THE LOSS OF SEAGRASS IN COCKBURN SOUND, WESTERN AUSTRALIA. II. POSSIBLE CAUSES OF SEAGRASS DECLINE

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ABSTRACT


This paper examines possible reasons for the extensive loss of seagrass in Cockburn Sound following industrial development. Transplanted seedlings survived poorly in Cockburn Sound compared with an adjoining embayment. Altered temperature, salinity, sedimentation and water movement do not explain the death of seagrass over wide areas, and there is no evidence for a role of pathogens. Oil refinery effluent reduced seagrass growth in aquaria at concentrations similar to those at the point of discharge, but could not account for the widespread deterioration observed in the field. Severe grazing by sea urchins was observed on meadows already under stress and does not appear to be a primary cause of decline; caged, transplanted seedlings also deteriorated.

Increased light attenuation by phytoplankton blooms may have affected the depth to which seagrasses could survive, but would have had little significant effect in shallow water; marked phytoplankton blooms were recorded only after extensive seagrass decline had taken place. Light reduction by enhanced growth of epiphytes and loose-lying blankets of filamentous algae in nutrient enriched waters is suggested as the most likely cause of decline. Heavy epiphyte fouling was consistently observed on seagrasses in deteriorating meadows, as well as on declining, transplanted seedlings, and is known to significantly impair photosynthesis in other systems. Extensive seagrass decline coincided with the discharge of effluents rich in plant nutrients.

INTRODUCTION

A marked reduction in the area of seagrass meadows has accompanied the establishment of industry along the shores of Cockburn Sound, Western Australia. The time-course of the reduction has been assessed in relation to

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the establishment of industry commencing in 1955: localized depletion took place by 1962, near to the point of discharge of effluent from an oil refinery, and there were localized losses due to scouring near pylons, and to physical processes such as dredging. However, widespread loss took place from 1969 onwards, and by 1978 accounted for 3300 ha, or some 97% of the area originally occupied by seagrass, representing a loss of some 83% of organic production by these plants (Cambridge and McComb, 1984).

The work described here was concerned with assessing, for Cockburn Sound, various factors which have been mentioned in the literature as contributing to a decline of aquatic macrophytes in other regions; these included altered temperature regimes, pathogens, effects of oil refinery effluent, increased grazing pressure, change in water turbidity and increased shading by epiphytes. Attention was also directed to transplanting seagrasses into the Sound from an adjoining, unpolluted embayment, so as to find out whether the plants still survive poorly in the Sound.

MATERIALS AND METHODS

Transplant experiments

Seedlings were collected from Warnbro Sound, an embayment 4 km south of Cockburn Sound (Fig. 1), where Posidonia meadows are relatively undisturbed, and still grow down to 11 m as they once did in Cockburn Sound (Cambridge and McComb, 1984).

An airlift was used to remove sediment from around the roots of 2–3-yr old seedlings of P. sinuosa Cambridge & Kuo. Comparable seedlings, each 2–3 leaves, were transferred to plastic tubes (8 cm diameter, 30 cm long). Forty plants were returned to Warnbro Sound, and 40 to the experimental site in Cockburn Sound. Twenty plants at each site were caged (0.5-cm mesh sides, 1.0-cm mesh top) to prevent grazing. Leaf lengths were measured once each week, and the cages brushed clean of marine growth either once or twice each week.

Grazing

The extent of sea urchin infestation was determined by underwater surveys, and densities of animals associated with the various stages of seagrass denudation recorded from randomly-placed 1-m² quadrats at the stations shown in Fig. 1.

Light, temperature, salinity and chlorophyll

These were measured every 2 months from August 1978 to November 1979 at the sites shown in Fig. 1. Temperature and salinity were measured with a temperature/salinity bridge (Hammond, Yeo-cal, Victoria).
Fig. 1. Cockburn Sound and Warnbro Sound, Western Australia, showing sites for seagrass transplants and collection of water samples. Numbered circles are sites at which sea-urchin densities were measured. Attenuation coefficients over seagrass meadows (Table IV) were measured at sites A--D.
Photosynthetically-active radiation was measured at 0.5-m intervals with a quantum sensor (LiCor Lambda LI-185, Quantum Radiometer), and attenuation coefficients calculated (Kirk, 1977).

