Aquatic Botany, 16 (1983) 137—148
Elsevier Science Publishers B.V., Amsterdam — Printed in The Netherlands

BIOMASS ACCUMULATION AND SHADING EFFECTS OF EPIPHYTES ON LEAVES OF THE SEAGRASS, *HETEROZOSTERA TASMANICA*, IN VICTORIA, AUSTRALIA

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(Accepted for publication 8 February 1983)

ABSTRACT

Bulthuis, D.A. and Woelkerling, Wm. J., 1983. Biomass accumulation and shading effects of epiphytes on leaves of the seagrass, *Heterozostera tasmanica*, in Victoria, Australia. *Aquat. Bot.*, 16: 137—148.

A method is described for estimating the rate of accumulation of epiphyte biomass on leaves of the seagrass, *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog and for estimating the effect of epiphyte biomass on photosynthesis of the seagrass. Epiphyte biomass was determined by comparison of the weight per unit area of epiphyte-covered and epiphyte-free leaf blades. Epiphyte weight increased as age of the seagrass leaves increased. Linear regression of epiphyte biomass vs. leaf age estimated the rate of biomass accumulation. Rates varied from 5.7 to 104 μg epiphyte dry weight per cm^2 of leaf surface per day at three sites in Western Port and Port Phillip Bay, Victoria. Rates of accumulation of epiphyte biomass were generally higher during December through March (summer) than in May (autumn), August (winter) or October (spring). Light attenuation by epiphytes increased linearly with biomass. The rate of biomass accumulation of epiphytes was compared with leaf growth rate, ambient photon flux density in *H. tasmanica* beds and the photosynthesis—photon flux density curve of *H. tasmanica*. This comparison demonstrated that epiphyte biomass can accumulate fast enough to shade *H. tasmanica* leaves and significantly reduce the time (to less than one half of the leaf life span) in which positive net photosynthesis of the leaf blade is possible.

INTRODUCTION

A number of studies on the epiphytes of seagrasses have identified and enumerated the plant and animal species present. Diatoms have been recorded on *Zostera marina* L. (Sieburth and Thomas, 1973; Main and McIntyre, 1974; Jacobs and Noten, 1980), *Thalassia testudinum* Banks ex König (Reyes-Vasquez, 1970; de Felice and Lynts, 1978; Sullivan, 1979), *Syringodium filiforme* Kütz. (reported as *Cymodocea filiforme* (Kütz.) Correll) and

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Halodule beaudettei (den Hartog) den Hartog (Sullivan, 1979). Other types of algal epiphytes have been reported on *Thalassia testudinum* (Humm, 1964) and *Zostera marina* (Brauner, 1975). In Australia, plant and animal epiphytes have been enumerated for *Amphibolis antarctica* (Labill.) Sonder et Aschers. (Ducker et al., 1977), *Ruppia maritima* L. sensu lato (Wood, 1959), *Posidonia australis* Hook *f.*, *Zostera capricorni* Aschers. and *Z. muelleri* Irmisch ex Aschers. (Womersley, 1956; Wood, 1959; May et al., 1978) and *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog (May et al., 1978, reported as *Zostera tasmanica*). Elsewhere, nitrogen, phosphorus and carbon fluxes between *Zostera marina* and its epiphytes have been investigated in a number of studies (Harlin, 1973; McRoy and Goering, 1974; Penhale and Smith, 1977; Sand-Jensen, 1977; Wetzel and Penhale, 1979; Penhale and Thayer, 1980; Smith and Penhale, 1980) and recent reviews by Harlin (1975, 1980) have summarised the plant and animal species reported to be epiphytic on seagrasses and what is known of the functional relationships between seagrasses and their epiphytes.

It has been suggested that rapid growth and biomass accumulation of epiphytes has resulted in the decline of seagrasses and of freshwater angiosperms in nutrient-rich waters, and that the major cause for the decline is shading of the leaf surface by the epiphytes (Sand-Jensen, 1977; Phillips et al., 1978; Cambridge, 1979; Johnstone, 1979). Sand-Jensen (1977) demonstrated that epiphytes reduced photosynthesis of *Z. marina* leaves by shading and Borum and Wium-Andersen (1980) reported a direct relationship between epiphyte biomass and light absorption of epiphytes in suspension. A higher biomass of epiphytes has been reported on older leaves than on younger leaves of *Z. marina* ((van den Ende and Haage, 1963; Borum and Wium-Andersen, 1980; Harlin, 1980), *Posidonia oceanica* (L.) Delile (van der Ben, 1969) and *Enhalus acoroides* (L. *f.*) Royle (Johnstone, 1979). This increased biomass on older leaves would be expected to increase shading of the leaf surface and thus decrease leaf photosynthesis. However, the importance of shading by epiphytes can be evaluated objectively only when data are available to compare the rate of epiphyte biomass accumulation with the growth rate of the seagrass leaves.

