NIWA
Taihoro Nukurangi

Subtidal *Ulva* within Tauranga Harbour: 1995/96

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prepared for
Environment B.O.P.

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EXECUTIVE SUMMARY

The extent of *Ulva* development within the subtidal reaches of Tauranga Harbour has not previously been documented, despite probable links between submerged growth and nuisance strandings. To address the gap in the ecological information on this problem seaweed, two approaches were recommended. Firstly a systematic survey of the distribution and abundance of the submerged *Ulva* population was proposed, and secondly, laboratory experimentation to gain relevant physiological information.

In 1995, a survey of thirty-four harbour sites took place in late February-early March and eleven of these sites were re-surveyed in mid-February 1996. SCUBA divers made observations of *Ulva* abundance and associated features across a wide range of water depths at these diverse locations. Plant material was collected for short term physiological experiments to determine the effects of light and nutrients on subtidal *Ulva* growth.

Results of the 1995 and 1996 surveys were similar. *Ulva* was recorded throughout the harbour at generally low abundance (average cover ≥5%). Biomass of marine macroalgae as a whole was also low at most sites (≥25%), and dominated by four Rhodophycean algae in addition to *Ulva*.

A number of factors were recognised to influence *Ulva* distribution and abundance in Tauranga Harbour. Subtidal *Ulva* biomass accumulation was seasonal in development as indicated by long-term NIWA monitoring (March 1994-present) at a representative site, and surveys were intentionally carried out during high biomass. The timing of peak subtidal biomass is apparently controlled by climatic factors including irradiance and temperature.

Light availability is considered to restrict the growth rate of subtidal *Ulva* at many locations in Tauranga Harbour. The light regime constantly fluctuates with the depth and clarity of overlying water, but even under conditions optimal for light availability, light intensities encountered at some sites were below levels experimentally shown to limit photosynthetic rate of subtidal plants. Although subtidal *Ulva* shows adaptation enabling efficient photosynthesis under unfavourable light conditions and may be capable of net growth, biomass is determined by growth in excess of rates of loss.

Survey observations and physiological experiments suggest that nutrients do not limit the development of subtidal *Ulva* in Tauranga harbour. Plant N:P ratios were close to optimal for algae and nutrient status did not relate to photosynthetic performance.

Hard substrates, shell and bivalve beds, provide initial recruitment points for attached plants. Mobilisation of attached plants as drift results from a complex interaction between current strength, substrate and the size of *Ulva* thallus. Both dislodgment of substrates used for plant anchorage and detachment at the base of the plant were observed. Mobile *Ulva* drift was common in mid-tidal currents, especially within channels, while large accumulations of drift fallout were observed within the Western Channel, southern basin, in areas where tidal currents slowed. Drift plants were frequently snagged around obstacles or accumulated within hollows in the substrate under low water movement, but most plants had become re-anchored in sandy substrates by limited burial. Burial was assisted by the action of polychaete worms in immobilising drifting plants in shallow sites, and by subsequent sedimentation processes, and this burial of tissue represents a large potential loss for the population.

Harbour circulation patterns developed for modelling sediment transport (Barnett 1985) are indicative of the major directions and pathways for *Ulva* drift within Tauranga Harbour. Obtaining data on the mobilisation threshold of *Ulva* and its transport velocities would enable drift movements to be modelled so source areas and intertidal accumulations can be predicted.

Survey results indicate *Ulva* growths can develop over much of the subtidal area of Tauranga Harbour on a seasonal basis. However the extent of variation in subtidal *Ulva* populations between years is not yet known. Likewise, the degree to which the subtidal populations are linked to prolific intertidal growths has yet to be defined. In this respect, representative subtidal sites should be re-investigated in the event of nuisance strandings, so that the linkages between subtidal and intertidal *Ulva* populations can be determined.

INTRODUCTION

Tauranga Harbour has experienced prolific intertidal growths of sea lettuce, *Ulva*, in past summers. These have proved undesirable for ecological, aesthetic and economic reasons and there have been calls for management action to reduce the frequency and severity of nuisance growths. The origins of intertidal material have not been definitively determined although dense subtidal populations of *Ulva* are believed to be an important source for strandings. The links between these two populations require further investigation.

A number of questions are raised in relation to the subtidal *Ulva* population in Tauranga Harbour. For example, what is the distribution and abundance of submerged plants? What proportion of total *Ulva* biomass do they comprise? What are the factors operating within the harbour that have the potential to influence the status of subtidal *Ulva*? Finally, is there a causal link between submerged *Ulva* growth and the occurrence of nuisance intertidal growths.

Until recently, there has been little investigation of submerged *Ulva*. In 1994 NIWA established a subtidal monitoring site at Otumoetai as a component of FRST funded research, in order to follow long term trends in *Ulva* abundance and identify influences on biomass accumulation. Over two and a half years of observations have now been completed. Because of limited funding and resources for this programme of study, the level of investigations in other parts of the harbour was restricted.

It was recommended to Environment BOP that a systematic survey of subtidal *Ulva* be undertaken to provide essential baseline information on the distribution and abundance of submerged populations within Tauranga Harbour. The first survey in the summer of 1995 provided important insight into the status of submerged *Ulva* and factors influencing its development (de Winton & Clayton 1995). A re-survey of selected sites in the summer of 1996 was recommended to indicate year to year variability in maximum *Ulva* development. The need for physiological experiments to determine the effect of light and nutrients on *Ulva* growth was also recognised, with the emphasis on observations which are relevant to harbour populations.

This report synthesises the results from both the 1995 and 1996 surveys of *Ulva* within the subtidal reaches of Tauranga Harbour. In addition, early results of physiological experiments are reported and related to field observations.

METHODS

Survey

In 1995 twenty-three subtidal sites were surveyed within the southern region of Tauranga Harbour on 27 and 28 February (sites A-W), and eleven sites surveyed within the northern region of the harbour on 1 March (sites I-XI). Profile sites were selected to represent all parts of the harbour as well as a range of water depths. NIWA's long-term monitoring site (Site F, Otumoetai) was also included so that observations here could be related to the whole harbour. Table 1 describes the position of survey sites and their location within the harbour is illustrated in figure 1.

In 1996, seven sites were resurveyed within the southern harbour on 13 and 14 February (sites C, F, G, J, L, P, W), and four sites within the northern harbour on the 12 February (sites I, III, VI, IX).

All depths in this report are reduced to metres below Chart Datum (approximately the Lowest Astronomical Tide). Actual depth at the time of the surveys was corrected according to tidal height and time of the tidal cycle. During the 1995 survey, tidal range was 0.2 to 1.8 m above Chart Datum and during the 1996 survey it was 0.2 to 1.7 metres (Hydrographic Office RNZN Tide Tables). At each site, observations were made at 0.5 m depth and every 1 m depth interval. Corrected depths were initially located by depth sounder and subsequently maintained to within 0.5 m by monitoring a dive computer (Dacor Omni^{TM}). Time lags were noted for tidal cycles within the inner harbour, for example M.H.W. at Omokoroa is 100 minutes later than the wharf (RNZN Tide Tables). However this delay represents only a slight correction error of generally less than 0.5 m.

The survey method was modified from Clayton (1983). At each depth a SCUBA diver observed a 2 m wide band of approximately 20 m length while swimming in the same direction as any current. Average covers of *Ulva* were subjectively scored with reference to the following modified Braun-Blanquet cover scale. 1=1-5%, 2=6-25%, 3=26-50%, 4=51-75%, 5=76-95%, 6=96-100%.

The maximum *Ulva* cover within any 2 m^2 area was also scored. Size of *Ulva* was recorded as the maximum and average greatest linear dimension (g.l.d.) of thalli. All *Ulva* species were included in observations, as it is impossible to accurately distinguish any species based upon morphological characteristics in the field (Adams 1994). Maximum and average covers were estimated for marine macro-algae as a whole and dominant species were noted. Algal identifications follow Adams (1994). Additional observations were made of substrate type, plant attachment and any signs of *Ulva* sporulation or grazing damage. During the 1995 survey underwater video footage was taken at 14 sites, as a permanent visual record of macro-algae abundance.

In 1996, penetration of Photosynthetically Available Radiation (PAR) through the water column was measured at 3 sites (F, P and VI) using a Licor LI 188B integrating quantum radiometer. Readings were taken for surface light (sensor in air), sub-surface light and at 0.5 m depth intervals to the harbour bottom. Readings were made under sunny conditions with light cloud cover, at about high tide, between 12 noon and 3 pm.

Physiological measurements

On both survey occasions, a number of measurements of the physiological condition of *Ulva* plants were made. Five plants were collected from a total of six sites from across the harbour. Three samples for analysis were taken from each plant by cutting a 2.5 cm^2 disc from an undamaged area of frond. Measurements were made of thallus dry weight, chlorophyll *a*, nitrogen and phosphorus contents, all of which were normalised to thallus area.

In addition, rates of photosynthesis were determined for plants from each collection site over a range of light intensities from 0 to 485 μmol photon m^{-2} s^{-1} at ambient temperature. Photosynthesis was determined as rate of change of oxygen concentration over time. Measurements at a range of light intensities enabled a mathematical formulation of the light-photosynthesis relationship to be derived. This took the form of the hyperbolic tangent function of Jassby and Platt (1976);

$P = Pmax.\tanh(\alpha\varepsilon/Pmax) - R$, where

P = rate of photosynthesis
$Pmax$ = light saturated rate of photosynthesis
α = slope of the curve at low light
ε = light intensity
R = respiration rate

RESULTS

Survey sites

There was considerable variation noted in the physical characteristics at different survey sites in terms of depth, slope, water clarity, substrate and current flow. Surveyed sites included large shallow subtidal areas (≤2 m), particularly within the inner reaches of both harbours (R, S, W, X, XI). An extensive shallow bank at the entrance of the southern harbour was also sampled (Centre Bank; T, U, V). Deep channels, a relatively small proportion of the harbour (figure 1), comprised well defined steep banks and flat channel base (eg. Western Channel sites G, H & I, site II), while marginal channels (eg. Otumoetai Channel, Town Reach, sites L, O, VI, VIII), had more gradual bathymetry.

