SEASONAL VARIATION IN STANDING CROP, DENSITY AND LEAF GROWTH RATE OF THE SEAGRASS, HETEROZOSTERA TASMANICA, IN WESTERN PORT AND PORT PHILLIP BAY, VICTORIA, AUSTRALIA

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ABSTRACT

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Standing crop, density and leaf growth rate of Heterozostera tasmanica (Martens ex Aschers.) den Hartog along with light, temperature, nutrient and sediment characteristics were determined monthly for fifteen months at three study sites in Western Port and one site in Port Phillip Bay, Victoria, Australia. Erect vegetative stems of H. tasmanica were frequently branched, were present throughout the year and accounted for 25-60% of the above-sediment biomass, with the stem proportion higher during winter than summer. At three of the four sites there was a unimodal seasonal pattern in which minimum leaf standing crop (27-61 g dry wt. m⁻²), density (600-2000 leaf clusters m^{-2}) and leaf productivity (0.34-0.77 g dry wt. m^{-2} day⁻¹) generally occurred during winter (June-August) and maximum leaf standing crop (105-173 g dry wt. m⁻²), density $(2700-5000 \text{ leaf clusters m}^{-2})$ and leaf productivity $(2.6-4.2 \text{ g dry wt. m}^{-2})$ day⁻¹) occurred during summer (December-February). A bimodal seasonal pattern with minimum standing crop and density during midsummer occurred at one site. This anomalous seasonal pattern may be due to exposure and desiccation stress during spring low tides. At the site receiving the lowest irradiance, standing crop, density and annual leaf production also were lowest, but length and width of leaves, shoot height and leaf growth rate per leaf cluster were the highest of the four study sites. On average, each leaf cluster at any one of the study sites produced 30-31 leaves per year with mean leaf turnover rates of 1.3-1.7% day'. Annual leaf production of H. tasmanica ranged from 410 to 640 g dry wt. m^{-2} at the four sites.

INTRODUCTION

The seasonal patterns of standing crop, density and leaf growth rate of temperate seagrasses have been the subject of a number of recent inves-

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tigations. Studies on Zostera marina L., for example, indicate that minimum standing crop $(0-140 \text{ g dry wt. m}^{-2})$, density $(0-900 \text{ shoots m}^{-2})$, and leaf growth rate (<0.06-1 g dry wt. m⁻² day⁻¹) occur during the winter months (Sand-Jensen, 1975; Thayer et al., 1975; Penhale, 1977; Jacobs, 1979; Nienhuis and de Bree, 1980). During spring, leaf growth rate, standing crop and density of Z. marina increase markedly, and maxima generally occur during mid-summer and may be as high as 1500 g dry wt. m⁻² for leaf standing crop, 4500 shoots m⁻² for density, and 13 g dry wt. m⁻² day⁻¹ for leaf growth rate (McRoy, 1970; Nienhuis and de Bree, 1980; see also reviews by McRoy and McMillan, 1977 and Zieman and Wetzel, 1980). Penhale (1977), however, reported a Z. marina community in North Carolina which had maximum standing crop during early spring (March) and which decreased during the remainder of the year, although productivity $(1.8 \text{ g C m}^{-2} \text{ day}^{-1})$ was at a maximum during late summer and autumn. For Posidonia australis Hook f. in Botany Bay, Jervis Bay and Port Hacking, New South Wales, Australia, West and Larkum (1979) and Kirkman and Reid (1979) reported very little seasonal change in leaf biomass, but leaf growth rate was markedly seasonal with a summer maximum (November-February) and a winter minimum (July-August). Similarly, for Z. capricorni Aschers. in Port Hacking, relative leaf growth rate was at a maximum in late summer and a minimum in winter (Kirkman et al., 1982).

There have been no reports on the seasonal patterns of growth and standing crop of *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog. *Heterozostera tasmanica* differs from Z. marina and P. australis in possessing lignified stems which represent a major proportion of the standing crop. Den Hartog (1970), Aston (1973), Tomlinson (1974), Cambridge (1975), and Jacobs and Williams (1980) state that these stems are shed during autumn and replaced by winter foliage, thus indicating a seasonal fluctuation in stem standing crop.

