors ultimately controls algal growth. To further expand such observations measurements of rainfall, water temperatures and solar input in the vicinity of the study area were obtained.

Methods and Materials

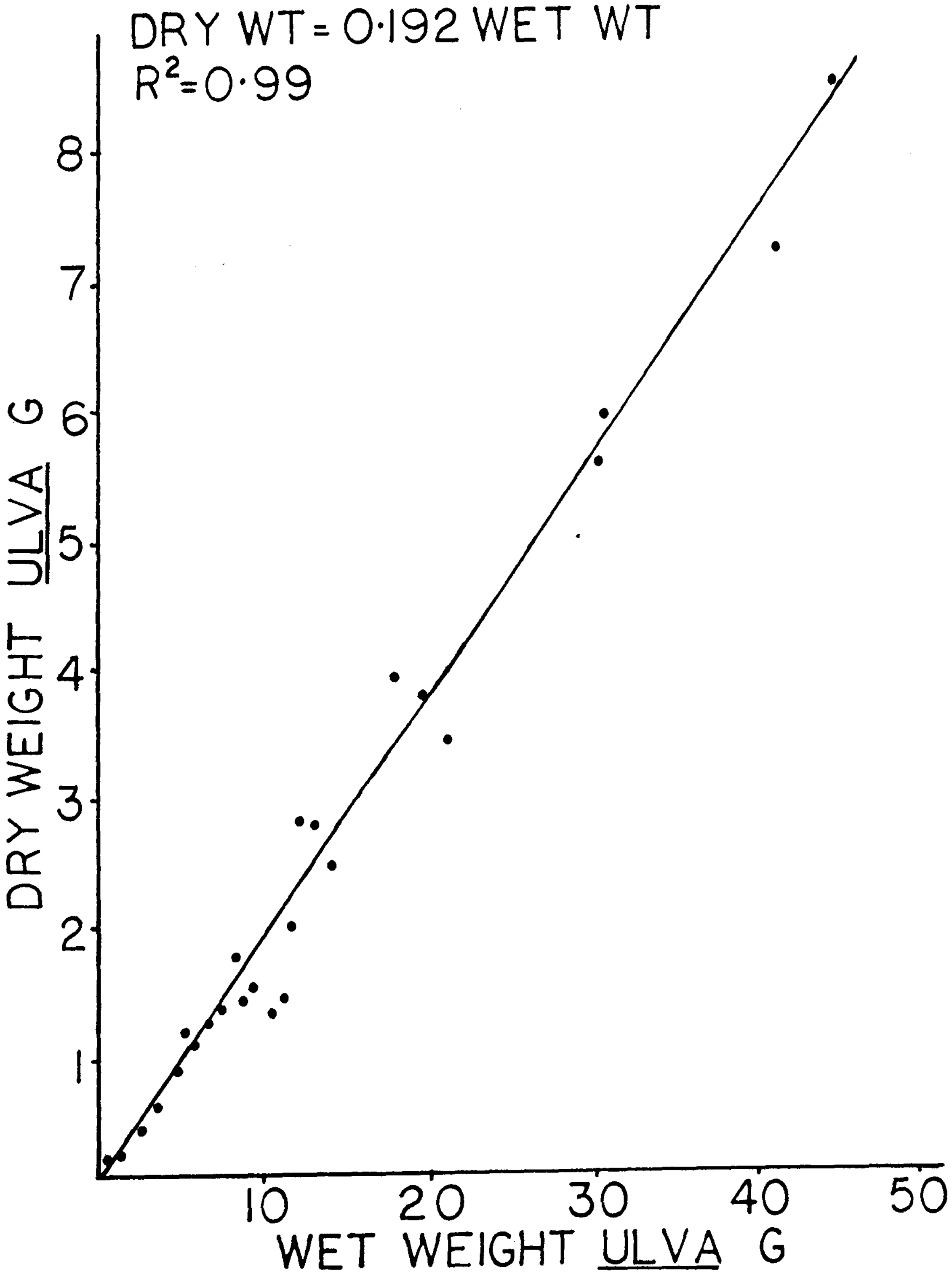
Standing Stock Estimation

The standing stock of *Ulva* was estimated in the Coos Bay estuary between Fossil Point and Pigeon Point at three intertidal levels. Monthly collections were made during the spring tide series in the middle of the month at a high intertidal site, 1.4 - 1.0 ft (January 1983 - December 1983), a mid intertidal site, 0.6 - 0.3 ft (March 1982 - October 1984), and a low intertidal site, -0.1 - -0.4 ft (January 1983 - October 1984); all heights are above MLLW. Because sampling occurred in the middle of a month the estimate of biomass actually covers the period from for example, mid March to mid April, although I will refer to the four week period by the first month that the period covers. All the *Ulva* within sixteen 0.125 m^2 quadrats randomly placed at each tidal height were gathered from the substrate. On return to the laboratory the algae were rinsed with fresh water, until any sediment or animals attached to the plants were removed, the animals were stored in 70% ethanol, and the algae dried at $60^{\circ}C$ for 24-48 hours after which they were weighed. The dry weight:wet weight relationship was determined during the first four months of sampling and is shown in Figure II-1.

Primary production of *Ulva*

Estimates of the growth of individual *Ulva* plants were made under field conditions at the mid and low intertidal sites using different techniques at each for reasons explained below.

FIGURE II-1. Dry weight: wet weight relationship for _Ulva_ spp. collected in Coos Bay.


DRY WT = 0·192 WET WT
R² = 0·99
DRY WEIGHT ULVA G
1
2
3
4
5
6
7
8
10
20
30
40
50
WET WEIGHT ULVA G

Mid intertidal.

The mid intertidal site consists of a broad rock platform with boulders and patches of shallow sediment. The growth of *Ulva* was measured at this site from March 1983 to September 1984. Removable artificial substrates were placed randomly throughout the site. The artificial substrates consisted of a 15 cm x 15 cm piece of plexiglass on which I glued three strips of 5 cm wide velcro tape. The hook side of the tape was attached to the plexiglass allowing the fuzzy side, on the back of which algae settled, to be pulled off. A 7 mm hole was drilled in the center of the plexiglass, through which a threaded stainless steel rod, hammered into the rock substrate was passed. The squares were held tight to the substrate with a wing nut screwed onto the rod. Before placing them at the study site the squares were seasoned in running sea water for two months; no green algae developed on the squares during this time. A total of 24 squares were placed in the intertidal over the 2 year period. Once *Ulva* began to settle on the squares individual strips of velcro with attached algae were removed, placed in a bucket of seawater, brought to the lab and the size of *Ulva* measured by making a photocopy. The *Ulva* blade was marked close to its margin with a series of small holes made with a disposable pipette to facilitate identification at a later date, and to determine if erosion was taking place at the edge of the blade. Whenever possible the squares were returned to the site on the same low tide, although in some cases the squares were kept over night in a tank of running seawater and returned the next day. Each strip of velcro was individually marked so that it was always replaced in the same orientation on its appropriate square.

I measured 128 Ulva plants in this manner in 1983, and 242 in 1984. The length of time between measurements varied from 2 to 11 days with a mean of 3.9 days. The average time that an individual plant was tracked was 7.7 ± 6.1 days; the longest period a plant was tracked was 33 days. To ensure that an alga growing on the squares was representative of the population, 30 plants were gathered at random using a 15 cm x 15 cm quadrat and their size was compared with 30 plants taken from 5 artificial squares; a t-test revealed no significant difference ($t = 0.52$, d.f.= 59, $p > 0.1$).

Low intertidal.

The low intertidal site is in a bed of *Zostera marina* and the absence of solid substrate prohibited the use of anchorable artificial substrates that would not be susceptible to sedimentation. As an alternative method to measure primary production here, *Ulva* was grown inside plastic chambers anchored to the substrate. *Ulva* was collected at random from the study site, and rinsed in running seawater to remove any sediment and organisms. The animals were preserved in 70% ethanol. The *Ulva* blade was spread flat on a piece of plastic and a copy made. A blade was placed in 40 cm x 31 cm transparent plastic bag which had 144 holes, 9 mm in diameter, punched through the bag. To ensure circulation of water through the bag, all four sides were held apart by wooden slats. A cord was attached to the slat at the bottom of the bag by which it was tied to a stake pushed into the mud. From May - September 1983 and May - September 1984 twelve bags were placed randomly at the site each month. The bags were left for periods of 3 - 6 days, after which the *Ulva* were again photocopied. In some cases, depending on the height of the low tide series, the algae were rinsed with seawater, replaced in the bag and returned to the study site for further growth experiments. The bags were never left in the field for more than 7 days.

Estimation of growth rates.

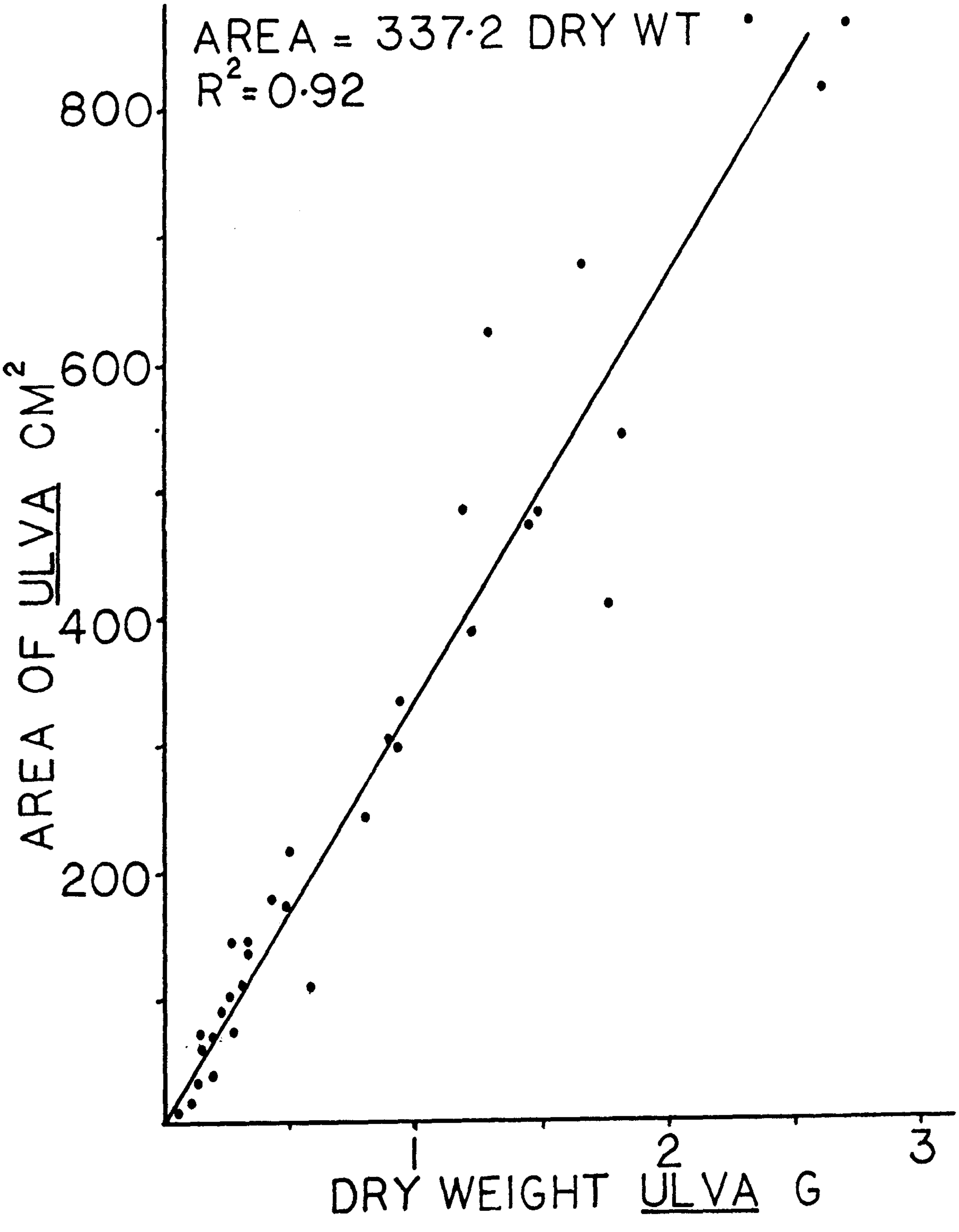
The area of the plants was measured from the photocopies with a plotting planimeter. At the end of three series of growth experiments from both the mid and lower intertidal sites the *Ulva* was dried and weighed and from these measurements the plant area:dry weight relationship was determined using linear regression techniques (Figure II-2). At both sites growth rates were estimated by the following formula:

$$\text{Growth rate} = \frac{\ln \text{Final plant weight} - \ln \text{Initial plant weight}}{\text{No. of days between initial and final measurement}}$$

When an individual plant was measured more than once more than one growth rate was obtained. A monthly growth rate for each tidal height was calculated by averaging the growth rates of the individual plants.

The algae growing on the squares are subject to grazing losses during the period in which growth measurements were calculated. To

FIGURE II-2. The relationship between area and dry weight for *Ulva* spp. collected in Coos Bay.


AREA = 337·2 DRY WT
R^2 = 0·92
AREA OF ULVA CM²
800
600
400
200
DRY WEIGHT ULVA G
1
2
3

account for this the number of herbivorous snails and amphipods found attached to the *Ulva* collected each month for biomass estimations were counted and the grazing rates of amphipods and snails were determined by conducting laboratory experiments. One to two grams of *Ulva* were placed in dishes of seawater with 10 amphipods in five dishes, 10 snails in another five dishes and five dishes with only algae as controls. The dishes were placed in a constant temperature box at $11^{o}C$ with a 14:10 hour light:dark cycle and the seawater was changed every other day. After one week I measured the difference in the wet weight of the algae and the wet weight of the invertebrates. Two sets of experiments were conducted, one in May, and one in August. The loss to grazers was estimated using the following formula:

$$\text{Grazing rate} = \text{No. of grazers/g } \underline{\text{Ulva}} \times \text{g } \underline{\text{Ulva}} \text{ eaten /day}$$

The amount of *Ulva* eaten during the lab experiments in May was used to calculate the grazing rates for March to June, and the amount eaten in August was used for the rates for July to August. The grazing rate for each month was added to the growth rate measured in the field.

During the growing season *Ulva* plants are torn from the substrate by waves and thus no longer contribute to production, unless they continue to grow as they drift around in the estuary. It was assumed that this removal occurs at a constant rate throughout the month. To account for this algal loss a constant (k) related to the change in biomass over the month was calculated as follows:

$$k = \frac{\log (Bt/Bo)}{t}$$

where Bt = biomass at time t
Bo = initial biomass
t = time (days)

Marked Ulva plants grown in running seawater in the laboratory showed that growth was equally distributed throughout the blade. Assuming that growth is always exponential, the production during a month was determined by the formula:

$$\text{Production} = \frac{Bo \times (e^{kt} - 1)}{k} \times r$$

where Bo = actual biomass at the beginning of the sampling period
e = exponential constant
k = constant related to the change in biomass over a month
t = time (days)
r = growth rate measured in the field with additions for grazing

The monthly production was added to the initial biomass to give a predicted final biomass which was compared with the biomass measured in the field each month. The difference between the two was attributed to losses of algal tissue to grazers, plant loss from the substrate and reproduction.

Physical parameters

Measurements of rainfall for each month of 1983 and 1984 were taken from data collected at the North Bend airport approximately 4 km upstream from the study site (NOAA 1983, 1984). Water temperatures are measured on average 5 times a week during high tide at the OIMB boathouse pier, approximately 3 km downstream from the study site and the means of each month's measurements for 1983 and 1984 were computed.

Information on the monthly solar input into the area was obtained from a monitoring station situated on the top of Tioga Hall, at the Southwestern Oregon Community College campus, approximately 5 km northeast of the study site.

