NIWA

Taihoro Nukurangi

Sea lettuce dynamics and ecophysiology in Tauranga Harbour, Bay of Plenty

NIWA Client Report:BRP802
May 1998

NIWA

Taihoro Nukurangi

Sea lettuce dynamics and ecophysiology in Tauranga Harbour, Bay of Plenty

M. D. de Winton
I. Hawes
J. S. Clayton
P. D. Champion
R. K. Smith

prepared for

Environment B.O.P.
Tauranga District Council
Western Bay of Plenty District Council

NIWA Client Report:BPR802
May 1998

National Institute of Water & Atmospheric Research Ltd
PO Box 11-115, Hamilton
New Zealand
Tel: 07 856 7026
Fax: 07 856 0151

CONTENTS

Reviewed by:

R.D.S. Wells

Approved for release by:

J. G. Cooke

Executive Summary

This report presents the results of studies on sea lettuce in Tauranga Harbour, undertaken for Environment B.O.P, Tauranga District Council and Western Tauranga District Council between 1994 and 1998. It also includes relevant information from a Government funded research programme.

The amount of sea lettuce present in the harbour changed annually and also varied between years. In 1994 to 1996, sea lettuce was most common over the spring to early summer and did not develop to 'bloom' levels. In 1997, the level of growth remained high through most of the year and by early 1998, record levels were observed and nuisance accumulations were commonly reported. These variations in sea lettuce presence are believed to be driven by changing plant growth rate. Also, a high plant presence at the beginning of spring seemed to increase sea lettuce accumulation in summer.

Laboratory experiments showed how the growth of sea lettuce plants would change with varying levels of light, nutrient status of the plants or temperatures. Measurements of light, plant nutrients and temperature for the harbour over seasons and years were then compared to observed sea lettuce growth and the following conclusions were drawn:

- The best temperatures for sea lettuce growth were in spring and early summer (15-20°C), and higher or lower temperatures restrict sea lettuce development.

- Light availability can restrict sea lettuce growth during winter, while the growth of plants in deep water (≥4 metres) would be limited year round by decreased light passing through the water.

- Sea lettuce can take up and store nutrients from the water for short periods of time. Therefore limited sampling of harbour nutrients would not show the potential for sea lettuce growth, while analyses of nutrient levels within plants did give a good indication. Plant N levels below 1.5% or P levels of 0.1% indicated growth limitation, with growth decreasing proportionally with reducing nutrient status.

- Nutrients, nitrogen (N) or phosphorus (P), limit sea lettuce growth in Tauranga Harbour where temperature and light are favourable for growth, such as in shallow depths over summer. High plant nutrient concentrations during 1992 would have allowed rapid growth and may partly explain the sea lettuce bloom

at that time, but the role of nutrient availability during the high sea lettuce abundance in 1997/98 will not be known until analyses are completed.

- The amount of sea lettuce growing on harbour sandflats is constantly replenished by drifting sea lettuce during flood tides. Sea lettuce drift tends to remain in the intertidal area because large marine worms (polychaetes) use plant fragments to form 'nests' that are anchored in the sand.

- Sea lettuce levels accrue from the 'rate' of growth and the 'principal' or initial amount of sea lettuce. Hence, the level of material that is present before the main spring growth period would make a large difference to annual development of sea lettuce.

Nutrient limitation of sea lettuce growth is the most promising management action to reduce sea lettuce 'blooms'. This requires that target water nutrient levels be identified which will limit the growth of sea lettuce at a critical time in its growth cycle. To be feasible, these targets would have to be higher than background coastal nutrient levels. In the meantime the policy to reduce nutrient loads to the harbour should be continued.

Technical Summary

This report presents research results from a NIWA study of sea lettuce (*Ulva*) within Tauranga Harbour, commissioned by Environment B.O.P., Tauranga District Council and Western Tauranga District Council. The report also includes results from a research programme, funded by the foundation of Research, Science and Technnology (FRST), with direct relevance to sea lettuce within Tauranga Harbour.

This report includes:

- A description of the temporal and spatial variations in sea lettuce abundance within intertidal and subtidal habitats over the past 4 years and the probable role of the physical harbour environment in influencing these patterns.

- Results of a physiological investigation into sea lettuce growth response to conditions of light, nutrient availability and temperature.

- Determination of the genetic and morphological variation within the sea lettuce population of Tauranga Harbour.

Sea lettuce in Tauranga Harbour showed large seasonal and inter-annual variations in abundance. During 1994-1996 a clear seasonal pattern was evident, with low sea lettuce abundance during winter months and peak abundance during late spring (November/December) to early summer (January/February). In 1997, a late summer (February/March) decline in sea lettuce presence did not take place as in previous years, and, although intertidal strandings were minimal in mid-winter 1997, the level of sea lettuce inocula was high prior to the usual spring growth period. Subsequent sea lettuce development over the 1998 summer led to the highest intertidal abundance recorded during the course of this study.

Sea lettuce within both the intertidal and subtidal habitats in Tauranga Harbour generally showed a similar pattern of abundance, however several observations suggest that drift originating from the subtidal is important in establishing and replenishing plants in the intertidal region. The actions of polychaete worms in trapping and anchoring drifting plants was recognised as particularly important for the development of high intertidal abundance.

The development of a sea lettuce bloom is considered to be driven predominantly by variations in growth processes rather than by fluctuating rates of removal. For

example, population dynamics were clearly linked to seasonal variations in temperature and light conditions in the harbour, and the extent of sea lettuce development across a depth gradient also reflected light availability. In contrast, losses for intertidal sea lettuce populations were greatest when growth rates became limited by other factors. However, shallow subtidal sea lettuce plants were especially prone to wave/current removal, with probable re-deposition in other areas including adjacent intertidal areas.

The growth of sea lettuce (measured as photosynthetic rate) was investigated under different laboratory conditions to indicate the relative importance of the light, nutrient and temperature environment of Tauranga Harbour. Sea lettuce growth increased with increasing intensity of light received, up to a 'saturation' light level beyond which further light did not increase plant growth. This saturation light level was found to be different for plants from various depths in the harbour. By comparing saturation values to light conditions at different times and depths in the harbour, it was possible to predict when and where light availability would limit sea lettuce growth.

In the intertidal and well lit, shallow water zones (<4m below chart datum) of Tauranga Harbour, plant growth was unlikely to be light limited for much of the spring to summer. In contrast, plants at depth (>4-8m below chart datum) appear to be growth limited by the levels of light received for much of the year. These deeper subtidal plants showed several adaptations to maximise the efficiency with which they captured light energy (increased pigment content, thicker blade), providing further evidence for the importance of light availability at depth. Deeper subtidal plants were also light saturated at lower light levels than intertidal or shallow plants, and showed a lower maximum rate of growth.

Sea lettuce growth was optimum at a temperature of just under 20°C at saturating light levels and decreased markedly below 15°C and above 20°C. This temperature optima correlates with harbour temperature conditions during spring to summer and the timing of sea lettuce development.

During experiments, sea lettuce showed an ability to take up nutrients from the water, to store excess nutrients within plant tissue and to use these nutrient reserves when external nutrients were no longer available. This feature, and the fact that water nutrient concentrations in Tauranga Harbour may fluctuate considerably, means that analyses of water nutrient samples alone is of limited value in understanding the importance of nutrient availability for sea lettuce growth. Instead, the amount of nutrients in plant tissues provides a better indication of their nutrient history and growth potential.

To assess the importance of major nutrients, nitrogen (N) and phosphorus (P), for sea lettuce growth in Tauranga Harbour, the intracellular nutrient content of plants from different sites, depths and collection times was compared to their growth rate under saturating light levels. Two important intracellular N levels were identified for plants; an optimum N (1.5-2%), above which the additional N was stored and did not lead to further increases in growth, and a minimum recorded N of 0.8%. Between these two values, growth rate increased with increasing intracellular nutrient status. Below the minimum %N value, little net growth would be possible. For P, a minimum intracellular value of 0.05% was identified, but there was little evidence that plants stored P, with growth increasing up to intracellular P contents of 0.1-0.12%.

From the results above it is considered that plants in the intertidal and shallow (≤ 4m) subtidal zones of Tauranga Harbour are most likely to experience nutrient limited growth at times when light and temperature conditions promote high growth rates. This nutrient limitation was apparent in summer 1997, when plants from shallow waters had intracellular nutrient contents that were slightly less than optimum values. More plants collected from the harbour were considered to be closer to P limitation than were close to N limitation based on intracellular nutrient content. Plants in the deeper subtidal reaches of the harbour were predominantly light limited and intracellular nutrient levels indicated adequacy.

There is evidence that intracellular nutrient levels of intertidal plants were higher during the last problem phase of high sea lettuce abundance in 1992 than they were during the recent low abundance years (1994-1997). Research results indicate a possible explanation for differences in abundance; showing how 1992 intracellular nutrient content would give rise to almost double the rate of sea lettuce growth than indicated by intracellular nutrients in 1997. The reasons for higher intracellular nutrient status of plants in 1992 is not known, but may be linked to coastal water features associated with the El Niño weather pattern.

The term sea lettuce includes several very similar species of the genus *Ulva*. Although a total of three species have previously been reported from Tauranga Harbour it was not known if all or one of these were involved in the observed population dynamics. A study of the genetic variation of plants in the harbour highlighted considerable diversity, but also identified site specific genetic character. Subsequent examinations of histology (cell structure) showed all specimens collected from a range of sites were attributable to *Ulva rigida* C. Agardh, based on accepted cell characteristics. Variable plant morphology did not indicate different species and instead reflected local environmental and habitat conditions.

In summary, sea lettuce accumulates because light and nutrient conditions in Tauranga Harbour are conducive to very rapid growth of this seaweed. As it would not be acceptable to reduce water clarity in the harbour to levels that would limit sea lettuce growth, management intervention to prevent or mitigate prolific sea lettuce accumulation in Tauranga Harbour would best be considered through nutrient limitation of plant growth rates.

At present, Environment B.O.P. has a policy of reducing nutrient discharge to the harbour, which should be maintained. However, to assess the feasibility of nutrient limitation of sea lettuce and to predict the outcome of nutrient management, certain information should be sought. For example, what is the harbour regime of nutrient availability that would bring about nutrient limitation at critical times in the growth cycle of sea lettuce? Is the reduction of harbour nutrient levels feasible against background nutrient levels of coastal waters? What is the role of episodic events (eg. El Niño) in introducing nutrient supplies which cannot be controlled by management action?

The most promising approach to forecast the outcome of nutrient changes on sea lettuce abundance is to adapt predictive models which have been developed overseas, to the harbour situation. Such a model could be built from research information on sea lettuce growth responses to nutrients, light and temperature, and by considering the present or proposed harbour environment, they would enable target nutrient levels to be set and the outcome of possible actions to be assessed.

1. INTRODUCTION

Tauranga Harbour occasionally experiences problem growths (blooms) of sea lettuce (*Ulva*) on extensive areas of tidal mudflats, similar to so called 'green tides' described from coastal embayments world-wide (Morand & Briand 1996). On these occasions prolific seaweed accumulation has prompted public consternation and calls for management intervention. However, because the exact causes or major influences on nuisance algal growth were not known, there was little information upon which to base management decisions.

Over the last four years NIWA has conducted a Foundation of Research, Science and Technnology (FRST) funded study which seeks to understand *Ulva* population dynamics and identify the factors leading to prolific growth. Using Tauranga Harbour as a study site, variations in sea lettuce abundance have been documented (de Winton *et al.* 1997) while other work has identified important influences on *Ulva* accumulation (Hawes & Smith 1995). Research has also been commissioned by Environment B.O.P., to obtain information more specific to harbours and estuaries of the Bay of Plenty (e.g. de Winton *et al.* 1996). This research closely links with NIWA's FRST programme but focuses on causal factors of prolific *Ulva* development that may be open to management intervention. NIWA research also intends to complement the information gathered by Environment B.O.P.

This report summarises NIWA's research on *Ulva* with relevance to Tauranga Harbour, including results from both FRST and Environment B.O.P. funded studies. This information is the result of both field studies from Tauranga Harbour and experimental culture studies on *Ulva* plant samples collected from the Harbour and forwarded to NIWA laboratories in Christchurch and Hamilton. Three main areas of research are presented. Results of a four year investigation of *Ulva* abundance at representative intertidal and subtidal harbour sites are described and patterns are compared with corresponding variations in the physical environment of the Harbour. A second section presents the results of physiological experiments to identify *Ulva* growth response to environmental conditions and to help explain the observed *Ulva* dynamics in Tauranga Harbour. A final section presents the results of a study on genetic and morphological variability within the Tauranga Harbour *Ulva* population.

2. *ULVA* ABUNDANCE CYCLES

2.1 Background

Ulva standing crop is the result of a balance between plant growth rates and the influence of loss processes, so that excessive algal biomass result when the balance is tipped towards growth production. Some studies have documented the main causes of fluctuations in macro-algal standing crop as variations in *in situ* production together with drift accumulation, interacting with tissue removal from sporulation (Niesenbaum 1988), drift export, decay/senescence, grazing (Lowthion *et al.* 1985, Shellum & Josselyn 1982) and burial (Price & Hylleberg 1982, Owens & Stewart 1983). Conditions which determine growth rate and *in situ* production include light intensity and daylength, temperatures and nutrient availability (Lowthion *et al.* 1985, Fillit 1995). The relative importance of these processes in contributing to the growth-loss balance for *Ulva* in Tauranga Harbour needs to be understood before effective management actions to control nuisance prolific accumulations of *Ulva* can be identified.

In this section we describe the dynamics of *Ulva* abundance across a habitat gradient within Tauranga Harbour and identify temporal and spatial patterns of *Ulva* development within intertidal and subtidal habitats. These patterns are then considered against a background of the changing physical environment of Tauranga Harbour in order to identify factors leading to biomass gain and loss, and the relative importance of these.

2.2 Methods

Ulva *population dynamics*

Monitoring of *Ulva* abundance began in late summer 1994, within adjacent intertidal and subtidal study sites in the Otumoetai region of Tauranga Harbour (Fig. 2.1), an area which had experienced *Ulva* accumulations in the past. Investigations were made at approximately fortnightly intervals over summer (Dec-Feb) and at monthly to 3 monthly intervals over the remainder of the year. Monitoring took place at times of low tide, with subtidal investigations timed for slack water periods.

The subtidal site covered a 30 m wide area, extending 300 m distance from chart datum (CD) to 6 m depth below CD. Over March to December 1994, a transect line was laid from CD down to the maximum depth of 6 m, and the number and size of plants which intercepted the line were recorded by SCUBA divers. Increasing problems with laying the transect line and interference by snagging *Ulva* drift led to

the adoption of a new recording method from 1995 onward, based on an established plant survey method of Clayton (1983). The average cover (%) of *Ulva* within a 2m wide profile was estimated across each metre depth interval, as marked by permanent intercept lines. The estimated maximum *Ulva* cover within any $2m^2$ area and the average and maximum 'greatest linear dimension' (GLD) of thalli (±10mm) were also recorded.

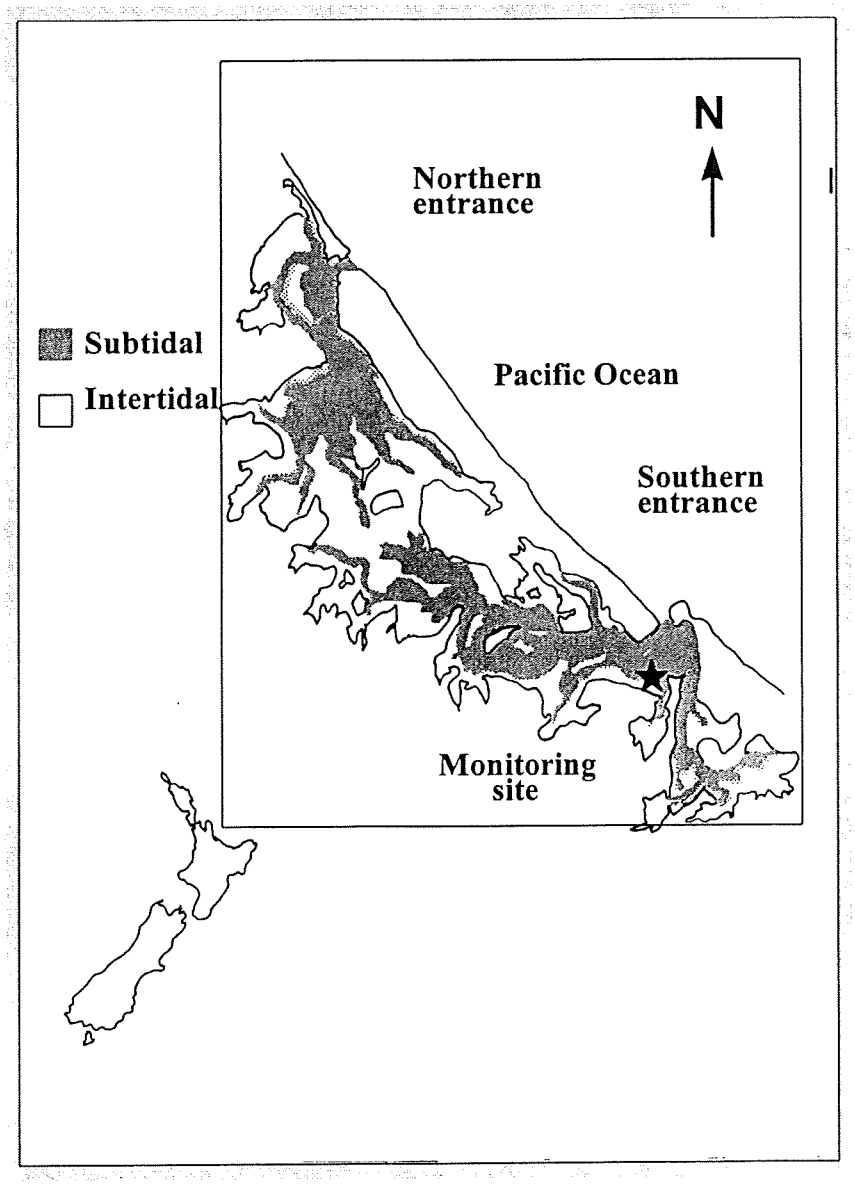

Figure 2.1 Location of monitoring site within Tauranga Harbour.

The intertidal site comprised a slightly depressed area (50 x 20m) between inner and outer (seaward) beds of *Zostera*, at a tidal height of c. 0.2-0.4m above CD. Within this area, 30 randomly placed $1m^2$ quadrats were examined and the % cover of *Ulva* was estimated for each quadrat. The attachment type of each plant was noted on each occasion except in January/February 1998, when attachment in 1-4 quadrats per visit could not be assessed due to high numbers of plants and plant fragmentation. On these occasions, or when plant biomass reached 100%, the quadrat was sampled for biomass (see below). Grazing damage and sporulation of plants were subjectively estimated for each quadrat on a scale of 0 (no visible effect) to 5 (severe damage).

The average standing crop of intertidal *Ulva* was measured periodically by collecting plant biomass within a subsample (5-10) of $1m^2$ quadrats. Maximum standing crop of subtidal *Ulva* was sampled in $1m^2$ quadrats, targeting areas of highest apparent biomass. Biomass samples were then rinsed in fresh water, dried at 80°C for 24 hours and weighed to $\pm$ 0.01 g.

Subtidal plant recruitment was investigated by deploying settlement lines (~1.5m length) of nylon braid (Donaghys Industries Ltd, 5.0 mm width) over the depth gradient. Six lines were set at each 1 metre depth interval, tied to fibreglass rods at about 300 mm off the bottom and 1-2 m apart. Settlement lines were placed on 16 May (1, 2, 3, 5 & 6 m) or 29 May (4 m) 1996 and recovered 195-209 days later. All plants which had settled on the line and which were discernible (>0.5 mm) were counted and the GLD of the largest plant on each line was measured. *Ulva* and other macro-algae were separated and dry weight was measured as described above.

Meteorological conditions

Local meteorological data provided an indication of harbour conditions for *Ulva* growth. Monthly means of solar insolation, which integrates intensity of irradiance and daylength, were calculated from daily measurements (LiCor LI200SZ) at the Tauranga Aerodrome, as were monthly means for maximum daily air temperature (YSI 703 thermistor). Measurements of daily wind run distances (Vaisala WAA15A) and direction (Vaisala WAV15A) were also accessed from aerodrome records. Mean daily sea surface temperatures for Tauranga Harbour were obtained from Environment B.O.P.'s NERMN data, calculated from 15 minute interval records, while the timing of extreme tides (2m+ high tide height) were identified from predictive tide tables.