For chlorophyll determinations, water (2 litres) was collected with a Niskin bottle a metre below the surface, at mid-depth and a metre above the bottom, passed through a glass-fibre paper (Whatman GFC), and chlorophyll a was determined after 90% acetone extraction of the ground paper (Strickland and Parsons, 1972).

Oil-refinery effluents

Seedlings of *P. sinuosa* and *P. australis* Hook f. were collected from Warnbro Sound as described for the transplant experiment. Four tubes were placed in cylindrical glass aquaria (55 cm tall, 14 cm diameter) filled with water from the collection site and maintained at 19 or 23°C in a constant-temperature water bath under natural light in a glasshouse. Seedlings were acclimatised for 14 days before a subsequent trial of 32 days; total leaf growth was measured every 4 days. The water was aerated vigorously.

In the refinery, sea water passed through a separator (from which floating oil residue was recovered), and the sea water, now containing oil components, discharged as an effluent on the shore of the Sound, at high-water mark. Effluent was collected in darkened plastic drums from the point of discharge into the Sound or, when higher concentrations were required, from the separator. Concentrations of effluent were expressed as hydrocarbons using infra-red spectrophotometry (Perkin Elmer 283), calibrated using hydrocarbons from the separator (APHA, 1976).

Treatments of 0, 50 and 100% effluent were given to 6 replicates, with the effluent—water medium changed every 8 days, giving an average maximum hydrocarbon content of 1 ppm. In another trial, changing of effluent—water medium every 2 days tested the effects of an average hydrocarbon content of 2 ppm. Hydrocarbon concentrations were monitored during the course of the trials, as aeration removed volatile components.

RESULTS AND DISCUSSION

Seagrass transplants

Attention was concentrated on *P. sinuosa*, the main meadow-forming species in the Sound. At the Warnbro station there was a marked gain in leaf area, whereas the plants at the Cockburn Sound station showed a progressive loss of leaf material (Figs. 2 and 3). New roots had grown on 90% of the plants at Warnbro, but there was no obvious root growth at Cockburn Sound.

There was a marked increase in amount of epiphytic algal growth at the site in Cockburn Sound (Fig. 3). Before transplanting, the leaves supported a
Fig. 2. Change in leaf area of *Posidonia sinuosa* seedlings following transplanting from Warnbro Sound to Cockburn Sound (circles) or to a control site in Warnbro Sound (squares). Half of the plants at each site were covered with cages to exclude grazers (broken lines), the other half were uncaged (solid lines). Vertical lines are standard errors.

A few colonies of encrusting coralline algae at their tips, and very few filamentous algae. In Warnbro Sound the plants remained relatively free of these filamentous epiphytes. However, in Cockburn Sound, less than 2 weeks after transplanting, the leaves were covered to within 2 cm of their bases with heavy epiphytic growths, especially at the senescent leaf ends. The main genera were *Ectocarpus* (Phaeophyta), *Ulva* and *Enteromorpha* (Chlorophyta) and *Polysiphonia* (Rhodophyta). Leaf surfaces of all plants were thickly coated by the third week. Strong wave action during a storm tore away many of the senescent leaf ends and filamentous algae, but a rapid build-up of epiphytes occurred again before termination of the trial.

In summary, the environment of Cockburn Sound is clearly detrimental to growth of seagrasses, and the effect can be observed within a few weeks of transplanting seedlings. Presumably the reason for this adverse effect is the same as that which caused the decline in seagrass meadows during industrial development.

*Temperature, pathogens and salinity*

One possibility is that there has been a significant change in the water temperature of the Sound, sufficient to bring about metabolic stress or perhaps allow the invasion of a pathogen (e.g. Rasmussen, 1977). However,
water temperatures measured in the Sound during the study were comparable with those in nearby coastal waters, and with long-term records at Fremantle (Hodgkin and Phillips, 1969).

The rapidity with which transplanted seedlings deteriorated in the Sound, the lack of seagrass dieback in adjacent marine embayments and the occurrence of the same species of seagrass over a wide latitudinal range (McComb et al., 1981), also rule out the possibility that a regional change in temperature might be responsible for the decline in Cockburn Sound.
It has been suggested that widespread mortality of *Zostera marina* L. is due to invasion by a microorganism (Rasmussen, 1977). In Cockburn Sound, seagrass loss has been largely confined to the eastern shore, has not occurred in adjoining embayments and has involved several species. Examination of plants from deteriorating meadows since 1970, and of transplanted seedlings, has not disclosed evidence for pathogens such as leaf lesions.