There was a link recognised between substrate type and current strength at sites. The inner harbour shallows consisted of extensive sandy flats (≤2 m) which were swept by tidal flows to and from the adjacent intertidal regions, with some having silty deposits. Shelly substrates were present in high current areas at the harbour mouths (sites E, I) or channel beds (sites V, VI). Strong water flows were also encountered at the Centre Bank area, where substrates varied from large sand ripples (V) to shelly sand (U) and 'shell lag' (site T).

Light profiles (% of surface light) show light conditions vary with site location and water depth (figure 2). Site P in the inner southern harbour had the lowest light penetration through the water column with 90% of incoming light lost by 4.5 m depth. Site VI close to the northern harbour entrance displayed greater light penetration with 90% of surface light to 7 m depth. Site F in the southern harbour had an intermediate level of light penetration. These measurements supported divers observations of reduced water clarity at inner harbour sites, particularly those close to river inflows (eg. sites Q, S, X) and clearer water at areas close to the harbour mouths (sites D, E, T). Reduced clarity was also observed in shallow areas where wave action disturbed silty substrates (site K).

1995 Survey

Ulva was widespread and was recorded from all 34 profile sites surveyed (tables 2 & 3), however there were no high cover growths at this time. Average covers of *Ulva* did not exceed 5%, except at two Western Channel sites (E, G) in the southern harbour and site II in the northern harbour. Here, average covers of up to 25% were recorded at some depths. The maximum cover recorded was up to 50%, again from Western Channel sites and sites I and II in the northern harbour. *Ulva* had an overall recorded depth range of 0.5 to 10 metres. There was no obvious pattern of plant abundance with depth, although the highest average and maximum cover values were within the 1 to 5 m depth range. The greater number of *Ulva* records from shallow water reflect the bathymetry of the harbour.

Ulva plants were small, usually less than 100 mm g.l.d. (tables 4 & 5), although thalli of up to 1 m were recorded. The largest thalli were associated with the high maximum cover sites, while plants of over 500 mm g.l.d. were only recorded from sites within the Western Channel (G, I, J) and Otumoetai (F), southern harbour.

The cover of marine macro-algae in total was also low (tables 6 & 7). Average covers of ≤25% were usual, exceeded only within the Western Channel, Te Puna Channel and site VI in the northern harbour. Approximately twenty-two species were recorded as dominant macro-algae, together with the tracheophyte *Zostera novazelandica* (table 8). Four Rhodophycean species; *Rhodymenia dichotoma*, *R. novazelandica*, *Hypnea nidifica* and *Spyridia filamentosa*, were frequently dominant. There was a pattern to the distribution of dominant macro-algae species. *Hypnea* and *Spyridia* were frequent within the inner reaches of the harbour while the *Rhodymenia* species dominated the outer reaches. *Gigartina circumcincta / atropurpurea* was conspicuous within the Town Reach, southern harbour.

Ulva did not display a preference for any one substrate type, but was recorded predominantly upon sand as the most common substrate type. Generally *Ulva* thalli were partially buried in sand substrates and in many cases appeared to have been anchored for some time, with decay and blackening of basal tissue evident. Upon shallow (≤2 m) sandy flats especially, burial was facilitated by the incorporation of *Ulva* into bundles of drift cemented together by mucus of polychaete worms (Nereidae). These polychaetes provided an initial attachment for *Ulva*, which was then subject to sediment processes. The actions of erosion and deposition could be seen around these bundles and over successive tides they were thought to form the uneven mini-dunes observed in these areas. Similar active burial was observed in areas of sand ripples. At site V sand ripples formed step-like ridges and troughs each 400 to 500 mm wide. Transported *Ulva* attached to shell fragments had sedimented in the lee of the steps with other coarse material. Migration of these formations with the predominant (flood) current was resulting in deposition over the accumulated *Ulva*.

Ulva plants were attached by holdfasts to shell debris, other algae and live shellfish, horse mussels (*Atrina zelandica*, eg. sites G, K, V, XI), pippis (*Paphies australis*, I) or scallops (*Pectin novaezelandiae*, L). In areas of shell lag substrates, numerous small plants (≤150 mm) grew attached to fragments (eg. I, T). No large plants were observed upon shell debris, however drag marks observed in sandy sediments near to site T (U, V) showed coarse fragments had been removed by currents and suggested the mobilisation of larger plants. Large holdfast attached plants were only observed upon live shellfish that were firmly embedded in the substrate.

Ulva drift was observed during times of high tidal flow, mainly at depth within defined channels (eg. M, N) and to a lesser extent on tidally 'swept' shallows. Mobile drift rolled across bottom sediments with the tidal currents and was only observed to enter the water column under high flow conditions in the base of main channels. There was also considerable sand movement observed within the bottom of major channels at peak current flow, in association with predominantly drift plants (eg. G, K). In local backwaters or in low current flow, unattached *Ulva* was often lodged in local depressions in sand substrates or snagged against obstacles.

1996 Survey

Ulva was present at all re-surveyed sites. *Ulva* cover was usually low (average ≤5%) except at site G in the Western Channel, where covers of 50% were recorded from 2 to 7 m depth (tables 2 and 3). Maximum covers were also highest at this site with *Ulva* covers up to 75% at some depths, forming a major component of dense drift accumulations of seaweeds. Elsewhere maximum *Ulva* covers were ≤25%.

Ulva plants at most sites were small, the median average size at 100 mm g.l.d. However large *Ulva* thalli (500 to 1000 mm g.l.d.) were frequently recorded from site G, Western Channel and Site F, Otumoetai (table 4). Large individual plants were also recorded from sites J, W and III (tables 4 and 5).

The total cover of marine macro algae was also generally low (average ≤5%), except site G in the Western Channel (tables 6 and 7). Here drift accumulations on the steep channel bank (2 to 7 m depth) usually exceeded 50% cover with 100% cover at some depths (table 6). Dominant species noted at most sites again included *Rhodymenia dichotoma*, *R. novazelandica*, *Ulva* sp., *Spyridia filamentosa* and *Hypnea* sp.

Ulva attachment types observed included burial, incorporation into polychaete refuges and attachment to shell fragments, live shells or tubeworm cases. *Ulva* drift was commonly moving deep within channels (eg. 7 to 9 m site G) with drift fallout on channel banks or in sandy depressions and snagging on obstacles to water flow. Unattached plants comprised the larger *Ulva* thalli recorded.

Physiological measurements

Nutrient concentrations within the tissues of *Ulva* thalli varied between sites. ANOVA identified two groups of sites, with site L (inner southern harbour) and site F (Otumoetai) having the highest mean % N, while material from sites III (Blakneys Channel), G (western Channel), I and II (outer northern harbour) were all significantly lower ($P<0.05$). There were no significant differences within the two groups of sites (figure 3). The ratio of N:P in plants from these sites did not differ significantly, the mean N:P ratio of 15.5:1 being close to the optimal ratio for algae (15:1).

Net photosynthetic rates per unit dry weight also varied between two groups of sites. Analysis by ANOVA found sites G, L and III had significantly higher photosynthetic rates than either sites I, II or F (figure 4). This grouping is different to that found for cellular N content. There was also no relationship by linear regression between either photosynthesis (normalised to chlorophyll *a* or dry weight) or respiration and % cellular nitrogen (figure 5).

Typical curves of light vs photosynthesis (figure 6) showed that subtidal plants had higher rates of photosynthesis *per unit area* at low light intensities than intertidal plants. This ability corresponded to the higher chlorophyll *a* concentrations of subtidal plants; an adaptation to maximise light absorbtion and hence to optimise low-light efficiency. In contrast, at high light intensities photosynthetic rates of subtidal plants were lower than intertidal plants.

Two critical light intensities were obtained from the light vs photosynthesis curves (figure 6). The light compensation point for photosynthesis, the light intensity at which net photosynthesis equals zero, for the subtidal plants averaged 12 μmol photons m^{-2} s^{-1} (figure 6). No *Ulva* growth would be possible below this light intensity. The saturation intensity, that beyond which increasing light has no effect on photosynthesis, was 100 to 150 μmol photons m^{-2} s^{-1} for subtidal plants (figure 6). Growth of subtidal plants will be light limited when ambient irradiance falls below this level.

DISCUSSION

An overview of factors with the potential to influence *Ulva* development has been obtained. Results of the 1996 survey were very similar to the 1995 results and re-enforce the information gathered during the more extensive survey. This suggests that accurate information on the status of subtidal *Ulva* within Tauranga Harbour can be obtained by the survey method. Such information will aid in the detection of important spatial or temporal differences in the status of *Ulva*, as surveys are repeatable and results from different locations are comparable. Results from physiological experiments will help interpretation of the response of *Ulva* growth to conditions in Tauranga Harbour.

The factors influencing *Ulva* development within the subtidal reaches of the Harbour, and the complex interactions between factors are considered below.

Seasonality

The harbour surveys were intentionally conducted during times of seasonally high *Ulva* development as indicated by regular monitoring of a site at Otumoetai (site F). Here, *Ulva* has a distinct seasonal cycle of abundance, with very low biomass over winter and peak development in summer.

Such seasonal plant growth cycles are determined by an interactive combination of climatic factors. For *Ulva*, changing temperature and irradiance are considered the most important factors for seasonal growth and the development of maximum biomass (Steffensen 1976, Thom & Albright 1990, Jeffery et al. 1992). By plotting the patterns of subtidal *Ulva* abundance at site F against key meteorological factors, the influence of changing climatic conditions can be seen for Tauranga. *Ulva* responded to increasing global radiation and sea temperatures over November/December with a rapid increase in abundance (fig. 7). Biomass was high over January, then declined in February/March. This reduction in abundance occurred while global radiation was still relatively high, and was independent of extreme tidal ranges that could cause *Ulva* removal by strong currents (fig. 7). One possibility is that water temperature, which lags a month or so behind changes in radiation, may have exceeded the favourable range for *Ulva* growth. Certainly temperature-growth experiments on a Christchurch population of *Ulva* showed growth rate rapidly fell above 20°C (Steffensen 1976) and sea surface temperatures at Tauranga exceed this value late in summer (fig. 7).