Underwater light climate

The attenuation of light within the water column was measured close to the Otumoetai monitoring station, at two to four weekly intervals from December 1996 to March 1997, using a LiCor Li188B submersible Photosynthetically Active Radiation

(PAR) sensor. From the resulting light vs depth profiles, the attenuation coefficient for PAR (K_d - m^{-1}) was calculated as:

$$K_d = \ln(E_o/E_z)/z$$

where E_o and E_z are PAR just below the surface and at depth z (m) respectively.

2.3 Results

Patterns of abundance

Seasonal and inter-annual variations in the development of Ulva were apparent. In 1994-1996, both intertidal and subtidal *Ulva* showed an annual pattern of minimum average cover (c. 1%) from April to October, a rapid increase in spring (October-December) and maximum average cover during late spring to early summer (Fig. 2.2). Annual patterns in 1997 and 1998 were unlike previous years in that *Ulva* did not decline in late summer and the growth season was extended. In winter 1997, a June reduction in cover was noted, but by mid September *Ulva* covers were equivalent to previous summer levels. During the recent 1998 summer, the average cover of *Ulva* within the intertidal habitat, at 38%, were the highest recorded in NIWA's four year data set.

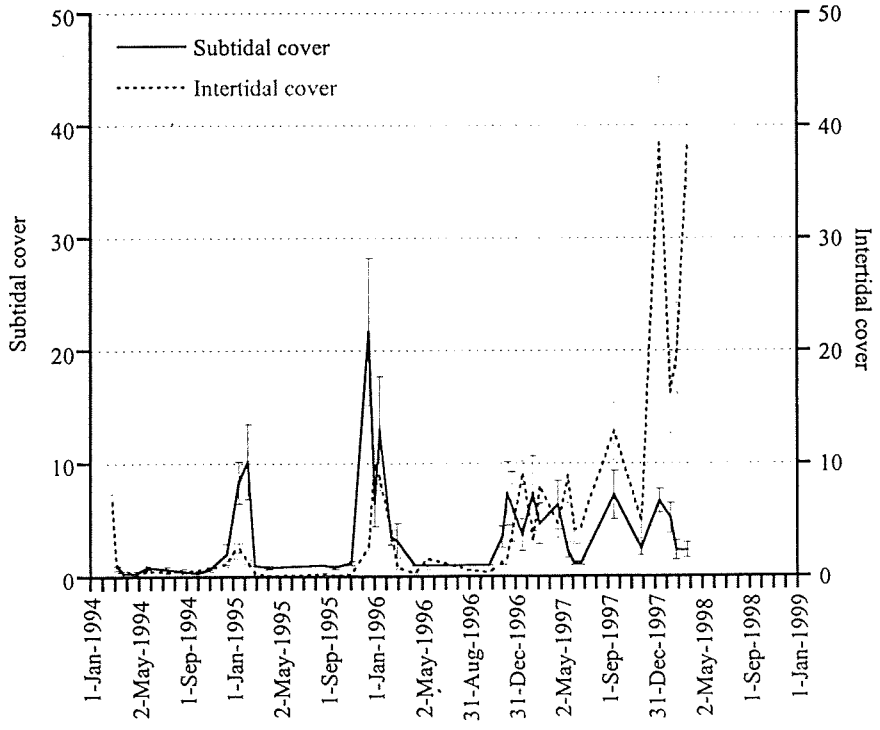

Fig. 2.2. Average cover of *Ulva* at the intertidal (n=30±se) and subtidal (n=6±se) monitoring sites.

Although intertidal and subtidal monitoring methods may not be directly comparable, it appears that the average subtidal *Ulva* covers were higher than intertidal values in both the 1994/95 and 1995/96 summers, were similar in the 1996/97 summer, but intertidal development greatly exceeded subtidal levels during the 1998 summer. The highest average subtidal *Ulva* cover of 22% was reported in December 1995. Some differences between the subtidal and intertidal habitats could also be seen in terms of the timing of *Ulva* biomass development (Fig. 2.2), with subtidal development often preceding intertidal development.

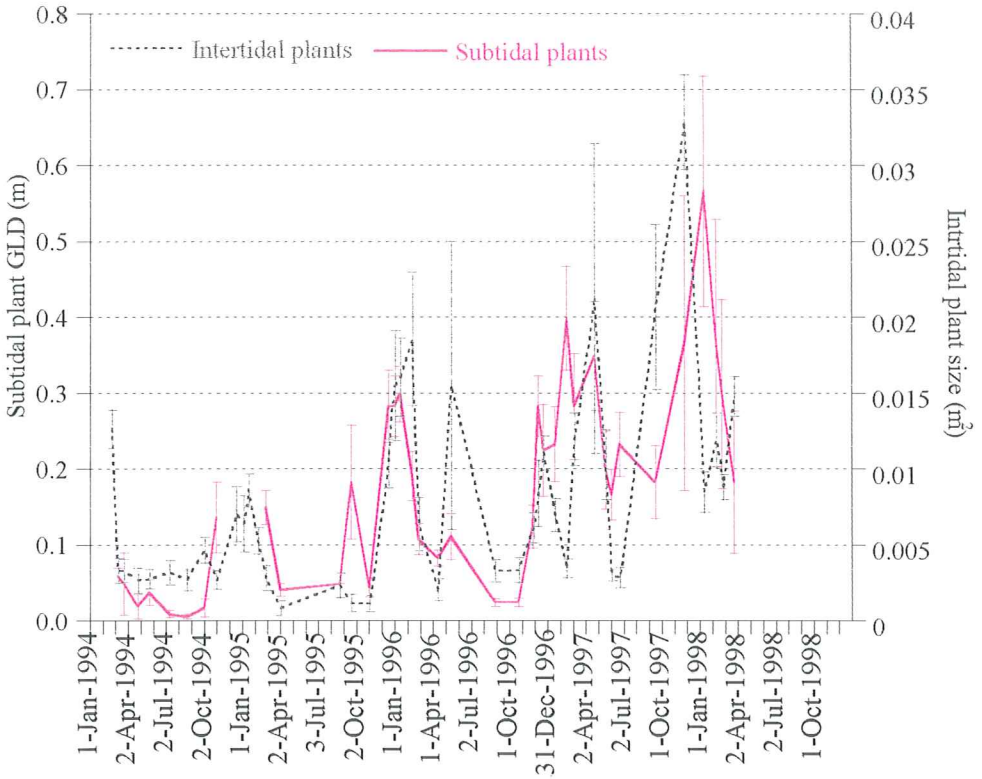

Fig. 2.3. Relative size of *Ulva* thalli over the monitoring period, as average greatest linear dimension (GLD, m) of subtidal plants (n=6 observations ±se) and average area (m^2) of intertidal plants (n=26-30 observations ±se).

Intertidal and subtidal abundance patterns were clearly linked to large changes in the size of individual plants (Fig. 2.3). Estimates of average plant GLD across the subtidal habitat were lowest at <0.1 m during the winters of 1994, 1995 and 1996 and increased in summer when plant abundance was higher. Average subtidal plant sizes tended to be greater in 1997 and 1998, with the highest value of 0.57 m recorded in the summer of 1998. The average size of intertidal thalli, calculated from plant cover and plant number and assuming all linear dimensions are the same, showed a similar temporal pattern as subtidal plants (Fig. 2.3), again with highest plant sizes values of

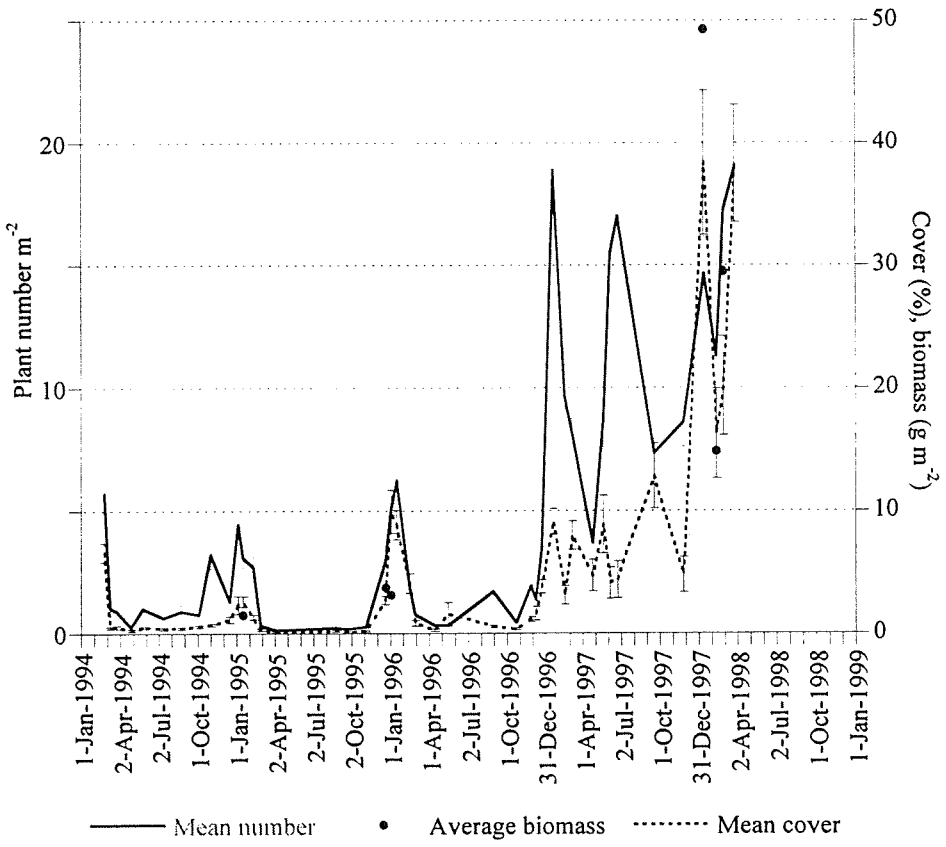

Fig. 2.4. Average number (n=26-30±se), % cover (n=30±se) and biomass (n=5-10) of *Ulva* plants within 1m^2 quadrats, randomly chosen within the intertidal site.

Prior to 1997, the mean numbers of plants recorded in intertidal quadrats varied over time in a similar pattern to *Ulva* cover (Fig. 2.4). Although plant numbers were low, generally ≤5 m^{-2}, short-term increases were associated with the higher *Ulva* cover over summer periods. In 1997 large increases in mean plant numbers of up to 18.9 m^{-2} were not linked with a corresponding increased cover (≤10%). From 1998 onwards, mean numbers of plants in intertidal quadrats have remained ≥5 m^{-2} with an average *Ulva* cover of above 15%.

The average standing crop of intertidal *Ulva* varied with plant cover, with mean biomass during periods of peak cover in 1995 and 1996 ranging from 1.53-3.74 g m^2 and a higher average biomass of 14.86-49.25 g m^2 at an equivalent time in 1998 (Fig. 2.4).

To determine the relationship between estimated intertidal plant cover and standing crop, cover/biomass data from individual quadrats was plotted, together with additional data from targeted quadrats of high cover collected during 1998. There was a linear relationship between estimated % cover and standing crop (g dry wt) within the 1 m^2 quadrats over the range of *Ulva* abundance sampled (Fig. 2.5). This

relationship is in keeping with results reported by Park (1994), although variable biomass may occur at the cover of ~100% due to the layering of plants.

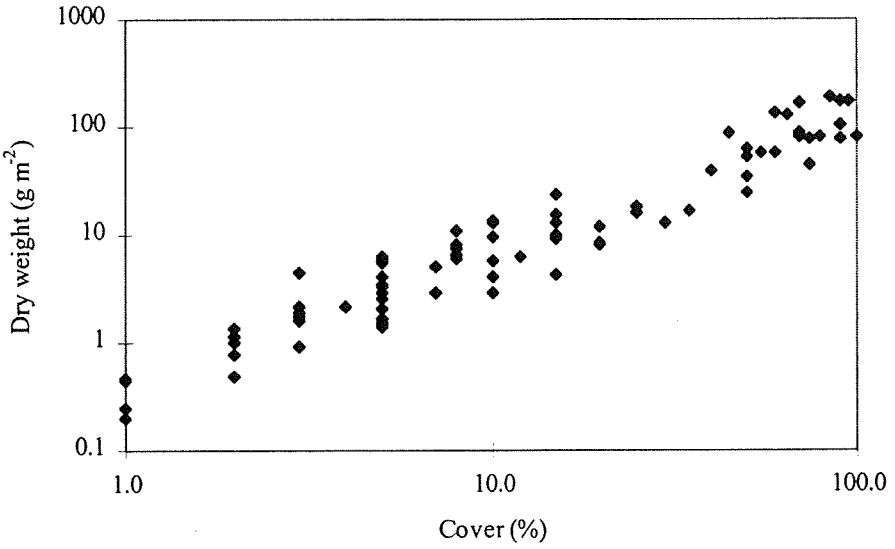

Fig. 2.5. Relationship between estimated cover (%) and sampled biomass for *Ulva* within $1m^2$ quadrats (n= 84).

Sporulation by intertidal plants was recognised by the presence of large white areas on parts of the thalli (e.g. Snow, 1996). This sporulation differed from the classic pattern of sporulation, where a narrow margin of clear tissue forms at the plant edge, which was observed in attached plants on a shallow subtidal site on at least 2 occasions (23 December 1996 and 26 March 1998). Both sporulation and grazing damage of intertidal thalli by macroinvertebrates was negligible during much of the monitoring period with few plants out of the population affected at any one time. Detectable damage was usually timed with higher intertidal covers, when plants were of a larger size (Fig. 2.6). However, in February 1998 it was noted that plants in high cover areas were prone to tearing and this that fragmentation had been exacerbated by grazing especially.

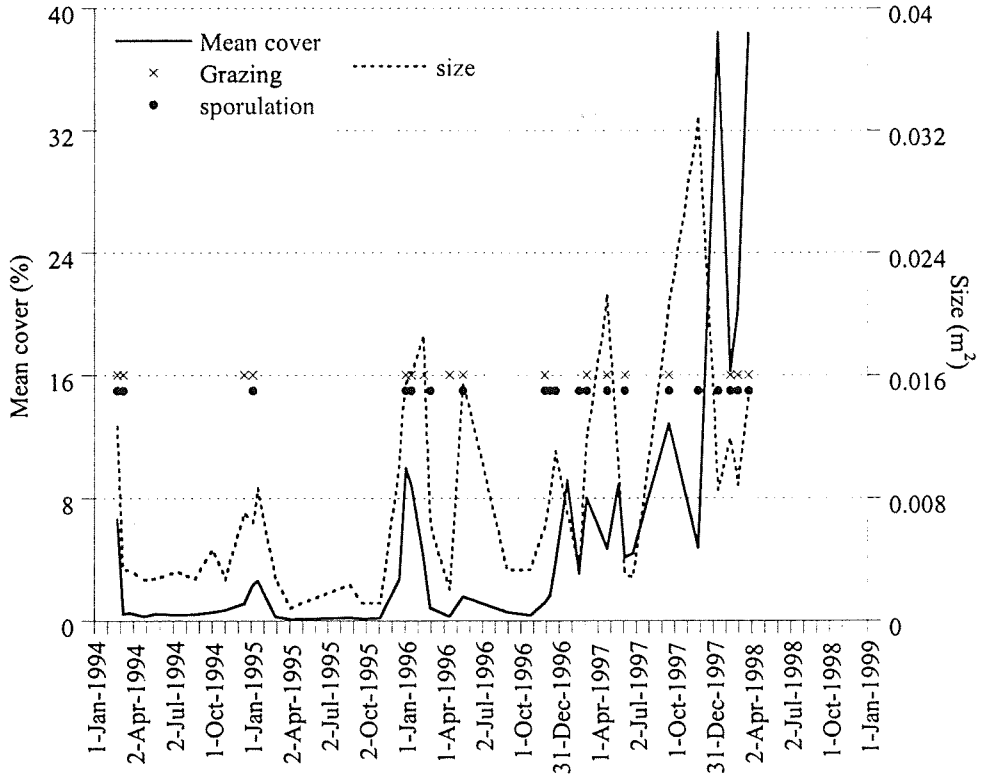

Fig. 2.6. Temporal patterns of detected grazing and sporulation damage within the intertidal population, in relation to average cover (%) and plant size (m^2).

Attachment of plants

There were changes in the form of attachment of intertidal plants over time (Fig. 2.7). During the late summer through to winter periods of 1994, 1995 and 1996, most plants were attached to shell fragments, but the predominant form changed in spring and summer to unattached plants that were either drifting freely or anchored by being incorporated into the debris associated with polychaete worm tubes. In contrast, from 1997 there was a substantial increase in the number of plants attached to shell and other solid substrata during all seasons (Fig. 2.7). In summer 1998, polychaete attached plants again became more frequent than shell attached plants and there was also a large increase in the presence of drift plants (Fig 2.7). Anchorage by burial of intertidal *Ulva* was negligible throughout the monitoring period and usually only detected at the time of highest plant cover.

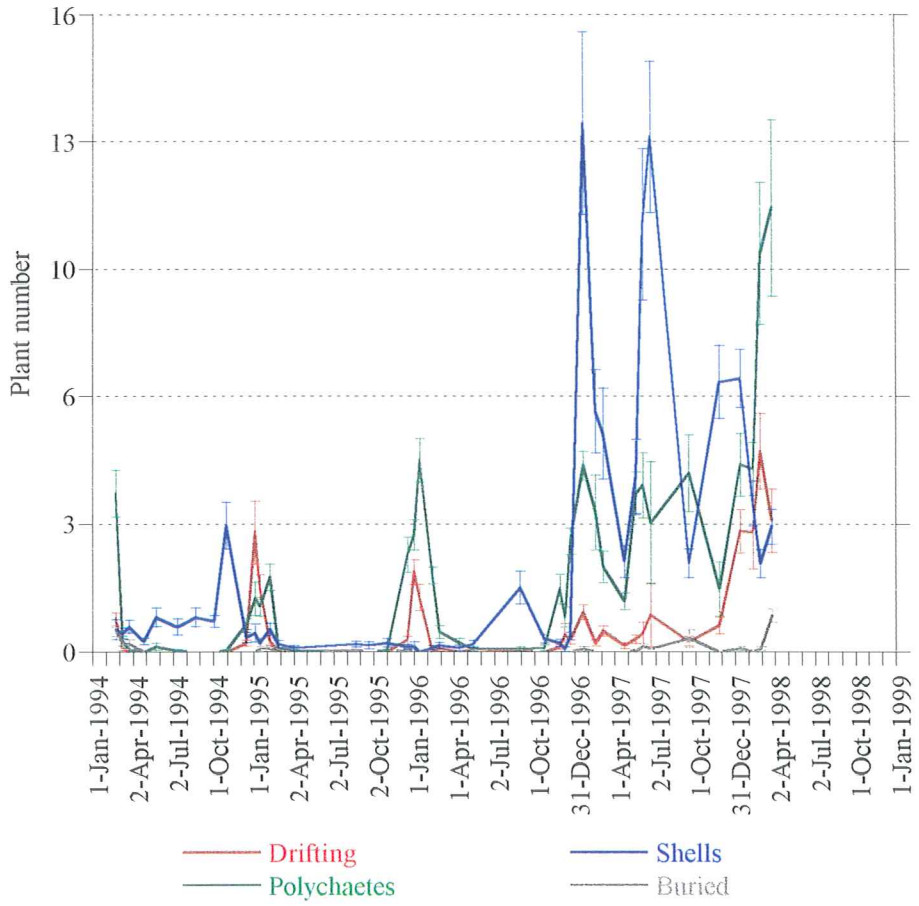

Fig. 2.7. Mean attachment types of plants within 1 m^2 intertidal quadrats (n=26-30±se).

The size of individual *Ulva* thalli was also observed to differ between attachment types, with shell attached plants in the intertidal usually being smaller than polychaete anchored or drift plants. For example, relationships between the % cover in intertidal quadrats and number of plants of a particular attachment type (Fig. 2.8) show that cover tends to be higher for any particular number of drift or polychaete attached plants than it was for the equivalent shell attached plants. For this reason, although shell attached plants were much more numerous during the extended 1997 growth season, associated plant cover did not increase greatly (Fig. 2.4).