Epiphyte biomass on leaves of *Z. marina* has been reported by Penhale (1977) and Borum and Wium-Andersen (1980). The pattern of accumulation of epiphytes on *Z. marina* leaves has been described qualitatively (Sieburth and Thomas, 1973). However, there apparently are no published quantitative data on the rate of biomass accumulation of epiphytes on seagrass leaves. Estimates of this rate cannot be based on biomass increment between average biomass for two sample dates because the loss of old epiphyte-covered leaves and production of new unepiphytised leaves are usually not measured. The objectives of the present study have been to develop a method for quantifying the rate of biomass accumulation of epiphytes on leaves of the seagrass, *H. tasmanica*, to determine the relationship between epiphyte biomass and shading of the leaf and to investigate the importance of this shading on photosynthesis of *H. tasmanica* in Western Port and Port Phillip Bay, Victoria.

METHODS

Epiphyte biomass on leaves of *Heterozostera tasmanica* was estimated by comparison of the weight per unit area of epiphyte-covered and epiphyte-free leaf blades from a single leaf cluster. All leaf blades with the attached epiphytes were removed from a leaf cluster, the position relative to the youngest leaf blade was noted, and leaf length and width measured. The leaf blades and attached epiphytes were rinsed carefully ($< 0.5\%$ of the epiphyte dry weight was lost during this procedure) in formic acid isotonic with seawater to remove inorganic salts which would otherwise contribute to the dry weight, dried to constant weight at 80° C, and muffled at 550° C to constant weight for ash-free dry weight (organic weight, Westlake, 1963). In each leaf cluster, the weight per unit area was determined for the youngest leaf blade (or second youngest when the youngest leaf blade was very small, < 50 mm long). These leaf blades had no epiphytes visible on the leaf surface (by light microscopy) other than widely scattered diatoms near the leaf tip. The $\mu g\ mm^{-2}$ (specific weight) of this reference leaf was subtracted from the specific weight of older leaf blades (with attached epiphytes) from the same cluster. The difference was an estimate of the weight of epiphyte biomass on the older leaf blades. This calculation assumes that the specific weight of the leaf blade does not change significantly with age. This assumption was tested by scraping the epiphytes from the leaf blades of eight leaf clusters collected at Charing Cross, Western Port on 29 August, 1979. There was no significant ($P > 0.05$) change in specific leaf weight with age (Table I), thus substantiating the assumption used in calculating epiphyte dry weight.

TABLE I

Dry weight of leaves of *Heterozostera tasmanica* which are free of epiphytes (nos. 1 and 2) or from which epiphytes have been removed (nos. 3 to 8). Leaves were collected 29 August 1979 at Charing Cross, Western Port. One-way ANOVA indicates no significant ($P > 0.05$) differences between leaves

Leaf no.	Dry weight ($mg\ cm^{-2}$)		
	Mean	s.e.	*n*
1 (youngest)	2.434	0.126	3
2	2.720	0.074	8
3	2.486	0.245	2
4	2.748	0.170	6
5	2.706	0.195	3
6	2.536	0.087	6
7	2.482	0.135	6
8 (oldest)	2.429	0.228	3

The rate of biomass accumulation of epiphytes was estimated by combining epiphyte biomass measurements with measurements of leaf age (days since leaf emergence). Leaf age was estimated from measurement of the plastochrone interval (the time interval between the initiation of two successive leaves in one leaf cluster) as described by Bulthuis and Woelkerling (1983). The least squares linear regression of epiphyte dry weight vs. leaf age was used to estimate the rate of biomass accumulation of epiphytes in μg per cm^2 of leaf surface per day.