The discharge of warm water may be detrimental to seagrass (Zieman and Wood, 1975). In Cockburn Sound, release of warm-water effluent is very localized on the eastern shore, showing an elevation of only 0.6°C at 1 m depth, 100 m from the oil-refinery outfall (December 1978). Any effect of warm effluent on seagrasses would inevitably be confined to a small zone around the point of discharge.

Also, it would not be possible to explain the time course of seagrass decline or the death of transplanted seedlings by a regional or local change in salinity. Salinities measured in Cockburn Sound, Warnbro Sound and the open ocean did not differ by more than 1‰.

Small quantities of groundwater flow into the nearshore shallows through beach sands (Layton Groundwater Consultants, 1979), but Johannes (1980), working some 50 km north of Cockburn Sound, found that groundwater is rapidly diluted after entering the ocean. Although there are no data on the effects of low-salinity interstitial waters in the substrate around the roots of seagrasses, any effect would be very localized.

*Altered sediment and water movement*

Rapid sediment accretion may reduce the area of seagrass meadows (Kirkman, 1978). However, in Cockburn Sound, the activities of man did not greatly modify existing sedimentation patterns (France, 1978), except locally, such as where scouring or dredging has occurred, and seagrasses were locally eliminated (Cambridge and McComb, 1984).

Excessive water movement may alter the sediment regime, and may also cause mechanical damage to plants. On the other hand, water movement is important in the transfer of metabolites to and from submerged plants (e.g. Sculthorpe, 1967). The construction of a solid-fill causeway (Fig. 1) has reduced wave and current action across the Southern Flats, apart from areas adjacent to the bridges where water is funnelled through relatively narrow openings. *P. sinuosa* grows vigorously in the lee of the causeway where annual primary production was the highest of all the stations measured (Cambridge and McComb, 1984), but where the water is very calm except under northerly wind conditions. In contrast, the entire eastern shore, where major loss of seagrass occurred, is subject to strong wave action.

*Grazing*

Increased grazing, especially by sea urchins, may be important in reducing the areas of seagrass meadows. For example, heavy grazing by sea urchins has
been reported from the United States in *Thalassia testudinum* Banks ex König (Camp et al., 1973) and *Zostera marina* meadows (Bak and Nojima, 1980). Ogden et al. (1973) recorded heavy grazing of seagrasses by a reef-dwelling urchin in the West Indies. Urchins have been found to graze *Posidonia oceanica* (L.) Delile in polluted areas of the Mediterranean, where *Posidonia* was declining (Kirkman and Young, 1981) and in Botany Bay, New South Wales, large populations of sea urchins have denuded *Posidonia* meadows, following alterations in water movement due to harbour construction (P. Anink, State Pollution Control Commission, New South Wales, personal communication, 1983).

In Cockburn Sound, seagrasses are grazed by the sea urchin *Temnopleuris michaelsenii* Döderlein, which is found in sheltered waters from South Australia to Shark Bay (L. Marsh, Western Australian Museum, personal communication, 1979). It is 1−3 cm in diameter, with sharp primary spines 3−4 mm long. Mortensen (1943) found only plant fragments, mainly seagrass, in the gut of this species collected from seagrass meadows. Grazed leaves of *Posidonia* were found to have a jagged apex similar to that described by Ogden et al. (1973) for seagrasses grazed by urchins in the West Indies; this effect differed from the scalloped edges produced by fish grazing. Marsh and Devaney (1978) report a survey of Cockburn Sound by the Western Australian Naturalist Club in 1958−60, well before the onset of seagrass loss, in which considerable numbers of this species of urchin were found on the muds of the deep, central basin of the Sound, but despite extensive sampling, no large concentrations of the animals were found in the seagrass meadows at that time.