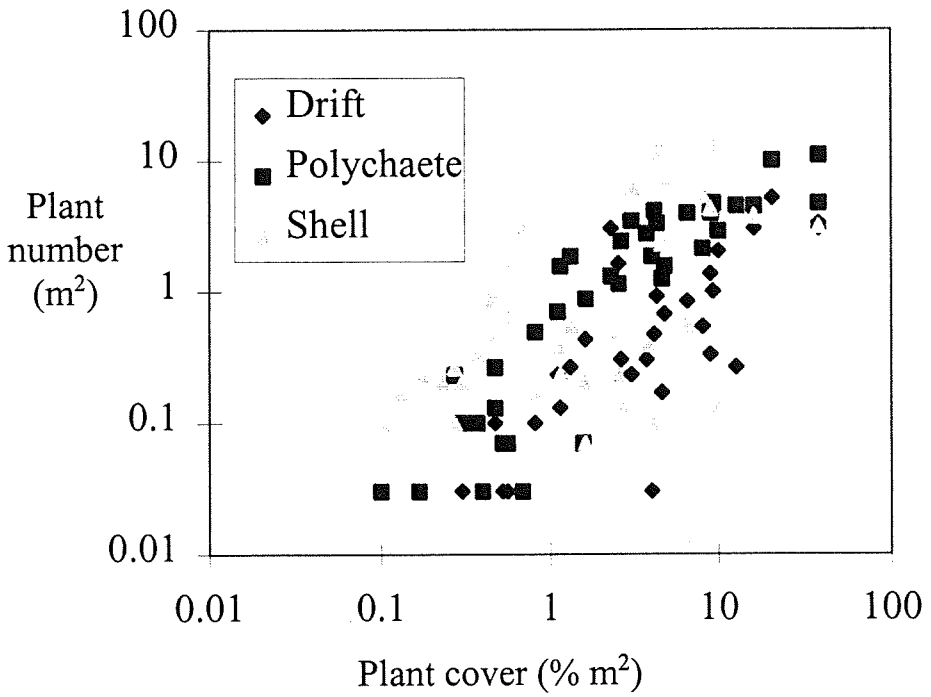

Fig. 2.8. Relationship between average *Ulva* cover (%) and mean number of plants of contrasting attachment type (n=31-42 observations).

Depth distribution

Ulva within the subtidal site showed a depth related pattern of abundance during the growth season (Fig. 2.9). The highest average plant covers were consistently recorded within the 1 to 3 m depth range, with average covers of 10-50% observed during peak abundance. Lower values were generally described for the 0 to 1 m and the 4 to 6 m depth range of the profile (Fig. 2.9).

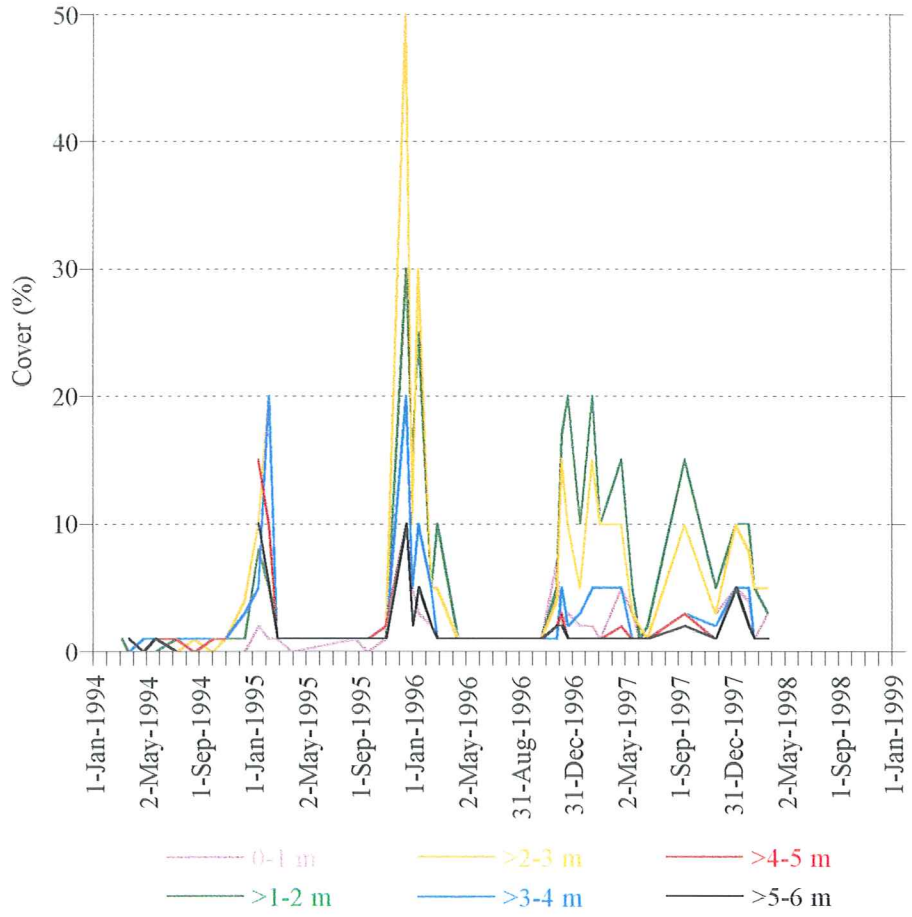

Fig. 2.9. Average cover (%) of subtidal *Ulva* across 1 m depth intervals.

The influence of depth on subtidal *Ulva* abundance is also apparent from maximum biomass samples. In January 1995, maximum biomass was greatest within 2-3 m depth (Fig. 2.10), at a mean of 64 g dry wt m^{-2}. Biomass was also relatively high (~30 g dry wt m^{-2}) at 1-2 and 3-4 m depth, but decreased below 5 m and above 1 m depth. In January 1996, the zone of highest biomass (20-30 g dry wt m^{-2}) was between 0 and 3 m depth and decreased below 3 m depth. These depth distributions of maximum biomass generally reinforced the patterns seen for average cover values described above.

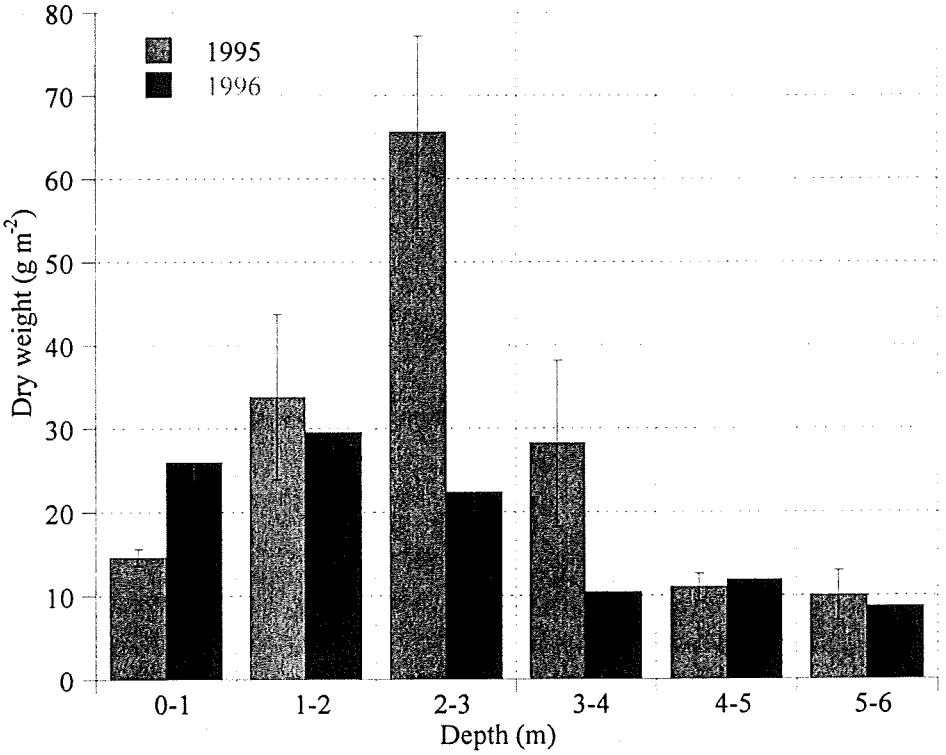

Fig. 2.10. Mean maximum *Ulva* biomass (g dry wt) within 1 m^2 quadrats (n=3±se) at 1 m depth intervals below CD, sampled on 17 January 1995 and 3 January 1996.

Subtidal *Ulva* recruitment also showed variations over the depth gradient. Recruitment was greatest at 2 m depth, with a mean of almost 80 plants settling per line (Fig. 2.11). In addition, the largest plants and highest *Ulva* biomass were recorded at 2 m depth, while *Ulva* also comprised the highest proportion of total macroalgal biomass (40%) at this depth. All values were uniformly low at 1, 5 and 6 m depth.

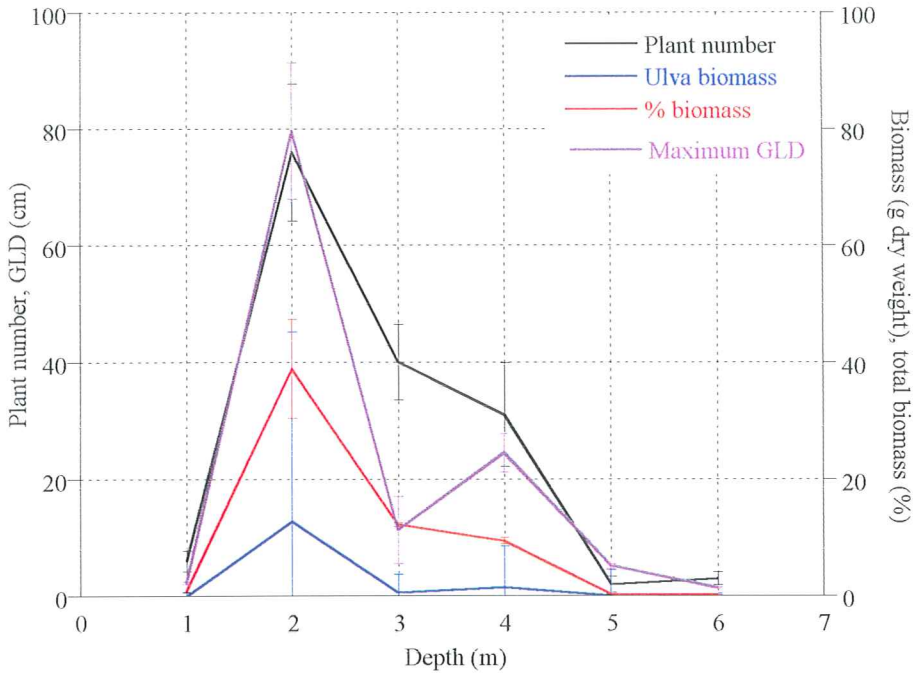

Fig. 2.11. *Ulva* recruitment on subtidal settlement lines over 195-209 days, as mean plant number per line, mean maximum thalli GLD, mean biomass (g dry wt) and % of total macroalgal biomass (n=5-6±se).

Harbour conditions

The levels of light available for *Ulva* growth within Tauranga Harbour change on a temporal basis due to changing daylength and variable incident solar radiation (Fig. 2.12). The % cover of *Ulva* populations was related to levels of solar insolation in terms of the timing of peak abundance phases, but showed little relationship in terms of the extent of development (Fig. 2.12). For example, solar insolation values were generally low during the 1996 summer, yet % cover of *Ulva* was higher than recorded in other summers. Although the timing and extent of external inputs of light energy are important, water clarity and tidal cycles would greatly modify the light climate experienced by *Ulva* growing within the harbour.

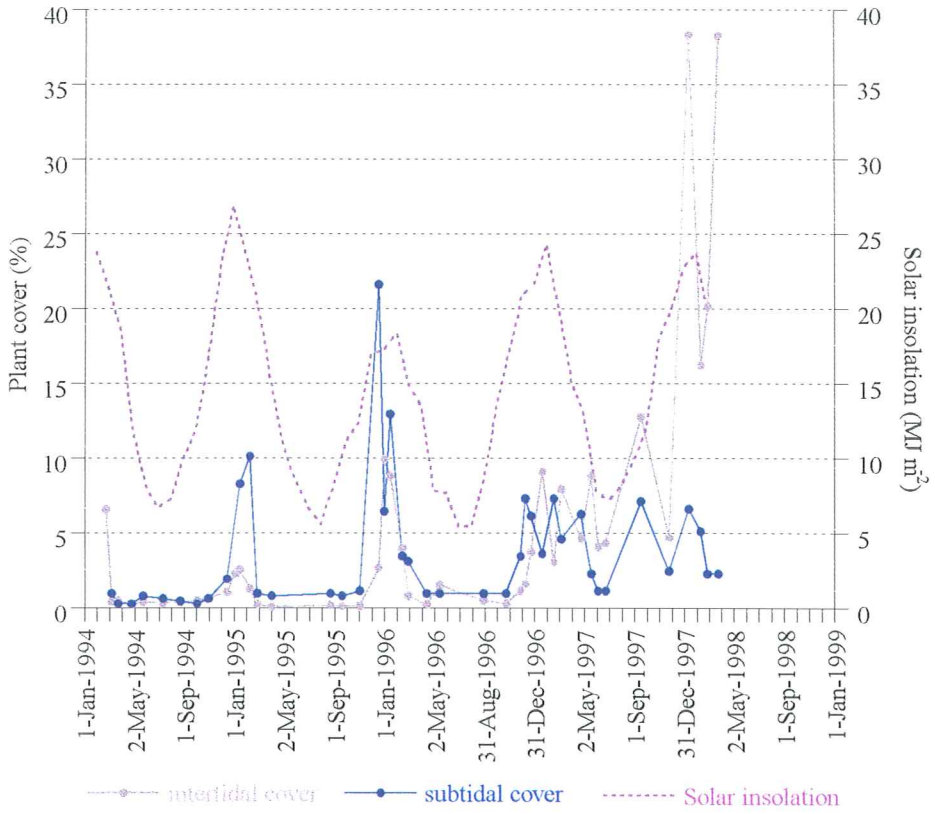

Fig. 2.12. Mean monthly values of solar insolation (MJ m^{-2}) at Tauranga, plotted against average intertidal and subtidal cover (%).

Light experienced at a specific point on the harbour floor will be dependent on the depth and clarity of the water. Both of these variables will vary over time, the former according to tidal height and the latter due to changes in particulate matter in the water column.

Overall for the period December 1996 - March 1997 we found a mean value for K_d of 0.33 m^{-1} (n = 6, se = 0.02). Percent transmission through the water surface was more variable, ranging from 73% in rough, overcast conditions to 94% in calm, sunny weather, with a mean value of 85%. The remarkable consistency of these data, particularly K_d, may reflect the single sampling location and also the lack of extreme weather as measurements tended to be made on days of good weather for logistic reasons.

Temporal changes in local temperatures are closely related to, and follow solar insolation after a delay of 1 to 2 months. Within the harbour, mean daily water temperatures ranged between 11.5°C and 22°C over an annual period, while mean monthly values for maximum air temperature at Tauranga ranged between about 13°C

and 26°C (Fig. 2.13). The temperatures encountered by *Ulva* populations would usually lie between these two sets of values, with subtidal plants experiencing lower and more stable temperatures and intertidal plants subject to higher and fluctuating temperatures.

The temporal development of *Ulva* was also related to temperature (Fig. 2.13). In all years, the initial seasonal increase of *Ulva* occurred when water temperatures first persisted at levels above 15°C. In late summer of 1995 and 1996, *Ulva* abundance declined suddenly as harbour temperatures rose rapidly to exceed 22°C. Following phases of decline, the *Ulva* population did not recover until the following summer, even though water temperatures entered the same range (15°C to 20°C) that had been associated with rapid *Ulva* development.

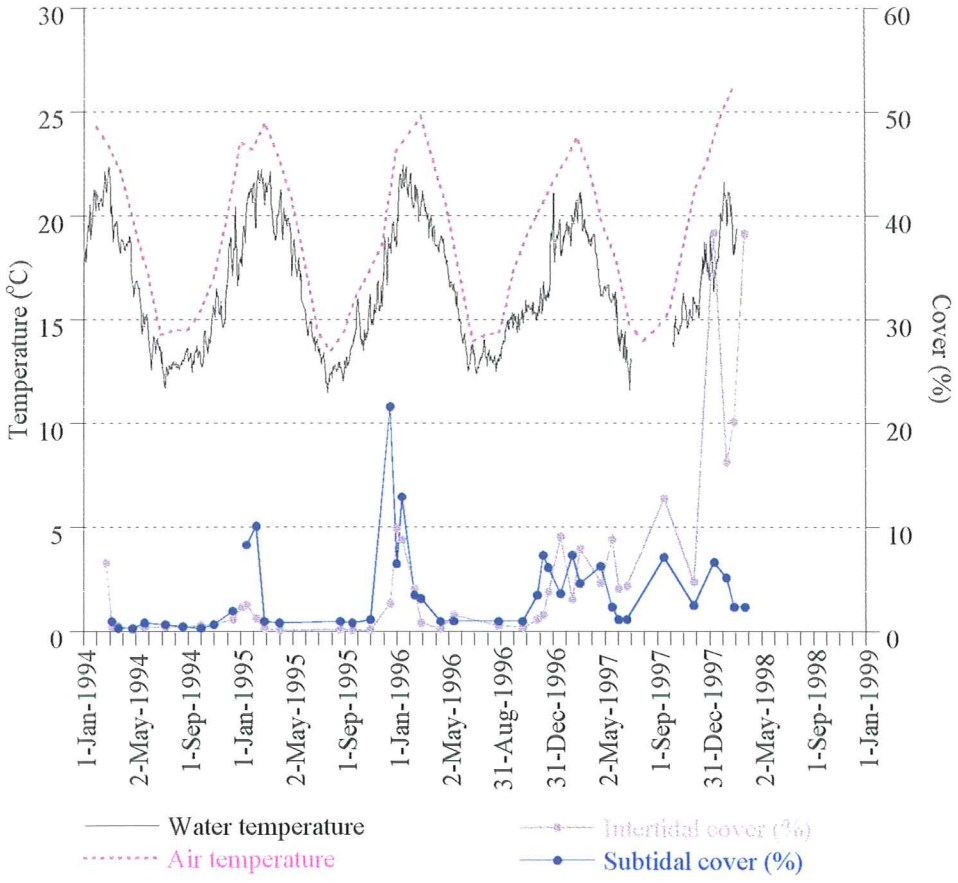

Fig. 2.13. Mean daily sea temperature for Tauranga Harbour and mean monthly values for maximum air temperature (°C), plotted in relation to average *Ulva* cover (%) in intertidal and subtidal habitats.

In 1997, water temperatures were cooler and only increased up to 21°C for short periods of time (Fig.2.13). These cooler sea temperatures may have been linked to

the development of an El Niño weather pattern in late summer 1997, which extended over the 1997/98 summer. In late summer, 1997 *Ulva* did not crash as in previous years and, instead, plants persisted until June, when a short mid-winter reduction in *Ulva* abundance was associated with water temperatures below 15°C. Harbour temperatures for the remainder of the winter period were unavailable due to equipment malfunction. Harbour temperatures in late 1997 and early 1998 were again cooler than 1994/95 or 1995/96, although water temperatures in February 1998 exceeded 20°C in association with unusually high air temperatures during that month. Concurrently, intertidal *Ulva* development was extremely high in January 1998, dropped in February and recovered to high levels again in March 1998.

Declines in *Ulva* abundance in both the intertidal and subtidal habitats were not apparently associated with extreme tide events (Fig. 2.14), suggesting that strong current flows were not responsible for the removal of biomass at times of *Ulva* decline. The potential for wind generated wave disturbance was also examined. The monitoring site has a NNE aspect with the longest fetch from the northerly quarter. A search of climatic records for major wind events (daily wind run >700 km) during periods when *Ulva* abundance was significant showed no obvious temporal relation to plant biomass declines (Fig. 2.14). However, in early 1997, there were short-term fluctuations in *Ulva* covers which appeared to relate to a sequence of cyclones. Subtidal plant covers dropped between mid-December 1996 and mid-January 1997 when cyclones Fergus and Drena had a large impact on the Bay of Plenty region, and decreased again around about the time of a large low pressure system in late February 1997. The greatest effect could be seen within 1-3 m depth, where average cover was reduced by ~10%. Interestingly, these subtidal losses were associated with corresponding increases in cover within the intertidal region (Fig. 2.2), suggesting that mobilised plants were contributing to the drift entering this habitat.