The temporal development of subtidal Ulva is strongly influenced by climatic factors.

Light

The proportion of surface irradiance available to submerged macro-algae depends upon attenuation of light by the water column, as determined by water depth and the presence of dissolved or suspended matter. Tauranga harbour presents a spatially and temporally fluctuating light regime for the photosynthesis and growth of subtidal *Ulva*, as water clarity varies from site to site and also changes over time, while water depth follows a tidal cycle. It is therefore difficult to determine the precise light conditions encountered by *Ulva* plants and their growth response.

Irradiance-depth profiles measured for three different sites in the harbour indicate that light levels commonly restrict *Ulva* photosynthetic rates. Light saturation of photosynthesis in subtidal *Ulva* from Tauranga Harbour occurs at c. 100-150 $\mu E\ m^{-2}\ s^{-1}$, and at lower light levels growth rates are below maximal (if other factors are not limiting). If the surface irradiance at noon on a sunny day in summer (c. 1500 $\mu E\ m^{-2}\ s^{-1}$) is considered, this saturation value is equivalent to 10% of surface light. As shown in fig. 2, 10% of surface light penetrates to 7 m at site VI and only 4.5 m at site P, inner harbour. In reality, surface irradiances are usually lower than 1500 $\mu E\ m^{-2}\ s^{-1}$ (eg. lower sun angle, cloud cover, low global radiation) and waters may be much more turbid than at the time of these measurements. Light would therefore limit *Ulva* growth rate across a wide range of depths, especially at sites of low water clarity.

Ulva has the capacity to adapt to different irradiance levels by altering photosynthetic apparatus (Vermaat & Sand-Jensen 1987). For example, subtidal plants from Tauranga Harbour have higher chlorophyll *a* levels per surface area than intertidal counterparts and so can utilise low light intensities efficiently. There were also differences in net photosynthesis found for plants from different sites within the harbour. The highest photosynthetic rates were recorded for plants from the inner harbour and lowest rates for plants collected from near to the harbour entrance. By acclimation to the predominant light regime, the alga can maintain efficient photosynthesis under fluctuating light conditions such as found in tidal inlets (Sand-Jensen 1988, Henley & Ramus 1989).

Ulva may persist under unfavourable light conditions. For example, adaptation to low light levels can enable net *Ulva* growth at irradiances as low as 0.6 μE m^{-2} s^{-1}, while plants can survive extended periods of dark (2 months at 4°C) with only temporary reductions in photosynthetic ability (Vermaat & Sand-Jensen 1987). Although capable of surviving under adverse light conditions, and even achieving net photosynthesis, it is growth in excess of loss rates which will determine *Ulva* biomass.

The absence of a clear depth distribution pattern for *Ulva* reflects the variability of spatial distribution of the plant, light conditions and physical heterogeneity of the harbour. *Ulva* is also mobile and can tolerate unfavourable light conditions. For example, although plants were recorded to a maximum depth of 10 m, material here may represent fragments recently transported from shallow depths which would not be viable in the long-term.

Light availability may limit Ulva growth rates over much of the subtidal reaches of Tauranga Harbour.

Nutrients

There were no patterns of *Ulva* distribution or abundance in Tauranga Harbour that could be related to nutrient supply. For example, the status of *Ulva* within both basins was similar despite the southern basin being enriched relative to the northern basin (Wilcock *et al.* 1990). In addition, experimental data on the relationship between nutritional status of collected subtidal plants and photosynthetic rates suggest that nitrogen content in the field is adequate to support growth requirements. Although the nutrient status of plants varied across sites, N:P ratios were well balanced, with no one nutrient obviously limiting to growth. This, and the absence of a relationship between photosynthetic rate and nutrient status suggests that nutrients play only a minor role in controlling the rate of *Ulva* biomass production.

Subtidal *Ulva* is less likely to be nutrient limited than intertidal plants because of the over-riding limitation of available light (eg. Lapointe & Tenore 1981). Also, even slight water movement has been shown to enhance nutrient uptake and growth of *Ulva* (Parker 1981) so the action of harbour currents may keep subtidal plants well supplied with nutrients.

Nutrient availability does not appear to limit subtidal populations of Ulva within Tauranga harbour.

Currents, substrates and attached *Ulva*

Current strength, substrate stability, *Ulva* attachment and contribution to drift are closely linked. Flow energies determine and are reflected by sediment type, attached plants grow on stable substrates, while the current velocities also contribute to the removal of attached plants.

Coarse shell materials comprise the substrate in areas of strong water movement, for example the shell lags depicted at the harbour mouths in a map of bottom sediment facies (Black 1985). These areas provide hard substrates for attached *Ulva* arising from over-wintering sporlings, persistent perennial holdfasts or for recruitment by spore settlement. One site providing significant shelly substrates is the shallow (0.4m) Centre Bank area near the mouth of the southern harbour. In January 1996, *Ulva* formed up to 100% cover patches around site T, with large plants (c. 500mm g.l.d.) attached upon live pippi/cockle shells and shell debris. Although similar shell substrates occur in the base of channels (Black 1985), these areas are unsuitable for attached growth, while on the predominant sand substrates attached plants are restricted to sparse horse mussels and other hard objects.

Attached plants may be mobilised together with their attached shell fragment, or become detached due to breakage of the stipe (Hawes & Smith 1995), and enter the drift population. Experiments in a recirculating flume shows there is a complex relationship between the plant size, strength of current and drag on the plant in determining the probability of stipe breakage (Hawes & Smith 1995). Dislodgment of attached plants would depend on these factors and also the weight/configuration of its anchoring fragment.

Attached plants develop on stable substrates which are of limited availability. Attached plants contribute to drift populations, their removal depending on plant size and the drag exserted by currents.

Drift movement

Drift moves with the predominant current and may wash back and forth with successive tidal flood and ebb. However, because the flow of water passing one spot is frequently greater during one tidal phase than the other (residual flow strength), passive drift has a net direction (Barnett 1985). Water circulation patterns developed to describe sediment transport with residual currents in Tauranga harbour (Barnett 1985, Black 1985) have relevance to *Ulva* as it too is transported by currents operating across the harbour bottom, although at a faster scale and different mobilisation threshold. The velocity of *Ulva* drift within Tauranga harbour has not yet been quantified but will have implications for the fate of drift. For example, drift originating near to the harbour entrance at the beginning of an ebb tide is likely to be lost from the harbour system if transport velocities are high.

Drifting material may actively grow during transport but is likely to be abraded, fragmented or could remain within deep channels unsuitable for growth. There is however, the likelihood of drift becoming re-anchored within favourable areas for growth.

This survey highlights the importance of polychaete worms in holding drift within shallow sandy areas. Anchorage of green algal mats by polychaetes is also described by Reise (1983). Here, algae upon North Sea tidal flats became anchored in the feeding funnels of lugworms and could resist removal by strong tidal currents. It was suggested that without this anchorage green algal mats would be washed away or confined to sheltered sites. Polychaete attachment within Tauranga Harbour has a similar role. Polychaete attachment and subsequent partial burial would help plants resist wave action or current removal and to remain in a high light environment conducive to rapid growth during the peak of the growing season. Initial polychaete colonisation may even involve small fragments which would not otherwise remain viable. Enhanced siltation and burial would counteract these benefits once conditions conducive for maximum productivity have passed.

Drift moves around the harbour with the predominant currents and may become anchored and re-mobilised a number of times.

Loss processes

Loss processes probably account for the rapid reduction in *Ulva* abundance at the monitoring site following peak summer biomass. If growth rates fall and are exceeded by loss rates, accumulated *Ulva* biomass may quickly be lost. Loss by wash-out from the harbour has been considered but is thought to only slowly 'dilute' populations, while neither significant sporulation nor grazing damage has been observed at the time of the decline.

The observations of *Ulva* burial suggest that this is an important loss process in Tauranga Harbour. *Ulva* is apparently tolerant of extended periods of dark, anoxic conditions at low temperatures (Vermaat & Sand-Jensen 1990), but burial in harbour sediments under summer temperatures may cause greater losses. Certainly burial was suggested to be a significant loss mechanism for another chlorophycean macro-algae (*Enteromorpha*, Owens & Stewart 1983) and losses of 4-5% per day were recorded for *Ulva* buried within natural sediments (Price & Hylleberg 1982). Under less favourable light conditions and active sediment processes such as encountered within deep channels of the harbour, lodged drift may not be sustainable as burial and decomposition of tissue must be matched by growth for plants to remain viable.

Observations at the monitoring site also suggest that little of the drift material incorporated into sediments during peak biomass successfully over-winters.

Loss processes such as burial result in rapid declines in Ulva biomass when they exceed growth rate in late summer.

Suggested scenario for subtidal *Ulva* development in Tauranga harbour

The seasonal cycle of submerged *Ulva* begins with the growth of over-wintering sporlings or perennial holdfasts in response to spring climatic conditions. The Centre Bank area appears to be the major region for the development of these attached plants due to the availability of stable substrates. 'Shell lag' substrates here comprise >80% cover of shell (Fig. 8, Black 1985), it is of shallow depth (0.4 m) and has high water clarity conducive to a rapid growth rate. Large plants develop here early in the summer.

Drift would be generated from the early growth and dislodgment of attached plants on the Centre Bank. Plant size and anchorage, current fields and the drag exerted on plants determine the probability of drift mobilisation. Field observations also suggest plants are mobilised from the Centre Bank.