Results

Standing Stock

The standing stocks of Ulva show a distinct seasonal pattern: biomass increases from March to August and then declines rapidly until almost all the Ulva is lost from the intertidal in November (Figure II-3). The biomass was higher for all months of 1984 than in the same month in 1983. All three levels sampled show a similar pattern of biomass accumulation and loss (Table II-1) although some Ulva plants are attached to the rock in the mid intertidal throughout the year, whereas all algae are lost from the low intertidal after October. Maximum standing stock occurs in August and the low intertidal site contributes the highest amount of algae. In 1983 83% of the standing stock was found at this level, and in 1984 88%. The high intertidal level contributes very little to standing stock; maximum biomass occurs here in May and biomass declines rapidly in the following months. The mid intertidal site shows considerable variation between years. The maximum standing stock in 1982 was over twice that reached in 1984, and almost four times the maximum seen in 1983. The timing of maximum standing stock at the mid intertidal level also differed between years, in 1982 the maximum occurred in July, in 1983 in August and in 1984 in June.

FIGURE II-3. Annual pattern of *Ulva* standing stock at Fossil Point: the line represents the combined results for all levels of the intertidal and the vertical bars are the standard errors of the means.

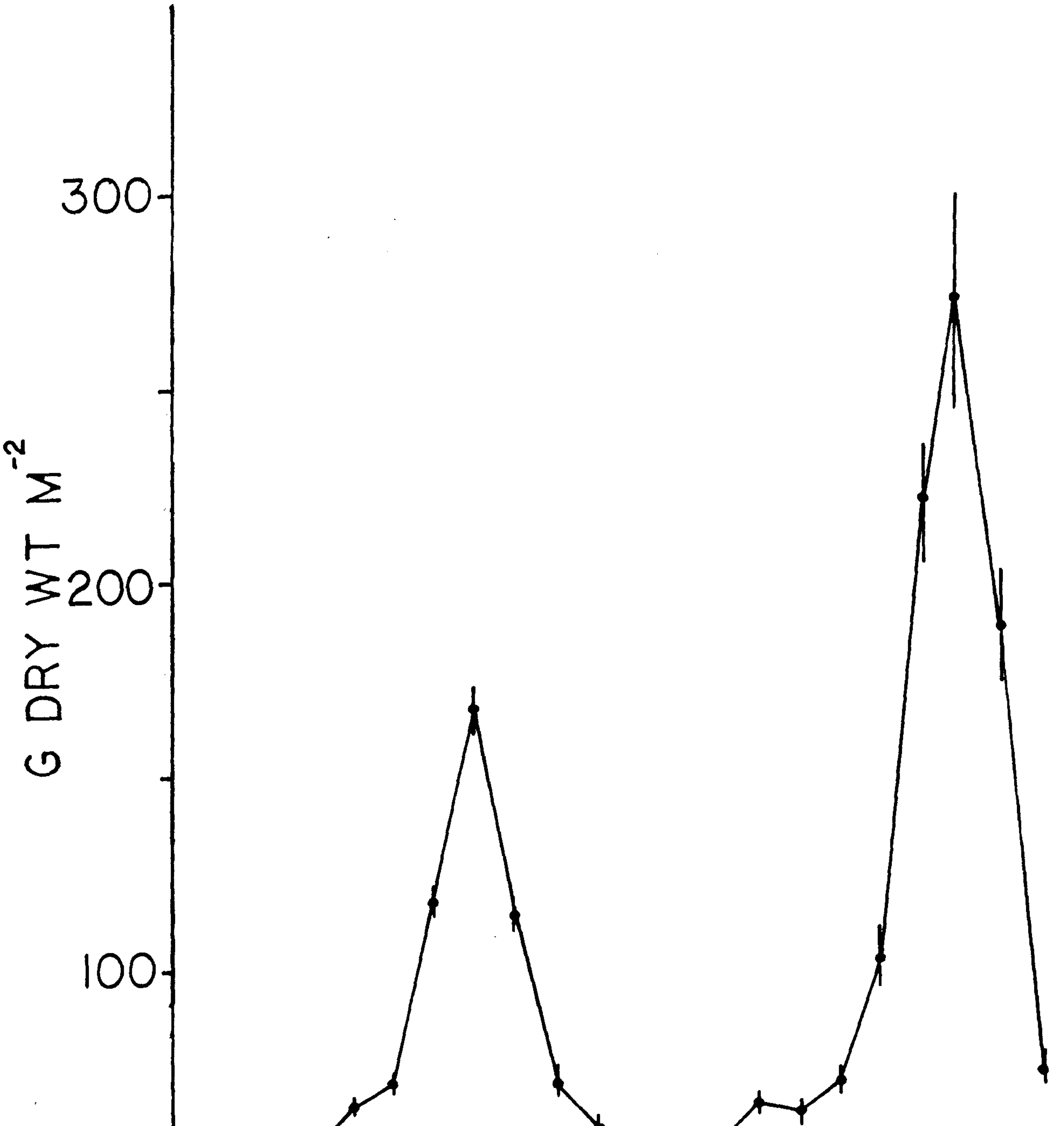

G DRY WT M^{-2}
300
200
100
J F M A M J J A S O N D J F M A M J J A S O
1983
1984

Table II-1. Biomass of *Ulva* at three tidal levels at Fossil Point
High 1.4-1.0 ft; Mid 0.6-0.3 ft; Low -0.1- -0.4 ft.
SE - standard error of the mean.

Date	High mean ± SE	Mid mean ± SE	Low mean ± SE
1982			
March		6.2 ± 0.6	
April		10.4 ± 1.1	
May		41.7 ± 5.9	
June		62.2 ±12.2	
July		73.7 ± 8.9	
August		44.1 ± 9.4	
September		35.9 ± 6.7	
October		8.9 ± 1.6	
November		5.9 ± 1.0	
December		2.5 ± 1.2	
1983			
January	0.2 ± 0.1	0.5 ± 0.2	0.0
February	0.1 ± 0.05	1.4 ± 0.2	0.0
March	0.9 ± 0.2	3.4 ± 0.5	0.0
April	1.0 ± 0.1	3.8 ± 0.2	0.0
May	4.3 ± 0.8	8.3 ± 1.7	1.3 ± 2.4
June	1.2 ± 0.3	11.0 ± 2.6	7.9 ± 5.0
July	1.5 ± 1.1	15.4 ± 3.4	59.6 ±11.6
August	0.8 ± 0.2	18.8 ± 5.9	97.4 ±17.3
September	0.5 ± 0.2	11.0 ± 1.8	60.3 ±10.6
October	0.1 ± 0.04	8.8 ± 2.0	9.4 ± 2.0
November	0.1 ± 0.03	6.6 ± 1.1	0.0
December	0.1 ± 0.03	0.5 ± 0.2	0.0
1984			
January		1.5 ± 0.6	0.0
February		4.4 ± 1.5	0.0
March		12.5 ± 1.8	0.0
April		10.4 ± 0.6	0.0
May		13.4 ± 3.5	3.9 ± 1.2
June		37.1 ±10.0	14.7 ± 4.5
July		25.4 ± 4.5	143.4 ±27.4
August		25.8 ± 5.6	195.2 ±48.8
September		16.6 ± 4.1	119.3 ±19.4
October		7.6 ± 4.0	10.9 ± 2.7

Net Primary Production

At the mid intertidal site growth rates for all months of 1983 are lower than those from 1984 (Table II-2), reflecting the trend seen in the biomass measurements. A similar trend exists in the low intertidal with the exception of August 1984. During both years the growth rate at both levels remains relatively constant from the beginning of the growing season to August, but is much lower in September. The growth rates of the low intertidal algae are higher than those of the mid intertidal with the exception of August 1984 and September 1983 and 1984.

During all months of the growing season the estimated biomass is larger than what is actually seen (Table II-3), indicating that algal material is lost from the population and becomes available to estuarine consumers. This contribution is shown in Figure II-4. Turnover of the algal population can be expressed as doubling time, the number of days it takes for the population to double its biomass. This ranges from 7.5 to 20.7 days in the mid intertidal and from 2.5 to 29.9 days in the low intertidal (Table II-3). In 1983 doubling times in the low intertidal are shorter than those in the mid intertidal for all months except September. This is also the case in 1984 with the exception of the longer time in the low intertidal in August.

Considerably more algae were available to the estuarine system in 1984 than in 1983 (Table II-4) indicating that year to year differences can be large and reflecting the trend seen in both biomass and growth

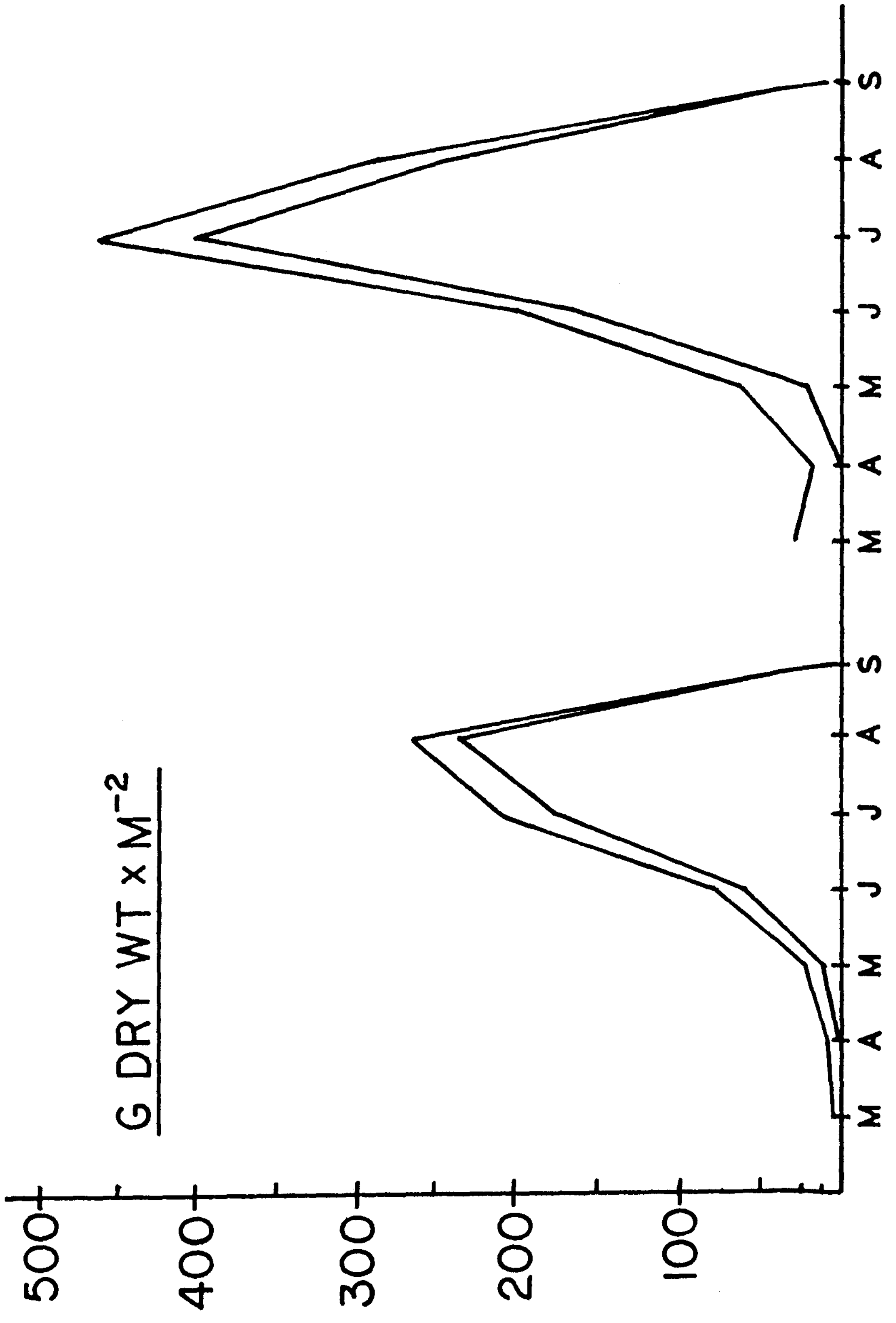
Table II-2. Daily growth rates of Ulva spp. at Fossil Point.
S.E. = standard error of the mean.

Month	Mid intertidal Mean ± SE	n	Low intertidal Mean ± SE	n
1983				
March				
	0.0437 ± 0.0174	9		
April				
	0.0516 ± 0.0150	10		
May				
	0.0469 ± 0.0077	21	0.0751 ± 0.0146	12
June				
	0.0333 ± 0.0072	20	0.0841 ± 0.0144	12
July				
	0.0540 ± 0.0047	27	0.0773 ± 0.0155	12
August				
	0.0597 ± 0.0050	25	0.0646 ± 0.0191	12
September				
	0.0168 ± 0.0161	16	0.0004 ± 0.0140	12
October				
1984				
March				
	0.0787 ± 0.0125	24		
April				
	0.0536 ± 0.0055	45		
May				
	0.0599 ± 0.0056	57	0.0841 ± 0.0149	12
June				
	0.0383 ± 0.0068	38	0.0961 ± 0.0183	12
July				
	0.0790 ± 0.0050	29	0.0793 ± 0.0140	12
August				
	0.0747 ± 0.0073	26	0.0516 ± 0.0150	12
September				
	0.0218 ± 0.0171	23	-0.0004 ± 0.0135	12
October				

Table II-3. Observed and estimated biomass of Ulva during the growing season in the mid and low intertidal at Fossil Point. N = 16. SE = standard error of the mean.

Date	Mid intertidal Observed biomass g dry wt m^{-2} mean± SE	Estimated biomass	No.of days to double	Low intertidal Observed biomass g dry wt m^{-2} mean± SE	Estimated biomass	No.of days to double
1983						
March						
	3.4± 0.5	8.1	13.0			
April						
	3.8± 0.2	12.7	9.0			
May						
	8.3± 1.7	21.8	11.8	1.3 ± 2.4	9.5	4.2
June						
	11.0± 2.6	24.1	13.7	7.9 ± 5.0	72.4	3.8
July						
	15.4± 3.4	43.2	11.0	59.6 ±11.6	237.8	7.8
August						
	18.8± 5.9	44.8	13.0	97.4 ±17.3	247.2	12.2
September						
	11.0± 1.8	16.0	20.6	60.3 ±10.6	60.6	29.9
October						
1984						
March						
	12.5± 1.8	39.6	9.8			
April						
	10.4± 0.6	29.5	10.6			
May						
	13.4± 3.5	55.3	7.5	3.9 ± 1.2	24.4	5.0
June						
	37.1± 9.9	72.7	15.3	14.7 ± 4.5	177.7	2.5
July						
	25.4± 4.5	88.4	8.9	143.4 ±27.4	542.2	8.2
August						
	25.8± 5.6	72.6	11.0	195.2 ±48.8	434.0	13.9
September						
	16.6± 4.0	24.1	20.7	119.3 ±19.4	118.8	-
October						

FIGURE II-4. Estimated *Ulva* production less observed biomass for monthly intervals during the 1983 and 1984 growing season. The upper line represents both the mid and low sites and the lower line represents the contribution of the low intertidal site.


G DRY WT x M^{-2}
500
400
300
200
100
M
A
M
J
J
A
S
1983
M
A
M
J
J
A
S
1984

measurements. The low intertidal site contributes a much larger amount of material to the estuary than the mid intertidal site, the majority of this occurring during July and August. (Table II-4).

The productivity of Ulva measured in this study lies in the mid range of values reported in the literature for marine macrophytes, but is comparable with that of other algal systems (Table II-5). The extremely high values reported by Davis (1981) for Enteromorphap and by Simenstad and Wissmar (1985) for Ulva/Enteromorpha are extrapolations of measured hourly rates of carbon fixation to a yearly period and thus may be subject to a number of errors.

Dry weight was converted to grams of carbon using the figure of 34.7% as reported for Ulva fasciata by Lapointe and Tenore (1981). A similar percentage was measured by Bach and Josselyn (1979) for Cladophora prolifera, and Westlake (1963) gives an average figure of 38% for all algae. The conversion results in an annual contribution of carbon to the estuary of 277g m^{-2} for 1983, and 541g m^{-2} in 1984. The total contribution can be estimated by using the area within the estuary that is suitable habitat for growth of Ulva (Figure II-5). The location of the eelgrass beds are taken from Gaumer et al. (1973), and the areas of hard substrate were determined in this study. Eelgrass bed locations mapped by Gaumer et al. did not differ substantially from locations and spatial area occupied by eelgrass ten years later (Hodder, pers observ.). From Figure II-5 I estimate that 27% of the lower portion of the estuary supports Ulva's growth. This implies an annual contribution of between 2.9 and 5.7 x 10^6kg carbon to the estuary.