The rate of biomass accumulation was estimated at three sites, Charing Cross and San Remo in Western Port which contains extensive beds of *H. tasmanica* (Bulthuis, 1981) and Edwards Point in Port Phillip Bay, Victoria. The physical and chemical conditions and the seasonal pattern of seagrass growth at these sites have been described in Bulthuis and Woelkerling (1981, 1983). Six leaf clusters were randomly sampled at each site during October through March (spring and summer), the season when earlier investigations had indicated epiphyte productivity was at a maximum (Penhale, 1977; Borum and Wium-Andersen, 1980). For comparison with other seasons, samples also were taken during May and August (late autumn and winter).

Light absorption by epiphytes on leaf blades of *H. tasmanica* was determined by measuring light transmission through scraped and unscraped sections of leaves with a Zeiss photomicroscope combined with a Zeiss microscope photometer. The light source was a Zeiss 60 W, 12 V tungsten illuminator. Light absorption was measured at 12—22 evenly spaced locations along the length of each leaf blade with epiphyte-free (scraped) sections of the same leaf as reference. The mean epiphyte absorption for each leaf was divided by two to estimate light absorption by a layer of epiphytes on only one side of a leaf.

RESULTS

The general nature of the early epiphytic community on *Heterozostera tasmanica* was similar qualitatively to that described by Sieburth and Thomas (1973) for *Z. marina.* Pennate diatoms were the first epiphytes present (visible by light microscopy) and these developed into a unialgal mat covering the whole of the leaf blade. Diatom frustules and detritus later formed an amorphous crust on which filamentous green algae and encrusting coralline red algae developed. The coralline algae were more prominent at the subtidal site, San Remo, than at the intertidal sites. Filamentous green algae generally accounted for about 20—60% of the biomass on older leaves, but contributed almost all of the biomass on older leaves during 'bloom' periods. Organic and inorganic detritus was present on most leaves, but generally appeared to account for less than 20% of the accumulated biomass. No attempt was made to separate the abiotic component from the living and dead epiphytes because all three contributed to light absorption.

As leaf age (measured in number of plastochrone intervals since emergence) increased, the dry weight of the epiphytes on the leaf blade also increased. This general pattern was evident at all sites on all sampling dates with data for March 1979 given as an example (Fig. 1). In March, 1979, the rate of biomass accumulation (and the maximum biomass observed on the oldest leaves) was lower at Charing Cross than at either of the other two sites (Fig. 1). At Charing Cross and San Remo the rate of accumulation was constant during the preceding 6 plastochrone intervals, resulting in an approximately linear relationship between epiphyte dry weight and plastochrone interval. At Edwards Point biomass accumulation occurred at two rates, one on the three youngest leaves, and a faster rate on the fourth through sixth oldest leaves (Fig. 1). The effect of a 'bloom' of epiphytes on the rate of biomass accumulation is illustrated by the November through January data for the San Remo site (Fig. 2). In November, the rate of accumulation was uniformly low, resulting in 1.15 mg cm^{-2} after eight plastochrone intervals. One month later (equivalent to three plastochrone intervals), there had been an increase in the rate of biomass accumulation with 4.35 mg cm^{-2} after eight plastochrone intervals. During the following month, this rate again decreased so that in January the bloom of the previous month was evident only on the seventh oldest leaf (Fig. 2).