Water circulation patterns in the outer part of the southern harbour (fig. 8) suggest the net direction of drift originating from the Centre Bank would be in-harbour, over a considerable distance (Barnett 1985). Actual pathways and drift velocities have not been determined but field observations agree with the circulation schema. For example at the Otumoetai monitoring site, large unanchored plants with remnant shell fragments contributed the bulk of material at peak biomass. These plants were thought to originate from attached communities observed earlier on the Central Bank. While at site G, Western Channel, large accumulations of drift material coincide with a large eddy in the circulation pattern; a probable deposition area.

Drifting plants become anchored in subtidal regions by polychaete attachment or partial burial. Light conditions at their location would determine their growth rate, which if it exceeds loss rates will result in biomass accumulation. Drift may be remobilised and anchored at a number of times and locations.

Stranding of subtidal drift probably initiates intertidal growths and may contribute much of the biomass of nuisance accumulations. Net directions of subtidal drift and an upstream source of material, together with features of the intertidal site may determine these accumulations.

CONCLUSION AND RECOMMENDATIONS

This survey provides the first detailed description of *Ulva* within the subtidal reaches of Tauranga Harbour and valuable baseline data for future investigations. Results show that *Ulva* develops large subtidal populations each summer, while intertidal populations appear to be primarily dependent upon strandings arising from subtidal populations.

Light and temperature are key factors controlling *Ulva* growth rate, and consequently the seasonal timing of subtidal population development. Plants initially develop attached to suitable substrates, which are largely restricted to areas of 'shell lag'. Subsequent dislodgment and drift mobilisation of attached *Ulva* plants is influenced by water velocity and the drag exerted on the growing plant. Drift moves with the predominant currents but can be captured and anchored by polychaetes resident in subtidal and intertidal sediments. Burial within mobile sand dunes, deposition in deep channels and harbour efflux would contribute to the rapid loss of *Ulva* populations once climatic conditions are no longer favourable for rapid growth.

In view of findings over the last two years the emphasis of investigations has shifted from studying the consequences of dense intertidal strandings, to those processes that generate strandings. The following actions are recommended to maximise the value of this information.

a) A re-survey of all survey sites in the event of an intertidal bloom, to detect critical differences in the distribution and abundance of subtidal *Ulva*, identify drift source areas and any local conditions of importance.

b) Investigate linkages between subtidal and intertidal populations by observing drift mobilisation on the Centre Bank, drift direction and rate of transport, with a view to modelling the circulation and fate of drift using the hydrodynamic harbour model (eg. Bell 1991).

c) Complete investigation on the effect of nutrient status and temperature on *Ulva* utilisation of light.

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Table 1. Global positioning reference and site description for 34 survey sites within Tauranga Harbour.

Profile Site	GPS Position	Description
A	S 37°39'60" E 176°09'60"	Rangataua Bay
B	S 37°42'10" E 176°10'75"	Inner Town Reach
C	S 37°40'60" E 176°10'29"	Outer Town Reach
D	S 37°38'32" E 176°10'72"	Pilot Bay
E	S 37°38'73" E 176°09'21"	South-east Matakana Island
F	S 37°39'64" E 176°09'57"	Otumoetai (monitoring site)
G	S 37°38'77" E 176°08'40"	Tilby Channel to Western Channel
H	S 37°38'52" E 176°08'01"	GRG beacon south of Duck Bay, Matakana Island
I	S 37°38'47" E 176°08'02"	South of Rangiwaeo Island
J	S 37°38'09" E 176°06'20"	Opunui Point
K	S 37°39'46" E 176°05'66"	North of Oikimoke Point, Wairoa river mouth
L	S 37°37'81" E 176°04'89"	G beacon north of Motuhoa Island
M	S 37°39'22" E 176°04'20"	G cone south of Motuhoa Island
N	S 37°39'16" E 176°03'40"	North of Te Puna Estuary
O	S 37°38'30" E 176°03'96"	Motuhoa Island opposite Omokoroa Beach
P	S 37°37'27" E 176°03'65"	Between Omokoroa point and Opureora landing
Q	S 37°38'04" E 176°03'17"	Omokoroa Jetty
R	S 37°36'84" E 176°02'93"	G beacon north of Omokoroa Point
S	S 37°37'59" E 176°02'04"	North of Ngakautuakina Point
T	S 37°38'66" E 176°10'52"	North-east of buoy platform on sandy plateau
U	S 37°39'02" E 176°09'63"	North-west of buoy platform on sandy plateau
V	S 37°39'15" E 176°10'25"	South-east of buoy platform on sandy plateau
W	S 37°39'13" E 176°04'47"	North of Te Puna Beach
I	S 37°28'71" E 175°55'87"	Matakana Island, adjacent to Katikati entrance
II	S 37°30'05" E 175°59'10"	Matakana Island, opposite Potu
III	S 37°29'72" E 175°58'13"	Ongare Point
IV	S 37°29'39" E 175°58'27"	From sandbar adjacent to Blakneys Channel
V	S 37°28'52" E 175°57'54"	GRG beacon at junction of Tuapiro and Blakneys Channels
VI	S 37°30'46" E 175°59'71"	Matakana Island, opposite Kauri Point
VII	S 37°30'83" E 175°58'76"	Kauri Point
VIII	S 37°30'83" E 175°58'76"	G cone south of Kauri Point
IX	S 37°31'69" E 175°59'84"	Inner harbour
X	S 37°31'90" E 175°57'53"	BY beacon east of Tahawi stream
XI	S 37°31'72" E 175°59'78"	Inner harbour

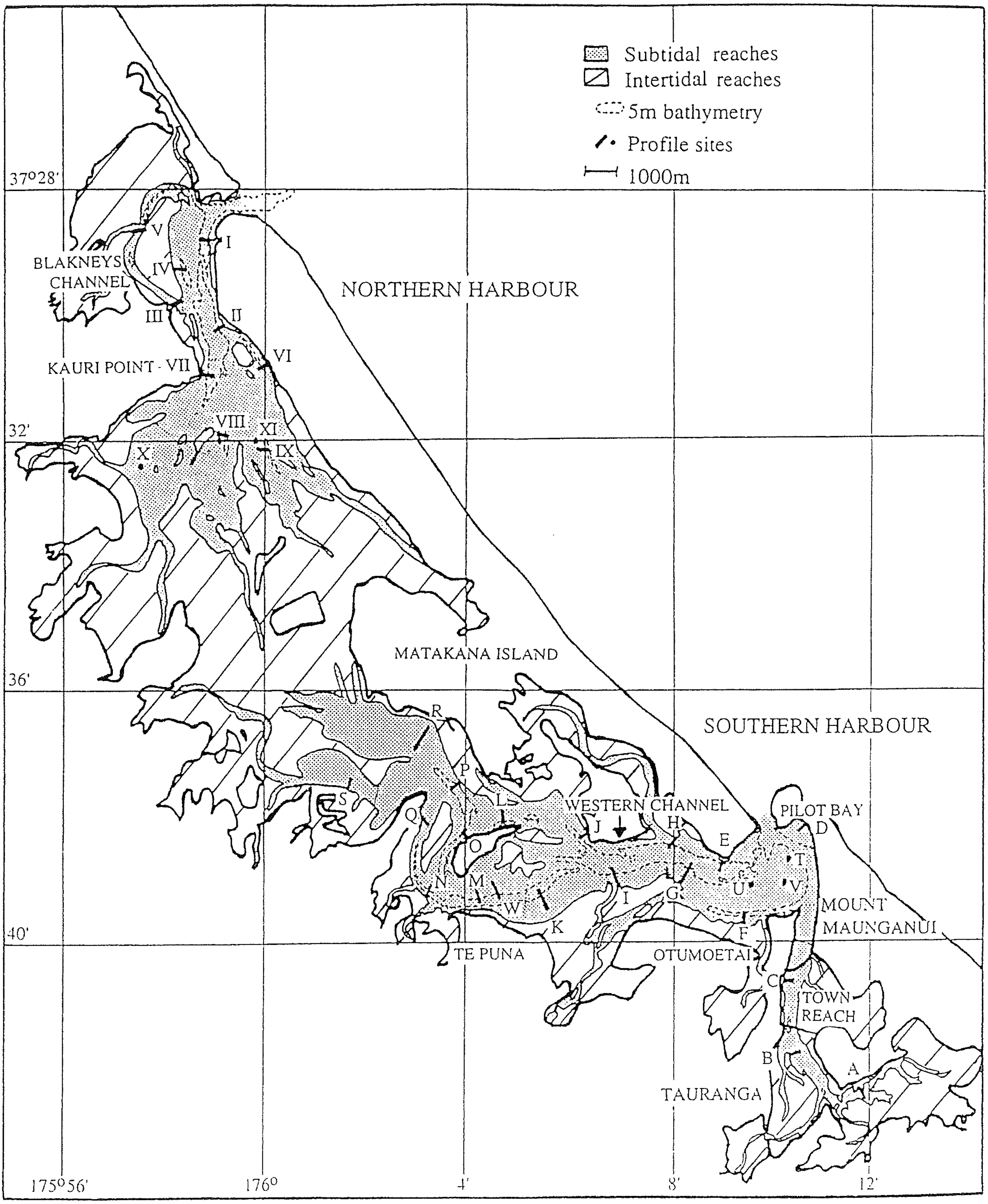

Fig. 1. Location of subtidal survey sites within Tauranga Harbour (map reproduced from RNZN hydrographic chart NZ 5411).