*T. michaelsenii* was found to be locally abundant on occasions during the present study. Table I shows densities recorded at stations along the eastern shore of the Sound in November 1972. The highest density was in an area carrying remnants of *Posidonia* meadows on the sand platform which was once continuously vegetated by seagrass. Sampling stations in the more severely-grazed meadow were divided into three categories: the centre of exposed sand patches recently denuded of seagrass cover contained the highest densities of urchins (up to 250 m$^{-2}$); in seagrass at the edges of sand patches where grazing was active, densities of urchins were found to be intermediate (100 m$^{-2}$); and in the centre of the meadow or in patches of seagrass between denuded areas leaves were less damaged and urchin densities were lowest (up to 40−60 m$^{-2}$). An underwater search made beyond the sampled regions showed the most severely grazed area to be localised. At the site of highest infestation, only a few animals could be found 6 weeks later. However, the leafless plants did not recover, and on visits to the area 2 and 4 years later, no *Posidonia* was found. Thus, although high densities of sea urchins appear to be short lived, their effects are more permanent.

Sea urchins invading in 1972 reduced much of the remnant meadow at Rockingham (Fig. 1), isolated by the dieback of large areas of the eastern shore meadows between 1969 and 1972, to bare sand. These were the most
### Table I

Densities of sea urchins at stations along the eastern shore of Cockburn Sound, November 1972

<table>
<thead>
<tr>
<th>Station No.</th>
<th>Depth (m)</th>
<th>Number of sea urchins m⁻²</th>
<th>Seagrass meadow</th>
<th>Denuded sand patches</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td></td>
<td></td>
<td>Centre</td>
<td>Edge of meadow</td>
</tr>
<tr>
<td>1</td>
<td>4</td>
<td>0.0</td>
<td>0.0</td>
<td>0</td>
</tr>
<tr>
<td>2</td>
<td>2</td>
<td>0.2</td>
<td>6.6,2</td>
<td>0</td>
</tr>
<tr>
<td>3</td>
<td>3</td>
<td>6.4</td>
<td>1.2</td>
<td>0</td>
</tr>
<tr>
<td>4</td>
<td>1-2</td>
<td>No seagrass</td>
<td>No seagrass</td>
<td>0</td>
</tr>
<tr>
<td>5</td>
<td>2-5</td>
<td>8.4</td>
<td>3,3</td>
<td>6</td>
</tr>
<tr>
<td>6</td>
<td>4</td>
<td>40,60</td>
<td>100,106</td>
<td>206,250</td>
</tr>
<tr>
<td>7</td>
<td>4</td>
<td>8.11</td>
<td>10,12</td>
<td>11</td>
</tr>
<tr>
<td>8</td>
<td>2.5</td>
<td>No seagrass</td>
<td>No seagrass</td>
<td>0</td>
</tr>
<tr>
<td>9</td>
<td>2-3</td>
<td>No seagrass</td>
<td>No seagrass</td>
<td>0</td>
</tr>
<tr>
<td>10</td>
<td>1.5</td>
<td>0.0</td>
<td>0.0</td>
<td>0</td>
</tr>
<tr>
<td>11</td>
<td>1</td>
<td>0.0</td>
<td>0.0</td>
<td>0</td>
</tr>
</tbody>
</table>

¹ Stations are given in Fig. 1. Duplicate quadrats were harvested at each site.

Severe outbreaks of urchin grazing which we observed, but urchin-damaged *Posidonia* leaves and *T. michaelsenii* were recorded on other occasions. For example, in November 1972 small areas of seagrass with grazed and damaged leaves were observed among undamaged seagrass on a small sand-covered reef at Site 2 in Fig. 1, with urchins present at 20–60 m⁻² adjacent to a grazed patch, and 0–20 m⁻² in the meadow. In December 1972, *Posidonia* adjacent to the southern bridge of the Garden Island causeway had urchin-damaged leaves, and dead sea-urchin shells were found among the sparse remaining plants. In November 1973, severe grazing was observed at Careening Bay; the meadow, which had originally extended down a sand slope to 5 m, had receded to 2 m. Another outbreak occurred at Woodman Point in November 1976.

Outbreaks were not confined to Cockburn Sound. At a 10-m-deep site in Warnbro Sound, in February 1978, sea urchins had removed all leaves for 5 m upslope from the original deeper boundary of the meadow. The animals were present at a density of about 200 m⁻² on 3 February and 6 March 1978, having grazed about 0.5 km along the edge of the meadow, as surveyed by underwater tow. No animals were found 4 weeks later. Green leaf material was present beneath the sand on 6 March, but by 4 weeks later, few living rhizome apices could be found, and there was no regeneration in the following year.