Table II-4. Production of Ulva available to the Coos Bay estuarine system.

Month	Intertidal Level					
	Mid			Low		
	Initial Biomass	Production	Final Biomass	Initial Biomass	Production	Final Biomass
	g dry weight m^{-2}					
1983						
March						
	3.4	4.7	8.1			
April						
	3.8	8.9	12.7			
May						
	8.3	13.5	21.8	1.3	8.2	9.5
June						
	11.0	13.1	24.1	7.9	64.5	72.4
July						
	15.4	27.8	43.2	59.6	178.2	237.8
August						
	18.8	11.0	44.8	97.4	149.8	247.2
September						
	11.0	5.0	16.0	60.3	0.3	60.6
October						
Total for 1983				798.2 = 277g C m^{-2}		
1984						
March						
	12.5	27.1	39.6			
April						
	10.4	19.1	29.5			
May						
	13.4	41.9	55.3	3.9	20.5	24.4
June						
	37.1	35.6	72.7	14.7	163.0	177.7
July						
	25.4	63.0	88.4	143.4	398.8	542.2
August						
	25.8	46.8	72.6	195.2	238.8	434.0
September						
	16.6	7.5	24.1	119.3	-	-
October						
Total for 1984				1,560.5 = 5414g C m^{-2}		

Table II-5. Annual production measurements for marine macrophytes.

Species	gC m^{-2} yr^{-1}	Reference
ALGAE		
Ulva	277 - 541	this study
Ulva/*Enteromorpha*	4644	Simenstad & Wissmar 1985
Ulva/*Monostroma*	321	Thom 1984(b)
Enteromorpha prolifera	2700	Davis 1981
Enteromorpha clathrata	430	Thom 1984(b)
Enteromorpha/*Blidingia*	125	Thom 1984(b)
Enteromorpha sp.	1100	Pregnall & Rudy 1985
Enteromorpha sp.	399	Baird and Milne 1981
Fucus vesiculosus	414	Josselyn & Mathieson 1980
Fucus vesiculosus and *Ascophyllum*	375	Brinkhuis 1977
Fucus distichus ssp. edentatus	964	Thom 1983
Ascophyllum	540	Josselyn & Mathieson 1980
Laminaria sp.	1225	Bellamy et al. 1968
Laminaria and *Agarum*	1750	Mann 1972(b)
VASCULAR PLANTS		
Zostera marina	1186	Kentula 1983
Zostera marina	806	Thom 1984(b)
Carex marsh	529	Simenstad & Wissmar 1985
Juncus - *Potentilla* marsh	956 -1108	Simenstad & Wissmar 1985

Physical parameters

The mean monthly water temperatures, the monthly amounts of rainfall and insolation for 1983 and 1984 are presented in Figure II-6. The rainfall pattern is similar in each year; rainfall is high during the months of October to April and falls to below 10cm during May to September. Thus rainfall levels are low during most of Ulva's growing season. Water temperatures are relatively constant in Coos Bay, with an annual range of 10 -15 °C. With the exception of October, water temperatures in 1983 were higher than those of 1984, probably as a result of the 1982/83 El Niño. The intensity of insolation remained relatively constant from May to September in 1983. In 1984 solar intensity was higher during May to August than in 1983.

Discussion

Each intertidal level sampled shows a similar pattern of seasonal biomass accumulation and loss. The mid intertidal site maintains a small population of algae over the winter months, but the plants in the lower intertidal are not attached to the substrate and are lost from the eelgrass bed with the advent of winter storms. The population of Ulva in the low intertidal does not form until conditions in the estuary are suitable for the growth and maintenance of unattached algal populations. The timing depends on river flow and wind strength and direction. In both 1983 and 1984 this population did not appear until late April - May. Similar unattached algal populations have been recorded from

FIGURE II-5. Area of the Coos estuary with *Zostera* beds with *Ulva* and rock outcroppings. The location of the eelgrass beds are from Gaumer et al. (1973).

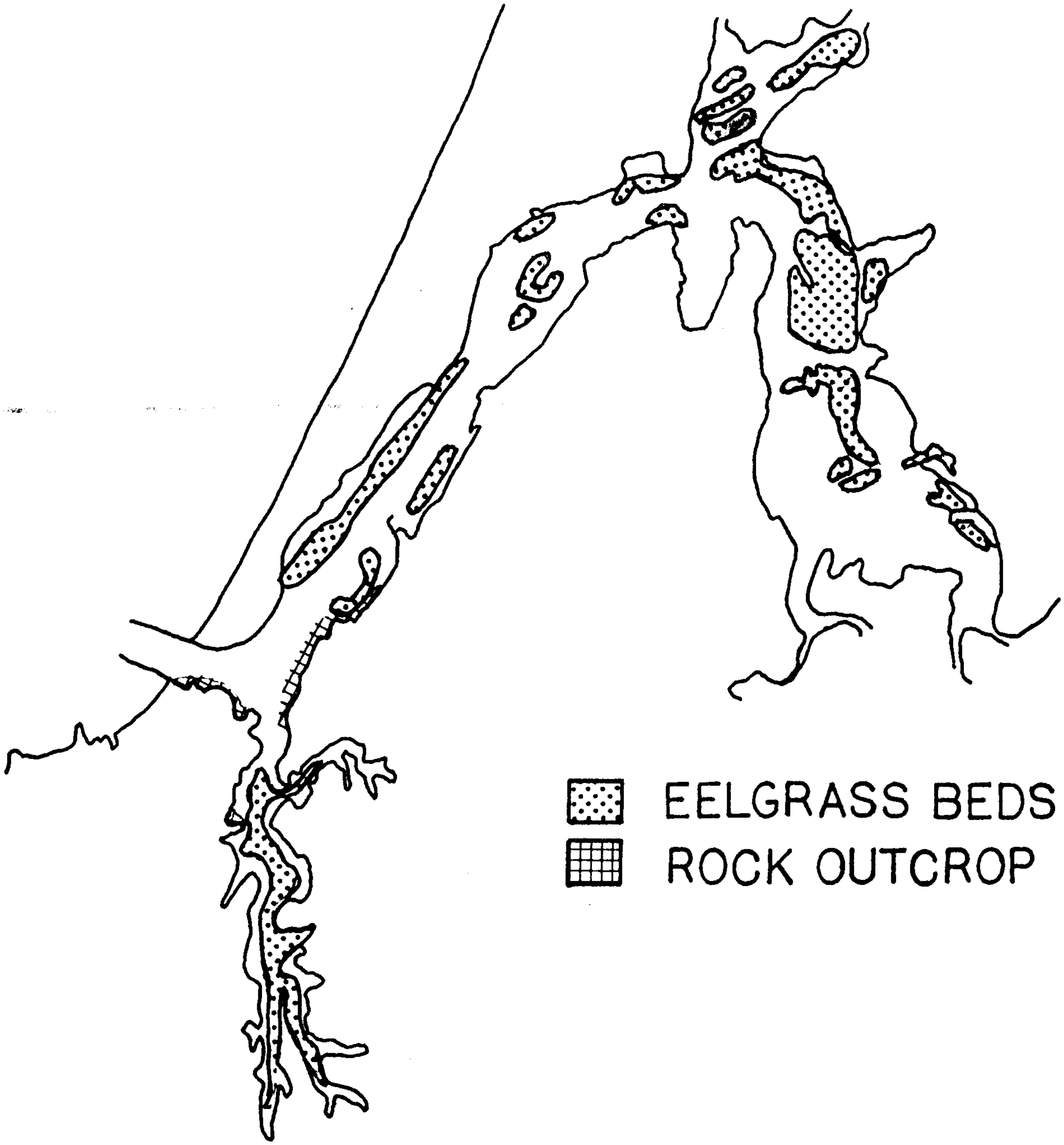
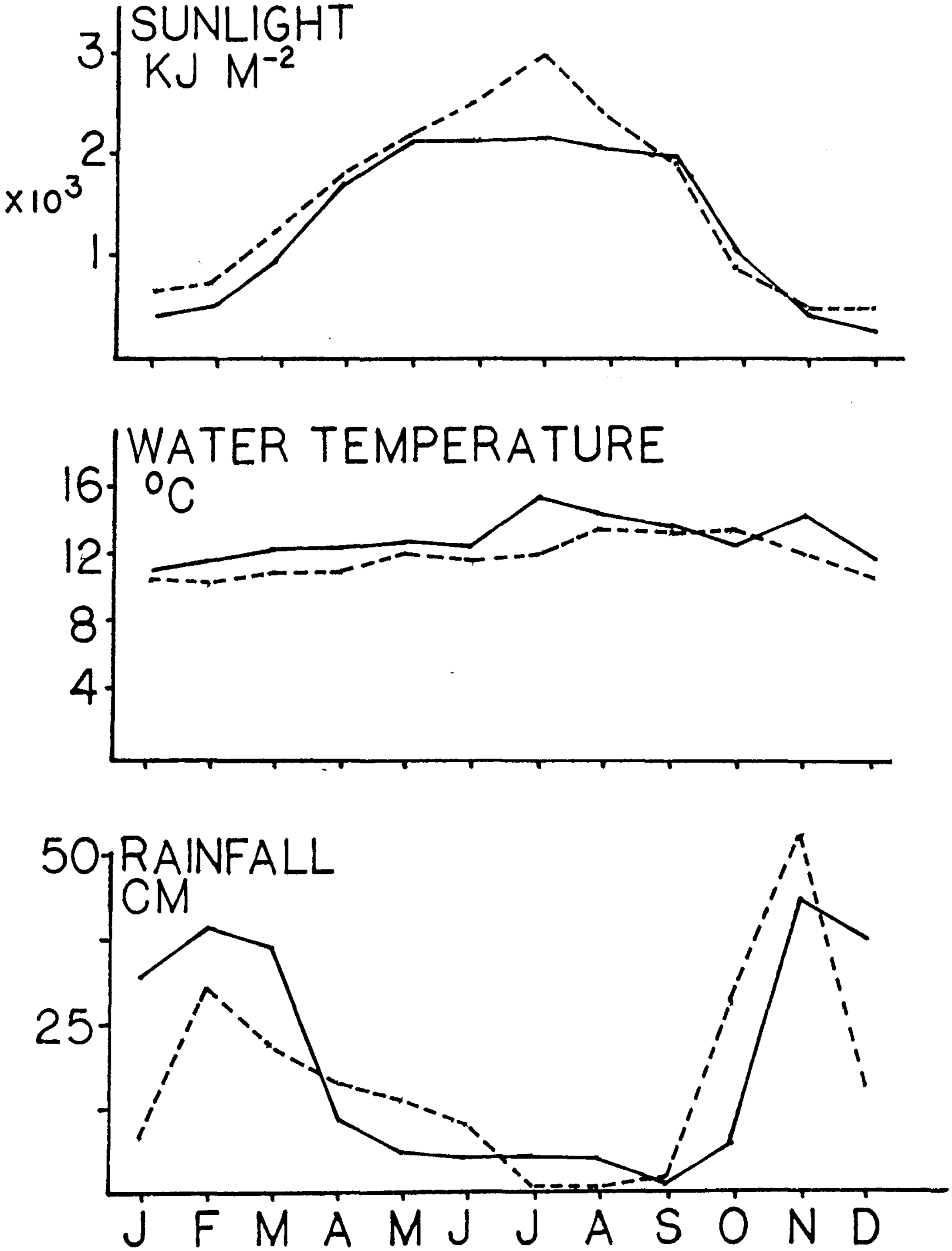

EELGRASS BEDS
ROCK OUTCROP

FIGURE II-6. The average monthly insolation, the monthly rainfall and the mean monthly water temperature in the area adjacent to Fossil Point, Coos Bay for 1983 and 1984. 1983, 1984


SUNLIGHT
KJ M-2
x10^3
3
2
1
WATER TEMPERATURE
°C
16
12
8
4
RAINFALL
CM
50
25
J
F
M
A
M
J
J
A
S
O
N
D

Washington (Price and Hylleberg 1982; Thom 1984a), for north-west Atlantic estuaries, where the brown alga, Ascophyllum nodosum forms large unattached populations (Chock and Mathieson 1983), and in Great Britain where a number of species exhibits this particular growth form (Burrows 1958).

The majority of Ulva plants in the low intertidal eelgrass beds are unattached so they are easily removed from the area by wind and wave action. Therefore, the calmer the conditions during the summer months, the greater will be the Ulva biomass at this site. Production however, may not be higher as nutrient or light levels may limit the growth of the algae. There is some evidence (Cadee and Hegeman 1974) that estuarine sediments probably supply adequate nutrients for the growth of macroalgae especially in areas where sewage effluents are released (Sawyer 1965; Burrows 1971). No measurement of nutrient levels were made in this study but an outfall from a sewage treatment plant is approximately 2 km upstream from the study site. The effect of this outfall on the growth rates and standing stock of the Ulva was not studied. High standing stocks can restrict light penetration to the lower levels of algae (Lapointe and Tenore 1981; Pregnall 1983a), this may limit production during calm periods.

Physical factors strongly influence the primary production and biomass of macrophytic algae. High algal standing stocks are associated with an increase in day length, lowered rainfall, and temporal distribution of infrequent storms (Horn et al. 1983; Josselyn and West 1985). This is certainly true for Ulva in Coos Bay, where standing stocks increase throughout the spring to a peak in August. During this period rainfall is relatively low, solar input is at a maximum and few storms are recorded. The decline after August is related to the inverse of the factors mentioned by Horn et al. (1983), and possibly to grazing pressures (Hatcher and Larkum 1983). Year to year fluctuations in standing stock similar to those in this study have also been reported by Price and Hylleberg (1982); Warwick et al. (1982) and Peckol and Searles (1984).

The net primary production of Ulva spp. in Coos Bay is as high as has been reported elsewhere for other macroalgae, and comparable with the often cited saltmarsh and seagrass ecosytems (see references Table II-5). In estuaries where intertidal flats or Zostera beds are extensive, as in many in the northeastern Pacific, green macroalgae can represent a significant carbon source. The green alga Enteromorpha has been shown to be highly productive in these estuaries (Davis 1981; Pregnall 1983b; Thom 1984a); Ulva, often found lower in the intertidal is as productive. These green macroalgae have been all but ignored as a source of organic matter in studies of estuarine food webs and nutrient cycling.

The growth rates of green algae are also influenced by changes in solar insolation (Davis 1981; Rosenburg and Ramus 1981), water temperatures, (Steffensen 1976b; Chock and Mathieson 1983) and precipitation (Thom 1980). Ulva has a high light saturation intensity (Lapointe and Tenore 1981) so that maximum growth does not occur unless light levels are high and suspended sediments low, conditions found in the estuary during the calmer summer months. Lapointe and Tenore (1981) working with Ulva fasciata obtained their maximum carbon fixation rate (4.6g C m^{-2} day^{-1}) at a density of 0.8kg wet wt m^{-2}; self shading reduced this rate at higher densities. Using the wet weight:dry weight conversion of Figure II-1 this represents 149.5 g dry wt m^{-2}. Only on one occasion, August 1984 in the low intertidal, did the observed biomass exceed this amount; the growth rate for this month was lower than for the previous three months and for August 1983. Moreover August was the only month when 1984 rates are lower than 1983. This lends support to their hypothesis that light levels are of primary importance in controlling growth rate.

Maximum growth rates occurred from March to August at the mid intertidal site, and May to August at the low intertidal. At both sites the growth rate in September was much lower. Rosenburg and Ramus (1981) found a similar pattern of growth for an Ulva population in North Carolina. Price and Hylleberg (1982) found that production of Ulva in False Bay, Washington was greatest in June and July.