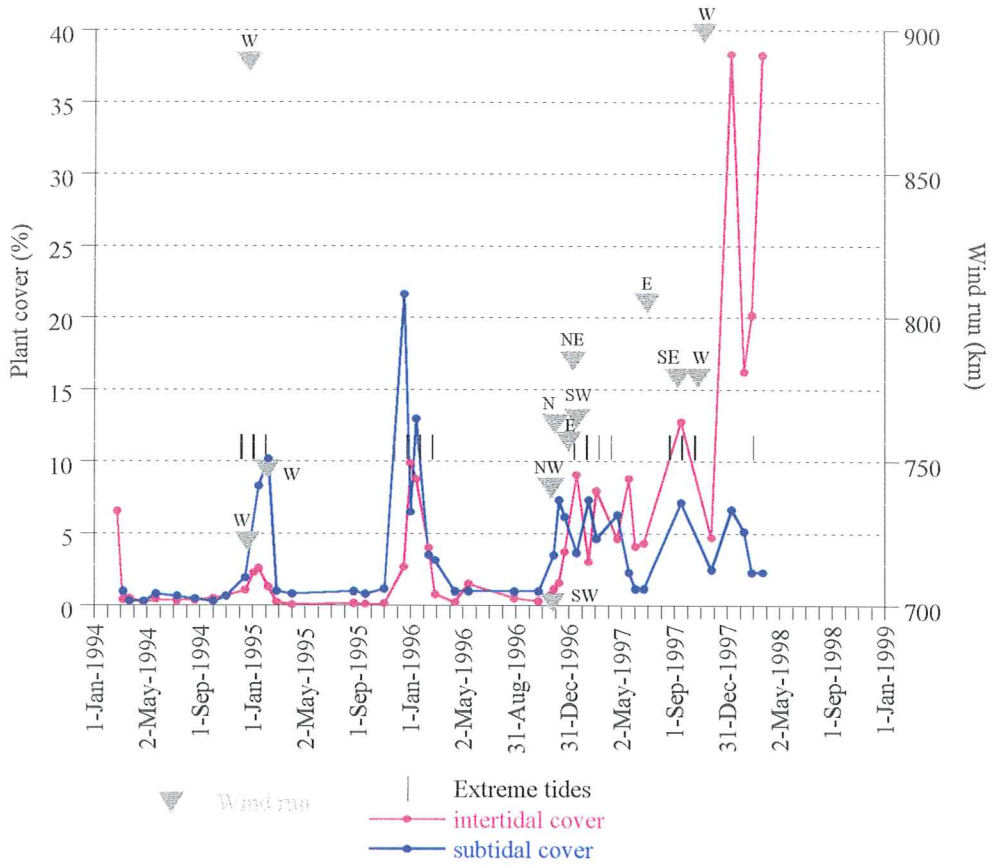

Fig. 2.14 . Windy events (daily wind run >700 km and direction) and timing of predicted extreme tide events, plotted for periods of *Ulva* abundance (Jan 1994-Mar 1994, Dec 1994-Mar 1995, Dec 1995-Mar 1996, Nov 1996-Mar-1998), together with mean *Ulva* cover (%) in the intertidal and subtidal habitats.

The predominant wind direction during the growth season for *Ulva* varied between years, with higher frequency of wind from the W-SSW (180-300°true) during 1996/97 and 1997/98 periods and an increase in NW-NNW winds (300-360°true) in 1998 (Fig. 2.15). This is in keeping with the development of an El Niño weather pattern in mid 1997-98, which tends to bring more wind from the west. Like most intertidal accumulation sites in Tauranga Harbour, the monitoring site has a NNE aspect and would be least disturbed by winds from the westerly sector.

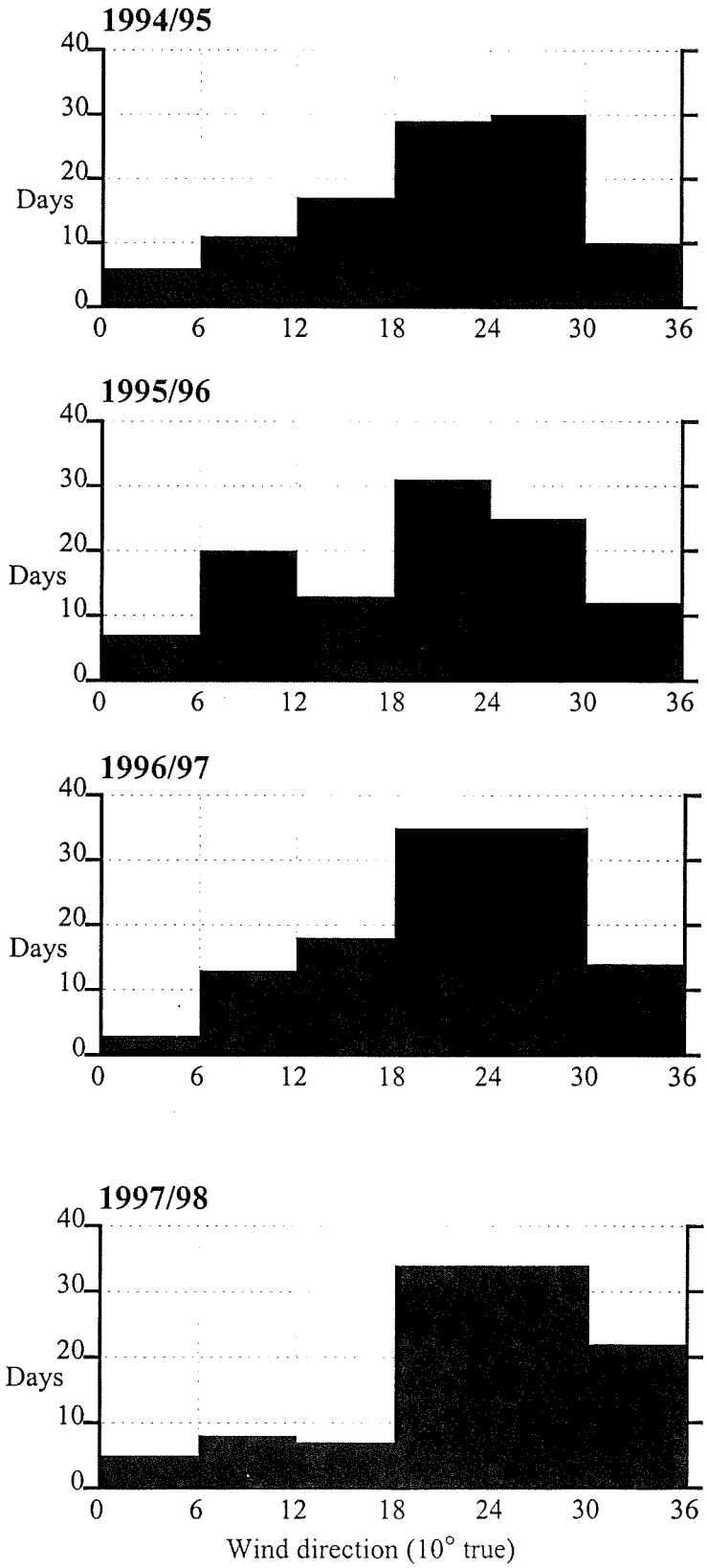

Fig. 2.15. Relative frequency (days) of wind direction (°true) during November-February of 1994 to1998.

2.3 Discussion

Ulva *population dynamics*

Ulva populations within Tauranga Harbour undergo temporal variations in abundance over different time scales. Firstly there are large inter-annual variations, which have created the history of 'bloom-bust' nuisance macro-algal accumulations. For example, this investigation initially described a low biomass phase of *Ulva* between 1994 to 1997, where average intertidal covers at Otumoetai did not exceed 15%. More recently during the summer of 1998, average intertidal covers have remained above 15% and began to approach covers of 40% or more recorded for this site during a high biomass phase of mid-1991 to early 1993 (Park 1996). Inter-annual variation such as this have been described for overseas locations which have experienced excessive macro-algal growths (Lowthion *et al.* 1985,)

Ulva abundance also changed significantly over an annual scale. During 1994-1996, both the intertidal and subtidal algal population developed on a seasonal basis, a feature commonly reported for *Ulva* and other opportunistic species (Thom & Albright 1990, Fong & Zedler 1993). In 1997 the previous seasonal pattern of development was not as pronounced, there was a high level of inocula present prior to the usual spring growth period, and subsequent increase over the spring to summer season of 1997/98 led to unusually high levels of intertidal sea lettuce. This suggests that under sustained positive growth rates, the level of overwintering material would have a key influence on biomass in spring and summer.

Environmental factors

Ulva dynamics can be considered against the background of a changing harbour environment to help identify the particular factors or factor interactions associated with *Ulva* development. In other studies this approach has identified temperature and irradiance as important factors in controlling the timing of seasonal growth and the development of maximum biomass of *Ulva* (Steffensen 1976, Jeffery *et al.* 1992). However, because environmental factors frequently operate in concert, it is often difficult to distinguish the exact causal relationships on algal development in the field (Thom & Albright 1990). For example one important feature of inter-annual climatic variation in New Zealand is the alternation of weather patterns, El Niño and La Niña. The recent (1997-98) El Niño event influenced several physical harbour parameters that potentially influence *Ulva*, however the relative importance of variations in temperature, wind direction or possible nutrient supply would be difficult to distinguish.

In this investigation, the timing of *Ulva* development appeared to respond to changes in harbour water temperatures. The sudden seasonal increases correspond to a

temperature range (15-20°C) which was considered optimal for the growth of an *Ulva* population within another New Zealand embayment (Steffensen 1976). Likewise the rapid seasonal decline also coincided with prolonged periods of water temperatures in excess of 20°C, which is thought to exceed the favourable range for *Ulva* growth (Steffensen 1976). Temperatures above optimum levels would cause a reduction in the growth rate of an alga and in other studies have been implicated in the recurrent summer dieback of *Ulva* in North American embayments (Rivers & Peckol, 1995), and linked to the reduced harbour development of green macro-algae in Southern England during some years (Lowthion *et al.* 1985). The fact that Tauranga's *Ulva* population did not recover once late summer water temperatures dropped to within the 15-20°C range might indicate other limiting factors operate, such as reduced daylength and incident solar radiation or nutrient availability (see below).

In contrast to seasonal light and temperature patterns, harbour nutrient concentration data does not show a regular and predictable variation (Park, 1996), reflecting the complex and dynamic nature of nutrient cycling. This behaviour, together with the ability of *Ulva* to take up and store external nutrients in excess of current growth requirements, means that a comparison of temporal variations in harbour nutrients and *Ulva* abundance has limited value. Nevertheless, we can consider the timing of some nutrient supply events that might be important for the dynamics of *Ulva* populations. For example, oceanic incursions of nutrient poor surface waters frequently reach the north-east coast of New Zealand in summer, and are characterised by a rapid increase in water temperature (Zeldis et al., 1998). Periods of rapid increase are seen in the temperature records for Tauranga Harbour and, as outlined previously, these were associated with a sea lettuce decline in 1995 and 1996. Conversely, periods of cool water temperatures may indicate wind driven upwelling of nutrient rich coastal waters, and such upwelling has proved important for *Ulva* growth elsewhere in the temperate Pacific (Fujita *et al.*1989). Moreover, El Niño weather is hypothesised to bring higher than usual concentrations of nutrients in oceanic surface waters which may be introduced in surface water intrusions (Zeldis et al., 1998), offering another possible explanation for the extended growth phase of sea lettuce over 1997-1998. It is also of interest to note that the diversion of sewage from a harbour to ocean outfall in mid 1995 did not lead to a corresponding change in *Ulva* abundance.

Although changes in solar insolation are not so obviously linked to *Ulva* biomass patterns in Tauranga Harbour, they would almost certainly be important. Radiation inputs not only direct subsequent temperature change, but *Ulva* biomass accumulation may also lag behind increasing solar insolation, therefore abundance cycles might appear better correlated to temperature conditions, when in reality they are driven by light conditions. For example, Thom & Albright (1990) found that irradiance determined temporal changes in the standing stock of benthic algae, but water temperature was the best predictor of biomass change.

In contrast to growth factors of light and temperature, there were no obvious temporal variations in factors which would act to remove *Ulva* biomass and hence modify patterns of production. For example, grazing damage, sporulation and burial of intertidal plants were not conspicuous and detectable only at times when biomass was high. Also, extreme tide and wind events which would remove *Ulva* did not tally with periods of declining abundance, although the potential for storm disturbance was recognised and shallow water communities are likely to be affected to some degree on a regular basis.

Ulva also displayed spatial patterns of abundance within Tauranga Harbour which related to physical conditions. The change in subtidal plant cover, biomass and recruitment/survival over a depth gradient supports the importance of light availability. The fact that the depths of 0-1 m had low *Ulva* development, despite receiving the highest light, appears to be due to plant removal from this shallow zone by strong tidal currents generated as waters ebb from, and flood the extensive intertidal zone (e.g. Lowthion *et al.* 1985). Furthermore, this zone represents the depth range receiving maximal disturbance during periods of wind induced wave action.

Drift influx

Drift movement within the harbour was seen as important in contributing biomass to the intertidal area. Both the timing of subtidal versus intertidal population development and the patterns of intertidal plant attachment suggest drift contribution from submerged sources. Conversely, attached plants which are most likely to have been recruited within the intertidal did not contribute as strongly to standing crop. This demonstrates that the rapid increases in *Ulva* need not be reliant upon the establishment of spore propagules, as colonising plants arise from thalli fragmentation and drift dispersal.

Polychaete worms (tentatively identified as Nereidae) contributed to the retention of drift material within the intertidal zone by providing anchorage for unattached *Ulva*, and similar interactions between macro-algae and polychaetes have been reported elsewhere, (Reise 1983, Woodin 1977). In Tauranga Harbour it is thought that large plants drifting onto the sandfats are rapidly 'captured' by polychaetes and are then incorporated into debris cemented together with worm mucus and anchored within the sediment. This action effectively increases the availability of intertidal habitat for *Ulva* growth which otherwise has limited suitable substrates for the development of attached plants.

Growth and abundance cycles

The apparent influence of light and temperature factors on both the temporal and spatial development of *Ulva* suggests that variations in growth rate are primarily responsible for seasonal fluctuations in macro-algal abundance. Likewise, the contribution to *Ulva* biomass by somatic growth especially suggests growth rate is of major importance. Another factor affecting growth rates, the availability of nutrient in harbour waters, was not examined here as *Ulva* growth is frequently 'uncoupled' from a fluctuating nutrient supply due to its ability to rapidly uptake and store N in excess of immediate needs (Fujita *et al.* 1989). In this respect, variations in *Ulva* intracellular nutrient concentrations over temporal and spatial scales (section 3) would provide a better indication of the availability of nutrients for growth.

Even small reductions in macro-algal growth rate due to adverse physical conditions may be sufficient to upset the equilibrium with loss processes and lead to rapid declines in standing crop. For example, unfavourable climatic conditions were considered to account for an initial decrease in *Ulva* growth rate within eutrophic Venice Lagoon, following which losses due to burial, grazing and reaping by authorities resulted in a significant and sustained regression of the macro-algae within this eutrophic embayment (Sfriso & Marcomini 1996). In Tauranga Harbour loss processes were mainly detected when *Ulva* biomass was high, so that if plant growth rates were limited at this time, biomass removal might account for the observed rapid declines in standing crop.

3. LIGHT, NUTRIENTS, TEMPERATURE AND THE GROWTH OF *ULVA* IN TAURANGA HARBOUR

3.1 Background

Growth of algae depends on the assimilation of inorganic carbon and nutrients, the first via photosynthesis and the second usually via uptake of inorganic ions from the surrounding seawater. In its simplest representation, algal growth uses photosynthesis to harvest light energy to form simple sugars from dissolved CO_2, a portion of which are metabolised to provide the energy required to assimilate other elements (nutrients) and to elaborate these intracellular nutrients with other carbon skeletons to form more complex organic molecules. Photosynthesis and nutrient uptake are clearly linked via energy, but it is frequently the case that these processes are not in perfect balance. Rates of nutrient uptake are dependent on rate of supply to the algal cell membrane and by the activity of nutrient uptake enzymes, which may be affected by temperature and internal processes. Under conditions of imbalance, either insufficient light is available to synthesise carbon skeletons to utilise the available intracellular nutrients (light limitation of growth) or insufficient intracellular nutrients can be taken up to match the amount of carbon which available light permits to be assimilated (nutrient limitation). Understanding the relative importance of nutrient and light limitation of growth of *Ulva* in the Tauranga Harbour is central to understanding the reason behind the observed growth cycles.

The relationships between light intensity and the rate of photosynthesis, and between external nutrient concentration and rate of nutrient uptake are not fixed. Algae have many adaptive mechanisms to optimise their performance in a given environment, For instance, under low light conditions, the areal concentration of light absorbing pigments can be increased, or under nutrient stress the number or type of nutrient uptake sites on their cell membranes can be changed. Also, the balance of light and nutrient limitation can vary over time and with location, due to changes to external nutrient concentrations, temperature or light intensities. This means that measurements of environmental variables alone are of limited use in estimating likely controls on growth rates. Instead, a combination of physiological and environmental data may provide a better indication of what is controlling growth. In this section we attempt to link growth rate with physiological constraints on the algae.

3.2 Approach

Light and Ulva *growth*

The upper limit to growth is set by the net rate of carbon fixation via photosynthesis (net photosynthesis equals gross photosynthesis minus respiration). Under any given physiological condition, this rate is related to light intensity by the relationship:

$$P = P_{max}.\tanh(\alpha.E/P_{max}) - R$$

where P is net photosynthesis at irradiance E, P_{max} is the light saturated rate of gross photosynthesis, R is the rate of respiration and α is the slope of the P *vs* E relationship as E approaches zero (Jassby & Platt 1976). By determining the parameters of this equation for plants from a range of depths and locations, and by estimating E at these depths, we were able to assess whether growth was likely to be light limited, and if so, when and where. These parameters are not fixed, but can vary with a number of factors, including previous light history, temperature and intracellular nutrient status.

Adaptation to low light intensity usually involves an increase in the cellular concentration of light absorbing pigments. In *Ulva,* this results in dark green thalli under reduced light, which absorb more incident light than paler green, high light plants. Associated with this adaptation, there is usually a reduction in P_{max} expressed on a dry weight or intracellular carbon basis. The upper limit to potential growth rate is therefore lower than in high light adapted plants.

Intracellular nutrients and Ulva *growth*

It has long been recognised that the concentration of intracellular nutrients within algal cells was much more important as a determinant of maximal photosynthesis and growth rates than the concentration in their surrounding medium (Hecky & Kilham 1988). The relationship is complicated by the ability of some algae, including *Ulva* species (Björnsäter & Wheeler 1990) to store nutrients inside their cells. Where storage occurs, the relationship between growth rate and intracellular nutrient concentration is typically hyperbolic, while in alga where no internal storage occurs, it is linear (e.g. Fujita *et al.* 1989; Hawes & Smith 1993). Typically, a minimal content below which no growth occurs, and an optimal content at which growth rate is saturated are recognised, and above the latter, luxury uptake and storage is inferred (Senft 1978). For *Ulva*, a number of estimations of minimal, maximal and content vs growth rate have been made, with N minima ranging from 0.7-2.4%, and maxima from 2.7 to 5.4% (Solidoro *et al.* 1997). Between these values, a near linear relationship between intracellular nutrient content and growth rate is usually observed. Intracellular P shows much less variability than N in *Ulva*, and is thought to be taken

up as required, rather than stored or depleted during growth (Solidoro *et al.* 1997). Internal nutrient stores are therefore useful indicators of degree of nutrient sufficiency in *Ulva*, where these can be related to potential growth rates.

While it is possible to be limited by more than one nutrient, usually the "law of the minimum" applies, in that one nutrient is more limiting than others. A consequence of this is that intracellular nutrient ratios deviate from an optimal value as one nutrient becomes increasingly limiting. Since N and P are the commonest limiting nutrients in inland and coastal waters, the N:P ratio is frequently taken as an indicator of N or P deficiency. Where it is close to an optimum value, either both, or neither is limiting, whereas under increasing N limitation for example, the N:P ratio tends to fall.

In this section we investigate the relative importance of light and nutrients as factors limiting *Ulva* growth in Tauranga Harbour. We use the intracellular nutrient contents as measures of nutrient sufficiency and relate these to rate of net photosynthesis as an indicator of potential growth rate. Experiments and field surveys were carried out to determine the intracellular nutrient requirements for growth of *Ulva* from the harbour. We have determined light *vs* photosynthesis parameters from plants from a range of depths and locations which, by combining with observations on the light conditions within the harbour, enable the probability of light limitation under *in situ* conditions to be assessed. The effect of temperature on photosynthetic rate was also examined. Our aim was to use these data to determine the balance between light and nutrient limitation of growth, and to test the physiological basis of hypotheses developed during the field research programme concerning the patterns of growth of the plant in Tauranga Harbour.