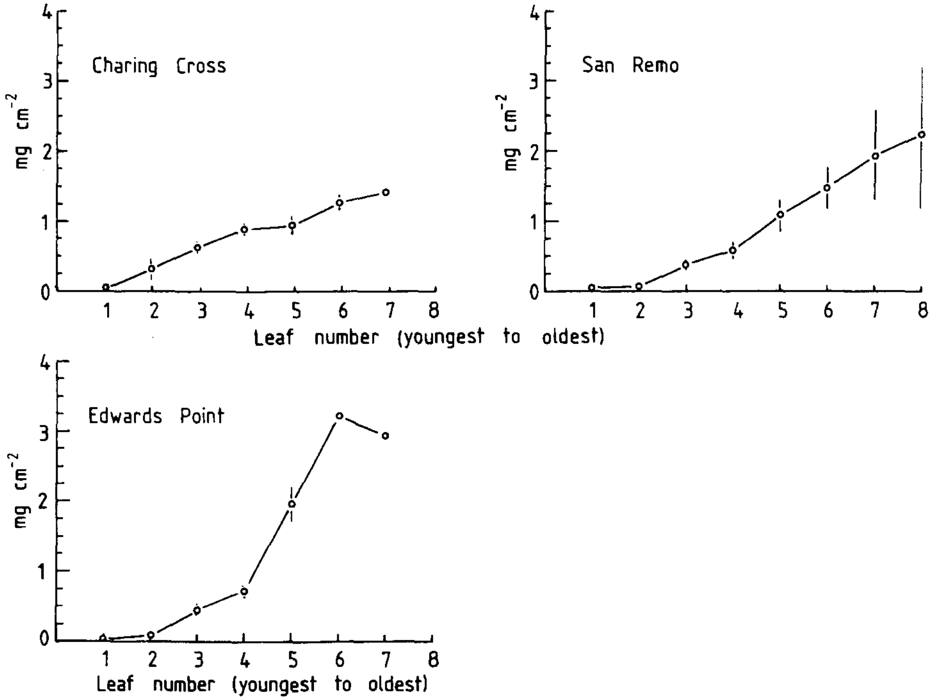

Fig. 1. Dry weight of epiphytes on successively older leaves of *Heterozostera tasmanica* at three sites in Western Port and Port Phillip Bay in March, 1979. mg epiphyte dry weight per cm^2 per leaf area, mean ± 1 s.e., n = 3—6 leaves.

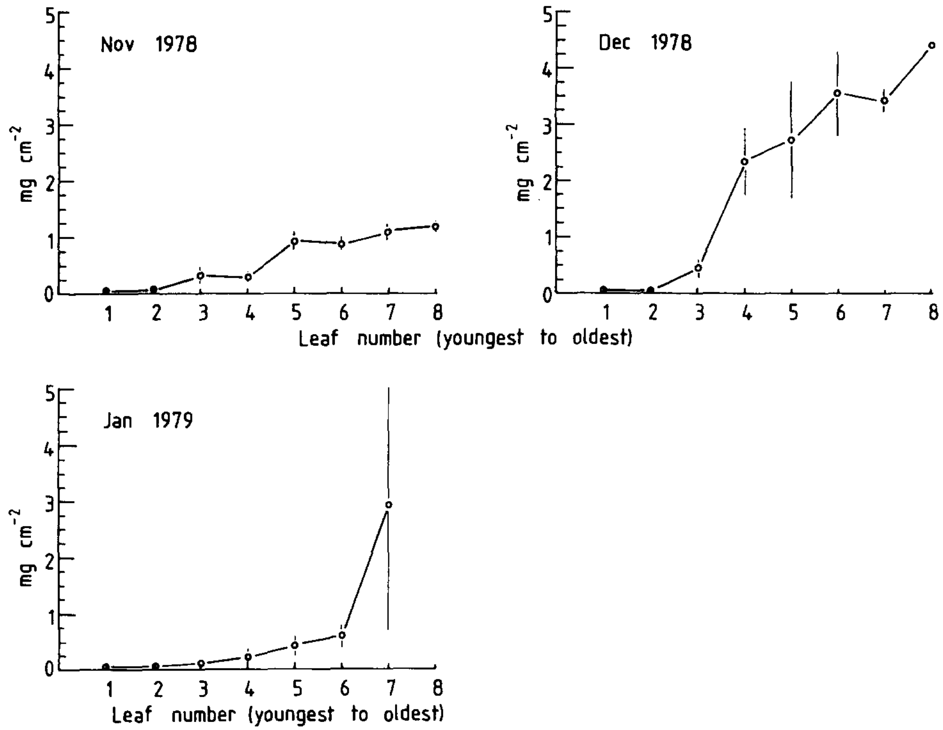

Fig. 2. Dry weight of epiphytes on successively older leaves of *Heterozostera tasmanica* at San Remo, Western Port before, during and after an epiphyte 'bloom' in December 1978. Mean ± 1 s.e., n = 3—6 leaves.

Ash-free dry weight of the epiphytes as a percentage of the dry weight did not change significantly ($P > 0.05$) at Charing Cross as leaf age increased (Table II). At San Remo, however, the percentage of ash-free dry weight decreased on older leaves. At San Remo, a greater abundance of encrusting coralline red algae was noted on older leaves, and these may have contributed to the increased ash content.