One factor was common to all observed instances of over-grazing of *Posidonia* by sea urchins; the meadow was already patchy, due either to
deterioration of a once continuous meadow, or to some natural environmental limitation such as depth. There were no outbreaks in a well-developed seagrass meadow with a dense, continuous leaf canopy.

These observations, and the results of the transplant experiment in which caged plants deteriorated (Fig. 2), suggest that the large populations of sea urchins which undoubtedly denude areas of deteriorating seagrass meadows, are not the primary cause of widespread loss of seagrasses.

Effects of oil-refinery effluent

Seagrasses grew well during the period of the trials (8 weeks, including 2 weeks acclimatization), with growth rates which were comparable with those observed in the field. Results of two of the trials are given in Table II, where it can be seen that a significant reduction in leaf growth was apparent when plants were subjected to an average concentration of 1 ppm hydrocarbon. This concentration is comparable with that entering the Sound at the high water mark, before extensive dilution upon mixing with the waters of the Sound. There was no effect on *P. australis* under the same conditions. Concentrations of 10 ppm, at least 5 times that which enters the Sound, were lethal to half of the seedlings within a period of 2 weeks.

The low sensitivity of the plants to effluent is in contrast with the very marked reductions in growth rates observed when seedlings were transplanted to the Sound (Fig. 3). The apparent short-term resistance of plants to oil refinery effluent is consistent with the observations of Hatcher and Larkum (1982), who found that leaf turnover of *P. australis* under controlled conditions was not affected within 40 days at the highest concentration of oil which they used (363 g l$^{-1}$).

It is possible that chronic poisoning by effluent components derived from various sources, not just the oil refinery, may be important. Chegwidden (1979) lists heavy metals, hydrocarbons and acids from effluents entering

TABLE II

<table>
<thead>
<tr>
<th>Temperature of trial (°C)</th>
<th>Approximate hydrocarbon level (ppm)</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>0</td>
</tr>
<tr>
<td>19</td>
<td>25.0 (1.0)</td>
</tr>
<tr>
<td>23</td>
<td>28.3 (2.3)</td>
</tr>
</tbody>
</table>

$^1$ Results from two trials are presented. Data are mean leaf growth, mm day$^{-1}$, with standard error, for 6 seedlings.

$^2$ Difference from control, $P = 0.05 - 0.1$.

$^3$ Different from control, $P < 0.01$. 

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the Sound. However, they were not detected in the waters of the Sound at levels likely to be lethal over the time scale of the transplant trials.

It is also significant that despite the commencement of release of effluent from the oil refinery in 1955, it was 7 years before deterioration in seagrass meadows could be seen in aerial photographs, as the loss of 4 ha of seagrass in the region; this is in contrast with the major dieback of seagrasses which occurred rapidly from 1969 onwards; approximately one year after the commencement of discharge from the fertilizer works (Cambridge and McComb, 1984).

It is concluded that while the oil refinery effluent could have caused localised death of seagrass near to the outfall, the extensive death of seagrass along the eastern shore cannot be readily attributed to oil refinery effluent, or to the discharge of inhibitory chemicals from other industries.

*Light attenuation in the water column*

*Posidonia* meadows once grew down the slopes of the peripheral banks to 10--12 m, as indicated by the fibrous remains of rhizomes beneath the sediment surface, but are now restricted to less than 3 m (Cambridge and McComb, 1984). It is usually accepted that plants will colonise suitable substrates to the depth where the light intensity allows photosynthesis to exceed respiration on a yearly basis. Thus, any significant reduction in light transmission through the water column will bring about a reduction in the depth at which plants will survive. For example, Larkum (1976) has suggested that increased turbidity has decreased the depth range of *P. australis* in Botany Bay, New South Wales, where remnants of seagrass meadows extend only to 2.5 m, as compared with 7--9 m in the clearer waters of other parts of the New South Wales coast.