3.3 Light and light-photosynthesis relationships

Methods

Two methods were used to measure the rate of photosynthesis in *Ulva.* Both relied on measuring the rate of change of oxygen concentration, over time, in sealed containers. In the first method, discs cut from *Ulva* thalli were incubated for 1 h, in sealed glass bottles, at a range of light intensities. At the end of the incubation, the oxygen concentration was determined by injecting samples into a couloximeter (Hawes & Schwarz 1996), and compared with controls which had been incubated under similar conditions, but without *Ulva* disks. In the second method, disks were incubated in a Hansatech photosynthesis measuring system. In this system, the disks were incubated in a 10 ml chamber, fitted with a stirrer and an oxygen electrode which was monitored continuously. The rate of change of oxygen concentration was measured over approximately 10 minutes, under constant agitation, and a range of irradiances were provided by an integral halogen light source.

In each case, estimates of photosynthetic oxygen evolution were obtained at a range of PAR intensities, and were fitted to the Jassby-Platt equation described above. Photosynthetic parameters were obtained from the best-fit curves fitted to the data using a variety of statistical packages.

Results

Light climate

Assuming that the field measurements of light give accurate figures for the extinction coefficient and surface transmission at the Otumoetai site, we are able to model the PAR at various depths at this location.

The time averaged depth of water above a specific subtidal point (relative to CD) can be estimated using the tabulated data on tidal heights for Tauranga Harbour. Given the limitation on the accuracy with which extinction has been measured, a useful approximation can be made over a period of a month, assuming that tidal amplitude does not vary with the spring-neap cycle, but rather oscillates between mean high water and mean low water according to a simple sine wave function. Using this assumption, water depth above a range of chart data was calculated. The irradiance incident to the water surface was obtained from mean daily values recorded at Tauranga Airport. Using mean daily incident PAR, PAR at each depth was computed using the values of surface transmission of 85% and K_d of 0.33 m^{-1} determined above. These computed values are shown in Fig. 3.1. The monthly average daily mean PAR over the August 1996 to March 1997 period are shown in Table 3.1.

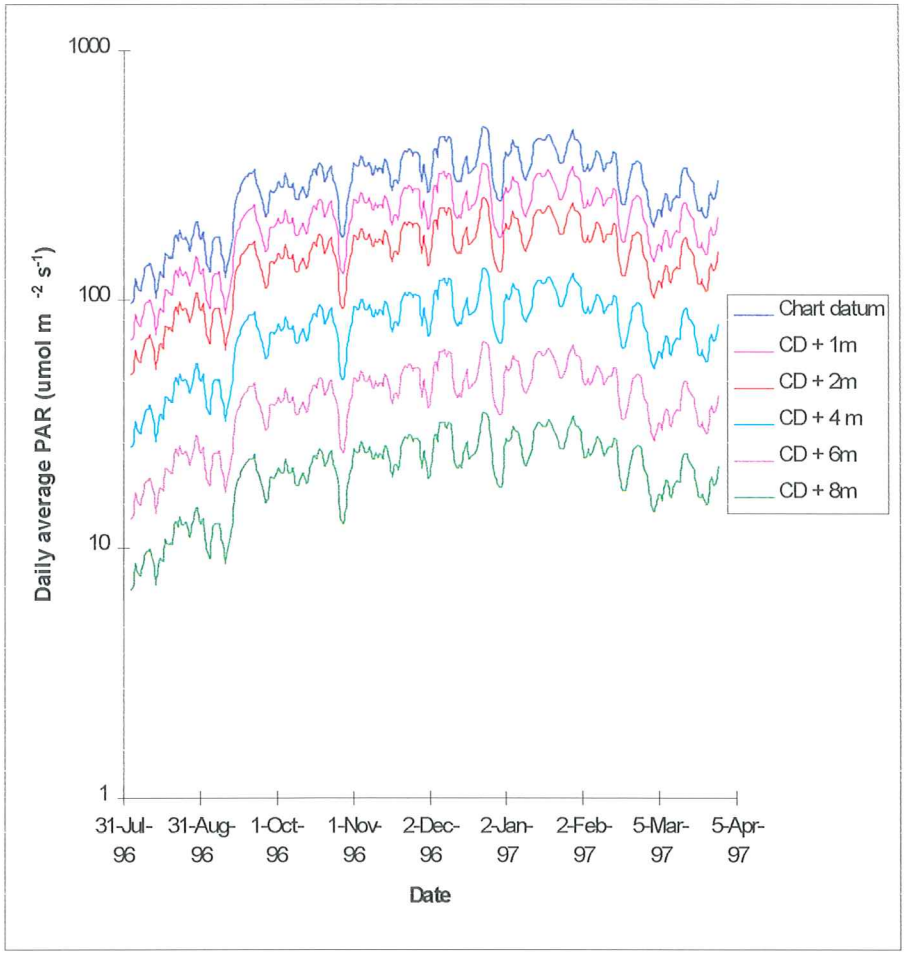

Fig. 3.1. Calculations of the daily average PAR at six depths at the Otumoetai study site during the 1996-97 study period. Calculations are based on mean extinction coefficient and surface transmission, incident irradiance at Tauranga Airport, and approximations of tidal heights (see text). Note logarithmic scale. To reduce variation, the plot is based on five-day running means of incident irradiance.

Table 3.1. Approximations of the monthly mean daily PAR (μmol photons m^{-2} s^{-1}) at various depths below chart datum (CD) at the Otumoetai study site.

Month	Chart	CD+1m	CD+2m	CD+4	CD+6	CD+8m
August	146	105	75	39	20	10
September	225	162	116	60	31	16
October	284	204	147	76	39	20
November	344	247	178	92	47	25
December	363	261	188	97	50	26
January	400	287	207	107	55	29
February	334	240	173	89	46	24
March	256	184	132	68	35	18

Experiment 1. Effects of collection depth at the Otumoetai site

This experiment was undertaken using both the Hansatech instrumentation and the Couloximetric method. Plants were collected five depths at the Otumoetai site, from 1.8 m below CD, to 7.5 m below CD. From each depth, the photosynthetic characteristics of two plants were determined. In addition, replicate cores were analysed for their Chlorophyll-a, nitrogen, phosphorus and dry weight content, according to standard laboratory procedures. Results of this experiment are summarised in Table 3.2.

Table 3.2. Summary of plant parameters across a depth gradient at the Otumoetai site, March 1997. Depths refer to m below chart datum. Each point is the mean of 3-5 replicates. P_{max} (μmol O_2 mg^{-1} h^{-1}) has been expressed on a dry weight and chlorophyll-*a* basis.

Depth (m)	%P	%N	N:P Molar	Dry wt (mg cm^{-2})	Chl *a* (μg cm^{-2})	P_{max} (Chl *a*)	P_{max} (g dry wt)	Resp (g dry wt)	E_k (μmol m^{-2} s^{-1})	E_c (μmol m^{-2} s^{-1})
1.8	0.08	0.88	24.13	2.24	1.13	0.74	0.37	0.029	140	11
3.4	0.08	1.22	31.94	2.67	2.92	0.48	0.52	0.037	120	10
4.5	0.08	1.29	36.01	2.82	3.09	0.46	0.48	0.050	110	11
6.5	0.11	2.17	44.35	3.02	10.18	0.12	0.39	0.043	83	9
7.4	0.12	2.08	38.31	2.85	9.22	0.13	0.39	0.054	75	10

These data show a number of interesting points. Firstly, there are clear trends in physiological features with depth. Dry weight and chlorophyll-*a* per unit area tended to increase with depth, as did the proportions of dry weight as both N and P. However, rate of light saturated photosynthesis per unit dry weight was maximal at intermediate depths. Increasing shade adaptation with depth was evidenced by the increasing chlorophyll-*a* content, declining value of E_k and declining chlorophyll-*a* specific P_{max}.

There was no clear pattern to respiration rate with depth, and photoadaptation did not reduce the value of E_c, the light intensity at which net photosynthesis equalled zero. This was close to 10 μmol m^{-2} s^{-1} in all samples. Reference to Fig. 3.1 suggests that, for much of the growing season, the shallowest plants were experiencing light levels which were saturating to photosynthesis (mean daily levels exceeded E_k). In contrast, plants at 6-8 m were operating at light intensity ranges consistently within those limiting to photosynthesis (mean daily values less than E_k). Plants in the 2-4 m depth range (see 3.4 m samples, Table 3.2) would appear to experience a light regime conducive to growth.

Light saturated rates of photosynthesis of 0.5 μmol O_2 mg^{-1} dry wt h^{-1}, sustained over a 14 hour photoperiod, would equate to fixation of approximately 85 mg C mg^{-1} dry wt d^{-1}, or, at a carbon content of 30%, a specific growth rate of 0.3 d^{-1}. This maximum growth rate is within the published range for *Ulva* of 0.21 - 0.5 d^{-1} (Solidoro *et al.*, 1997).

In the context of the relative importance of light and nutrients in limiting growth rate, it would appear that the accumulations of *Ulva* in water deeper than 4 m below CD at the Otumoetai site, are likely to be predominantly light limited. Those at shallower depths (<4 m) experience a more equitable light climate, hence are more likely to be subject to nutrient limitation. Increasing light limitation of growth below 4 m depth is consistent with observations of the vertical extent of *in situ* growth and settlement described in section 2. Lower dry wt specific P_{max} in the 1.8 m material than in the mid-zone samples suggests lower growth rates, despite sufficient light for photosynthesis, hence these samples may have been nutrient limited. These data suggest that, under field conditions, N and P contents of >2.0 and 0.1% respectively (6.5 and 7.4 m) are indicative of nutrient sufficiency, contents of 1.3 and 0.08% (3.4 and 4.5 m) are indicative of high growth rates, while an N content of 0.9% (1.8 m) may have been associated with nitrogen limitation of growth. Chlorophyll-*a* contents approaching 9-10 μg cm^{-2} show extreme shade adaptation and may be indicative of light, rather than nutrient, limitation of growth.

3.4 Intracellular nutrient status

Intracellular nutrient status of plants throughout the harbour.

To further investigate the relationships between photosynthesis and intracellular nutrient status, we examined plants from a range of locations that would reflect a wide range of harbour nutrient conditions. Light saturated rates of net photosynthesis (Pn_{max})were determined at a temperature of 16°C and ambient intracellular %P and %N contents. At each site, three replicate samples were analysed for all variables, and a mean calculated. The intention was to determine if a consistent relationship could be demonstrated between Pn_{max} and any intracellular nutrient, as would be expected from considerations discussed in the introduction to this section.

Plants were collected from subtidal locations (depth usually 2-4 m below CD), on five occasions. Overall, the distribution of intracellular N followed a log-normal distribution. Such a distribution pattern is consistent with a minimum N content, below which further plant growth is not possible. The minimum intracellular N was found to be 0.6% by dry wt (Fig. 3.2). There was no evidence for a maximum intracellular N content, suggesting that the *Ulva* plants had a capacity to take up N in excess of immediate requirements.

A different pattern was seen for phosphorus, where there was no clearly defined minimum, and the data did not fit the expected log-normal distribution (Fig. 3.3). It was notable that intracellular P values were clustered around the median more closely than N values, suggesting less tendency to store P than N. This tendency to store N but not P is reflected in the fact that much of the variability in N:P molar ratios was related to the N content (Fig. 3.4). This implies that, for *Ulva* populations in Tauranga Harbour, N:P ratios need to be interpreted with care. High N:P ratios are not specifically evidence of low P availability, but rather of excess stored N relative to P, even when P is also in adequate supply.

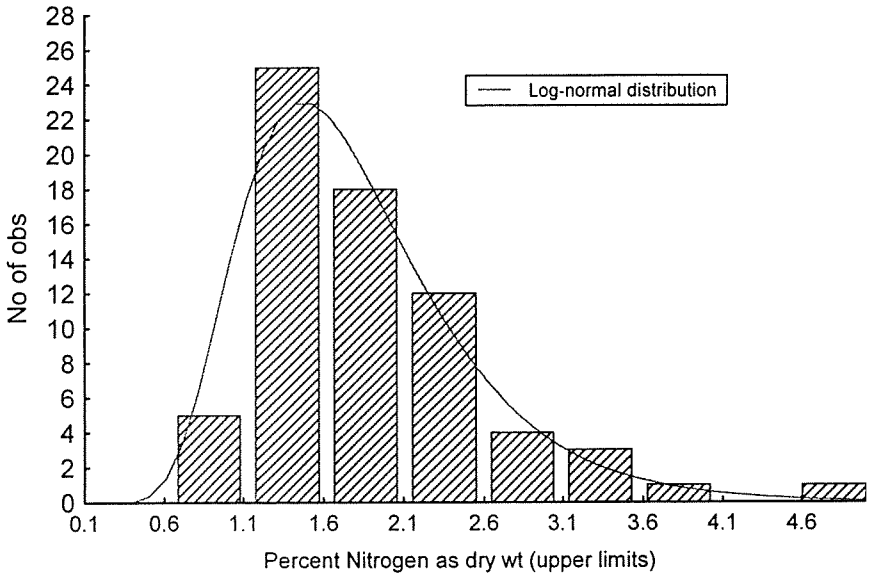

Fig. 3.2. Distributions of %N in plant samples collected on four dates, from 6 sites in the Tauranga Harbour. The data closely fits a log-normal distribution (chi-squared test, $p>>0.05$), with a lower cut-off of 0.6%N and a median of 1.3%.

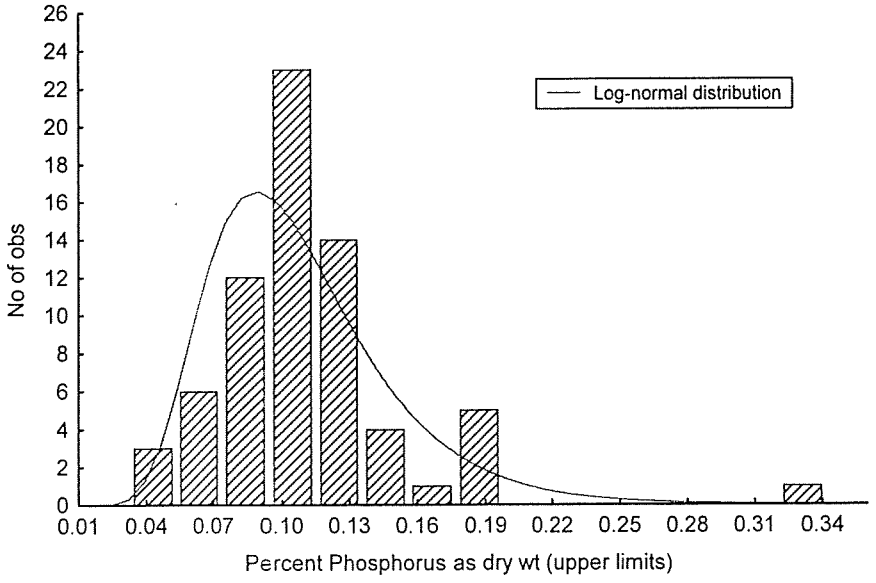

Fig. 3.3. Distributions of %P in plant samples collected on four dates, from 6 sites in the Tauranga Harbour. The data does not fit log-normal or normal distributions (chi squared test, p <0.05). There is a poorly defined lower cut-off of 0.04%P, and a median of 0.1%.

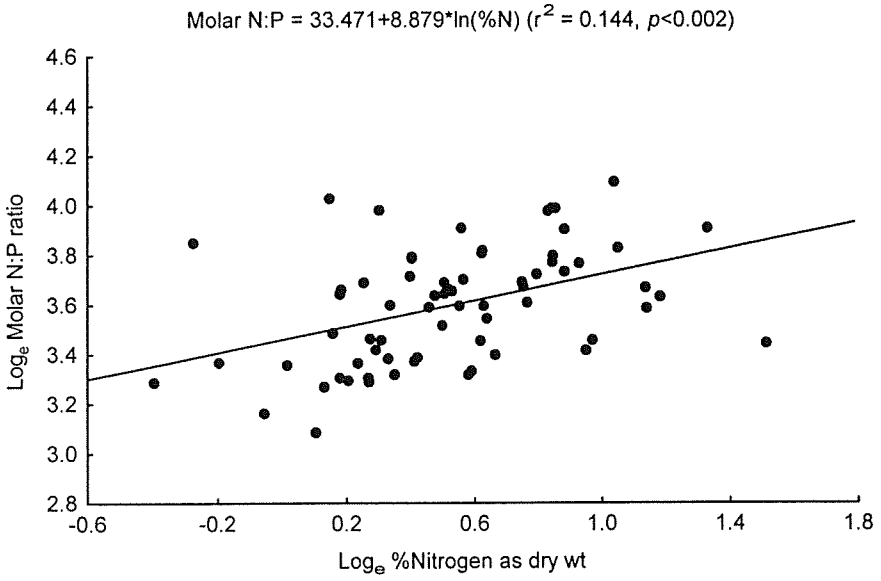

Fig. 3.4. The relationship between Molar N:P ratio and %N of plant samples. Both variables have been log_e transformed to normalise their distributions, thus making regression analysis statistically valid.

When the light saturated rates of photosynthesis were plotted against intracellular N and P, saturation and minimum effects were again evident. Saturation of photosynthesis occurred at an intracellular N of around 1.5-2% (Fig. 3.5), and an intracellular P of 0.10-0.12% (Fig. 3.6). Minimum values, at which point photosynthesis fell to zero, were close to 0.05% for P, and were less well defined at 0.8% N. Maximum light saturated rates of photosynthesis were sustained at intracellular N only slightly above the minimum, while from 0.05 to 0.1% P a gradual increase in light saturated rates was observed. On this basis, approximately 7% of the 69 samples in Fig. 3.2 and 3.3 show signs of incipient N limitation, and 22% of P limitation.

These data are consistent with inferences made based on the depth profile at Otumoetai, where high rates of photosynthesis were observed where N was below 1% dry weight. The intracellular P of 0.08% in the three shallowest samples at Otumoetai may have been slightly below optimum, suggesting potential limitation by this nutrient.

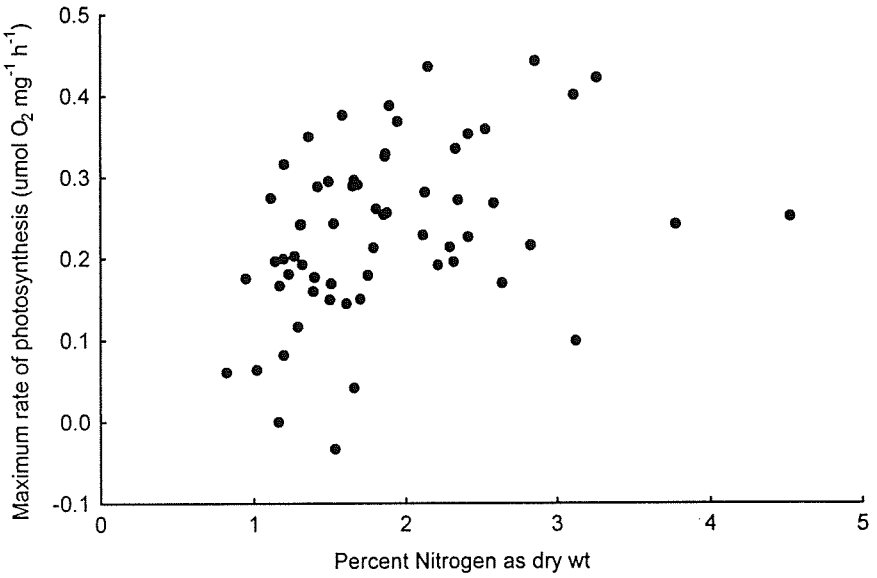

Fig. 3.5. Relationship between %N and light saturated rate of photosynthesis in plant samples collected on four dates, from 6 sites in the Tauranga Harbour. No clear pattern is evident, though photosynthetic rate tends to decline as %N approaches its minimum of 0.8% and there is evidence of a saturation effect above approximately 2%N.