TABLE II

Organic weight (as a percentage of dry weight) of epiphytes on successively older leaves of *Heterozostera tasmanica* at an inter-tidal (Charing Cross) and subtidal (San Remo) site in Western Port. Mean ± s.e., n = 10 sample dates with 2—6 leaves per sample date

Site	Leaf number (youngest to oldest)						
	2	3	4	5	6	7	8
Charing Cross	75.7 ±2.0	76.6 ±2.1	74.6 ±2.7	71.5 ±3.3	72.9 ±2.3	66.2 ±4.2	71.1 ±3.1
San Remo	79.5 ±2.5	78.7 ±1.7	71.9 ±2.3	68.2 ±2.7	64.6 ±3.8	63.2 ±2.5	58.5 ±3.6

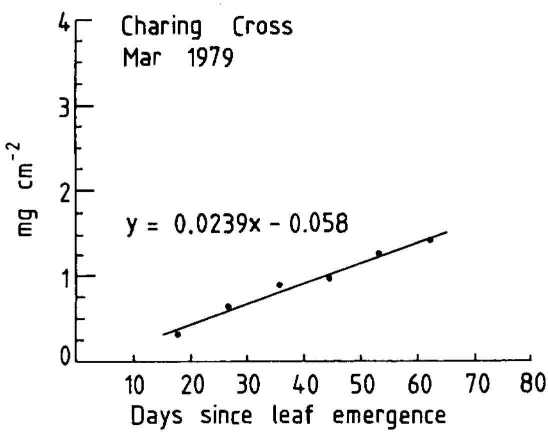

Fig. 3. Rate of epiphyte biomass accumulation on leaves of *Heterozostera tasmanica* at Charing Cross, Western Port, in March 1979. The line and equation are the least squares linear regression of the points shown ($r^2 = 0.978$). The slope (0.0239) is in mg cm^{-2} day^{-1}. The slope was calculated for each sampling date and used as the best estimate of epiphyte biomass accumulation rate for that date.

TABLE III

Rates of biomass accumulation of epiphytes on leaf blades of *Heterozostera tasmanica* at three sites in Western Port and Port Phillip Bay in μg cm^{-2} day^{-1}. Rates were determined by linear regression as illustrated in Fig. 3. r^2 for the linear regressions are given in parentheses

Month	Charing Cross	San Remo	Edwards Point
Aug. '78	5.7 (0.80)	44.6 (0.92)	31.3 (0.86)
Oct. '78	9.7 (0.93)	15.7 (0.95)	36.8 (0.99)
Nov. '78	9.8 (0.91)	19.5 (0.90)	*
Dec. '78	24.4 (0.95)	58.4 (0.92)	35.8 (0.80)
Jan. '79	8.8 (0.72)	14.9 (0.99)	46.4 (0.95)
Feb. '79	12.9 (0.82)	48.3 (0.99)	104 (0.92)
Mar. '79	23.9 (0.98)	50.1 (0.99)	91.8 (0.95)
May '79	27.4 (0.97)	15.7 (0.98)	21.8 (0.99)

*No data available.

When the leaf number is replaced by the length (in days) of the plastochrone interval, the rate of biomass accumulation can be expressed in μg cm^{-2} day^{-1} (Fig. 3). Least squares linear regression of these points from Charing Cross, March 1979, had an r^2 of 0.978 and a slope of 0.0239. That is, biomass of epiphytes accumulated on the leaf blades of *H. tasmanica* at a rate of 0.0239 mg cm^{-2} day^{-1} (or 23.9 μg cm^{-2} day^{-1}). Similarly, least squares linear regression for the straight line portion (e.g., leaves 2—6 for San Remo, January 1979, Fig. 2) on each sampling date was used to estimate the rates of epiphyte biomass accumulation (Table III). Rates at San Remo

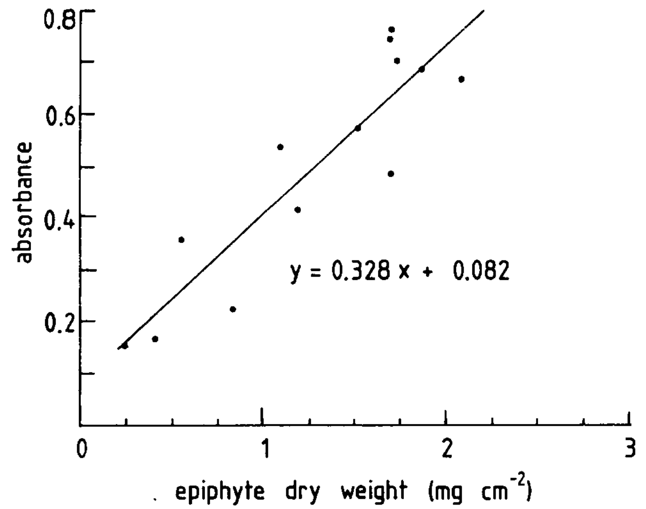

Fig. 4. Dry weight vs. absorbance of epiphytes on leaves of *Heterozostera tasmanica* at Charing Cross, Western Port, August 1979. The line and equation are the least squares linear regression of the plotted points ($r = 0.878$).