The mean light attenuation coefficient of water in Cockburn Sound was generally twice that of the open ocean (Table III). Warnbro Sound was

**TABLE III**

Mean (S.E.) light attenuation and chlorophyll *a* concentrations for the plots shown in Fig. 4

<table>
<thead>
<tr>
<th>Attenuation coefficient</th>
<th></th>
<th></th>
</tr>
</thead>
<tbody>
<tr>
<td>Ocean</td>
<td>Warnbro</td>
<td>Cockburn</td>
</tr>
<tr>
<td>0.07 (&lt;0.01)</td>
<td>0.10 (0.01)</td>
<td>0.13 (0.01)</td>
</tr>
</tbody>
</table>

<table>
<thead>
<tr>
<th>Chlorophyll <em>a</em> (μg l&lt;sup&gt;-1&lt;/sup&gt;)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Ocean</td>
</tr>
<tr>
<td>Warnbro</td>
</tr>
<tr>
<td>Cockburn</td>
</tr>
<tr>
<td>0.4 (&lt; 0.1)</td>
</tr>
<tr>
<td>0.8 (0.2)</td>
</tr>
<tr>
<td>3.1 (0.3)</td>
</tr>
</tbody>
</table>
similar to the open ocean in summer, but had higher attenuation coefficients in winter (Fig. 4a), because of increased suspension of particulates by the high wave energy of winter storms and westerly swell.

Attenuation of light in Cockburn Sound was usually considerably higher than in Warnbro Sound; thus seagrasses at comparable depths would receive less light in Cockburn than in Warnbro. Chlorophyll-a concentrations were also considerably higher in Cockburn than in Warnbro Sound, where concentrations were generally similar to those of the open ocean (Table III, Fig. 4b). The higher chlorophyll levels in Cockburn Sound are attributed to the discharge of effluents rich in plant nutrients, of which nitrogen availability is critical (Chiffings, 1979; Chiffings and McComb, 1981).

Attenuation coefficients were generally greater over seagrass meadows in Cockburn and Warnbro Sounds (Table IV) than the mean for the whole water body (Table III). This may have been because of sediment resuspension, or materials released from the seagrass meadows.

Fig. 4. Attenuation coefficient (above) and chlorophyll a content (below) for Cockburn Sound (solid line), Warnbro Sound (dashed line) and a site in the open ocean (dotted line). Sites are given in Fig. 1.
Shading by phytoplankton blooms, and by localized suspension of particulate matter, may well have been important in the decline of seagrasses in deeper water, where light was already at critical levels. On the other hand, it seems unlikely that increased sediment resuspension, or algal blooms of the magnitude of those recorded here, would have seriously impaired light availability to meadows in shallow waters, down to about 5 m. In the transplant experiment, the caged plants in Warnbro Sound received approximately the same light as the uncaged plants in Cockburn Sound (Table V), yet the plants in Cockburn Sound grew at a much lower rate than those in Warnbro (Fig. 2).

### TABLE IV

Attenuation coefficients at four seagrass stations in Cockburn and Warnbro Sounds, 1977—1979

<table>
<thead>
<tr>
<th>Date</th>
<th>Site and Depth</th>
<th>Warnbro Sound A 2.5 m</th>
<th>Shoalwater Bay B 3 m</th>
<th>Cockburn Sound C 2.5 m</th>
<th>Cockburn Sound D 1.0 m</th>
</tr>
</thead>
<tbody>
<tr>
<td>12 Dec. 1977</td>
<td>0.14</td>
<td>0.17</td>
<td>0.18</td>
<td>0.32</td>
<td></td>
</tr>
<tr>
<td>26 Jan. 1978</td>
<td>0.18</td>
<td>0.24</td>
<td>0.18</td>
<td>0.26</td>
<td></td>
</tr>
<tr>
<td>31 Mar. 1978</td>
<td>0.26</td>
<td>0.14</td>
<td>0.18</td>
<td>0.24</td>
<td></td>
</tr>
<tr>
<td>30 May 1978</td>
<td>0.40</td>
<td>0.25</td>
<td>0.39</td>
<td>0.94</td>
<td></td>
</tr>
<tr>
<td>1 Aug. 1978</td>
<td>0.22</td>
<td>0.17</td>
<td>0.30</td>
<td>0.20</td>
<td></td>
</tr>
<tr>
<td>29 Sept. 1978</td>
<td>0.08</td>
<td>0.12</td>
<td>0.11</td>
<td>0.21</td>
<td></td>
</tr>
<tr>
<td>16 Nov. 1978</td>
<td>0.09</td>
<td>0.13</td>
<td>0.10</td>
<td>0.14</td>
<td></td>
</tr>
<tr>
<td>Mean (S.E.)</td>
<td>0.19 (0.04)</td>
<td>0.17 (0.02)</td>
<td>0.21 (0.04)</td>
<td>0.33 (0.10)</td>
<td></td>
</tr>
</tbody>
</table>