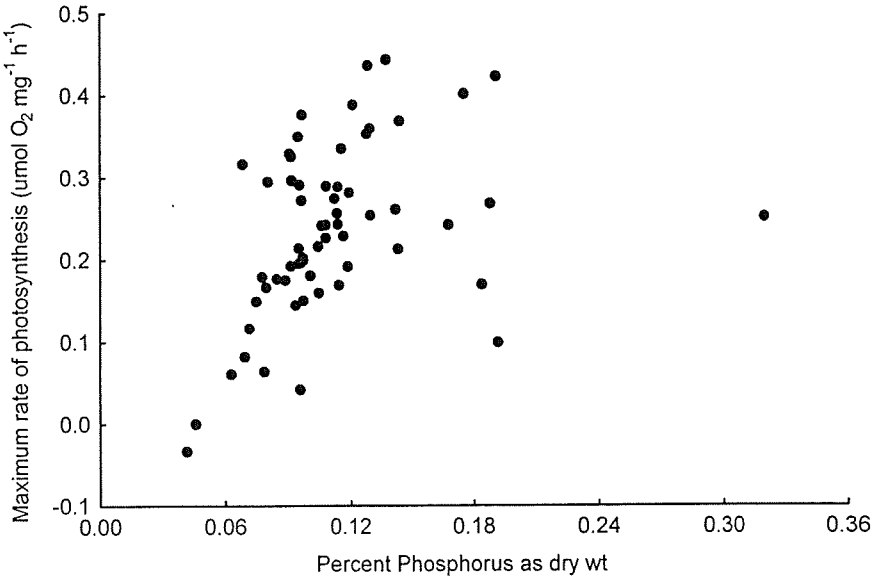

Fig. 3.6. Relationship between %P and light saturated rate of photosynthesis in plant samples collected on four dates, from 6 sites in the Tauranga Harbour. There is a tendency for photosynthetic rate to decline as %P falls below 0.01.

Laboratory estimation of minimum N and P contents

In order to verify the estimates of minimum intracellular N and P contents of 0.8 and 0.04% respectively, in samples obtained from field studies in Tauranga Harbour, experiments were undertaken under laboratory conditions. Six plants from approximately 2 m below CD at the Otumoetai site were incubated for 25 days, under near ambient light and temperature conditions, but in seawater with very low nutrient concentrations. The intracellular nutrients were monitored during this period by removing replicate disks of tissue. After 25 days of nutrient starvation, three plants were introduced to nutrient enriched seawater, while three remained under nutrient starved conditions. Intracellular N and P were monitored for a further 7 days after this transfer. Rates of light saturated photosynthesis were determined at the beginning of the experiment, and again in the two groups of plants after nutrient enrichment.

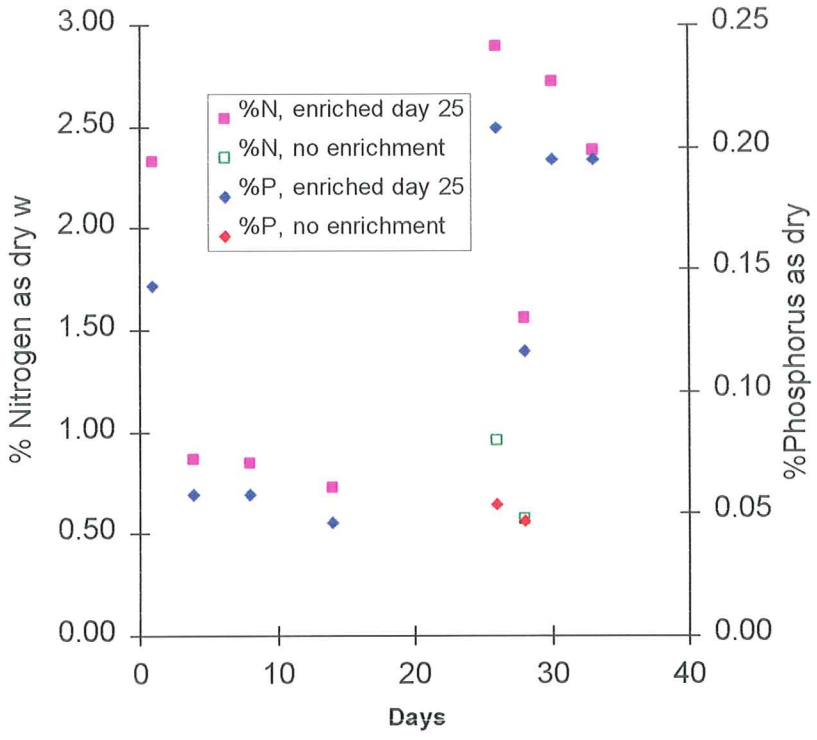

Fig. 3.7. Time series of intracellular N and P in plant material starved for 25 days, then either transferred to nutrient rich medium, or left under starved conditions. Each point is the mean of 3 or 6 plants, each plant the mean of 3 replicate analyses.

Intracellular nutrients declined rapidly during the starvation period (Fig. 3.7), with N falling to approximately 0.75%, and P to 0.05%. After nutrient enrichment of the seawater, both %N and %P increased rapidly, to 2.5% and 0.2% respectively. The

minimum values reached during the starvation period are consistent with estimates of minimum quotas obtained from field material.

The average light saturated photosynthetic rate at the start of the experiment was 0.43 mmol O_2 mg^{-1} dry wt h^{-1}. This fell to 0.02 mmol O_2 mg^{-1} dry wt h^{-1} in the starved plants at 27 days. Following three days of nutrient enrichment, this had risen to 0.18 mmol O_2 mg^{-1} dry wt h^{-1}, rising to 0.25 mmol O_2 mg^{-1} dry wt h^{-1} after 1 week of high external nutrients. These data again support the field data, in that net photosynthesis was barely detectable in plants with minimum intracellular nutrients, but rose rapidly when intracellular nutrients became available.

Spatial variability in intracellular nutrient status

During surveys of the abundance of *Ulva* in February 1995 (de Winton *et al.* 1996), samples were collected from a range of sites for %N and %P analysis. At each site, six plants were collected, and four replicate samples were analysed from each plant. Site codes and locations are shown in Fig. 3.8.

The data were analysed (analysis of variance, ANOVA) to determine whether at each site plants were significantly different, and whether there were significant differences between sites which could be related to site characteristics. Where differences were found, these were identified using Tukey's HSD test. Differences were considered significant at $p<0.05$. For both %N and %P, no difference could be shown between plants within any given site. For %P, significant differences between sites were determined by site 7, where %P was higher than sites 2, 5 and 6 (Fig. 3.9). Sites 3 and 4 tended to have high %P, but the differences were not statistically significant. For %N, two groups of sites were separated, sites 2, 5 and 6 had low %N, sites 3 and 4 had high %N, while site 7 was between these groups (Fig. 3.10). Site 1 had a very wide range of both %N and %P contents.

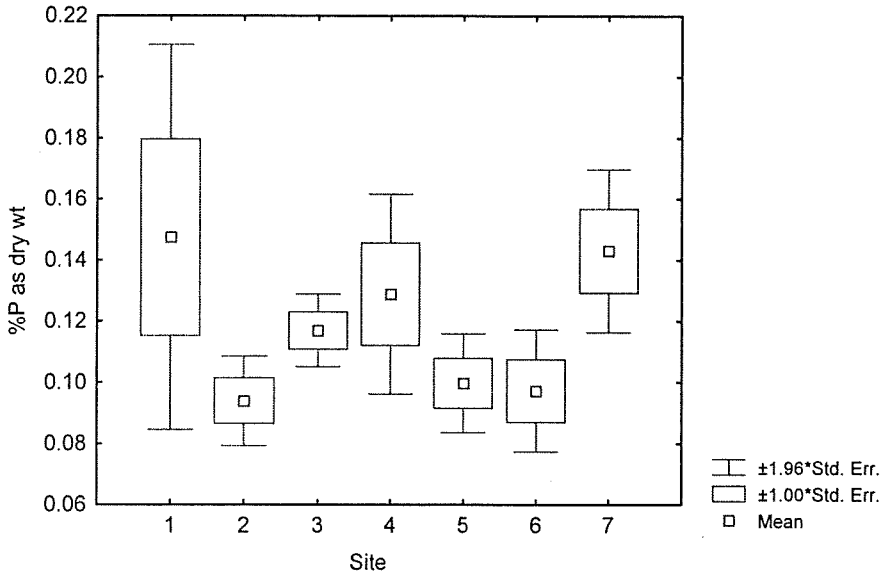

Fig. 3.9. Box and whisker plot of intracellular %P of plants from seven sites in February 1995.

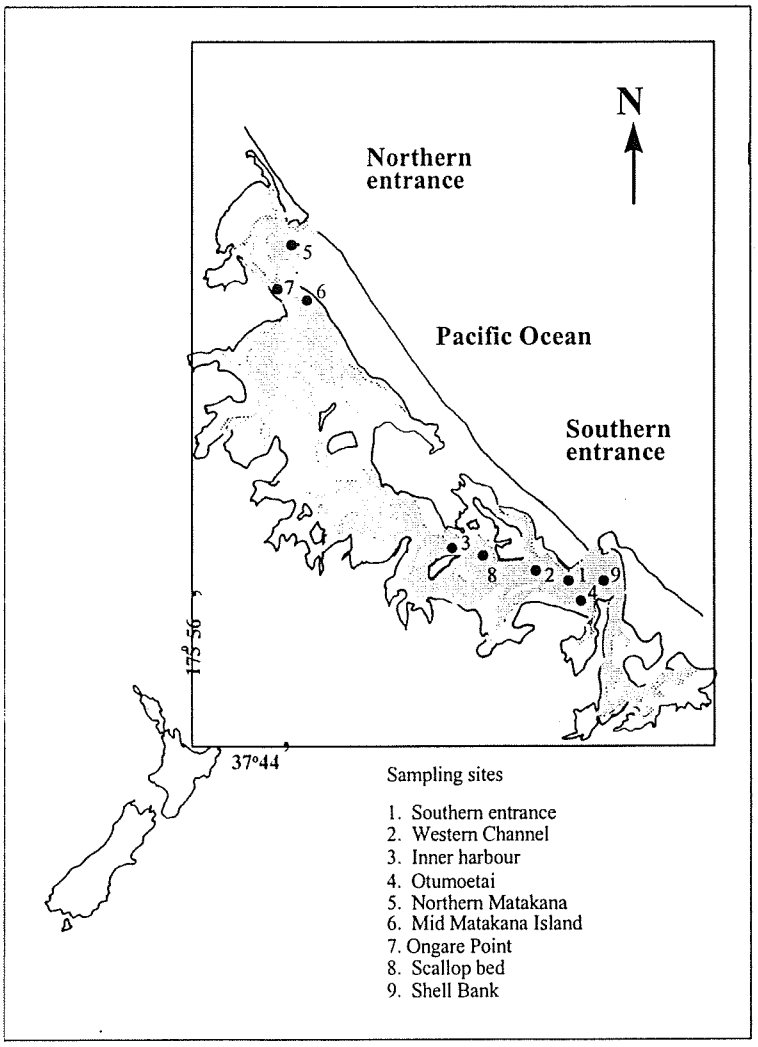

Fig. 3.8. Map of Tauranga Harbour showing sample collection sites for physiological experiments (section 3) and genetic analyses (section 4).

It was evident that, although there was a wide range of N and P contents in the site 1 samples, the N:P ratio was relatively constant (Fig. 3.11). A possible interpretation of this is supply of the two nutrients at this site varied due to differences in water movement, and that this, rather than local variation in the concentrations of nutrients in the seawater surrounding the cells, led to the high degree of variability. High N:P ratios at sites 3 and 4 reflect the high N content, whereas at site 2, these are due to a low P content.

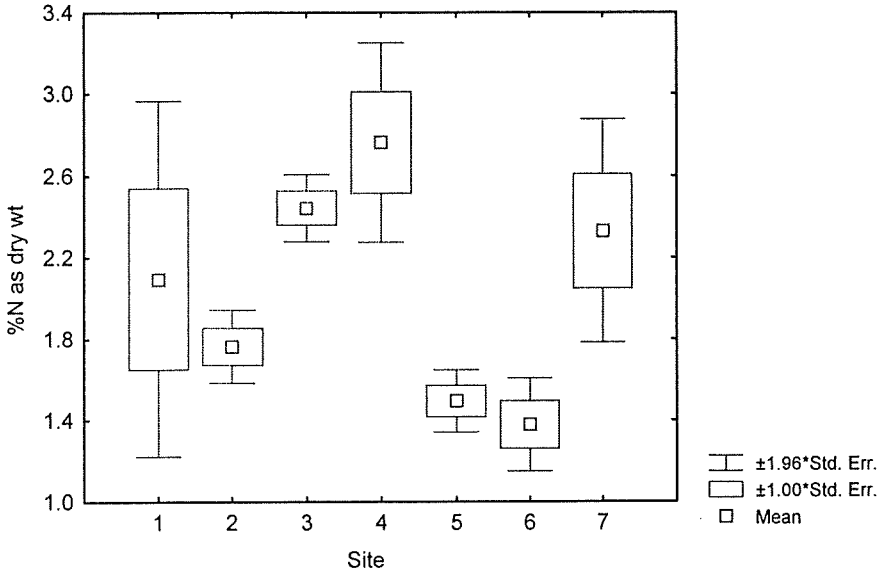

Fig. 3.10. Box and whisker plot of %N of plants from seven sites in February 1995.

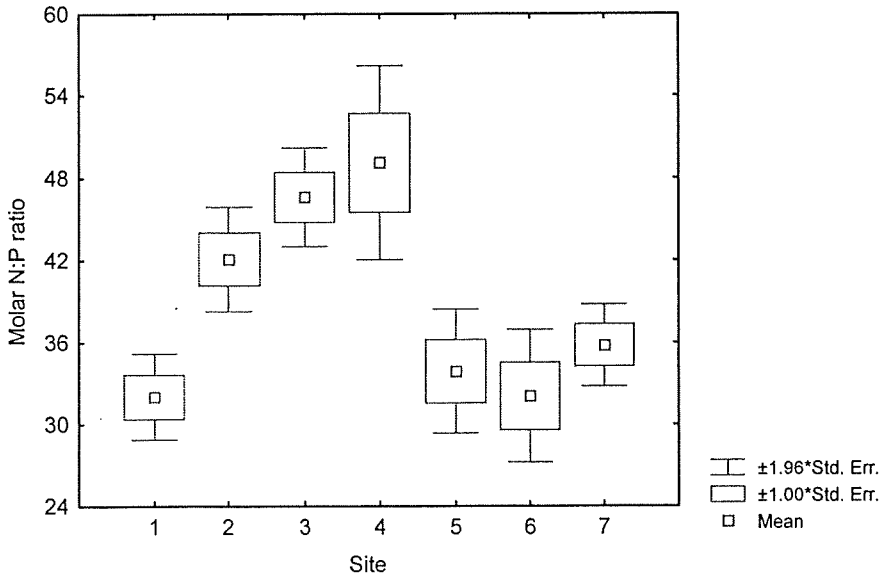

Fig. 3.11. Box and whisker plot of molar N:P ratio of plants from seven sites in February 1995.

In summary, Ongare Point had a high intracellular %P, and intermediate %N, the inner harbour and Otumoetai sites had high %N and lower %P, while the Western Channel and both Matakana sites had low %N and %P. The Southern entrance site had a very wide range of both %N and %P. However, no sites showed mean intracellular N or P which would indicate strong nutrient limitation at the time of

sampling. The highest probability of nutrient limitation of growth would be at sites 4, 5 and 6, where %P was low.

Light saturated rates of photosynthesis also varied between sites (Fig. 3.12). Lowest rates were observed at the central bank and sites 5 and 6 where nutrient limitation was implied. The nutrient replete sites, Inner Harbour, and Ongare Point showed highest rates of photosynthesis. At Otumoetai, where plants appeared to be nutrient replete, maximal rate of photosynthesis was low, though this was probably more a function of shade adaptation than intracellular nutrient status. The high areal chlorophyll-*a* content reinforces this view (Fig. 3.13).

Chlorophyll-*a* contents of plants showed no relationship with either intracellular nutrients or rate of photosynthesis (Fig. 3.13). Concentrations probably reflect more the light history of the plants, and the absence of very high concentrations (c.f. deep plants at Otumoetai (Table 3.2) suggests that none of these sites was highly light stressed during February 1995.

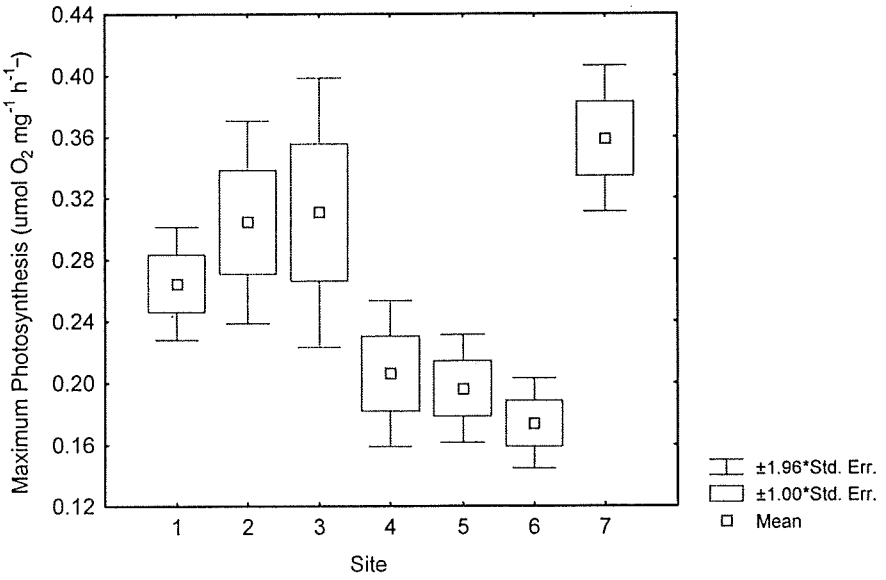

Fig. 3.12. Light saturated rates of photosynthesis at a range of sites in the Tauranga Harbour.

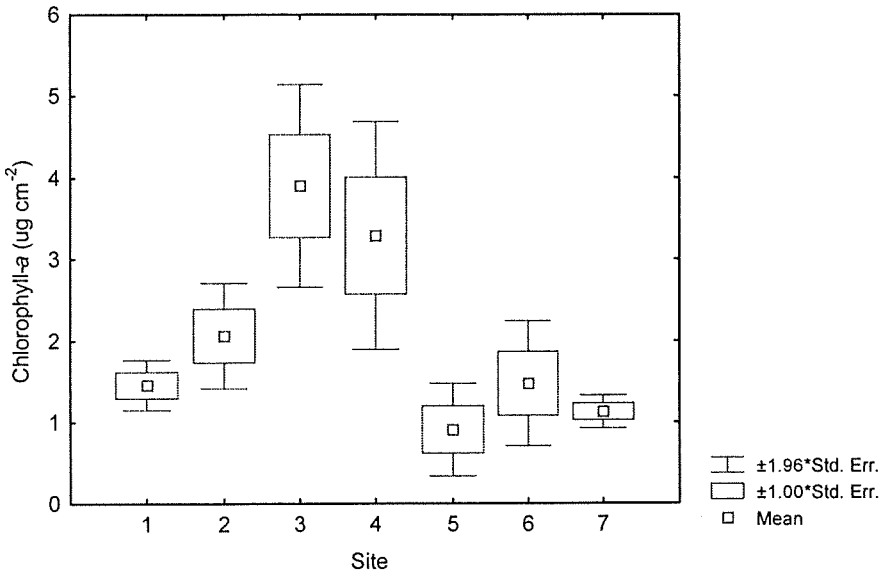

Fig 3.13. Areal chlorophyll-*a* concentrations at a range of sites in the Tauranga Harbour.

Variation over samplings at Otumoetai

The spatial data discussed above were obtained in 1995, a year of quite high *Ulva* biomass at the 2-4 m sampling depth (section 2). Comparisons of intracellular nutrient contents of plants collected at the same depths at the Otumoetai site, at different times, were made using ANOVA to determine how consistent these were from year to year (Fig. 3.14 and 3.15). During the 1994-1995 summer, concentrations of N were high enough to indicate that it was available in excess to that required for growth. Likewise, %P was consistently above 0.08% at this time, indicative of a high potential for growth.

Overall, if any nutrient limited growth at this time it would have been P. However, in the two subsequent summers (both years of low *Ulva* biomass) plants had significantly lower intracellular nutrient contents, particularly %N. While %N did not fall to starvation levels, there may have been occasions when it was limiting growth rate, and %P levels at times approached the 0.05-0.10% range where P was having a negative impact on growth. This is again consistent with conclusions drawn from the depth profile data at this site.