As a result of the high net productivity and because the majority of biomass is not stored as standing crop there must be a high turnover of algal material. The ratio of production to the average biomass can be used as a measure of the turnover rates of populations, and to make comparisons, not only between primary producers, but between secondary and higher levels of production (Valiela 1984). When combined with net production measurements, the production:biomass (P/B) ratio can give an indication of the amount of carbon that has to be used by the plant for activities other than biomass addition. For example, the P/B ratio for Macrocystis is estimated to be about 1.0, and the average net production to be 800 - 1000g C m^{-2} y^{-1} (Mann 1982). Laminaria, on the other hand, has a net production ranging from 1225g C m^{-2} y^{-1} (Bellamy et al. 1968) to 1750g C m^{-2} y^{-1} (Mann 1972b), and a P/B ratio in the range of 2-7 (Mann 1982). A low P/B ratio such as that of Macrocystis indicates that considerable energy is used in the maintenance of plant tissue (Mann 1982). The P/B ratio for the Ulva population at Fossil Point was 4.4 in 1983 and 4.8 in 1984. No measurements of maintenance costs were made in this study but the high P/B ratio and high net productivity of the Ulva population reflect a situation similar to that of Laminaria in that a large turnover occurs annually and relatively little carbon is used for the maintenance of biomass. P/B ratios have been determined for only a few macroalgae. Short term studies in which production is measured by incorporation of ^{14}C or the evolution of oxygen do not lend themselves to accurate estimation of these ratios unless seasonal variation is represented by a number of measurements from different times of the year.

A considerable amount of algal material in the form of Ulva biomass is transferred to estuarine waters during the growing season. Few estuaries in the north-east Pacific have large areas where benthic algae can attach, but intertidal eelgrass beds are common, and the majority of Ulva production occurs at these lower intertidal levels. Benthic algae, primarily Ulva spp. comprised an average of 14% of the total standing stock of macrophytes in an Alaskan eelgrass bed (M^{c}Roy 1970), and between 10-70% of the macrophyte biomass during the summer months of an eelgrass bed in Coos Bay (Gonor et al. 1979). Thus production by _Ulva_ can make an important contribution to estuarine productivity not only in the late summer when the algae in the eelgrass beds are removed by storms but also during the spring and summer growing season. If predictions of the importance of macroalgae in estuarine food webs in the Hood Canal (Simenstad and Wissmar 1985) hold true for all northeastern Pacific estuaries, _Ulva_ has the potential to be a large contributor of carbon to higher trophic levels.

CHAPTER III

OUTPUTS OF ULVA PRODUCTION

Introduction

Once carbon has been fixed by photosynthesis it is transferred to estuarine waters in a number of ways. These include direct consumption by grazers, release of reproductive products, loss of algal tissue from the substrate due to wave action, and exudation of dissolved organic materials. The majority of estuarine macrophytes are not consumed as living plants (Mann 1972c), but rather enter a detrital cycle where they are used by microorganisms that in turn provide food for detritivores and suspension feeders, until finally the plant material is broken down into small molecules. However, estuarine algae, unlike seagrasses and salt marsh plants, can be attractive to grazers and therefore are subject to direct consumption. This is particularly true of the green algae (Montgomery and Gerking 1980).

Field manipulations on rocky shores have shown that grazers can control the development of algal populations (Castenholz 1961; Paine and Vadas 1969; Lubchenco 1980). These experiments involve the comparison of areas from which grazers have been excluded with areas that are grazed naturally. Both invertebrates and vertebrates are known to eat

Ulva. The major vertebrate grazers of green algae are waterfowl, and in Coos Bay the main species that eats *Ulva* is the Brant Goose, *Branta bernicla*. These birds are present in Coos Bay during March and April, the time of spring algal growth. They eat both *Zostera marina* and *Ulva*. Because they have no cellulose digesting enzymes in their digestive tract (Mattocks 1971) the geese have to rely on mechanical means to break open the cells so they can digest the cell contents. They are thus rather inefficient grazers and must eat large quantities of material to satisfy their nutritional requirements. Their effect on the size and temporal development of the *Ulva* population was determined by using herbivore exclusion cages.

Herbivorous fish are uncommon in temperate areas (Kikuchi 1980), both buffalo sculpins, *Enophyrs bison* (Davis 1981) and top smelt, *Atherinops affinis* (Sousa 1979) will at times eat *Ulva*. Data from seining studies conducted in areas adjacent to the study site were used to indicate the seasonal occurrence of these two fish species. Invertebrates grazing directly on living algal tissue include amphipods, isopods, crabs and gastropods. Their impact was examined by determining the numbers of the most abundant grazers, amphipods and snails, present at the study site, and by using lab experiments to determine the amounts of algae consumed.

Species of *Ulva* are capable of frequent reproduction so that the potential input of material to the estuarine particle pool in the form of zoospores and gametes is large. *Ulva* displays the classic alternation of isomorphic generations characteristic of the family

Ulvaceae. Fruiting occurs at fortnightly intervals normally correlated with the spring tides (Smith 1947; Thiadens and Zeuthen 1967; Chihara 1968; Subbaramaiah 1970; Oza et al. 1985), when both gametes and zoospores are liberated as the exposed plants are covered by the rising tide (Subbaramaiah 1970). Fruiting during neap tides has been reported (Sawada and Watanabe 1974; Okuda 1975) but appears to be less common. Asexual reproduction occurs in culture, with new _Ulva_ fronds initiated from cells sloughed from the plant and from fragments of the blade (Bonneau 1978). The quantity of zoospores and gametes releases by _Ulva_ and contributed to the estuarine particle pool was estimated during this study.

The amount of algae torn from the substrate by wave action can be substantial. Monthly strand line collections made just before the highest monthly tide were used by Josselyn (1978) to estimate the relative amounts of plant material that entered the particle pool. Initially I conducted surveys of the strand lines at the study site and adjacent areas to see if I could estimate the amount of drift _Ulva_ being deposited on the shore. This method was found to be unsatisfactory because input of material into the strand line was temporally very patchy, both on a daily basis and with each tidal cycle. Large amounts of algae deposited in the strand line at Fossil Point on one tide cycle were often gone the next day, or on other occasions were partially buried in the sediments. Changes in tidal levels, the passage of storms, and periods of calm can have pronounced effects on drift deposition (Perkins 1974). In Coos Bay summer winds blow relatively constantly from the northwest, whereas winter winds blow from the south. This no doubt affects where drifting material is cast up on the shore. As an alternative I estimated the amount of material drifting away from the study site on an outgoing tide and compared this amount with a qualitative assessment of the amount of material washed up in the drift line by wind action. Josselyn's 1978 method was also not suitable because _Ulva_ cast up on the shore quickly lost its green color and began to break up into small pieces. This was particularly true when the sun dried the drift algae. To determine how quickly the _Ulva_ broke down into small particles once it was part of the wrack line I measured the rate of loss of _Ulva_ from drift bags tethered in the wrack line.

Release of dissolved organic carbon (DOC) by aquatic macrophytes represents a proportion of their total primary productivity (Fankbonner and de Burgh 1977; Brylinsky 1977; Pregnall 1983a). Estimates of DOC's importance vary, but the large amounts suggested by early work (Khailov and Burlakova 1969; Sieburth 1969; Gallagher et al. 1975) may be attributed to stresses such as desiccation (Moebus et al. 1974) or damage to the plants prior to the experiment (Fankboner and de Burgh 1977). The most common technique for estimating DOC release from aquatic plants involves the use of carbon 14 tracers which approximate the flow of carbon 12. In this study I used ^{14}C labelled sodium bicarbonate to estimate the amount of DOC released by _Ulva_ spp. during photosynthesis.

In conjunction with the DOC release experiment I also measured the uptake of ^{14}C during photosynthesis. Many investigators (e.g Littler and Murray 1974; Littler and Arnold 1982; Heine 1983) estimate algal production by measuring carbon fixation over a short period of time, usually only a few hours. The limitations of this method, especially as a way of estimating annual productivity, have already been pointed out (Chapter II), but for comparative purposes I have included the results of this short term experiment.

Methods and Materials

Vertebrate Grazing

Consumption of Ulva by geese at Fossil Point was estimated by caging an area of the intertidal in such a way as to exclude waterfowl. Angle iron cages, $1m^2$ with legs 15 cm long, were wired to posts driven into the rock substrate. Both the top and the sides of the cage were open. Six cages were used in 1983 and eight in 1984. Two cages were placed in the intertidal below the Oregon Institute of Marine Biology's (OIMB) boat house in 1983, an area where geese have not been observed to graze, to act as controls for any caging effects.

The cages were placed at the mid intertidal site in February before the Brant arrived, and removed once the Brant left at the end of April. Monthly biomass samples of Ulva were collected from inside the cage during the period the Brant were present and until the collected biomass was not significantly different from that outside the cage. Biomass samples were treated in the same way as previously noted (Chapter II).

The quantity of Ulva eaten by the Brant was determined as follows: the rate of increase in the algae within the areas protected from grazing by geese was calculated as:

$$\alpha = \frac{\ln Bt - \ln Bo}{t}$$

where:

α = rate of increase
Bo = initial biomass
Bt = biomass at time t

Using this rate the amount of *Ulva* that would be expected to be present in grazed areas, if no goose grazing had occurred, can be estimated by adding the production, calculated as follows to the biomass present at the beginning of the month to give a predicted biomass.

$$\text{production} = \frac{Bo \times (e^{kt} - 1)}{k} \times$$

where:

$k = \frac{\log Bt/Bo}{t}$
t = time (days)

The difference between the biomass measured in the field in areas not protected from goose grazing and the predicted biomass gives an estimate of the amount of *Ulva* lost as a result of grazing by Brant Geese.

The numbers of Brant Geese in the study area were counted during mid to low tide periods, when the *Ulva* were accessible to grazing, on 22 occasions between March 3 and April 29 1982. During this period in 1983 and 1984 the number of Brant in the study area was noted on all visits. The consumption of *Ulva* by fish was not measured directly, but results from seining studies conducted by students in the 1983 Estuarine Biology and Vertebrate Ecology classes taught by Dan Varoujean at OIMB were used to give an indication of whether top smelt or buffalo sculpins, both of which are known to eat Ulva (Sousa 1979; Davis 1981), were present in the vicinity of the study site. The mean number of these fish from repeated, duplicate hauls of a beach seine at Point Adams and the Empire boat landing (Figure I-1) was determined. The net was 40m long by 2m high with a 1.5cm mesh.

Invertebrate Grazing

As noted in Chapter II the grazing rates of amphipods and snails were determined by conducting laboratory experiments. The seasonal variation in small grazers, the herbivorous snails and herbivorous amphipods, found attached to the Ulva collected each month for biomass estimations were counted.

Reproduction

Four $0.125m^2$ plots randomly selected within the mid intertidal study site were cleared of Ulva bimonthly from April 1983 to February 1984. The collections were sorted in the laboratory into non-reproducing and reproducing plants. Fertile portions of the blade change from bright green to yellow/green or brown/green during the formation of gametes or zoospores and thus are relatively easy to distinguish (Chihara 1968; Okuda 1975), although fertile gametophytes cannot be distinguished from fertile sporophytes (Okuda 1984). The fertile plants were photocopied and the area of the reproductive portion calculated. On several occasions some plants had already discharged their swarmers by the time I surveyed the site and only the empty thallus cells were left on the plant. In these cases the plants were also collected and photocopied to determine the proportion of the plant that had reproduced. The part of the plant that remains as empty thallus cells will eventually detach from the growing plant and become drift material. To determine the percentage of the reproductive part of the plant the empty thallus cells represent the area:dry weight ratio of the photosynthesizing part of the plant was compared with the area:dry weight ratio of the empty thallus cells. Occasionally the population was checked during neap tides to determine if any fruiting was occurring (Sawada and Watanabe 1974; Okuda 1975); none was observed.

Drift

The quantity of macrophytes drifting free in the water column was sampled monthly from November 1983 to October 1984 using a duplicate net system towed just below the surface, from the side of a 17ft boat, on a transect line across the bay from point A to point B (Figure I-1). The entrance to each net was 0.25 m^2 and the flow of water through one of the nets was measured with a flow meter. Sampling began one hour before the high tide and continued through the descending tide cycle to one half-hour after the low tide. In this way any material leaving the estuary from the study site and the mud flats upstream fom the site on the outgoing tide was sampled. The samples collected by both nets were sorted, dried and weighed. The amount of water leaving the estuary between high and low tide depends on the difference between the tidal levels. Tidal prism is a measure of this difference multiplied by the area of the estuary, and it provides a way to compare the volume of water leaving the estuary on different sampling days. The rate of flow can be calculated by dividing this volume by the period of time between the high and the low tide. This assumes the rate of flow is constant over the tidal cycle. The tidal prism and the rate of flow for each date are shown in Table III-1. The amount of algae drifting away from the study site close to the bottom during an ebbing tide was measured monthly from November 1983 to October 1984, with the exception of January, by placing a series of nets on the bottom just outside and downstream of the bed. The nets were held open by a triangular frame 82 cm on a side. Three nets were placed on the bottom half an hour after the high tide and left for 4.5 - 5 hours, after which they were pulled to the surface and the collected algae were sorted, dried and weighed. The flow of water through one of the nets was measured with a flow meter.

To determine how quickly the Ulva in the wrack line broke down into small particles, mesh bags, 30cm x 40cm with a mesh diameter of 5 mm, containing fresh drift algae were tied to stakes pushed into the sediment at Fossil Point at the level of the wrack line. Drift Ulva was collected, blotted dry, weighed and placed in the bag. The bags were left for 5 days, the algae removed, blotted and reweighed, and returned to the intertidal for a further 4 days when the algae were reweighed. A total of twelve bags were placed in the intertidal over a period of 3 months.

Table III-1. Tidal prism and flow rates from Coos Bay on the days that surface drift was sampled.

Date 1984	Tidal Prism $m^3 \times 10^7$	Flow rate $m^3hr^{-1} \times 10^7$
Jan 28	9.372	1.7323
Feb 12	8.712	1.1662
Mar 28	7.260	1.0567
Apr 13	8.316	1.2505
May 12	6.424	1.0925
Jun 7	6.820	1.0103
Jul 23	1.320	0.2808
Aug 6	1.760	0.3809
Sep 21	2.684	0.5400
Oct 20	4.180	0.7256
Nov 17	7.26	1.2305
Dec 1	3.872	0.6400

Dissolved Organic Carbon and Photosynthetic Rates

Ulva was gathered from the study site, rinsed free of sediment and invertebrates, blotted dry, weighed and placed in 300ml BOD bottles with synthetic seawater (Rila Sea Salts). The dissolved carbon dioxide, bicarbonate, and carbonate concentration of the seawater was determined prior to the experiment using the methods of Stricklands and Parsons (1972). 5μCi NaH^{14}CO was added to each of six bottles which were incubated at 14°C, an average summer water temperature at the study site, outside on a sunny day for two hours from between 11.00 and 13.00 hrs in a shaking water bath. A stream of running water was maintained through the water bath to keep the bottles cool. Three dark controls were placed in black bottles which were wrapped in aluminum foil. I took 3 ml samples of the water from the bottles just after the introduction of the label to establish initial background activities and at 15 minute intervals throughout the experiment. After taking the sample each bottle was shaken to disrupt metabolically induced diffusion gradients. The samples were acidified to pH 2 with hydrochloric acid. Carbon dioxide free air was bubbled through them for 10 minutes to drive off the labelled inorganic carbon; samples were prepared for liquid scintillation by adding 12 ml of scintillation cocktail. Counts were recorded on a Beckman LS 150 Liquid Scintillation Counter and were corrected for quench using the appropriate curves. The resulting counts provided a measure of the dissolved organic carbon released during the two hours of photosynthesis.

At the end of the incubation I rinsed the algae with hydrochloric acid to remove any adhering inorganic carbon, and then with distilled water to remove the acid, and placed them in 25ml of dimethyl sulphoxide (DMSO) in a 60°C oven for eight hours to extract the photosynthetic pigments. DMSO has been shown to be as efficent as the more commonly used acetone for extracting chlorophyll and superior in terms of chlorophyll stability (Hiscox and Israelstam, 1979; Filbin and Hough, 1984). The extract was then counted with liquid scintillation to determine carbon fixation during photosynthesis.