1 Locations of Stations shown in Fig. 1.

### TABLE V

Effect of water and cages on light penetration during seagrass trials

<table>
<thead>
<tr>
<th>Locality</th>
<th>Attenuation coefficient in water</th>
<th>Light reaching seagrasses</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Above cages (μE m⁻² s⁻¹)</td>
<td>Within cages (% of Warnbro cages)</td>
</tr>
<tr>
<td></td>
<td>%</td>
<td>Cleaned</td>
</tr>
<tr>
<td>Warnbro Sound</td>
<td>0.13 (0.01)²</td>
<td>965</td>
</tr>
<tr>
<td>Cockburn Sound</td>
<td>0.18 (0.02)</td>
<td>717</td>
</tr>
</tbody>
</table>


² Standard error.
Deterioration of meadows occurred over the full depth range during the period of major losses, and was not confined to a retreat of the deeper limit of the meadow into shallower waters. Further, the onset of the major period of seagrass dieback (1969) preceded the time (circa 1975) when phytoplankton blooms became prominent in the area. It is concluded that increased light attenuation, brought about by phytoplankton blooms, was not the primary cause of extensive loss of seagrass meadows.

The importance of epiphytes

Large quantities of epiphytes were consistently observed on seagrasses where meadows were thinning, and growth of epiphytes was very marked in the transplant trial (Fig. 3). On deteriorating meadows there were heavy growths of red algae (including Acrochaetium, Laurencia, Centroceras and Polysiphonia), green algae (including Enteromorpha and Ulva) and brown algae (including Asperoococcus). Individual plants were frequently large, up to 25 cm long. These larger algae were much less common in Warnbro Sound, and in Cockburn Sound where meadows were intact; in these areas crustose coralline algae such as Melobesia were relatively more prominent. In addition to true epiphytes, loose-lying blankets, up to 1 m thick, of fine filamentous algae, predominantly Ectocarpus, were sometimes found over remnants of seagrass meadows in Cockburn Sound.

As heavy epiphyte loads have been found to cause shading in seagrass leaves sufficient to reduce photosynthesis and growth (Sand-Jensen, 1977; Bulthuis, 1983; Bulthuis and Woelkerling, 1983; Orth and Montfrans, 1984), it is suggested that the enhanced growth of epiphytes in nutrient-enriched waters has brought about the decline in seagrass meadows in Cockburn Sound.

Nutrient levels are high in Cockburn Sound relative to nearby oceanic waters, and favour phytoplankton growth (Chiffings and McComb, 1981). Nitrogen is of particular importance in controlling phytoplankton growth in the Sound (Chiffings and McComb, 1981) and, by implication, for the growth of epiphytes as well.

Figure 5 shows the estimated levels of nitrogen entering the Sound from industrial sources, with a summary of major events in the seagrass loss. A marked increase in nitrogen loading coincided with the period of major seagrass decline, providing circumstantial evidence for a link between increasing nitrogen loads, enhanced epiphyte growth and deterioration of seagrass. This suggestion is consistent with the findings of other studies, which have reported increased growth of epiphytes and mats of filamentous algae following nutrient enrichment (e.g. Moss, 1976; Phillips et al., 1978; Harlin, 1980; Harlin and Thorne-Miller, 1981), and Fitzgerald (1969) and Shacklock et al., 1973 (cited Phillips et al., 1978) have emphasised the importance of nitrogen availability.
CONCLUSION

It is suggested that the following events have led to the major depletion of seagrasses in Cockburn Sound:

1. Increased nutrient loading, especially nitrogen, stimulated the growth of epiphytes and unattached, filamentous algae.

2. Increased algal growth significantly reduced the light available to seagrass leaves.

3. Phytoplankton growth continued to increase water turbidity, further reducing light intensity in areas distant from the points of nitrogen entry, so that the deeper limit of these meadows retreated.

4. As the canopy thinned, the seagrass meadow became vulnerable to grazing by sea urchins.

The third paper in this series more directly examines the hypothesis that shading by epiphytes has been the primary cause of the loss of seagrass meadows in the nutrient-enriched waters of Cockburn Sound (Silberstein et al., 1986).

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