for November, December and January indicate the sharp increase in December at the time of a 'bloom' of epiphytes (Table III, Fig. 2). The rates of accumulation of epiphytes at Charing Cross, San Remo and Edwards Point varied from 8.8 to 104 μg dry weight cm^{-2} leaf surface day^{-1} during the spring and summer months of October to March. Rates above 40 μg cm^{-2} day^{-1} were recorded during December, February and March at San Remo and during January to March at Edwards Point. The highest rate of epiphyte biomass accumulation recorded in the present study was 104 μg cm^{-2} day^{-1} at Edwards Point during February 1979. Biomass accumulation rates during spring and summer were generally highest at Edwards Point and lowest at Charing Cross (Table III). Rates during May and August (autumn and winter) were usually lower than during summer (December to March).

The accumulated biomass of epiphytes on the leaf blades of *H. tasmanica* reduced light penetration to the leaf surface (Fig. 4). There was a direct relationship between dry weight of epiphytes and light absorbance over the range of 0.35—2.05 mg epiphytes cm^{-2} leaf surface. At an epiphyte dry weight of 2 mg cm^{-2} and, thus, an absorbance of 0.7 (Fig. 4), only 20% of the irradiance reaching the upper surface of the epiphytes would be transmitted to the upper surface of the leaf blade.

DISCUSSION

The present study has demonstrated a method for quantifying the rate of biomass accumulation of epiphytes on leaf blades of *H. tasmanica*. With minor modifications in measuring the plastochrone interval, the same method is applicable to most other seagrasses. Because seagrasses continually produce new substrate for epiphyte colonisation, a set of samples from a single date (plus an estimate of the plastochrone interval) can be used to estimate a rate.

The method also was attempted in an area of high silt accumulation where fine silt becomes enmeshed in the epiphyte community and may account for more than 50% of the total dry weight. This fine silt, however, was very easily disturbed and the physical handling involved in removing leaf blades from the field to the laboratory jarred various amounts of silt off the leaf. The method is not applicable at such sites.

The increase in epiphyte dry weight with leaf age found in the present study is consistent with the qualitative description of epiphyte colonisation on the seagrass *Z. marina* by Sieburth and Thomas (1973) and the higher epiphyte biomass reported on older than on younger leaves for various seagrasses (van den Ende and Haage, 1963; van der Ben, 1969; Johnstone, 1979; Borum and Wium-Andersen, 1980; Harlin, 1980).

The accumulated dry weight of epiphytes in the present study includes both living and dead plant and animal epiphytes and any debris which may have become enmeshed in the community. The rates measured in the present study are a measure of changes in the total epiphyte biomass over time and indicate the magnitude of the effect that epiphytes may have on seagrasses (for example, in reducing light intensity at the leaf surface, Fig. 4). The rate of biomass accumulation is not an estimate of net primary production because no attempt has been made to measure dissolved organic carbon losses, physical sloughing of epiphytes off the leaves, senescence of epiphytes or grazing. Grazing, particularly, may significantly reduce epiphyte biomass on seagrass leaves (Mook, 1977; Howard, 1982; Robertson and Mann, 1982; Van Montfrans et al., 1982).