Results

Vertebrate Grazing

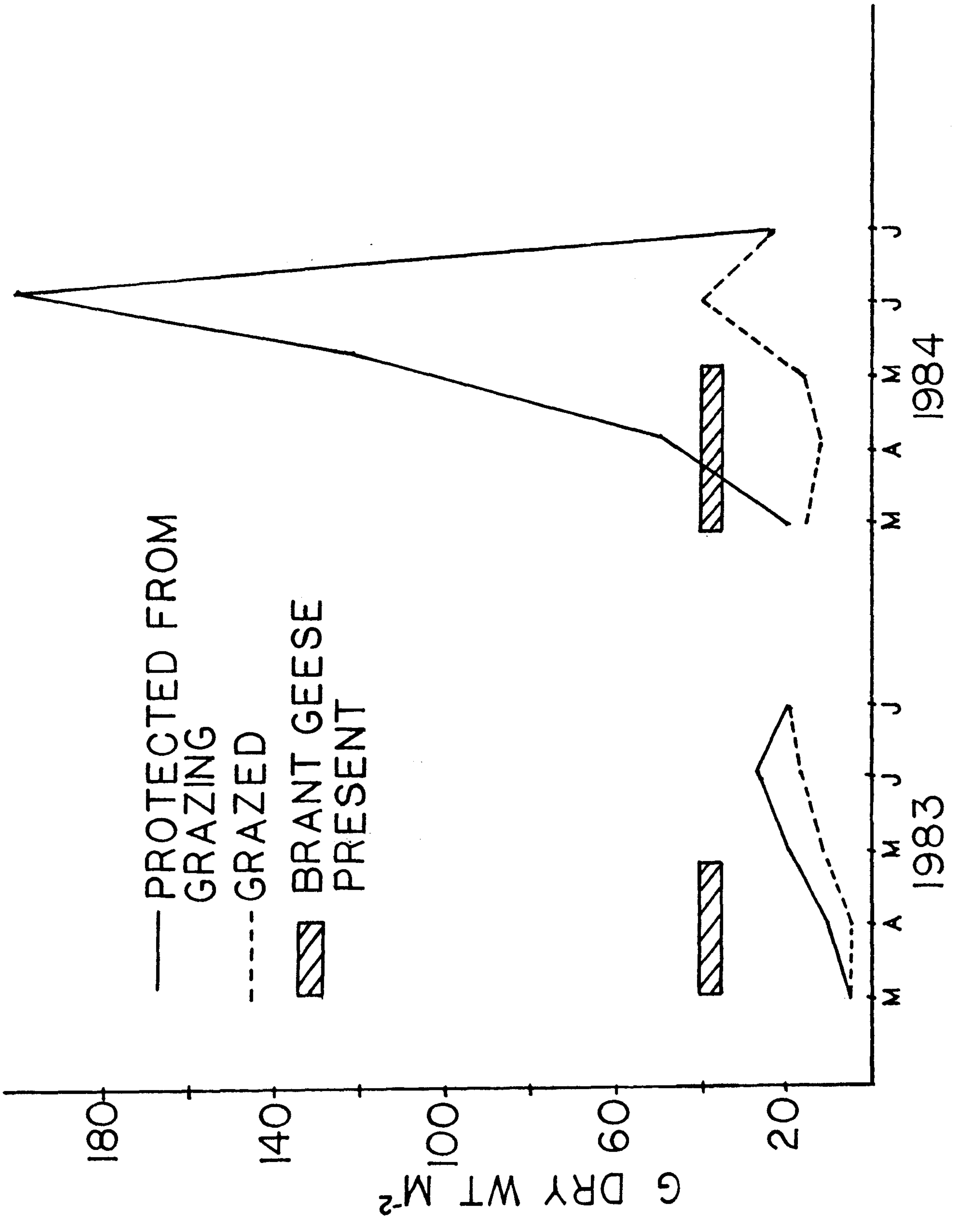
The principal waterfowl grazers, Brant Geese are present in Coos Bay during the migration from their wintering areas in Mexico to the breeding grounds of the Arctic tundra. They arrive in Coos Bay at the beginning of March and most are gone by early May. A few individuals are present during June and occasionally non-breeding geese are seen during the summer months but these few animals have little impact on the algal populations. During March 1982 an average of 297 ± 177 (SD) Black Brant fed in the study area during low tide periods (n=13), and in April 1982, 191 ± 108 geese were sighted (n=11). Fewer geese were seen in 1983 although fewer visits were made to the study area than in 1982. In March 1983 an average of 120 ± 78 birds fed during low tides (n=6) and in April 1983 51 ± 32 geese were observed (n=4). In 1983 almost all the Brant had left Coos Bay by April 29, considerably earlier than in 1982 or in 1984. The average number of geese feeding in the study area in

1984 appeared to be greater than in 1983, although fewer observations were made than in the previous two years. In March 496± 240 birds fed during low tide periods (n=3), and in April 255 145 geese were recorded (n=3).

The amount of *Ulva* eaten and the percentage of the biomass it represents were greater in March of both years than in April (Table III-2). More *Ulva* was available in 1984 than in 1983 and a higher percentage of the biomass was eaten in 1984. In 1983 the geese ate approximately one-quarter of the March biomass, but the quantity available was not large. In April 1983 fewer birds were present and grazing pressure was lighter with only 0.4g of *Ulva* m^{-2} (dry weight) being consumed. In 1984 goose grazing had a much more significant impact. During March 25.2g *Ulva* m^{-2} was eaten representing 71% of the biomass produced in that month; grazing pressure in April was not so high as fewer birds were present. In both years this may be an underestimation of the amount of biomass eaten as Brant were also observed eating *Ulva* from the drift line.

The difference in amounts of *Ulva* available between the years is shown graphically in Figure III-1. In areas protected from goose grazing in 1984 the biomass of *Ulva* is considerably higher than in the grazed areas. This is not only true for the period during which the Brant are present, but continues to be the case until July when there is no significant difference in the biomass between the grazed and ungrazed areas. There was no significant difference between the growth rates of *Ulva* inside or outside the cages. The presence of the cages alone was

FIGURE III-1. A comparison of the biomass of _Ulva_ inside and outside geese exclusion cages in the mid intertidal at Fossil Point.


G DRY WT M-2
180
140
100
60
20
— PROTECTED FROM GRAZING
- - - GRAZED
▨ BRANT GEESE PRESENT
M
A
M
J
J
1983
M
A
M
J
J
1984

not responsible for the change in biomass. The standing stocks inside and outside the cages at the control site, the OIMB boathouse, were not significantly different ($t=0.97$, d.f.$=5$, $p>0.1$).

Table III-2. The impact of grazing on Ulva by Brant Geese at Fossil Point, Oregon. Biomass figures are means with standard errors of the means in brackets. N = 16.

Date	Initial biomass g dry wt. m^{-2}	Increase rate	Final Biomass Predicted g dry wt m^{-2}	Final Biomass Actual g dry wt m^{-2}	Grazing by geese g dry wt m^{-2}	% biomass grazed
1983						
March	3.4 (0.51)	0.015	5.0	3.8 (0.21)	1.2	24.0
April	3.8 (0.21)	0.029	8.7	8.3 (1.66)	0.4	4.6
1984						
March	12.5 (1.76)	0.067	35.6	10.4 (0.92)	25.2	70.7
April	10.4 (0.92)	0.026	19.7	13.4 (2.80)	6.3	32.0

Grazing by fish was probably not important. No buffalo sculpins were seined from either of the two areas sampled and the number of top smelt was low (Table III-3).

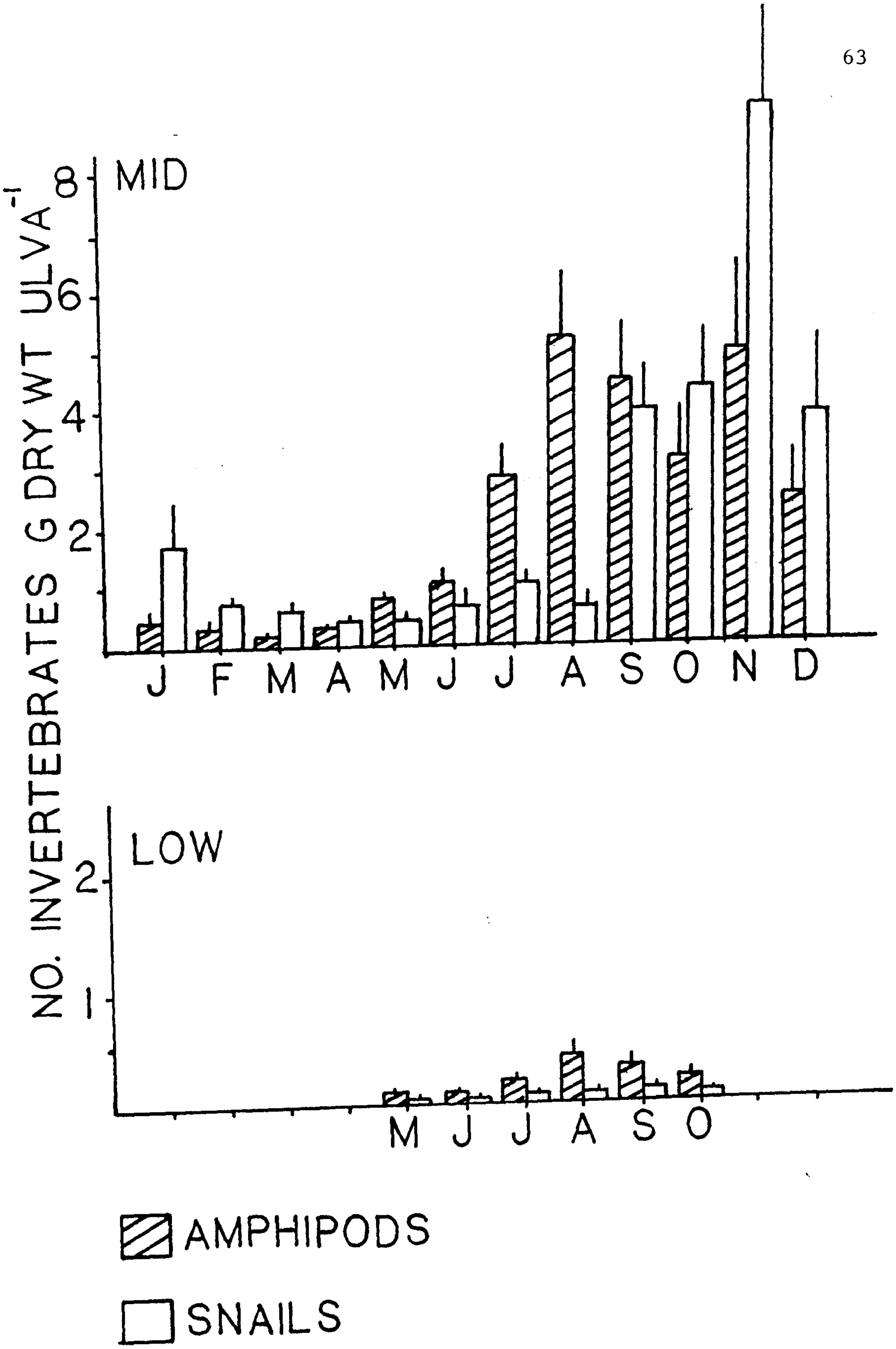
Table III-3. Mean number of top smelt taken in two beach seines at Point Adams and Empire boat launch, Coos Bay, 1983.

Month	Point Adams	Empire
April	1	8
May	0	3
June	6	1
July	0	0

Invertebrate Grazing

The number of invertebrates per gram of *Ulva* was much higher in the mid intertidal than in the low (Figure III-2). The physical characteristics of each site might account for this difference. The mid intertidal is a rock substrate and is more frequently exposed to the air, whereas the low intertidal site is an eelgrass bed with its associated sedimenting nature. Invertebrates at the mid intertidal site might cluster on the algae for shelter and to prevent desiccation during low tide periods, the time at which the samples were taken. At the low site there is almost always a small amount of water on the mudflat surface and invertebrates might not need to cluster on the algae to prevent desiccation. The *Zostera* plants and their epiphytes may also provide alternative shelter for invertebrates. Far fewer invertebrates were found at this site probably because of the absence of a rock

Figure III-2. Monthly mean number of snails and amphipods per gram of
Ulva from the mid and low intertidal at Fossil Point.
Vertical lines are standard error of the mean.


NO. INVERTEBRATES G DRY WT ULVA^{-1}
MID
8
6
4
2
J
F
M
A
M
J
J
A
S
O
N
D
LOW
2
1
M
J
J
A
S
O
AMPHIPODS
SNAILS

substrate, and perhaps because predation pressure can be more intense in the lower intertidal as it is covered with water for a much longer period (Race 1982). All herbivorous snails were *Lacuna* spp., principally *L. marmorata*. Amphipods were much more varied and were not identified from every sample. Several samples were examined and the principal species were gammarids such as *Ampithoe lacertosa*, *A. valida*, *Eogammarus confervicolus*, *Allorchestes angusta*, *Microjassa litotes*, and *Ischyrocerus* sp.

At the mid intertidal site the highest number of invertebrates were found on the *Ulva* from August to December (Figure III-2) when algal biomass is either constant or declining. Lowest numbers of invertebrates occurred from February to May, the period of spring growth of *Ulva*. Mean numbers of invertebrates from algae growing in cages protected from goose grazing were not significantly different from the mean numbers in areas grazed by geese (ANOVA $p > 0.05$). At the low intertidal site the number of invertebrates per gram of *Ulva* was relatively constant throughout the season (Figure III-2).

Grazing rates of amphipods and snails vary depending on the time of year (Table III-4). In May amphipods have a much lower grazing rate than they have in August, whereas the reverse was true for snails. The grazing rate of snails in May was very variable, perhaps because some snails layed eggs during this experiment.

Table III-4. Grazing rates of amphipods and snails on *Ulva* in the laboratory during May and August. (Values are means with standard deviations in brackets).

		May			August	
	Control	Amphipod	Snail	Control	Amphipod	Snail
Initial weight *Ulva* (g wet wt)	1.01 (0.49)	0.80 (0.12)	0.90 (0.30)	1.83 (0.31)	1.20 (0.14)	1.20 (0.56)
Final weight *Ulva* (g wet wt)	1.37 (0.48)	0.89 (0.18)	0.92 (0.29)	2.50 (0.63)	1.29 (0.05)	1.43 (0.42)
% change	36%	11%	2%	37%	8%	19%
Grazing Rate:						
g *Ulva* (g grazer)$^{-1}$ week^{-1}		0.57 (0.55)	3.05 (2.97)		2.41 (0.25)	1.71 (0.34)
g *Ulva* grazer^{-1} week^{-1}		0.024 (0.016)	0.038 (0.032)		0.050 (0.033)	0.045 (0.041)

Reproduction

Reproductive products were released by *Ulva* throughout the year, although the percentage of reproductive plants during the winter months was much lower than in the spring or the summer (Table III-5). The percentage of an individual plant that released its cell contents as gametes or zoospores is relatively constant for each month sampled, being on average about 50%. The empty thallus cells left attached to the plant after the release of gametes or spores weighed 67.4 ± 11.2% of the photosynthesizing plant's weight. This indicates that on average

32.6% of the reproductive portion of the plant is released as spores or gametes. The remaining empty thallus cells detach from the green portion of the plant and become drift material.