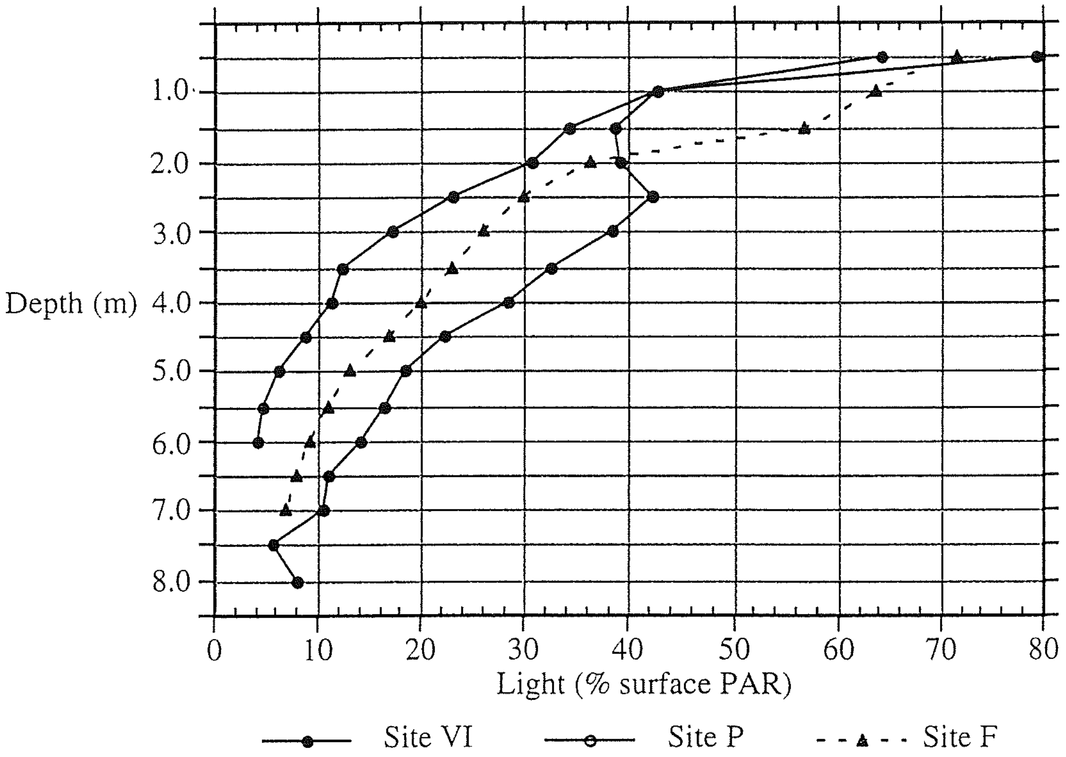

Fig. 2. Irradiance-depth profiles (% surface PAR) at three sites within Tauranga

Table 2. *Ulva* cover values across depth increments at each site surveyed within the southern harbour in 1995, and selected sites re-surveyed in 1996. Cover scale 1=1-5%, 2=6-25%, 3=26-50%, 4=51-75%, 5=76-95%, 6=96-100, – = *Ulva* not recorded.

Depth (m)	**Town Reach**				**Pilot Bay**	**Shallow bank**			**Otumoetai**		**Western Channel**							**Te Puna**					**Inner southern harbour**							
	A	B	C		D	T	U	V	F		E	G		H	I	J		K	M	W		N	O	L		P		Q	R	S
Year			'95	'96					'95	'96		'95	'96			'95	'96			'95	'96			'95	'96	'95	'96			
Average cover																														
0.5	-	1		-	-	1	1	1	-	1	1	1		-	1	-	-	1	1	1	1	-	-	1	-	-	1	-	1	1
1	1	1	-	1	-				1	1	1	1	2	-	1	1	1	1	-	1	1	-	-	1	-	1	1	-	1	-
2	1	1	1	1	-				1	1	2	1	3	-	1	1	1	1	-	1	1	-	-	1	1	1	1	-	1	-
3	1	1	1	1	-				1	1	2	1	3	1	1	1	1	1	-	1	1	1	-	1	1	1	1	1	1	-
4	-		1	1	1				1	1	2	2	3	1	1	1	1	1		1	1	-	-	-	1	1	-	-	-	-
5			1		-				1	1	1	2	3	1	1	1		-		-	-		-	1	-	1	-			-
6					-				1	1	1	-	3	1	1	-		-		-	-		1	-	-	1	-			
7					-						1	1	3	-	1			-		-							-			
8					-						-	1	2	-																
9													2	-																
10														1																
Maximum cover																														
0.5	-	1		-	-	1	2	1	-	1	1	1		-	2	-	-	1	1	1	1	-	-	1	-	-	1	-	1	1
1	1	1	-	1	-				1	1	1	2	2	-	2	1	1	1	-	1	1	-	-	1	-	1	1	-	1	-
2	1	1	1	1	-				2	2	2	1	4	-	1	1	2	1	-	1	1	-	-	1	1	1	1	-	1	-
3	1	1	1	1	-				2	2	3	2	4	1	1	2	1	1	-	1	1	1	-	1	1	1	1	1	1	-
4	-		1	1	1				2	1	3	3	3	1	1	1	1	1		1	1	-	-	-	1	1	-	-	-	-
5			1		-				2	1	2	3	4	1	1	1		-		-	-		-	1	-	1	-			-
6					-				2	1	1	-	4	1	1	-		-		-	-		1	-	-	1	-			
7					-						1	1	4	-	1			-		-							-			
8					-						-	1	3	-																
9													2	-																
10														1																

Table 3. Ulva cover values across depth increments at each site surveyed within the northern harbour in 1995, and selected sites re-surveyed in 1996. Cover scale 1=1-5%, 2=6-25%, 3=26-50%, 4=51-75%, 5=76-95%, 6=96-100, _ = Ulva not recorded.

Depth (m)	**Outer northern harbour**				**Blakneys Channel**			**Kauri Point**	**Inner northern harbour**						
	I		II	IV	III		V	VII	VI		VIII	IX		X	XI
Year	'95	'96			'95	'96			'95	'96		'95	'96		
Average cover															
0.5	1	1	1	1	1	1	1	-	-	1	1	-	-	1	1
1	1	1	2	-	1	1	-	1	1	1	1	-	-		
2	1	1	2	-	1	1	-	1	1	1	1	1	1		
3	1	1	1	-	1	1	1	1	1	1	1	1	1		
4	1	1	1	1	1	1	1	-	1	1	1	1	1		
5			1	1	1		1	-	1	1	-	-	-		
6			1	1	1		1		1	1			-		
7			1				1		1						
8			1												
Maximum cover															
0.5	2	1	1	2	1	2	1	-	-	1	1	-	-	1	1
1	3	1	3	-	1	1	-	1	1	1	1	-	-		
2	2	1	3	-	1	1	-	1	1	1	1	1	1		
3	2	1	1	-	1	1	1	1	1	1	1	1	1		
4	2	1	1	1	1	1	1	-	1	1	1	1	1		
5			1	1	1		1	-	1	1	-	-	-		
6			1	1	1		1		1	1					
7			1				1		1						
8			1												

Table 4. Greatest linear dimension (g.l.d., mm) of *Ulva* across depth increments at each site surveyed within the southern harbour in 1995, and selected sites re-surveyed in 1996. – = *Ulva* not recorded.

Depth (m)	Town Reach				Pilot Bay	Shallow bank			Otumoetai		Western Channel							Te Puna					Inner southern harbour							
	A	B	C		D	T	U	V	F		E	G		H	I	J		K	M	W		N	O	L		P		Q	R	S
Year			'95	'96					'95	'96		'95	'96			'95	'96			'95	'96			'95	'96	'95	'96			
Average g.l.d.																														
0.5	-	50		-	-	50	100	50	-	50	50	50		-	200	-	-	50	150	100	100	-	-	100	-	-	100	-	50	20
1	50	50	-	100	-				100	100	50	100	200	-	200	100	200	100	-	100	100	-	-	100	-	20	50	-	50	-
2	50	50	≥10	100	-				100	100	100	200	300	-	100	200	50	100	-	100	300	-	-	80	100	20	50	-	50	-
3	50	50	50	100	-				100	300	100	300	300	50	100	100	50	50	-	50	100	10	-	50	100	20	50	50	50	-
4	-		50	100	5				100	200	100	400	300	50	100	50	50	100		50	100	-	-	-	100	20	-	-	-	-
5			100		-				200	200	100	400	200	50	200	50		-		-	-		-	50	-	20	-			-
6					-				200	200	100	-	400	50	100	-		-		-			20	-	-	20	-			
7					-						100	100	500	50	100			-		-							-			
8					-						-	50	300	-																
9													300	-																
10														50																
Maximum g.l.d.																														
0.5	-	100		-	-	300	400	50	-	300	50	100		-	300	-	-	50	150	300	200	-	-	350	-	-	100	-	50	40
1	100	100	-	100	-				200	400	100	200	800	-	400	200	200	300	-	200	200	-	-	500	-	40	200	-	300	-
2	150	50	≥10	200	-				250	600	200	600	500	-	300	700	800	200	-	200	600	-	-	150	100	50	100	-	300	-
3	150	50	50	200	-				400	1000	200	400	1000	50	500	300	200	150	-	100	300	10	-	100	200	80	50	50	50	-
4	-		100	100	5				500	1000	300	1000	600	50	500	100	200	100		50	300	-	-	-	100	50	-	-	-	-
5			200		-				1000	600	400	1000	1000	50	600	50		-		-	-		-	50	-	60	-			-
6					-				1000	500	400	-	800	100	200	-		-		-	-		20	-	-	20	-			
7					-						200	200	1000	50	200			-		-							-			
8					-						-	100	500	-																
9													300	-																
10														50																

Table 5. Greatest linear dimensions (g.l.d., mm) of *Ulva* across depth increments at each site surveyed within the northern harbour in 1995, and selected sites re-surveyed in 1996. – = *Ulva* not recorded.