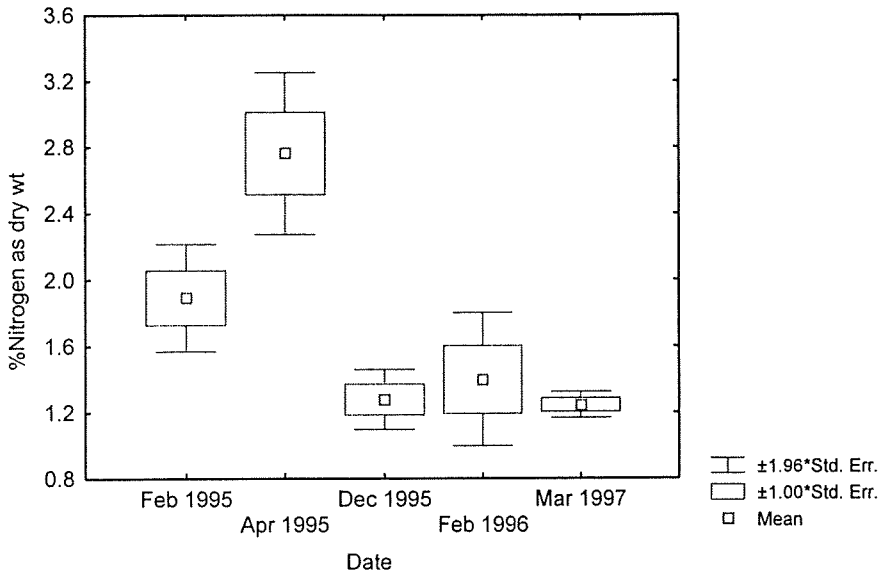

Fig. 3.14. Comparison of nitrogen content of *Ulva* from the Otumoetai site on five occasions.

Other sites for which data from 1995 and 1997 are available show a similar pattern of lower intracellular nutrient concentrations in 1997 (Table 3.3), suggesting that there was a harbour-wide reduction in nutrient availability in the later of the two years.

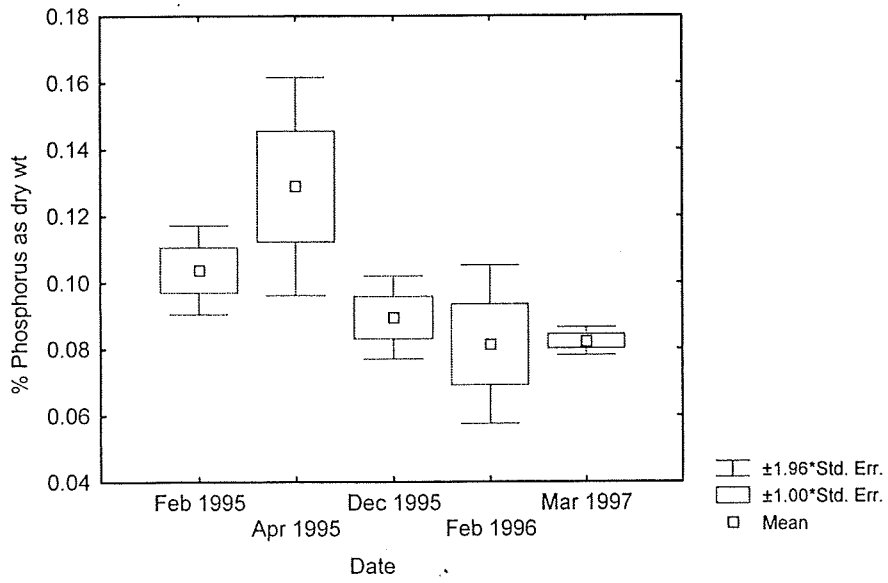

Fig. 3.15. Comparison of phosphorus content of *Ulva* from the Otumoetai site on five occasions.

Table 3.3. Mean and range of intracellular %N and %P at three sites within the Tauranga Harbour in February 1995 and March 1997. Ranges are in parentheses.

Site	1995 %N	1997 %N	1995 %P	1997 %P
S. entrance	2.09	1.12	0.14	0.075
	(1.20-4.53)	(1.05-1.24)	(0.068-0.320)	(0.056-0.088)
Otumoetai	2.76	1.22	0.129	0.084
	(2.21-3.78)	(1.16-1.29)	(0.095-0.191)	(0.079-0.090)
Mid Matakana	1.34	1.08	0.097	0.075
	(1.12-1.79)	(0.88-1.42)	(0.071-0.143)	0.070-0.079)

Variation of intracellular N and P with depth is indicated in Table 3.2, while subtidal plants collected for maximum biomass (section 2) showed a tendency for N and P contents to increase with depth (Fig. 3.16, 3.17). This is consistent with increasing light limitation with depth, with N and P contents of the shallowest plants being sufficiently low to suggest that they were nutrient limited.

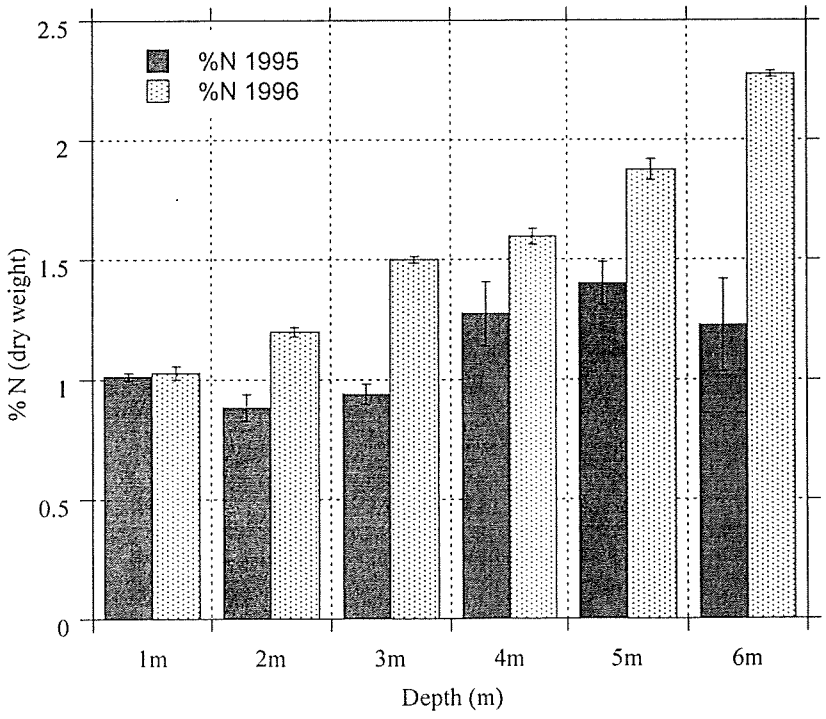

Fig. 3.16. Intracellular %N content of plants (n=2±se) from areas of maximum biomass at 1 m depth intervals, on 17 January 1995 and 3 January 1996.

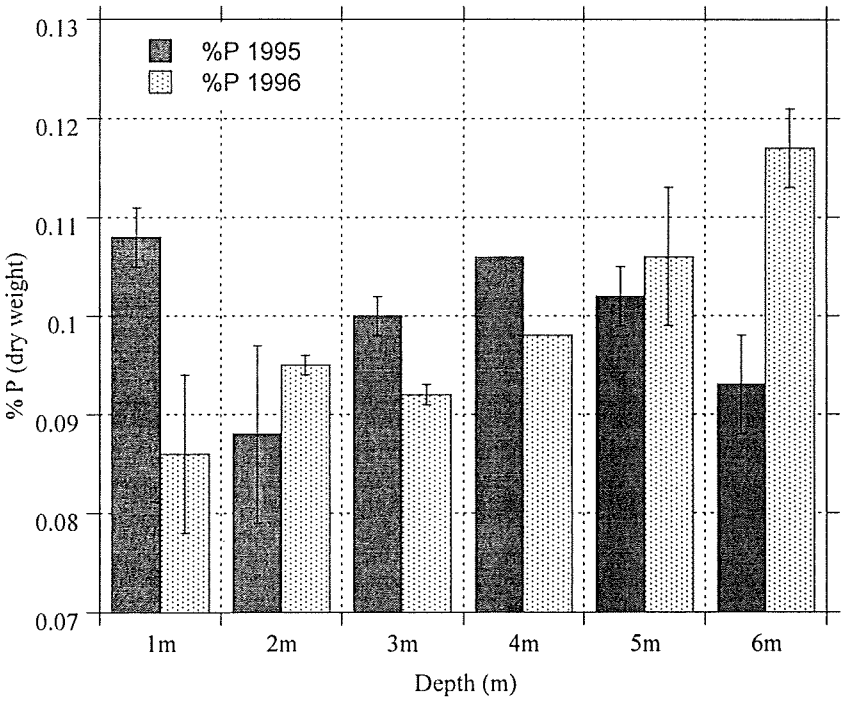

Fig. 3.17. Intracellular %P content of plants (n=2±se) from areas of maximum biomass at 1 m depth intervals, on 17 January 1995 and 3 January 1996.

3.5 Effects of temperature on photosynthesis

The effects of temperature on net photosynthesis were examined using the Hansatech instrumentation, in late summer, 1997. Plants were acclimated to 10, 15, 20 and 25°C for 1 h prior to incubation in the oxygen measuring chamber in the dark (respiration) and at saturating light intensity (net saturated photosynthesis). Plants from 1 and 6 m below CD were used. When expressed on a dry weight basis, there was no significant difference in photosynthesis between plants from the two depths at any given temperature. Both respiration and photosynthesis showed non-linear relationships to temperature (e.g. Fig. 3.18). A reasonable fit to the data was obtained using a quadratic expression, which indicated an optimum temperature of just below 20°C.

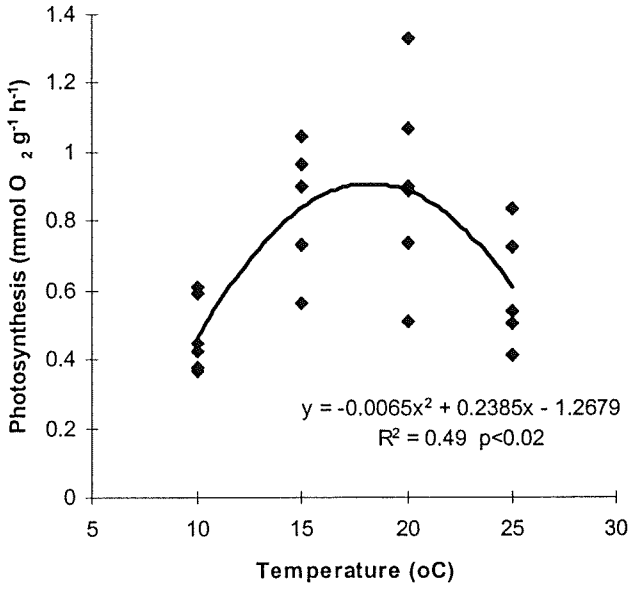

Fig. 3.18. The relationship between temperature and net photosynthesis at saturating light.

3.6 Comparison with literature data

Recently, Solidoro *et al.* (1997) published a model of the growth of *Ulva rigida* in the Venice lagoon. The model was designed to model the rate of uptake of external nutrients, hence the intracellular nutrient concentrations. Growth rate of *Ulva* was then modelled from the effects of light, temperature and intracellular nutrient status. The aim was to predict seasonal and spatial biomass changes in the plant population from the predicted growth rate and an estimate of mortality. The model proved successful at predicting the main features of *Ulva* growth in the lagoon. In estimating the parameters of this model, Solidoro *et al.* (1997) comprehensively reviewed existing information on the growth physiology of *Ulva* species. In this section we place our study in context, by comparing parameters which we derive from Tauranga, with their values (Table 3.4).

Solidoro *et al.* (1997) concurred with other workers in considering intracellular P to be unrelated to growth, in that P was not stored but was taken up as required. Our data confirm one aspect of this, in that there was little evidence of storage of P, although Fig. 3.3 indicates that growth (as net photosynthesis) fell when intracellular P was below 0.08%.

Table 3.4. Comparison of parameters selected from literature data by Solidoro *et al.* (1997) as the best estimates for *Ulva* species, with values derived in this study.

Parameter	This study	Solidoro *et al.* (1997)
Maximum growth rate	0.28 d^{-1}	0.45 d^{-1}
Minimum intracellular N	0.8%	1.0%
Maximum intracellular N	3-4%	4.5%
Saturating light	130 μmol m^{-2} s^{-1}	140 μmol m^{-2} s^{-1}
Maximum rate of photosynthesis	0.50 μmol O_2 mg^{-1} dry wt h^{-1}	0.86 μmol O_2 mg^{-1} dry wt h^{-1}

To examine the sensitivity of *Ulva* growth in the Tauranga Harbour to nutrients, we re-worked the Solidoro model, incorporating parameters and functional relationships measured at Tauranga and introducing a phosphorus limitation step based on best fit to Tauranga data. The model is structured in the following way. Growth rate (μ) and light saturated rate of photosynthesis as fractions of maximal rates (e.g. μ/μ_{max}) are expressed as functions (g) for each potentially limiting process, here intracellular N and P, temperature (T) and light (E). For example, g(N) is a function which describes the proportion of maximum growth rate at a given N content. Overall growth rate is given by the product of individual functions:

$$\mu = \mu_{max}.g(N).g(P).g(T).g(E)$$

The functions used by Solidoro *et al.* (1997), and derived from our data are shown in Table 3.5. Using the maximum rates of photosynthesis and growth given by Solidoro *et al.* (1997), we were able to use our formulations of g coefficents to predict rates of photosynthesis at a range of realistic combinations of variables (e.g. Fig. 3.19).

Table 3.5. Functional expressions relating *Ulva* growth to environmental conditions derived from this study and by Solidoro *et al.* (1997).

Functional expression	This study	Solidoro *et al.* (1997)
$g(N)$	$= (N-0.8)/(N-0.3)$	= (N-1)/N-0.8)
$g(P)$	$= (P-0.03)/P$	$= [P]/(0.01+[P])^*$
$g(T)$	$= 0.26T - 0.007T^2 - 1.41$	$= 1+\exp(-0.3(T-10))^{-1}$
$g(E)$	$= \tanh(E/E_k)$	$= 1-\exp(-E/162)$

* $[P]$ is the external concentration of phosphate

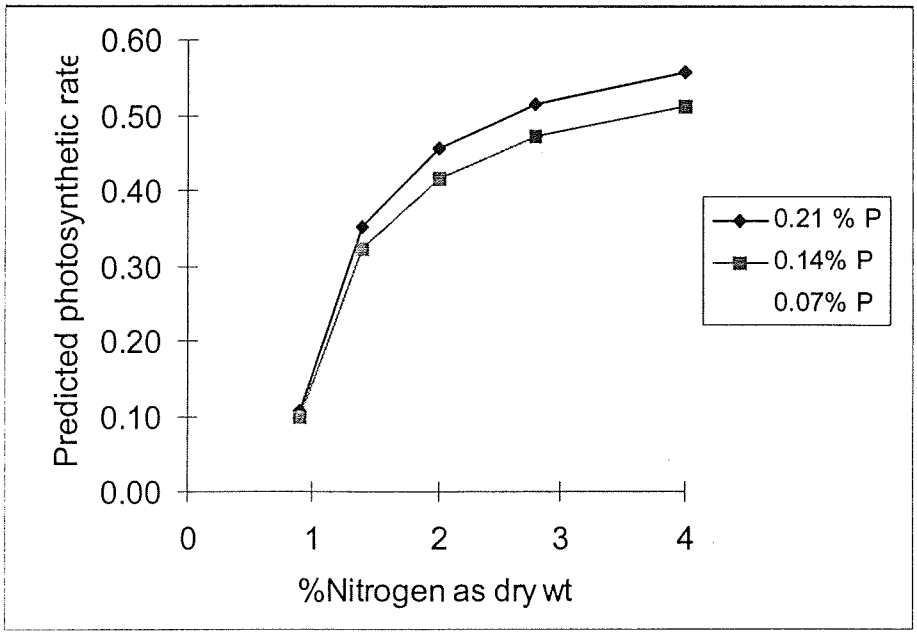

Fig. 3.19. Model predictions of photosynthetic rate at a range of intracellular N and P, at 20°C and 250 μmol photons m^{-2} s^{-1}.

These predictions are in line with observed rates of photosynthesis, and clearly indicate that, at the range of %P seen in this study, it is likely to be having a significant effect on *Ulva* growth. It is also interesting to compare predicted growth rates for plants during a high growth year (1992) and a low growth one (1997). Environment B.O.P. data from the 1992 period show mean intracellular N and P of plants from Otumoetai to be 2.51 and 0.13 respectively. Used in this model, at temperatures of 20° C and a light flux of 300 μmol m^{-2} s^{-1}, these values yield a P_{max} of 0.45 μmol O_2 mg^{-1} h^{-1}. This is almost twice the predicted value of 0.28 μmol O_2 mg^{-1} h^{-1} based on the intracellular N and P of 1.3 and 0.1% recorded in 1997.

The reasons for the lower intracellular nutrients in 1995-97 compared to 1992 cannot be determined from our data. The intracellular nutrient decline coincides with a low biomass phase of *Ulva*, and with the diversion of sewage discharge from the harbour to an ocean outfall. However, the importance of sewage diversion may depend on the relative importance of tidal flushing and in-harbour discharges to the nutrient balance. In this context, it is of interest that the periods of low external nutrient supply and *Ulva* growth coincide with periods of high sea surface temperature. These high temperatures may be an indication of advection of low nutrient, sub-tropical water to the coast during these years. Along this coast, high water temperatures are often brought about by dominance of south easterly winds, which promote onshore flow of subtropical water. In contrast, low sea temperature years tend to be maintained by dominance of north westerly winds, which promote offshore surface currents, and hence upwelling of cool, nutrient-rich bottom water at the coast.

4.0 MORPHOLOGY AND GENETIC ANALYSIS OF *ULVA* FROM TAURANGA HARBOUR

4.1 Background

Ulva plants within Tauranga Harbour are morphologically very diverse, encompassing the range of habitat forms described by Adams (1994). Three taxonomic entities have previously been collected from this harbour; *U. laetevirens, U. lactuca* and *U. rigida* (Park 1996). These species may be reliably distinguished by their histology (Phillips 1988).

Genetic studies on the *Ulva* population within Tauranga Harbour were initiated for three main reasons. Firstly, with recognised problems in identifying *Ulva* species by morphological features (Phillips 1988), a genetic analysis might assist histological studies to determine if more than one entity was commonly represented and if one particular entity constituted the nuisance species. Secondly, genetic analyses might reveal a basis for observed morphological and physiological variability. Finally, the spatial distribution of genetic character was investigated to detect if there were relationships between site populations which could result from the production and dispersal of drift within the harbour.

4.2 Methods

Ulva material was collected for histological analysis from one intertidal and three subtidal sites in Tauranga Harbour. Collections were made at the following sites (Fig. 3.8): Site 4 (Otumoetai - intertidal, subtidal at 3 and 6 m depth), Site 7 (Ongare Point - 1 m depth) and Site 9 (Shell Bank - 1 m depth). Where possible attached material was collected, but at Ongare Point (Northern Harbour) none was available so thalli with thickened basal areas were selected. A range of habitat forms including long and short ribbons, deeply dissected lobed, and large undivided sheets, each varying in thickness, were sampled.

Material from each site was sectioned in the basal region of the thallus and photographed at x160 magnification.

Ulva material was collected for genetic analysis from one intertidal and four subtidal sites in the Southern Harbour. Ten *Ulva* plants were collected at each of the five following sites (Fig. 3.8)

Site 2. Western Channel

Site 4a. Subtidal Otumoetai

Site 4b. Intertidal Otumoetai

Site 8. Scallop bed

Site 9. Shell bank

To analyse for DNA, these collections were washed in tap water and blotted dry. Material was frozen in liquid nitrogen, then ground in a pestle and mortar. Duplicates of each sample were processed separately as follows. Ground material was mixed with extraction buffer and left to stand. Nucleic acids were precipitated by adding absolute ethanol with sodium acetate, freezing then centrifuging. The resulting pellet was re-suspended in Tris-EDTA buffer.

DNA yield was quantified spectrophotometrically and compared with standards using electrophoresis (Sambrook *et al.* 1989).

DNA in the samples were then amplified using the following RAPD protocol. Samples were mixed with a combination of *Taq* polymerase, one of nine DNA primers, dNTP and PCR buffer. Tubes were sealed with mineral oil and processed in a thermocycler; running through 40 cycles of denaturation (at 94°C), annealing (at 35° C) and extension (at 72°C). All RAPD reactions were repeated at least twice.