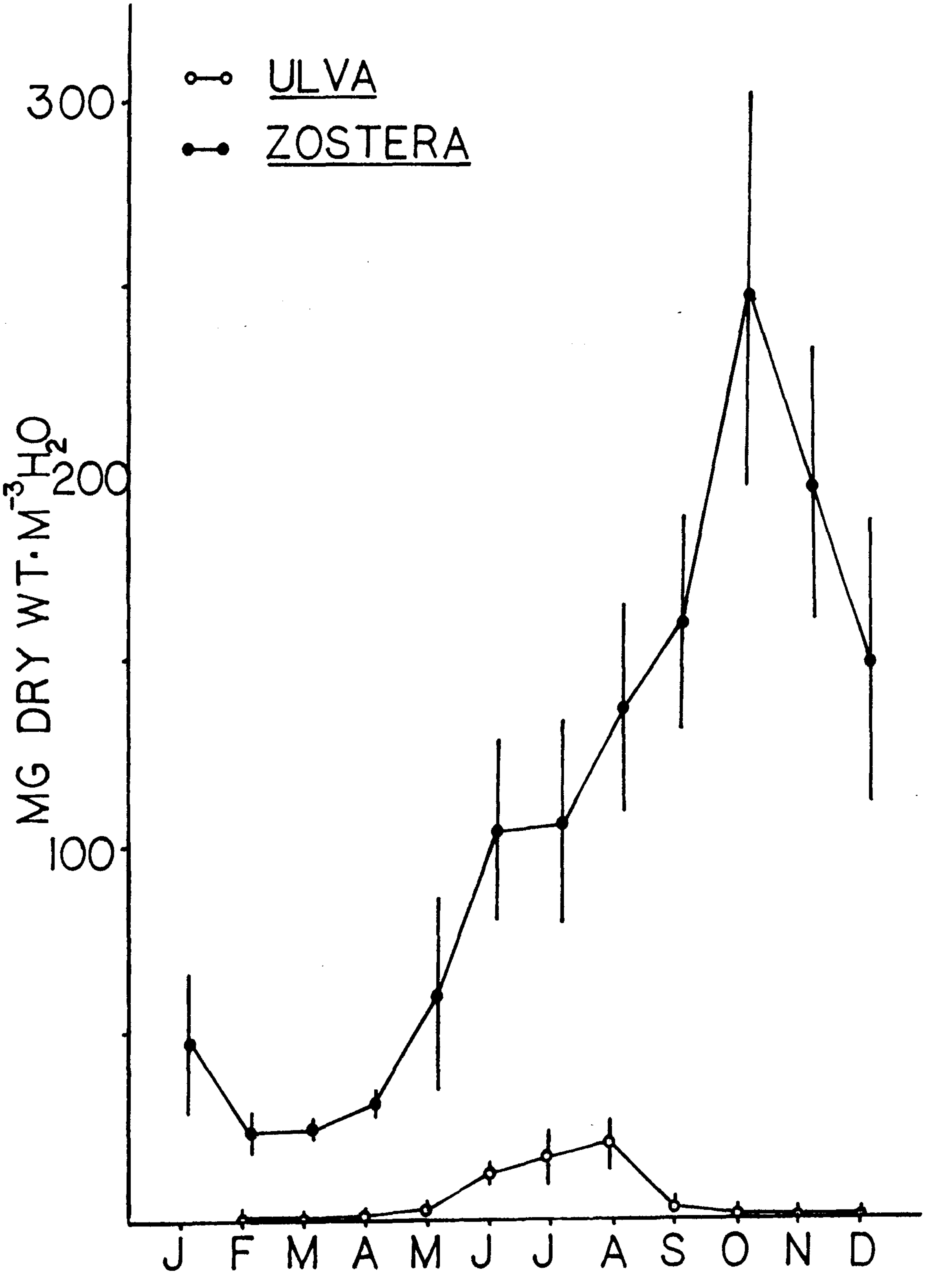
Table III-5. The percent of reproductive Ulva plants from the mid intertidal at Fossil Point and the percentage of the plant that had reproduced, measured on a bimonthly basis from February - December 1984. Samples are from 0.125 m^{-2}quadrat, N=4. Values are means standard deviations.

Month	% of plants which were in reproductive condition	% of an individual plant that had reproduced
February	49.4 ± 9.8	47.4 ± 12.1
April	92.1 ± 5.3	51.9 ± 14.7
June	93.0 ± 4.7	49.7 ± 11.7
August	89.6 ± 9.1	52.8 ± 12.4
October	71.2 ± 11.5	44.7 ± 10.2
December	47.2 ± 11.4	43.2 ± 12.0

Drift

Only small amounts of Ulva were found in drift samples taken during the flooding tide. By far the largest amount of macrophyte material that drifts out of Coos Bay is Zostera marina (Figure III-3). Larger amounts of Ulva were found in the drift between June and August;

FIGURE III-3. The amount of _Ulva_ and _Zostera_ per m^3 of water filtered collected drifting at the surface downstream from the study site. Points are means and the vertical bars standard error of the means.


ULVA
ZOSTERA
300
200
100
MG DRY WT·M^{-3}H$_2$O
J
F
M
A
M
J
J
A
S
O
N
D

corresponding to the period of maximum biomass accumulation. Very little drift material was seen in April or May, a time of rapid growth of the population, as well as in September, the fall decline. The amount of algae trapped in the nets on the bottom of the bay was relatively small (Figure III-4). Qualitative estimates made by visual surveys showed that during the late summer large quantities of _Ulva_ are cast up in the wrack line, particularly after a strong north-west wind which dislodges much of the loosely attached or unattached material in the eelgrass beds. Attempts to measure this input were not successful as the amounts are extremely variable on a tidal and daily basis, but it seems likely that much of the material that is torn from the substrate or washed out of the _Zostera_ beds is cast up on the shore and incorporated into the beach sediments. This is also suggested by the small quantities of _Ulva_ trapped in the drift nets placed on the bottom (Figure III-4).

Once cast up breakdown of _Ulva_ was rapid. Drift algae placed in bags in the wrack line were rapidly broken down into particles smaller than 5 mm in diameter (Figure III-5). _Ulva_ was lost at a rate of 10.55% day $^{-1}$, nine days after the initial placement, almost all of the algae had disappeared from the bag. Six of the 12 bags were partially buried in the sediment when retrieved on day 5 indicating that much of the algae that are cast up in the wrack line becomes buried. In the low intertidal zone, below _Callianassa_ sp. beds, burial of _Ulva_ in situ occurs during the growing season and during the fall decline. In August 1984 8.0 ± 11.5% of the _Ulva_ I collected from the low intertidal site was

FIGURE III-4. The average amount of Ulva per m^3 water filtered drifting on the bottom during an ebbing tide downstream from the study site at Fossil Point. Points are means and vertical bars are standard errors of the means.

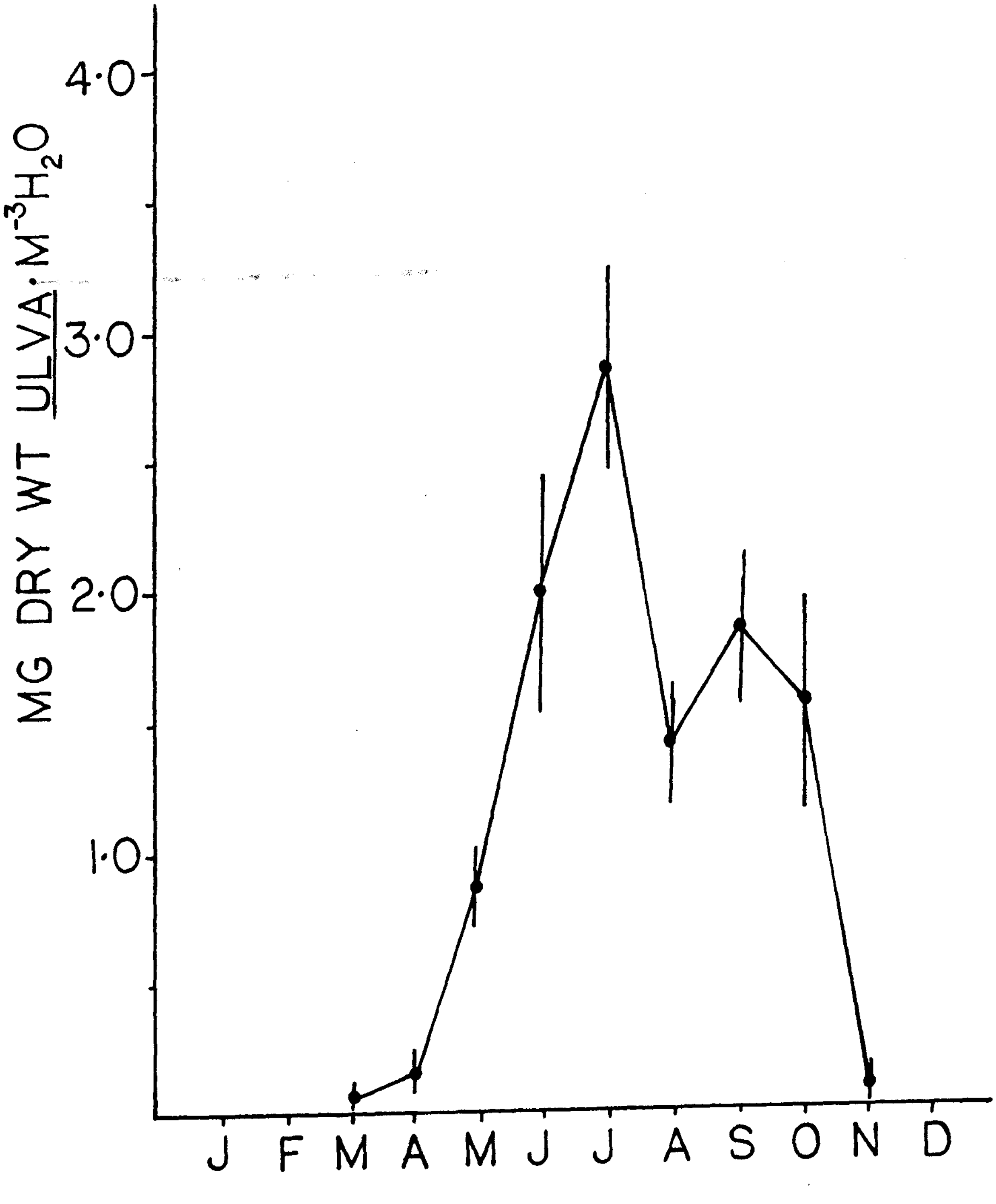
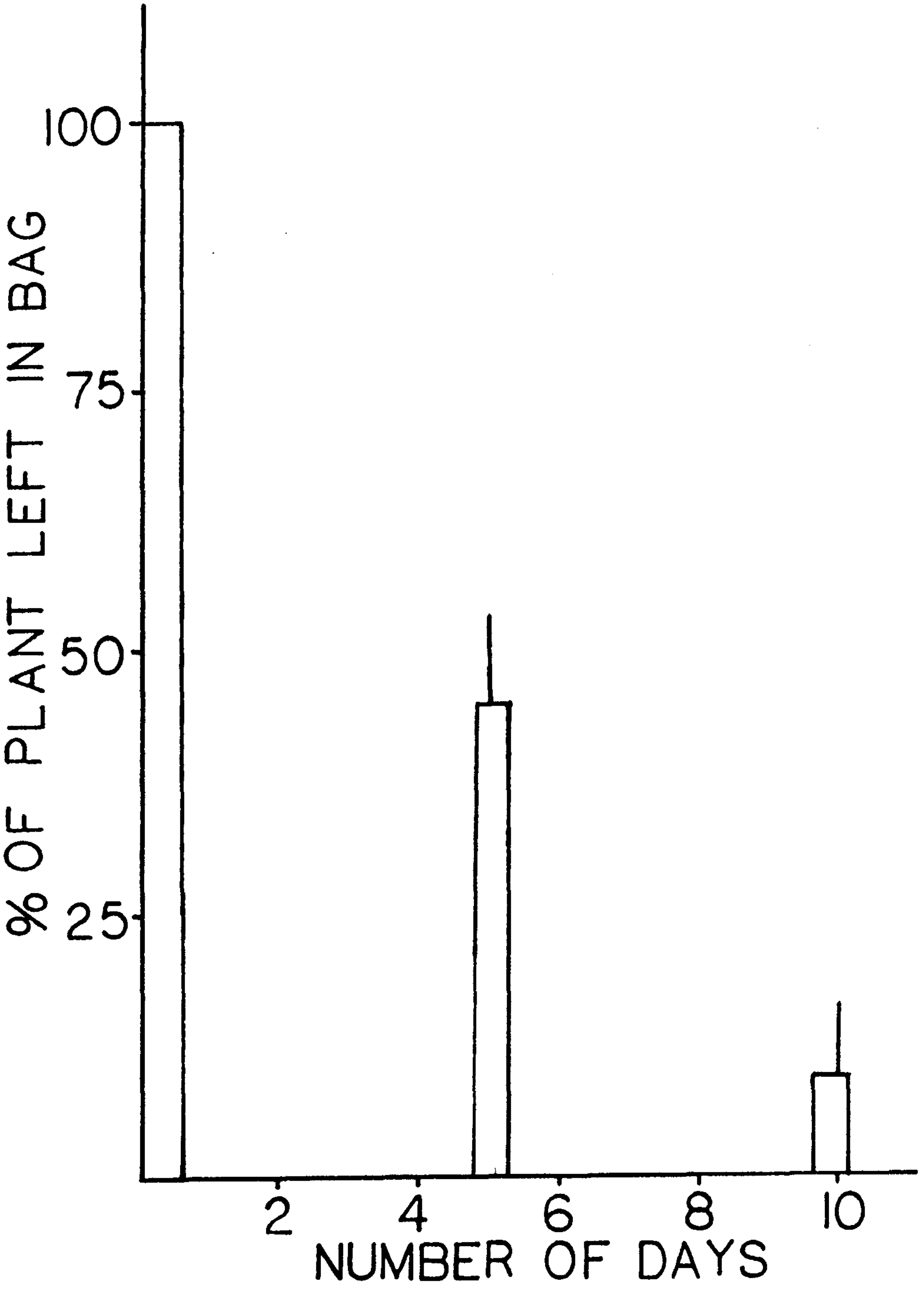

MG DRY WT ULVA·$M^{-3}H_2O$
4·0
3·0
2·0
1·0
J
F
M
A
M
J
J
A
S
O
N
D

FIGURE III-5. The rate of breakdown of *Ulva* in mesh bags staked in the intertidal drift line at Fossil Pont. Values are means and the vertical bars are standard deviations.


100
75
50
25
% OF PLANT LEFT IN BAG
2
4
6
8
10
NUMBER OF DAYS

partially buried in the sediment, and in October 1984 21.8 23.7% was buried.

Dissolved Organic Carbon and Photosynthetic Rates.

In seven 2 hour incubations of Ulva in 30°/oo seawater, the carbon fixation rate averaged 1.01± 0.63 mg C (g dry wt algae)$^{-1}$ hr^{-1} , and the amount of carbon released by the photosynthesizing plant averaged 0.090± 0.074 mg C (g dry wt algae)$^{-1}$ hr^{-1}. This represents an average of 7.8% of the recently fixed carbon (Table III-6). Some carbon was fixed by algae incubated in the dark bottles and on average 18.5% of this was released as organic carbon, although this quantity represents only 2.2% of the amount released during photosynthesis. A comparison of the rate of carbon incorporation during photosynthesis was made with values from the literature (Table III-7). The value for g C m^{-2} day^{-1} from this study was determined by taking the biomass from the low intertidal site in August 1984 (195.2g) and assuming that day length during this period was 12 hours.

Discussion

Brant Geese are present at a time that corresponds to the begining of the spring growth period of Ulva, and the geese are then the principal consumers of algal material. Grazing rates will be influenced by the size of a grazer's population, the migratory movements of animals and the availability of plants. In some years the grazing activities of

Table III-6. Photosynthetic rates and release of dissolved organic carbon (DOC) from *Ulva* measured using ^{14}C labelled sodium bicarbonate. (SD = standard deviation)

	Carbon Fixation Rate	Dissolved Organic Carbon	% DOC
	mgC (g dry weight Ulva^{-1}) hr^{-1}		
Light Incubation			
	0.28	0.016	5.7
	0.33	0.017	5.2
	0.64	0.053	8.3
	0.97	0.071	7.3
	1.43	0.090	6.3
	1.52	0.171	11.3
	1.93	0.209	10.8
mean ± SD	1.01 ± 0.63	0.090 ± 0.074	7.8 ± 2.4
Dark Incubation			
	0.004	0.001	25.0
	0.013	0.001	7.7
	0.014	0.004	28.6
	0.014	0.002	14.3
	0.018	0.003	16.7
mean ± SD	0.013 ± 0.005	0.002 ± 0.001	18.5 ± 8.4

Table III-7. Daily Production figures for *Ulva* sp.