Depth (m)	**Outer northern harbour**				**Blakneys Channel**			**Kauri Point**	**Inner northern harbour**						
	I		II	IV	III		V	VII	VI		VIII	IX		X	XI
Year	'95	'96			'95	'96			'95	'96		'95	'96		
Average g.l.d.															
0.5	100	100	200	100	150	50	50	-	-	100	20	-	-	30	20
1	150	100	200	-	150	50	-	100	10	50	30	-	-		
2	100	100	200	-	150	100	-	50	50	100	50	100	100		
3	100	100	200	-	100	100	100	100	50	100	50	100	100		
4	150	100	150	100	100	300	50	-	30	100	20	100	100		
5			150	100	100		50	-	30	30	-	-	-		
6			150	100	100		50		40	30			-		
7			150				200		40						
8			100												
Maximum g.l.d.															
0.5	300	20	200	200	300	300	50	-	-	100	20	-	-	30	40
1	400	300	200	-	400	300	-	100	10	100	80	-	-		
2	300	100	300	-	400	200	-	50	50	200	100	300	300		
3	300	100	300	-	300	300	100	150	100	400	100	100	300		
4	250	200	300	200	300	1000	250	-	50	250	20	200	200		
5			400	200	200		50	-	30	50	-	-	-		
6			400	200	200		100		40	70			-		
7			400				300		40						
8			250												

Table 6. Cover values for all marine macro-algae across depth increments at each site surveyed within the southern harbour in 1995, and selected sites re-surveyed in 1996. Cover scale 1=1-5%, 2=6-25%, 3=26-50%, 4=51-75%, 5=76-95%, 6=96-100, – = marine macro-algae not recorded.

Depth (m)	Town Reach				Pilot Bay	Shallow bank			Otumoetai		Western Channel							Te Puna					Inner southern harbour							
	A	B	C		D	T	U	V	F		E	G		H	I	J		K	M	W		N	O	L		P		Q	R	S
Year			'95	'96					'95	'96		'95	'96			'95	'96			'95	'96			'95	'96	'95	'96			
Average cover of all marine macro-algae																														
0.5	-	1		-	-	1	1	1	-	1	1	1		-	1	-	1	1	1	1	1	1	-	1	-	1	1	1	1	1
1	1	1	1	1	-				1	1	1	1	2	-	1	1	1	1	-	1	1	1	1	1	-	1	1	1	1	1
2	1	1	1	1	-				1	1	2	2	4	-	1	2	2	1	-	1	1	1	1	1	1	1	1	1	2	1
3	1	1	1	1	-				1	1	2	2	4	1	2	1	1	1	-	1	1	1	1	1	1	2	1	1	1	1
4	-		1	-	1				2	1	2	5	4	1	2	1	1	2		1	1	1	1	1	1	1	1	1	1	1
5			2		-				2	1	1	5	6	1	2	1		2		1	1		1	1	-	1	1			1
6					-				2	1	1	-	6	1	3	1		3		1	1		1	1	1	1	-			
7					-						1	2	4	1	3			3		-							-			
8					1						1	2	3	-																
9													2	-																
10														1																
Maximum cover of all marine macro-algae																														
0.5	-	1		-	-	2	2	1	-	1	1	1		-	2	-	1	1	1	1	2	1	-	1	-	1	1	1	1	1
1	1	2	1	1	-				1	1	1	2	3	-	2	1	1	2	-	1	2	1	1	1	-	1	1	1	1	1
2	1	2	1	1	-				2	2	2	3	5	-	2	3	2	2	-	1	2	1	1	1	1	2	1	1	2	1
3	1	1	1	1	-				2	2	3	3	4	1	2	2	2	1	-	1	2	1	1	1	1	2	1	1	1	1
4	-		1	-	1				5	1	3	6	6	1	3	1	2	2		3	2	1	1	1	1	1	1	1	1	1
5			3		-				3	1	2	6	6	1	4	2		3		3	2		1	1	-	1	1			2
6					-				3	1	1	-	6	1	5	1		3		3	1		1	1	1	1	-			
7					-						1	2	4	1	4			4		-							-			
8					2						2	2	4	-																
9													2	-																
10														1																

Table 7. Cover values for all marine macro-algae across depth increments at each site surveyed within the northern harbour in 1995, and selected sites re-surveyed in 1996. Cover scale 1=1-5%, 2=6-25%, 3=26-50%, 4=51-75%, 5=76-95%, 6=96-100, – = Marine macro-algae not recorded.

Depth (m)	**Outer northern harbour**				**Blakneys Channel**			**Kauri Point**	**Inner northern harbour**						
	I		II	IV	III		V	VII	VI		VIII	IX		X	XI
Year	'95	'96			'95	'96			'95	'96		'95	'96		
Average cover of all marine macro-algae															
0.5	2	1	1	1	1	1	1	-	-	1	1	-	-	1	2
1	1	1	2	-	1	1	-	1	1	1	1	-	-		
2	2	1	2	-	1	1	1	1	1	1	1	1	1		
3	1	1	1	-	1	1	1	1	1	1	1	1	1		
4	2	1	2	1	1	1	1	1	1	1	1	2	1		
5			1	1	1		1	1	2	1	-	1	1		
6			1	1	1		1		3	1			1		
7			1				1		1						
8			1												
Maximum cover of all marine macro-algae															
0.5	2	1	1	2	1	2	1	-	-	1	1	-	-	1	3
1	3	1	3	-	1	2	-	1	1	1	1	-	-		
2	2	3	3	-	1	2	1	1	2	1	1	1	1		
3	4	3	1	-	1	1	1	1	1	1	1	2	1		
4	2	2	2	1	1	1	1	1	1	1	1	3	1		
5			2	1	1		1	1	2	1	-	2	1		
6			1	1	1		1		4	1			1		
7			1				1		2						
8			1												

Table 8. Marine macro-algae and tracheophytes recorded among the dominant plants at survey sites, with species ordered from frequently dominant to rarely recorded.

Rhodymenia dichotoma Hook. *f.* et Harvey
Rhodymenia novazelandica Dawson
Spyridia filamentosa (Wulfen) Harvey
Hypnea nidifica J. Agardh
Ulva spp.
Codium fragile (Suringar) Hariot ssp. *novae-zelandiae* (J. Agardh) Silva
Gigartina chapmanii Hook. *f.* et Harvey
Gigartina circumcincta J. Agardh / *atropurpurea* (J. Agardh) J. Agardh
Enteromorpha spp.
Gracilaria chilensis Bird, McLachlan et Oliveira
Zostera novazelandica Setchell
Cladophora spp.
Polysiphonia sp.
Plocamium costatum (C. Agardh) Hook. *f.* et Harvey
Corallina officinalis Linnaeus
Aeodes nitidissima J. Agardh
Stenogramme interrupta (C. Agardh) Montagne
Microcladia/ *Ceramium* sp.
Myriogramme denticulata (Harvey) Kylin
Cladhymenia oblongifolia Harvey
Codium convolutum (Dellow) Silva
Hormosira banksii (Turner) Descaisne
Dictyota sp.

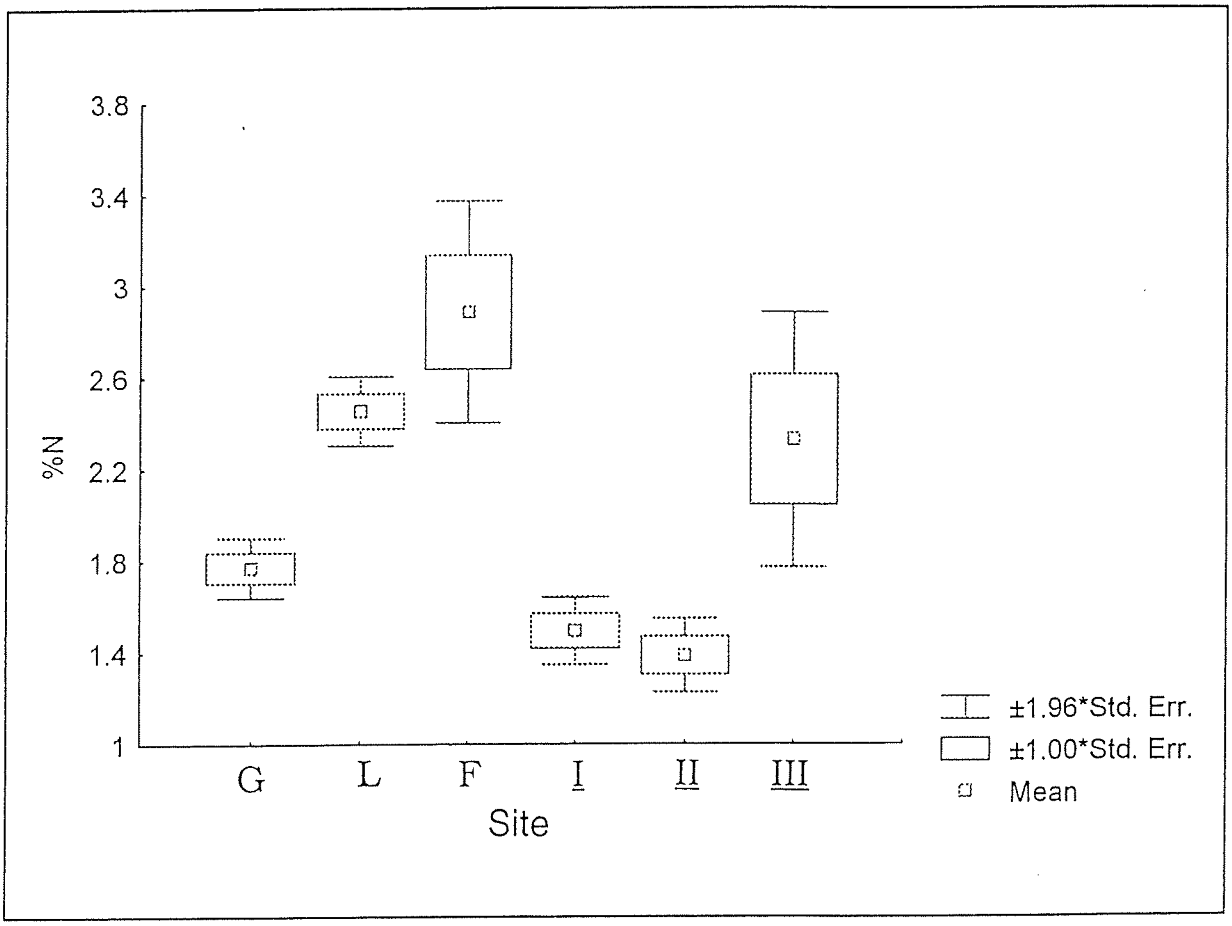

Fig. 3. Nitrogen content of *Ulva* material from six sites, Tauranga Harbour (see fig. 1 for site locations).