The conditions for epiphyte growth and accumulation of biomass were more favourable at Edwards Point than at either San Remo or Charing Cross (Table III). At Edwards Point, ammonium concentration of the water was slightly higher and phosphate concentration was eight times higher than at the other two sites (Bulthuis and Woelkerling, 1983). These higher nutrient levels in the water may account for the higher rates of biomass accumulation of epiphytes observed at Edwards Point. Rates of epiphyte biomass accumulation also were higher at San Remo than at Charing Cross (Table III). Nutrient levels in the water were similar at these two sites (Bulthuis and Woelkerling, 1983), but snail populations were conspicuously abundant at Charing Cross and may account for the lower epiphyte biomass observed at this site (cf. Mook, 1977; Robertson and Mann, 1982; Van Montfrans et al., 1982). Rates of biomass accumulation of epiphytes at all sites were generally higher during December through March than during the other months that were measured (Table III). These may indicate seasonal differences in the rate of biomass accumulation of epiphytes and further study of seasonal trends is warranted. Increases in the rate of biomass accumulation during summer may be particularly deleterious to *H. tasmanica* because field (Bulthuis, 1983b) and laboratory (Bulthuis, 1983a) studies indicate that *H. tasmanica* is most sensitive to light reduction during the warmer months.

Epiphytes occur ubiquitously on seagrasses and the effect on the seagrass may be deleterious because of shading, lowering of the bicarbonate concentration at the leaf surface (Sand-Jensen, 1977; Borum and Wium-Andersen, 1980) or competition for water-borne nutrients. In freshwater, Phillips et al. (1978) suggested that under conditions conducive to rapid growth of epiphytes, submerged angiosperms may die and be excluded from certain lakes. Similarly, the disappearance of the seagrass, *Posidonia australis*, from much of Cockburn Sound, Western Australia, has been attributed to growth and development of epiphytes (Cambridge, 1979). Sand-Jensen (1977) and Johnstone (1979) have suggested that seagrasses generally have high leaf growth rates and thus produce new photosynthetic tissue faster than epiphytes can shade, nutrient-filter, or damage the leaf tissue. Data from the present study provide evidence that epiphyte biomass accumulates during a 'bloom' at a rate fast enough to lower leaf photosynthesis significantly. For example, during December 1978, epiphyte biomass accumulation at San Remo was 0.0584 mg cm^{-2} day^{-1} (Table III), irradiance at the water surface at noon on a cloudless December (summer) day is about 1500 μmol m^{-2} s^{-1}, irradiance at the top of the seagrass canopy at San Remo was 12% of surface irradiance (Bulthuis and Woelkerling, 1983), the instantaneous light compensation level for a leaf blade of *Heterozostera tasmanica* at 20°C is about 30 μmol m^{-2} s^{-1} (Bulthuis, 1983a) and epiphyte dry weight vs. light absorption is characterised by absorbance = 0.328 dry weight + 0.0819 (Fig. 4). Under these conditions, 36 days after leaf emergence the epiphytes reduced light intensity below the light compensation point; and at noon on cloudy December days, this point was reached for leaves 11 days after emergence. Mean leaf life span at San Remo in December was 64 days from emergence to abscission (Bulthuis and Woelkerling, 1983). Thus, leaf blades at San Remo in December 1978 were so quickly shaded by epiphytes that they did not have a positive net photosynthesis, even at noon, for more than half of their life span. Similar conclusions were indicated for the 'bloom' at Edwards Point in February 1979. Therefore, high rates of biomass accumulation of epiphytes on *H. tasmanica* leaves may significantly lower photosynthesis of the seagrass by shading and deleteriously alter the chances of survival. On the other hand, at Charing Cross, where rates of epiphyte biomass accumulation were lower and light at the top of the seagrass canopy higher, on clear December days at noon, even the oldest and most heavily encrusted leaves received more than the light saturation level of irradiance. Shading by epiphytes, thus, would not be expected to be a major factor for *H. tasmanica* at Charing Cross, Western Port.

The present study has shown that rates of biomass accumulation of epiphytes on *H. tasmanica* leaves varied from 5.7 to 104 μg cm^{-2} day^{-1} at three sites in Western Port and Port Phillip Bay. Rates were highest at Edwards Point where nutrient concentration of the water was highest, lowest at Charing Cross where the snail population was the densest and generally higher during December through March (summer) than during May (autumn), August (winter) or October (spring). At the rates measured in the present study, epiphyte biomass can accumulate fast enough to shade *H. tasmanica* leaf blades and significantly reduce the time span in which positive net photosynthesis of the leaf blade is possible.

ACKNOWLEDGEMENTS

Sincere thanks are due to the technical staff of the Marine Science Laboratories for assistance with field collections and with processing samples in the laboratory, and to Mr. E. Hyduke for computing assistance. The views expressed in this paper do not necessarily reflect those of the Victorian Ministry for Conservation.

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