Species	Production		Reference
	g C m^{-2} day^{-1}	mgC (g dry Wt^{-1}) hr^{-1}	
Ulva sp.	2.4	1.01 ± 0.63	this study
Ulva californica	3.1	3.3	Littler & Murray 1974
Ulva expansa		10.3 ± 0.4	Davis 1981
Ulva fasciata	4.6		Lapointe & Tenore 1981
Ulva taeniata		3 - 11	Littler & Arnold 1982
Ulva lobata		9.5	Littler & Arnold 1982
Ulva rigida		5.5	Littler & Arnold 1982
Ulva californica		2.5	Littler & Arnold 1982
Ulva sp.		3.5	Littler & Arnold 1982
Ulva sp.	2.2		Price & Hylleberg 1982
Ulva sp.	1.04 2.50		Blinks 1955

figures are means (± standard deviations) the geese can severely depress the population of algae, thus restricting its potential for growth and reproduction, and colonization of new sites. The effect the geese have on the suppression of biomass is evident for approximately two months after they have left the area. After this time no differences in the biomass is evident suggesting that other factors then become more important in controlling the Ulva populations.

Aside from the removal of algal material by direct consumption Brant also act as algal shredders. Much of their fecal material is made up of small pieces of undigested algae. By their grazing activities Brant Geese increase the rate of passage of Ulva to the detrital cycle. A similar situation has been described for green turtles (Chelonia mydas) feeding on Thalassia (Thayer et al. 1982), although in this case cellulases are present in the turtle's digestive tract, so that food is more thoroughly processed.

Measuring invertebrate grazing by the number of snails and amphipods found on the Ulva plants at low tide indicates that in the mid intertidal the greatest amount of grazing occurs during the late summer and fall months. Peak numbers of amphipods were also found then by Price and Hylleberg (1982) on algae in False Bay, Washington. In the low intertidal the number of grazers is lower and there was very little variation throughout the growing season. This may be related to zonation patterns of invertebrates that are the result of predation (Lubchenco and Menge 1978; Dayton 1984). Grazing rates from this study are comparable to those obtained for amphipods feeding on Ulva by Price and Hylleberg (1982) and by Pregnall (1983a) for amphipods and snails feeding on *Enteromorpha*.

Reproduction can reduce the amount of biomass. Rhyne (1973) attributed the early summer decline of *Ulva curvata* and *Ulva rotundata* on the North Carolina coast to the rate of reproduction outstripping vegetative growth, coupled with the detachment of thalli from their substrate. He did not determine the relative importance of either loss.

The largest amounts of *Ulva* were found drifting in the bay between June and August, very little was collected in September, the fall decline of the populations. This was surprising, as the fall decline in estuarine algae is sometimes attributed to removal from the substrate by storms (Price and Hylleberg 1982) and one would expect to find considerable amounts of *Ulva* drifting in the estuary at this time. Rapid breakdown of the drift algae occurs and it is thus possible that by mid September the large amount of biomass produced in August had already broken down into small particles or had been incorporated into sediments. Although not measured in this study, the decomposition rate of algae is more rapid under submerged conditions (Josselyn and Mathieson, 1980). Smith and Foreman (1984) found that flat blades of algae decomposed much more quickly than morphologically more complex types and that the highest producers (which are often flat bladed) decompose most rapidly.

From the small amounts of *Ulva* found in the drift samples, the amounts of *Ulva* buried in the sediments, and the qualitative assessments I made at the study site throughout the year, much of the *Ulva* that is either torn from the rock, or dislodged from the eelgrass beds as a result of wind-induced wave action is retained in close proximity to the study site. These drift algae are either washed up onto the shoreline where they rapidly decompose or are incorporated into the sediments *in situ*. Incorporation of algae into the sediments has been documented for populations of algae growing on mudflats (Price and Hylleberg 1982; Owens and Stewart 1983). Price and Hylleberg (1982) found that 8 - 20% of the September biomass of *Ulva* produced in False Bay, Washington was incorporated into the sediments during October. The *Ulva* was trapped by the shifting sediments after a storm. Litter derived from *Fucus distichus* and *Iridea cordata* growing in the intertidal and shallow subtidal respectively was retained exclusively within the shallow subtidal (Smith and Foreman 1984). Smith and Foreman (1984) indicated that the distribution of litter in the shallow subtidal was very patchy as in this study.

The breakdown of *Ulva* into small particles is rapid, so that algae torn from their substrate and washed up on the shore will quickly fragment and be utilized by microbes. Algae are broken down into small particles 3-10 times faster than vascular plants (Josselyn 1978). Algal detritus is colonized and mineralized more rapidly by microrganisms than detritus from vascular plants (Tenore 1977a), and it is also a superior food for invertebrates (Tenore 1977b). The importance of macroalgae as a food source was shown by Simenstad and Wissmar (1985) who found that detritus from algal sources and eelgrass was the primary sources of organic carbon in detritus-based food webs in Puget Sound. The decaying algae may themselves be an important food source for invertebrates. Findley and Tenore (1983) found that when the polychaete *Capitella capitata* was fed on rapidly decaying algal detritus it derived a major portion of its nitrogen from the algal substrate, whereas when fed on slower decaying marsh grass detritus the microbes colonizing the grass were the important nitrogen source.

The drift *Ulva* is rapidly broken down and becomes available for invertebrate consumption or is incorporated into the detritivore cycle, and because input is not totally concentrated in a fall peak, as in most vascular plants, fixed carbon from the *Ulva* will be available to estuarine food webs throughout the growing season of the algae. In contrast, detritus from vascular plants, which decompose much more slowly, acts as a long-term food resource as it is available during winter months when primary production is low. In this respect the two types of detritus are serving different roles.

Carbon is most rapidly transferred from the living algal blade to estuarine waters through the release of dissolved organic carbon (DOC) during photosynthesis. The estimate from this study is a little higher than those in the recent literature, but is much lower than in cases where desiccation stress or damage to the plant have resulted in very high rates of DOC release (Khailov and Burlakova 1969; Sieburth 1969). Hall and Fisher (1985) estimated that 4% of the photoassimilated carbon of algae growing in a brackish marsh was released as DOC. A similar estimate of 5% was made by Pregnall (1983b) for *Enteromorpha*.

CHAPTER IV

A MODEL OF THE PRODUCTION DYNAMICS OF THE *ULVA* POPULATIONS IN THE COOS ESTUARY, OREGON

Introduction

The experiments and measurements detailed in chapters II and III can be used to construct a model of the production biology of *Ulva* in the Coos estuary. Such a model integrates the measurements of growth and the estimates of production with the data on grazing, reproductive outputs and loss of algae from the substrate. It provides a way to evaluate the relative importance of these outputs, both seasonally and at different levels in the intertidal.

The following data from 1984 were used to construct this model:

1. biomass and growth measurements obtained in the field;
2. mean number of invertebrates (amphipods and snails) found on the *Ulva* and the estimation of grazing rates from the lab experiments;
3. estimation of consumption of *Ulva* by Brant Geese from Chapter III;
4. the percentages of reproductive plants and reproductive output measured in the field.

Construction of the Model

The biomass predicted for each month (Bp) was partitioned into a number of compartments using the data collected in the field and the laboratory. The compartments can be summarized as follows:

$$Bp = Ba + Hi + Hv + R + D$$

where

Ba = biomass measured in the field
Hi = amount eaten by invertebrates
Hv = amount eaten by vertebrates
R = release of reproductive products
D = drift algae

As noted in chapter II biomass samples were taken during the low tide series in the middle of each month so that, for example, the estimate for March actually covers the period from mid March to mid April.

Because *Ulva* produces spores or gametes once a fortnight, the biomass was divided into two equal parts, representing the growth over two, 2-week periods. The loss of algae as a result of grazing by invertebrates during the first two weeks was then calculated by the formula:

$$Hi/2 = Bp/2 \times NG \times GR$$

where

NG = number of grazers per gram *Ulva*
GR = grazing rate

Grazing rates were measured in laboratory experiments as previously noted (Table III-4), and the number of invertebrates estimated by counting those attached to the algae collected for biomass measurements.

The grazing rate obtained in the lab in May was used for March - June calculations and the rate from August for July, August and September calculations. During March and April the amount of Ulva eaten by Brant Geese was determined (Table III-2). For both of these months the quantity (Hv) was divided by 2, combined with the amount eaten by invertebrates and subtracted from the predicted biomass.

It was then assumed that the Ulva reproduced and the quantity released as gametes was estimated as follows:

$$R/2 = (Bp/2 - Hi/2 - Hv/2) \times PR \times PG \times 0.326$$

where
PR = fraction of the population that reproduced
PG = fraction of the plant that produced gametes
0.326 = fraction of the reproductive portion of the plant released as gametes (from Chapter III)

For months where no estimate of reproductive condition was measured the estimate from the following month was used.

This process was repeated for the final 2 week period of the month and the amount grazed and lost in reproduction summed with that from the first period. These outputs and the actual biomass measured in the field were subtracted from the predicted biomass as follows:

$$D = Bp - Hi - Hv - R$$

This gives the quantity of Ulva unaccounted for in these calculations which represents the loss of material from the substrate; algae that were either removed from the site as drift or were buried in the sediments. At the low intertidal site in September and at both levels in October no net growth occurred. In these cases the actual biomass from the previous month was used as the predicted biomass value.

Results and Discussion

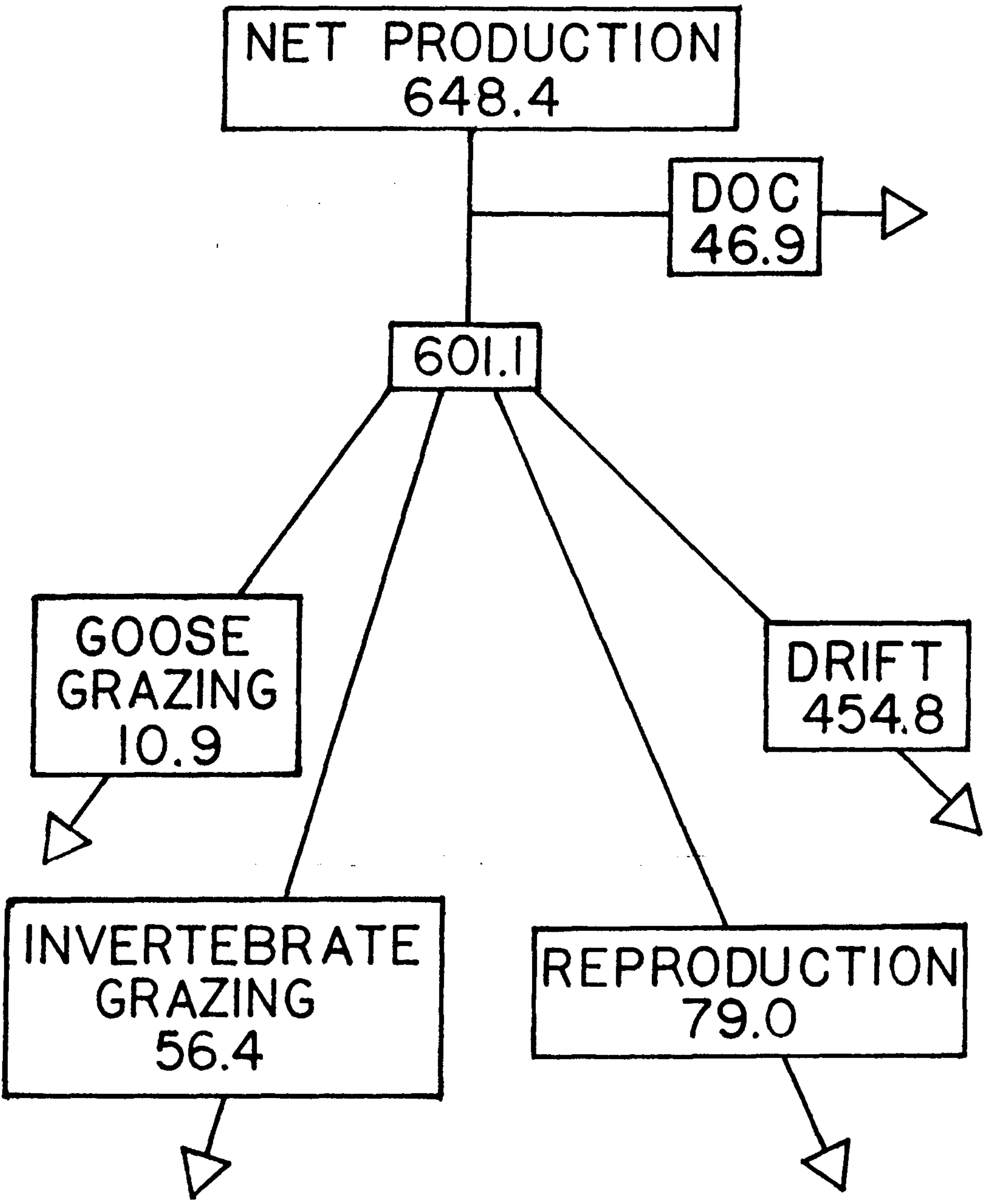
The output of the model is presented in Table IV-1, which gives the grams of *Ulva* per m^2 that are eaten, produced as gametes or lost as drift. In this table drift refers to material that was removed from the study site as whole or partial plants torn from the substrate, as empty thallus cells lost after reproduction, or as fragments of plants as a result of senescence, and whose fate it was not possible to determine; it is either incorporated into sediments or drifts free in the water column. To assess the amount of organic carbon that different production outputs represent, the values for g dry weight m^{-2} were converted to g C m^{-2} using the figure of 34.7% carbon reported by Lapointe and Tenore (1981) for *Ulva fasciata*. These results are shown in Figure IV-1. The most important pathway by which carbon fixed by *Ulva* enters estuarine waters is in the form of drift material. This output accounts for 70% of net production.

Grazing is of less importance, accounting for 10.4% of net production (Figure IV-1). This intensity of grazing is consistent with the hypothesis that only a small amount of estuarine plants is consumed directly (Correll 1978; Kikuchi 1980; Baird and Milne 1981). It is in contrast to Price and Hylleberg (1982) who estimated that amphipod populations could have consumed over half the annual net production of *Ulva* in False Bay, Washington. Grazing is most important during the early and latter part of the growing season. During the early part of the growing season grazing removes a considerable percentage (26.8 -

Table IV-1. 1984 Production Outputs of _Ulva_ in the Coos Estuary. All values are in g dry wt per m^2.

Month	Predicted Biomass	Grazing		Reproduction	Drift
		Geese	Invert.		
March					
	39.6	25.2	2.1	1.6	10.7
April					
	29.5	6.3	1.6	3.4	18.2
May					
	79.7	0	4.7	11.2	63.8
June					
	250.4	0	7.6	36.6	206.2
July					
	630.6	0	47.1	90.0	493.5
August					
	506.6	0	62.8	68.5	375.3
September					
	143.4	0	24.0	12.3	107.1
October					
	52.6	0	12.5	4.1	36.0
November					
Total	1732.4	31.5	162.4	227.7	1,310.8
%		1.8	9.4	13.1	75.7

FIGURE IV-1. Model of the production outputs of *Ulva* from Fossil Point in 1984. All values are gC m^{-2} yr^{1}.


NET PRODUCTION
648.4
DOC
46.9
601.1
GOOSE
GRAZING
10.9
DRIFT
454.8
INVERTEBRATE
GRAZING
56.4
REPRODUCTION
79.0

68.9%, Fig. IV-2) of algal biomass from the mid intertidal. This can almost entirely be attributed to grazing by Brant Geese. This removal could enhance the growth rate of the remaining algae as Lapointe and Tenore (1981) found that at low biomass levels growth was more rapid than at higher levels, but it is more likely that because the geese remove entire blades of algae they reduced potential algal production by removing biomass. Extrapolation of the results of waterfowl grazing to Coos Bay as a whole is not totally accurate; Brant Geese are more common in the study area than in many other areas of Coos Bay. This is partially a result of the decline in the numbers of Brant in recent decades probably due to hunting and loss of feeding habitat (D. Bauer, U.S. Fish and Wildlife Service, pers. comm.)