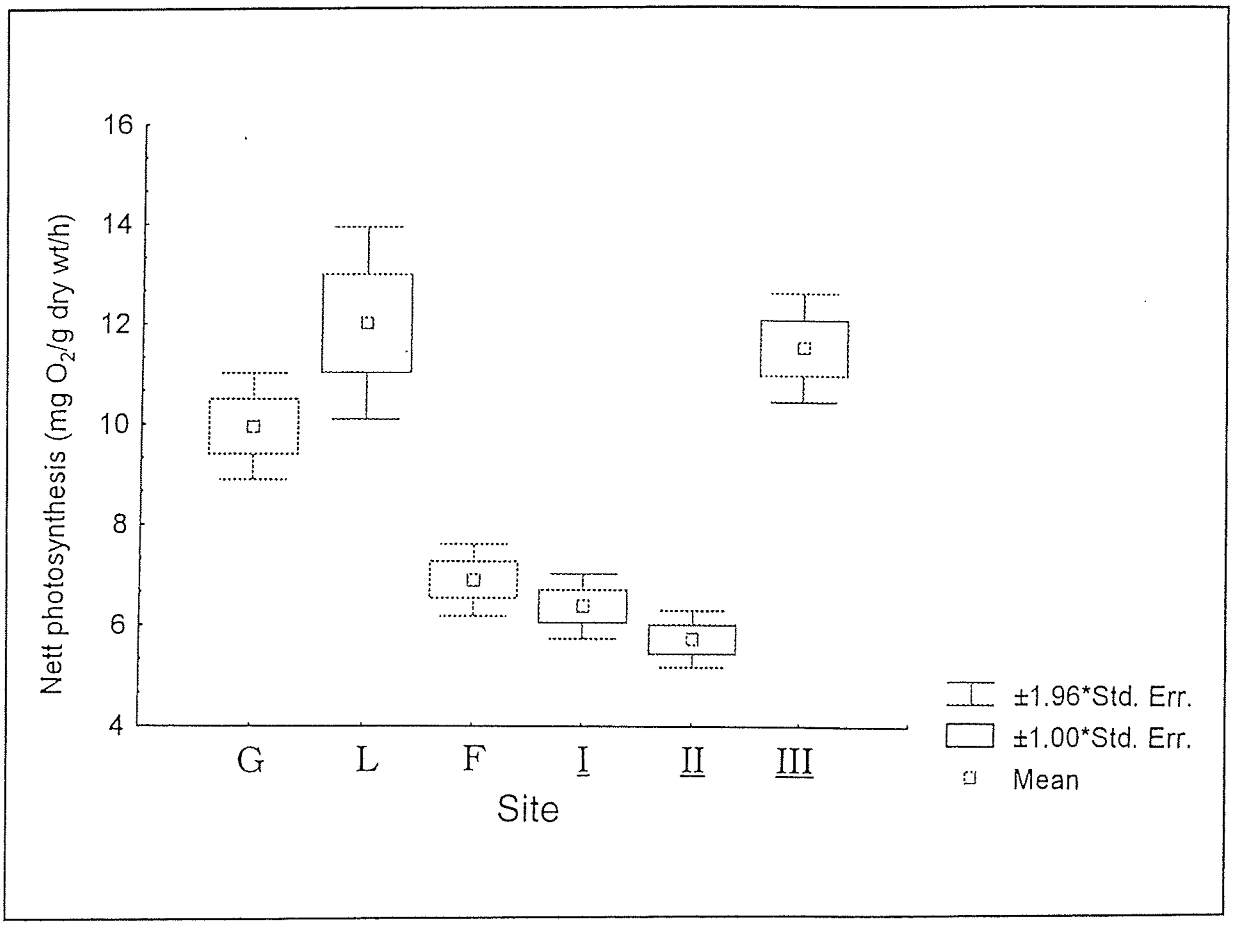

Fig. 4. Net photosynthetic rates of *Ulva* material from six sites, Tauranga Harbour (see fig. 1 for site locations).

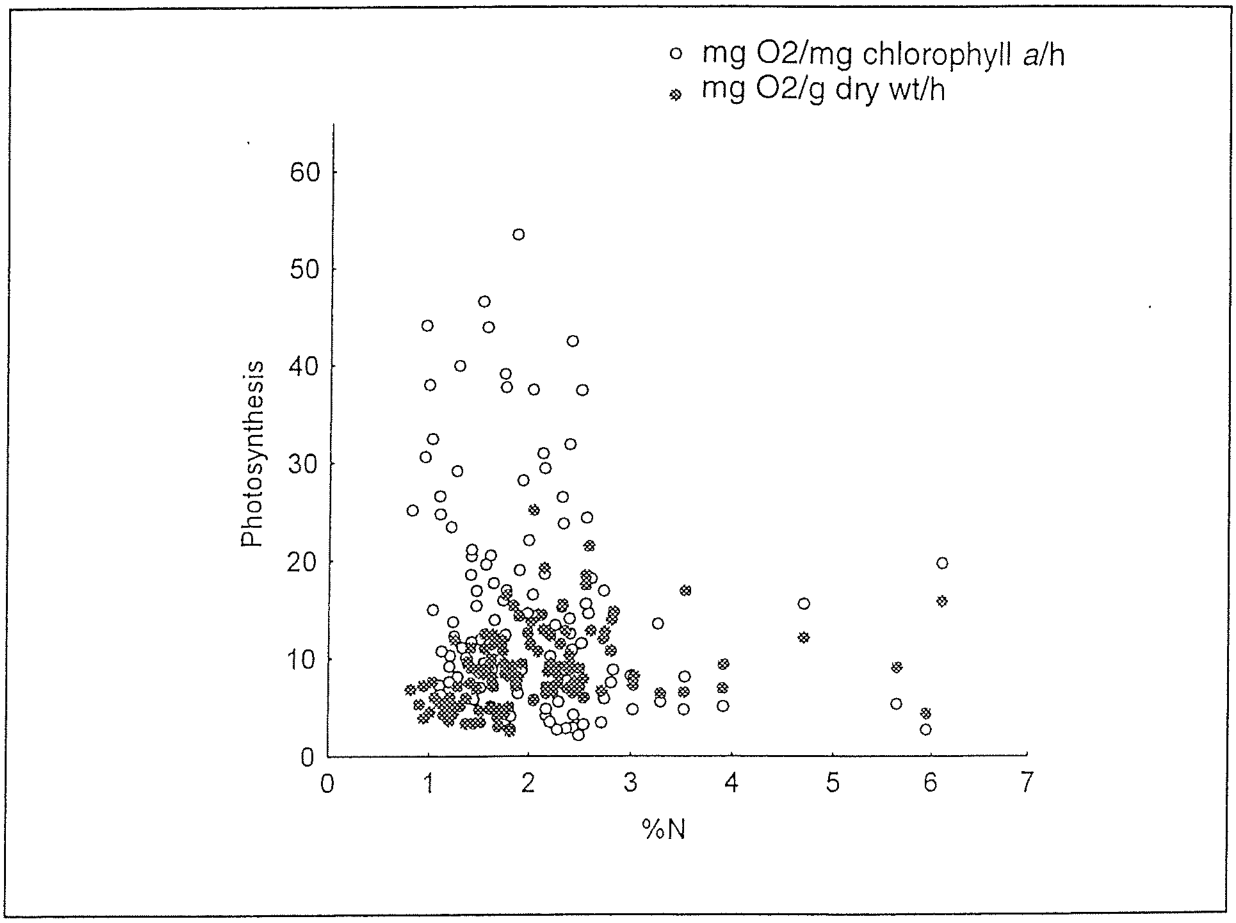

Fig. 5. Photosynthetic rate of *Ulva* material from Tauranga Harbour plotted against respective nitrogen status.