Amplification products were analysed by electrophoresis, visualised under UV light after staining with ethidium bromide, compared with standards (ladders) with known base pair numbers. The resultant DNA patterns were scored for each sample (and duplicates) by presence/absence of bands for each primer. Results of this scoring were analysed using the RAPDistance package (Armstrong *et al.* 1994) calculating pairwise distances between samples using several algorithms and using these to construct a Neighbour-Joining Dendrogram.

Samples were also amplified for DNA sequencing in the ITS region, performed by the Waikato University Sequencing facility. Samples were sequenced and compared changes within the 20 and 432 base-pair region.

4.3 Results and Discussion

A large degree of variation between individuals was observed in all dendrograms produced by each RAPD algorithm (Fig. 4.1). Analysis of molecular variance (WINAMOVA) results apportioned 75% of variation between individuals. However, individuals from each sample site generally clustered together, with sub- and inter-tidal Otumoetai plants forming one group, shell bank plants a second group and Western Channel and scallop bed plants a third group. The Western Channel and scallop bed sites are situated within the same channel, approximately 4 kilometres apart.

These RAPD results indicate there is a genetically diverse population of *Ulva* within the Southern Harbour, with evidence of some local variation between sample sites. Results of ITS sequencing were generally very poor with only 11 of 27 samples giving good sequences. A total of 3 different haplotypes were discerned from these samples. These variations were based on a point mutation at base-pair position 406, or a premature termination site and variations were not confined to any one sample site. These variations and the fact that only 11 of 27 samples produced a product corresponding in size to the ITS region would reinforce the assertion that a genetically diverse population occurs within Tauranga Harbour.

Histological investigations of *Ulva* collected within the harbour have revealed that all samples investigated fit the species *U. rigida* based on cross sections cut from basal thallus regions (Phillips 1988). These are illustrated in Plates 4.1 to 4.5. *U. rigida* is distinguished from *U. lactuca* by the presence of palisade-like basal cells, being more than twice as high than they are wide, compared with almost square cells in *U. lactuca*. The basal cells of *U. laetevirens* are conical rather than rectangular in shape.

It would thus appear that *U. rigida* is the only *Ulva* species sampled within Tauranga Harbours, although this does not exclude the possibility of other species being present. Populations at each site are genetically diverse, but there is some level of similarity within plants sampled from each site and within plants sampled in the same channel.

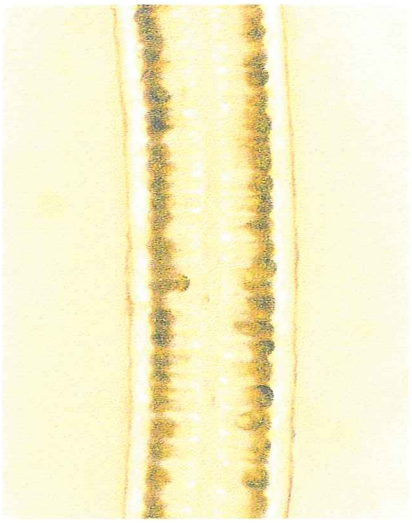

Plate 4.1. Cross sections of basal region of *Ulva* thalli (x160) from the intertidal region at Otumoetai.

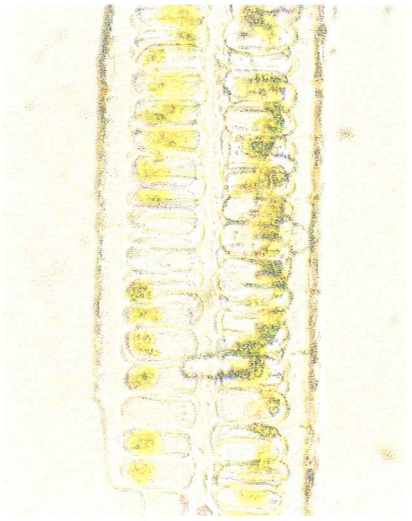

Plate 4.2. Cross sections of basal region of *Ulva* thalli (x160) from the deep subtidal region (6 m) at Otumoetai

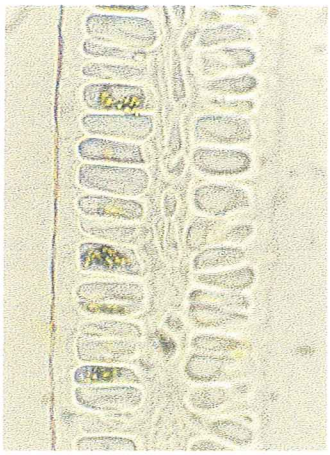

Plate 4.3. Cross sections of basal region of *Ulva* thalli (x160) from the shallow subtidal region (2-3 m) at Otumoetai

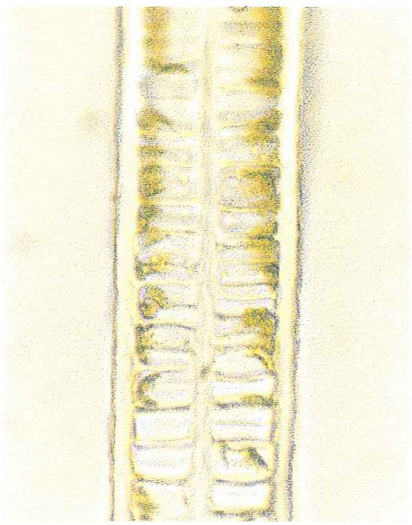

Plate 4.4. Cross sections of basal region of *Ulva* thalli (x160) from Ongare Point.

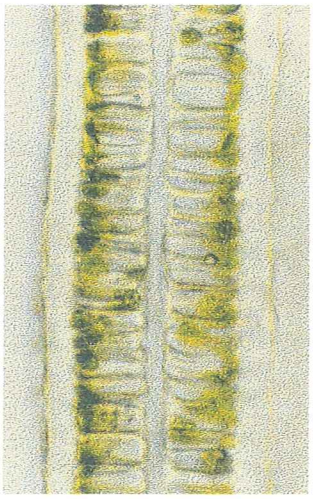

Plate 4.5. Cross sections of basal region of *Ulva* thalli (x160) from the shelly bank area.

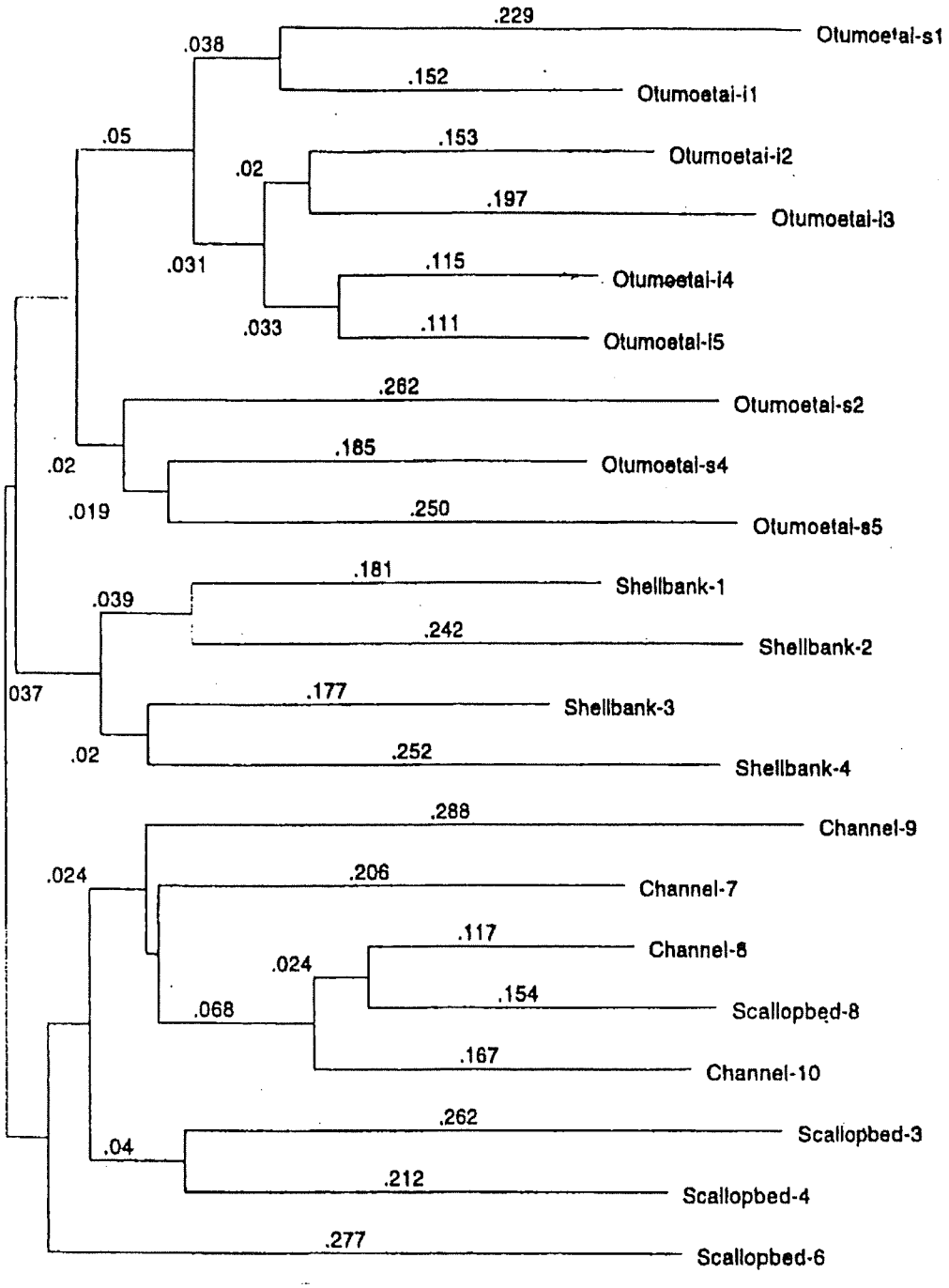

Fig. 4.1. *Ulva* neighbour-joining tree based on RAPD data for 4-5 plants from 5 locations: Otumoetai subtidal (s), Otumoetai intertidal (I), shell bank, Western Channel and scallop bed (see Fig. 3.8).

5. RECOMMENDATIONS

- Management of prolific *Ulva* populations in Tauranga Harbour would be best sought by reducing plant growth rates, as variations in *Ulva* abundance appear to be predominantly driven by changing growth rate.

- The most promising avenue of management action to control *Ulva* growth is via nutrient limitation. Growth factors of temperature and incident radiation are clearly beyond management control, while reductions in harbour clarity which would result in light limitation of a significant proportion of *Ulva* are unlikely to be acceptable.

  These studies have identified optimum intracellular N and P values for *Ulva*, with reductions below this optimum producing proportional reductions in plant growth. Management of external nutrient supplies which result in nutrient limitation of *Ulva* would set the growth potential of harbour populations. The feasibility of achieving significant nutrient limitation of *Ulva* over the growth season depends on two main factors for which there is insufficient information currently.

  a) The nutrient uptake kinetics, storage and utilisation behaviour of *Ulva*: Information is required on what harbour water nutrient concentrations, nutrient forms and flow regimes are required by *Ulva* to maintain nutrient sufficiency and also how long stored intracellular nutrients may support plant growth in the absence of sufficient external nutrients. Presently, NIWA is investigating nutrient uptake kinetics of *Ulva* at different levels of water nutrient concentrations, flow and intracellular nutrient status to provide preliminary information on sea lettuce nutrient requirements.

  b) The limits to the extent or timing of harbour nutrient reductions: Reductions in nutrient discharges into the harbour cannot decrease levels below that of background concentrations in coastal waters. These background levels would have to be low enough to significantly limit *Ulva* growth at critical times of the year. In this respect, the occurrence of events that enrich coastal waters (eg. El Niño), and which are beyond control, could have the potential to negate management actions. Sampling of nutrients in harbour and coastal waters over an ecologically relevant time scale during the *Ulva* growth season would provide some of these answers.

- A model should be developed to help predict changes in *Ulva* abundance from changes in key conditions. The possibility of adapting overseas models developed to predict *Ulva* growth and biomass accumulation should be investigated for

Tauranga Harbour. If successful, such a model could not only provide an explanation for variations in *Ulva* presence but also ascertain the likely impact of various nutrient reduction scenarios on *Ulva* growth and biomass accumulation.

- Early indicators of problem accumulations should be assessed. For example, a high over-wintering biomass could signal a high abundance year, because it represents a higher 'principal' for incremental growth. The benefit of such indicators is that managing authorities would have the opportunity to budget for beach clearing activities in the likely event of a bloom.

6. ACKNOWLEDGEMENTS

This study was funded in part by Environment B.O.P, Tauranga District Council and Western Bay of Plenty District Council and also by the Foundation for Research, Science and Technology. The authors were assisted in the field by A. Taumoepeau, R. Wells, T. Dugdale and C. Kemp (NIWA). Meteorological data was retrieved by M. Bellingham and N. Eynon-Richards (NIWA) and Environment B.O.P provided sea surface temperature data for Tauranga Harbour. The Waikato University Sequencing facility performed DNA sequencing. Dr L. Dijkstra and Dr D. Hoffstra contributed to genetic studies of *Ulva*, C. Stanger, F. Richards provided laboratory assistance and Dr A-M Schwarz (NIWA) provided valuable comments.

7. REFERENCES

Adams, N.M. (1994). Seaweeds of New Zealand: An illustrated guide. Canterbury University Press, Christchurch, New Zealand, 360 pp, 116 plates.

Armstrong, J.S.; Gibbs, A.J.; Peakall, R.; Weiller, G. (1994). 'The RAPDistance Package.' obtainable via WWW.

Bjornsater B.R.; Wheeler P.A. (1990). Effect of nitrogen and phosphorus supply on growth and tissue composition of *Ulva fenestrata* and *Enteromorpha intestinalis* (Ulvales, Chlorophyta). *Journal of Phycology*, 26: 603-611.

Clayton, J.S. (1983). Sampling aquatic macrophyte communities. *In*: Biggs, B. J.; Gifford, J. S.; Smith, D. G. (eds.) Biological methods for water quality surveys. *Water and Soil Miscellaneous Publication 54,* Wellington, Ministry of Works and Development.

de Winton, M.D.; Clayton, J.S.; Hawes, I. (1996). Subtidal *Ulva* within Tauranga Harbour ; 1995/1996. *NIWA Consultancy Report No* BPR70205/1, 31 pp.

de Winton, M.D.; Clayton, J.S.; Hawes, I. (1997). Intertidal and subtidal *Ulva* dynamics in Tauranga Harbour, New Zealand. Abstracts of the 13th annual conference of the Australasian Society for Phycology and Aquatic Botany. 22-24 January, 1997, CSIRO Marine Laboratories, Hobart. pg 61.

Fillit, M. (1995). Seasonal changes in the photosynthetic capacities and pigment content of *Ulva rigid*a in a Mediterranean coastal lagoon. *Botanica Marina*, 38: 271-280.

Fong, P.; Zedler, J.B. (1993). Temperature and light effects on the seasonal succession of algal communities in shallow coastal lagoons. *J. Exp. Mar. Biol. Ecol.*, 171: 259-272.

Fujita, R.M.; Wheeler, P.A.; Edwards, R.L. (1989). Assessment of macro-algal nitrogen limitation in a seasonal upwelling region. *Mar. Ecol. Prog. Ser.,* 53: 293-303.

Hawes, I.; Schwarz, A., (1996) Epiphytes from a deep-water characean meadow in an oligotrophic New Zealand lake: species composition, biomass and photosynthesis. *Freshwater Biology,* 36: 297-313.

Hawes, I.; Smith R.A. (1993). Effects of localised nutrient enrichment on the shallow epilithic periphyton of oligotrophic Lake Taupo, New Zealand. *New Zealand Journal of Marine and Freshwater Research*, 27: 365-372

Hawes, I.; Smith, R.A. (1995). Effect of current velocity on the detachment of thalli of *Ulva lactuca* (Chlorophyta) in a New Zealand estuary. *Journal of Phycology*, 31: 875-880.

Hecky, R.E.; Kilham, P. (1988). Nutrient limitation of phytoplankton in freshwater and marine environments: A review of recent evidence on the effects of enrichment. *Limnol. Oceanogr.*, 33: 796-822.

Jassby, A.D.; Platt, T. (1976). Mathematical formulation of the relationship between photosynthesis and light for phytoplankton. *Limnol. Oceanogr.*, 21: 540-547.

Jeffrey, D.W.; Madden, B.; Rafferty, B.; Dwyer, R.; Wison, J.; Allott, N. (1992). Algal growths and foreshore quality. Dublin Bay water quality management plan, Environmental Research Unit technical report No. 7.

Lowthion, D.; Soulsby, P.G.; Houston, M.C.M. (1985). Investigation of a eutrophic tidal basin: part 1 - factors affecting the distribution and biomass of macro-algae. *Marine Environmental Research*, 15: 263-284.

Morand, P.; Briand, X. (1996). Excessive growth of macro-algae: a symptom of environmental disturbance. *Botanica Marina*, 39:491-516.

Niesenbaum, R.A. (1988). The ecology of sporulation by the macroalga *Ulva lactuca* L. (Chlorophyceae). *Aquatic Botany*, 32: 155-166.

Owens, N.J.P.; Stewart, W.D.P. (1983). *Enteromorpha* and the cycling of nitrogen in a small estuary. *Est. Coast. Shelf Sci.*, 17: 287-296.

Park, S. (1994). Environment B.O.P natural environment regional monitoring network coastal and estuarine ecology programme 1993/94. *Environment B.O.P. Report Number 94/20*, 137 pp.

Park, S. (1996). Sea lettuce monitoring in the Bay of Plenty - changes in abundance, nutrients and environmental influences for the period July 1992 - June 1996. *Environment B.O.P. Environmental Report 96/23*, 50 pp.

Phillips, J.A. (1988). Field, anatomical and developmental studies on southern Australian species of *Ulva* (Ulvaceae, Chlorophyta). *Australian Systematic Botany, 1:* 411-456.

Price, L.H.; Hylleberg, J. (1982). Algal-faunal interactions in a mat of *Ulva fenestrata* in False Bay, Washington. *Ophelia*, 21: 75-88.

Reise, K. (1983). Sewage, green algal mats anchored by lugworms, and the effects on Turbellaria and small Polychaeta. *Helgoländer. Meeresuntersuchungen*, 36: 151-162.

Rivers, J.S.; Peckol, P. (1995). Summer decline of *Ulva lactuca* (Chlorophyta) in a eutrophic embayment: interactive effects of temperature and nitrogen availability? *J. Phycol.*, 31: 223-228.

Sambrook, J.; Fritsch, E.F.; Maniatis, T. (1989). Molecular cloning: a laboratory manual, 2nd Edition, Cold Spring Harbour Laboratory Press, Cold Spring Harbour, NY.

Senft,W.H. (1978). Dependence of light-saturated rates of algal photosynthesis on intracellular concentrations of phosphorus. *Limnol. Oceanogr.*, 23: 709-718.

Snow, J.A. (1996). Life history of *Ulva* in Tauranga Harbour. Unpublished MSc Thesis, University of Auckland.

Sfriso, A.; A Marcomini (1996). Decline of *Ulva* growth in the lagoon of Venice. *Bioresource Technology*, 58: 299-307

Shellum, B.H.; Josselyn, M.N. (1982). Physiological ecology of *Enteromorpha clathrata* (Roth) Grev. on a salt marsh mudflat. *Bot. Mar.*, 25: 541-549.

Solidoro, C.; Pecenik, C.; Pastres, G.; Franco, R.; Dejak, D. (1997). Modelling macroalgae (*Ulva rigida*) in the Venice lagoon: Model structure identification and first parameters estimation. *Ecological Modelling,* 94 (2-3): 191-206

Steffensen, D.A. (1976). The effect of nutrient enrichment and temperature on the growth in culture of *Ulva lactuca* L. *Aquatic Botany*, 2: 337-351.

Thom, R.M.; Albright, R.G. (1990). Dynamics of benthic vegetation standing-stock, irradiance, and water properties in Central Puget Sound. *Marine Biology*, 104: 129-141.

Woodin, S.A. (1977). Algal 'gardening' behaviour by Nereied polychaetes: effects on soft-bottom community structure. *Marine Biology*, 44: 39-42.

Zeldis, J.; Sharples, J.; Uddstrom, M.; Pickmere, S. (1998). Fertilising the continental shelf: biological oceanographic studies on the northeastern New Zealand continental margin. *Water & Atmosphere,* 6 (1): 13-16.