During the middle of the growing season grazers consume only a small amount of the biomass at both levels (Figure IV-3). Towards the end of the growing season (August - October) grazing again becomes more important. Herbivorous snails and amphipods remove between 12.4 and 23.8% of the total net production (Figure IV-2). This grazing contributes to the fall decline in biomass. At this time not only is growth slowing because light levels are decreasing and algae are being stripped from the intertidal by winds, but invertebrate grazers are more numerous and remove algal material. Warwick et al. (1982) suggested that grazers could be partially responsible for the fall decline in _Enteromorpha_ populations growing on mudflats. The activities of invertebrate grazers are more important in the mid than in the low intertidal (Figure IV-3); from July to October grazers consume between

FIGURE IV-2. The monthly outputs of reproductive products, drift and grazed algae as a percentage of the estimated monthly net production of *Ulva* at Fossil Point in 1984.

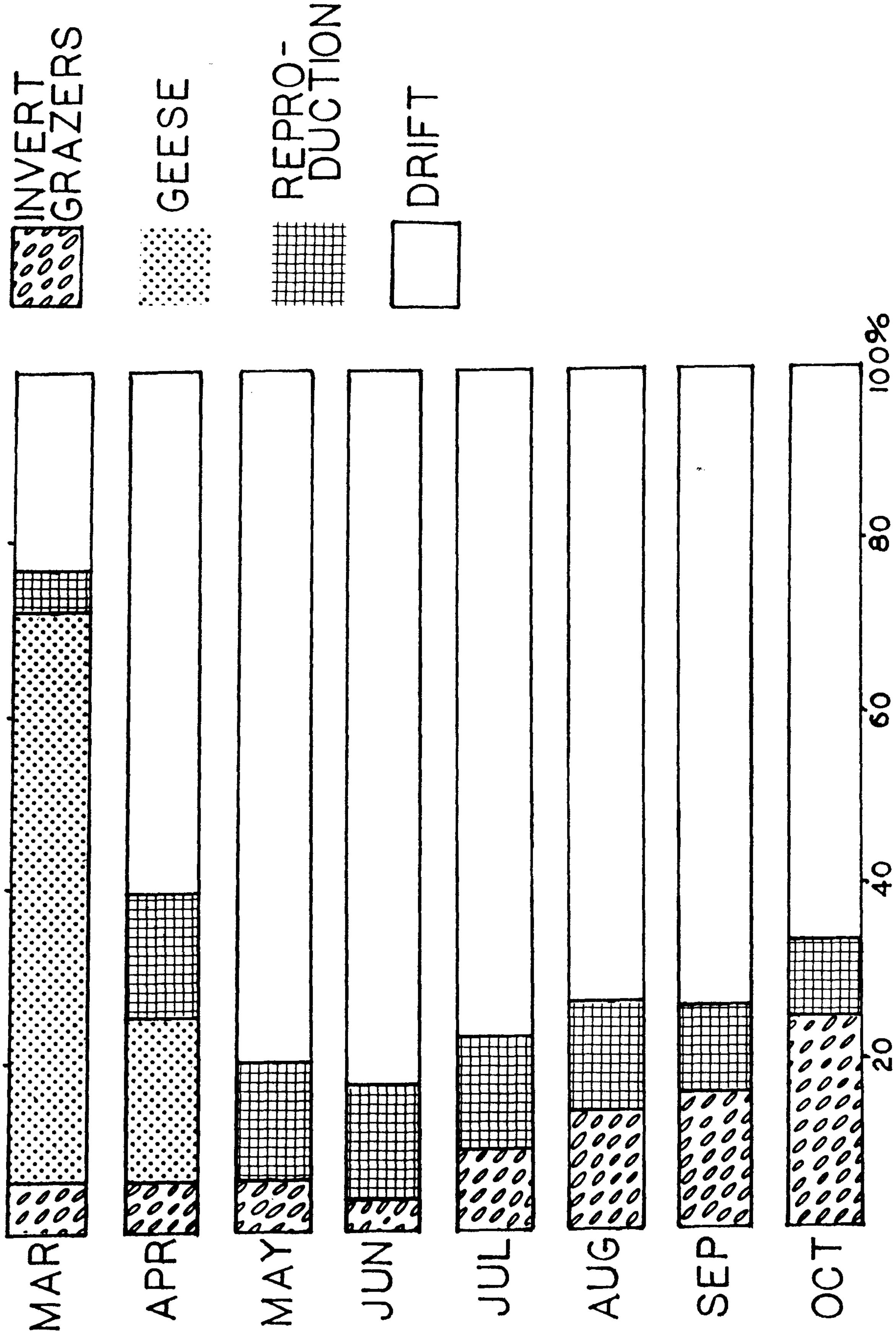
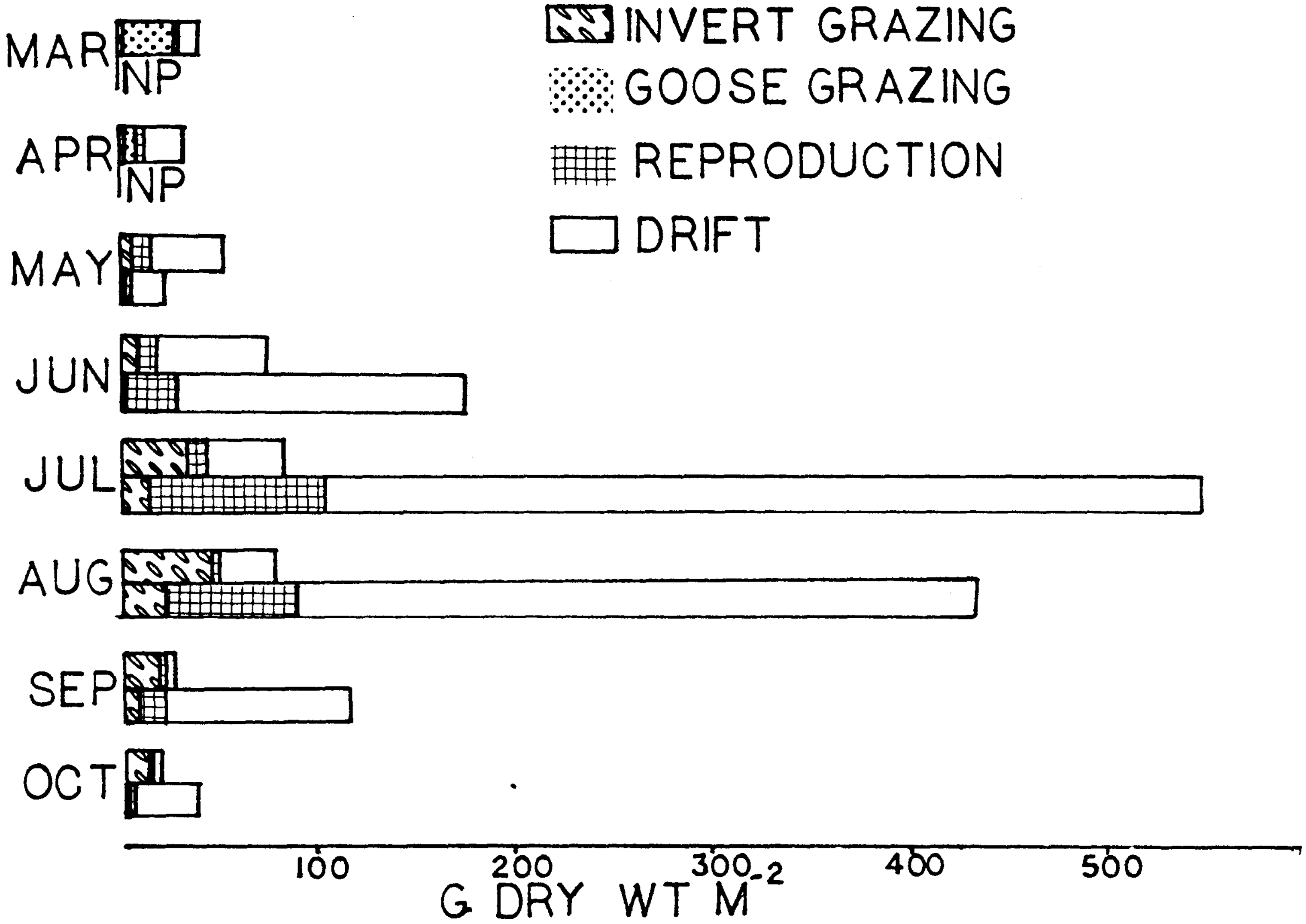

MAR
APR
MAY
JUN
JUL
AUG
SEP
OCT
20
40
60
80
100%
INVERT GRAZERS
GEESE
REPRO-DUCTION
DRIFT

FIGURE IV-3. The amount of monthly net production of _Ulva_ that is eaten by grazers, released as gametes or zoospores, and lost from the study site as drift algae in 1984. The top bar for each month represents the mid intertidal and the lower bar the low intertidal. NP: no production at the site.

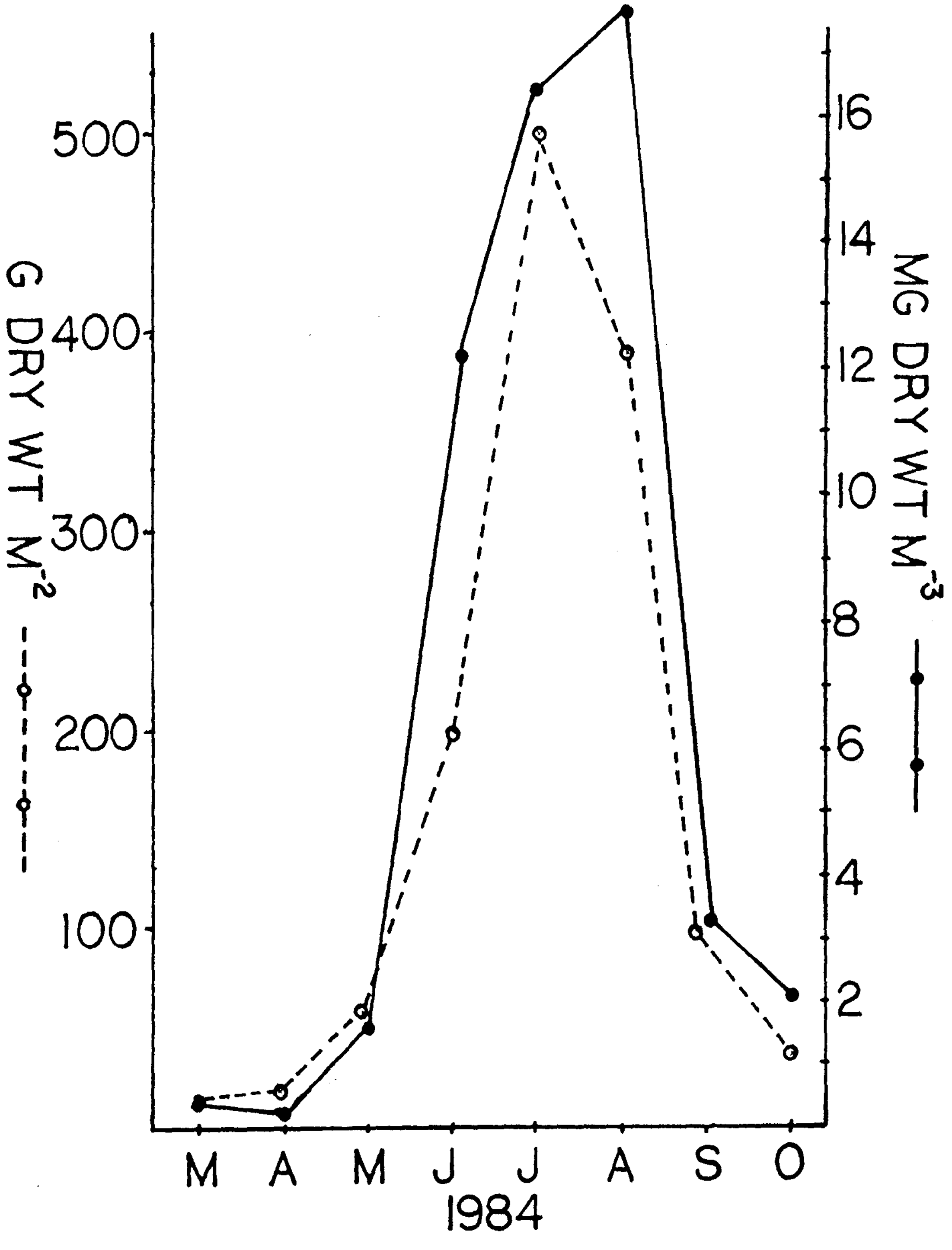

INVERT GRAZING
GOOSE GRAZING
REPRODUCTION
DRIFT
MAR
NP
APR
NP
MAY
JUN
JUL
AUG
SEP
OCT
100
200
300
400
500
G DRY WT M^{-2}

37 - 78% of the predicted biomass in the mid intertidal.

The biweekly release of gametes accounts for 12.2% of net production (Figure IV-1). Rhyne (1973) attributed the spring decline of *Ulva* in North Carolina partially to the rate of reproduction outstripping vegetative growth. Although reproduction results in a loss of biomass in the present study it was not responsible for a decline in the population biomass during the growing season. Growth rates of the two populations were similar if doublings per day are compared (0.08 - 0.69, this study; 0.02 - 0.33, Rhyne 1973). Reproductive rates could be low in the Coos Bay population. Subbaramaiah (1970) found that *Ulva fasciata* plants growing in Veraval, India were reduced in size from 20 -150cm to less than 5cm as a result of the formation of swarmers.

The amount of *Ulva* that becomes drift material is large, ranging from 61 - 82% of the net production for most of the growing season (Figure IV-2). Growth declines in September and the majority of the production is lost from both intertidal levels just prior to this period, i.e. at the end of August (Figure IV-3), with drift accounting for over 75% of the output. One way to assess the validity of the amount of drift material predicted by this model is to compare its output for this component with the quantity of material seen in the field. It is not possible to do this directly as production of drift material was determined by measuring the amount of *Ulva* found per m^3 of water filtered through nets towed at the surface or placed on the bottom and was not estimated directly from the substrate. It can be done, however, relatively by a graphical comparison as shown in Figure IV-4.

FIGURE IV-4. A graphical comparison of the amount of drift *Ulva* trapped downstream from the study site each month (in mg dry weight m^{-3} water filtered) and the amount of drift material estimated to leave the study site each month (in g dry weight m^{-2}).


G DRY WT M-2
500
400
300
200
100
MG DRY WT M-3
16
14
12
10
8
6
4
2
M
A
M
J
J
A
S
O
1984

The relative proportion and the temporal relationship of the estimated drift and that measured in the field are quite similar, suggesting that the quantities of drift estimated in the model are realistic. The fate of the algal material stripped from the substrate is unknown. As discussed in Chapter III some *Ulva* is buried in the sediments where it will decay quite rapidly (Price and Hylleberg, 1982). Burial of *Enteromorpha* in estuarine sediments during the growing season was observed by Owens and Stewart (1983), but quantities were not estimated. Some other material will drift around in the bay or be washed up in the wrack line. Josselyn and Mathieson (1980) showed that drift algae, in this case *Ascophyllum nodosum*, can represent a significant component of particulate organic matter in the estuary.

The release of dissolved organic carbon (DOC) by photosynthesising *Ulva* represents 7.8% of the recently fixed carbon. DOC is immediately available for use by bacteria (Brylinsky 1977; Pregnall 1983) and by some invertebrates (Sorokin 1973; Fankboner and Druehl 1976; Stewart 1979), and represents a rapidly utilized carbon source. This fixed carbon is lost from the plant before the estimate of production was made in the field, and so is not accounted for directly in this model. However an estimate of the annual amount of DOC can be made from the predicted biomass (Table IV-1), with the assumption that 7.8% is representative of the entire growing season. The estimate for DOC release is 46.9 g C m^{-2} in 1984. This is similar to the amount of carbon transferred through invertebrate grazers (Figure IV-1). Possibly the amount of DOC released annually is an underestimate because it does not take into account fluctuations that occur as a result of exposure to air and subsequent reimmersion, and to differing salinities (Sieburth, 1969; Penhale and Smith, 1977; Pregnall, 1983b).

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