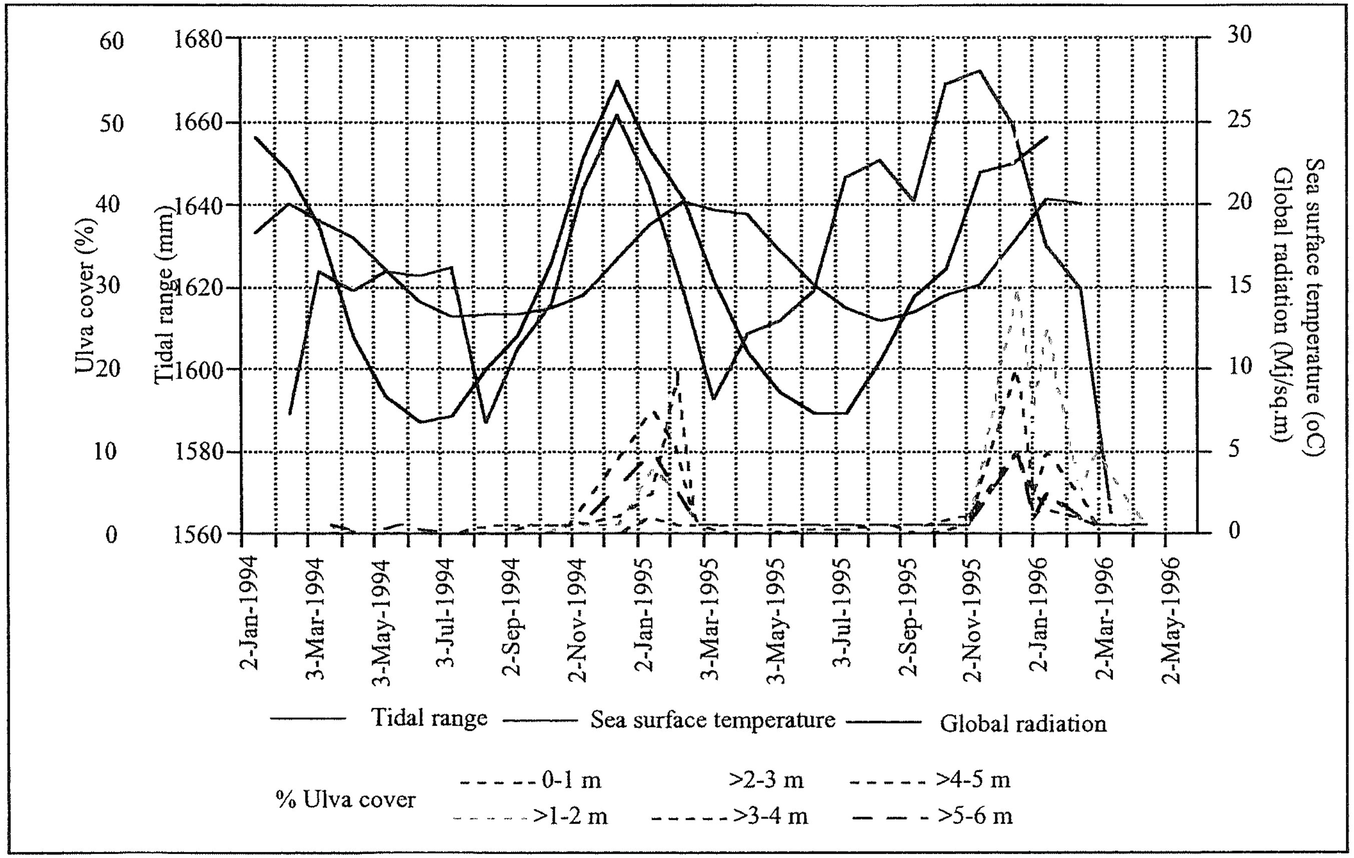

Fig. 3. Seasonal development of subtidal *Ulva* (average cover) at site F, plotted with mean monthly values for global radiation (Tauranga aerodrome), sea surface temperature and tidal range (Moturiki Island).

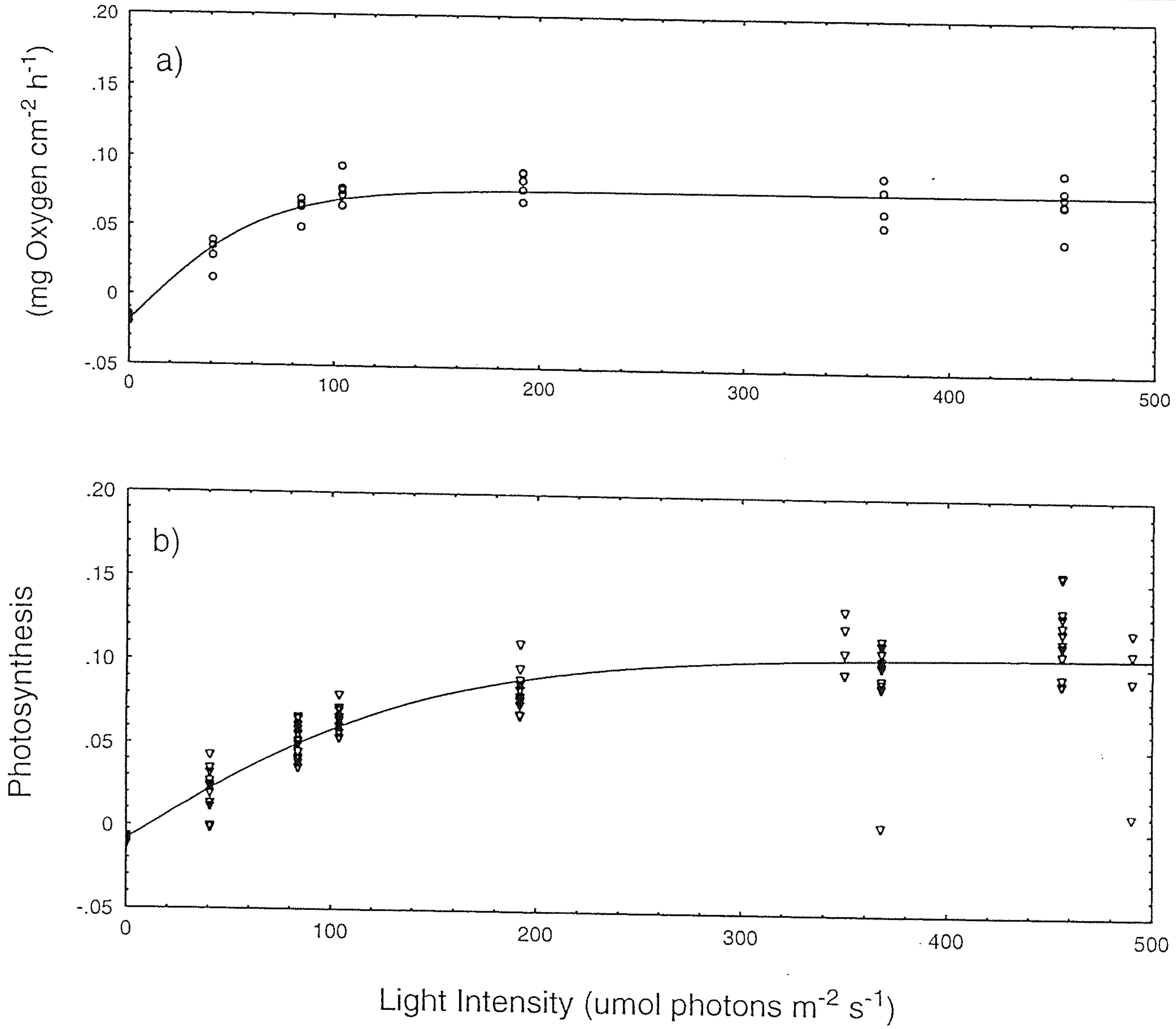

Fig. 6. Photosynthetic rate across a range of light intensities for a) subtidal *Ulva* and b) intertidal *Ulva* from site F, Tauranga Harbour.

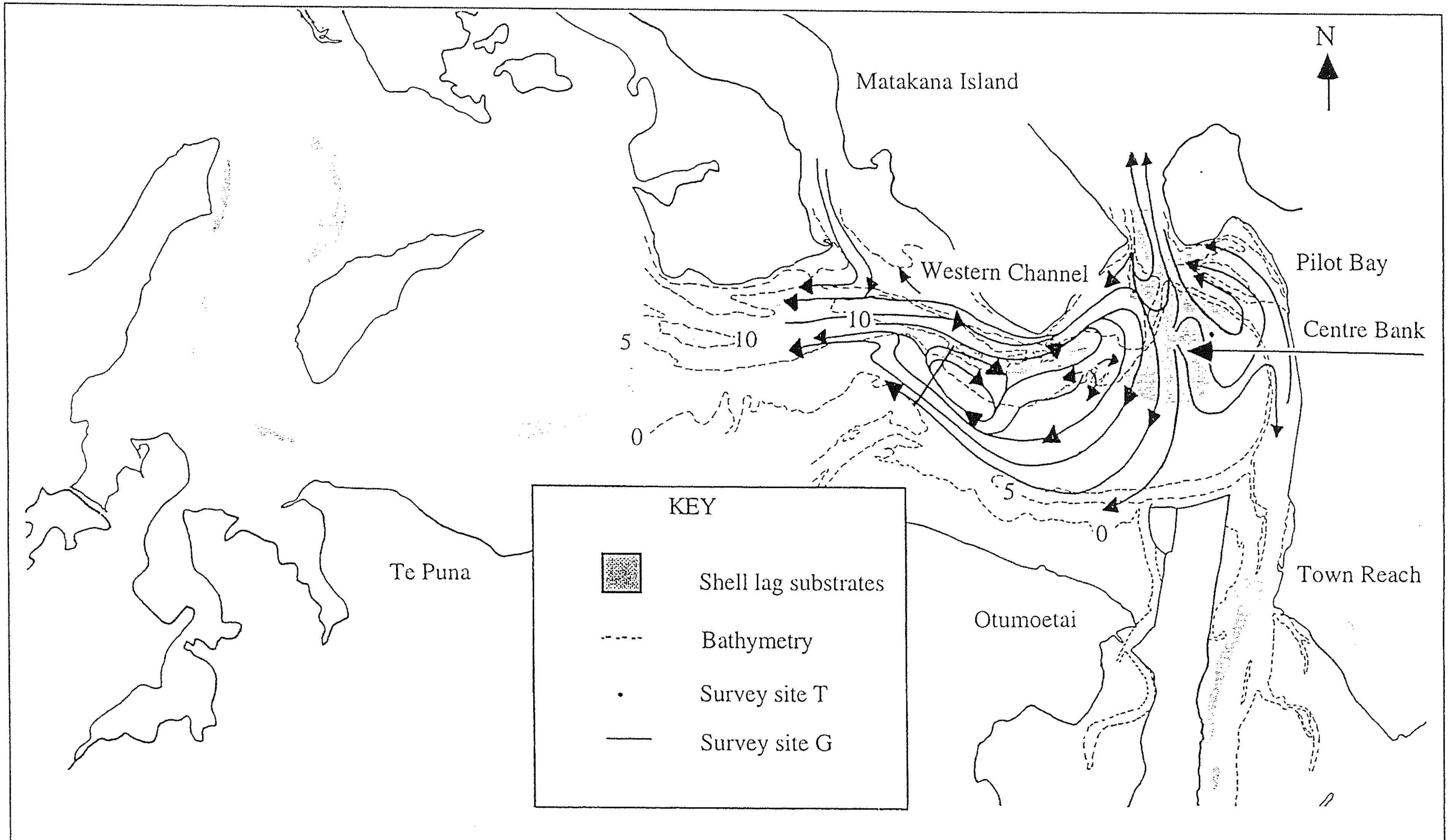

Fig. 8. Areas of 'shell lag' substrates (>80% shell cover) and the predominent circulation pattern for the outer southern basin, Tauranga Harbour (from Black 1985 and Barnett 1985).