The objectives of the present study have been (1) to investigate the seasonal patterns of leaf and stem standing crop, erect shoot and leaf cluster density and leaf growth rate of *H. tasmanica* at four study sites in Western Port and Port Phillip Bay, Victoria, Australia, (2) to relate these patterns to the physical and chemical characteristics of these sites, and (3) to compare the general seasonal pattern of growth and leaf production of *H. tasmanica* to other temperate seagrasses.

STUDY SITES

At three study sites in Western Port and one in Port Phillip Bay (Fig. 1) the standing crop, density and leaf growth rate of *H. tasmanica* were determined monthly for fifteen months. These four sites were selected from among 50 potential sites to represent the diverse light, nutrient and depth conditions in which *H. tasmanica* grows. At all four sites *H. tasmanica* covered an area of at least 50×100 m. The Charing Cross site (38° 15'



Fig. 1. Location of study sites in Western Port and Port Phillip Bay at which growth and standing crop of H. tasmanica were determined.

30" S, 145° 21' 55" E) was located within extensive intertidal banks covered with H. tasmanica in the Upper North Arm, the section of Western Port which has the greatest area and highest standing crop of H. tasmanica (Bulthuis, 1981). Earlier investigations at this site had indicated that nitrogen limits the leaf growth rate of H. tasmanica during spring and early summer (Bulthuis and Woelkerling, 1981). The San Remo site (38° 13' 30" S. 145° 23' 50" E) is subtidal. The Spit Point site (38° 21' 15" S. 145° 31' 15'' E) received less light than the other intertidal sites because of the more turbid overlying water. The Edwards Point site (38° 13' 20" S, 144° 41' 45" E) in Port Phillip Bay, had the highest levels of phosphorus in the water of any site and was the only intertidal site with a perceptible bottom gradient (approximately 40 cm over the 50 m width of the site) which facilitated water runoff during low tide. The sediments next to the Edwards Point site on the shallower side were either bare or were covered with Zostera muelleri Irmisch ex Aschers.; those on the lower side of the site were covered with H. tasmanica. In Western Port, H. tasmanica surrounded each of the three sites for at least 500 m in all directions.

The physical and chemical characteristics of the four sites are summarised in Tables I–III. Sediments at all sites were anaerobic muds beginning less than 1 cm below the surface and organic carbon ranging from 0.7% at San Remo to 6.5% at Charing Cross (Table I). The presence of lignified stems to a depth of 30-45 cm at the three Western Port sites implies that *H. tasmanica* had been growing at the sites for several years at least.

TABLE I

Depth (below mean water), tidal amplitude (of spring tides), organic carbon of surface (upper 5 cm) sediments (mean \pm s.e. of 10 samples), depth of anaerobic mud and stems and rhizomes (mean of 2 one-metre cores) and bottom slope of four study sites in Western Port and Port Phillip Bay at which growth and standing crop of *H. tasmanica* were determined

	Charing Cross	Spit Point	San Remo	Edwards Point
Depth (m)	1.0 Intertidal	1.0 Intertidal	3.6 Subtidal	0.6 Intertidal
Tidal amplitude (m)	3.1	3.1	3.0	1.1
Surface sediment	Anaerobic mud	Anaerobic mud	Anaerobic mud	Anaerobic mud
Organic carbon (% of dry wt.)	6.5	2.5	0.7	4.9
Depth of anaerobic muds (cm)	60	30	>90	*
Depth of old stems and rhizomes of H. tasmanica (cm)	45	30	45	*
Bottom slope	<10 cm × 100 m ⁻¹	< 10 cm × 100 m ⁻¹	<10 cm × 100 m ⁻¹	40 cm × 50 m ⁻¹

*No data.

TABLE II

Nutrient concentrations and salinity of water at four study sites in Western Port and Port Phillip Bay at which growth and standing crop of *H. tasmanica* were determined. Mean and range of monthly samples from March 1978 to May 1979

	Charing Cross	Spit Point	San Remo	Edwards Point
Nitrogen	n (µg at N l ⁻¹)			
`NH,	0.34	0.32	0.26	0.41
	< 0.1 - 0.9	< 0.1 - 1.2	0.1 - 0.9	< 0.1 - 1.3
NO ₃	0.23	0.73	0.38	0.24
-	0.1 - 1.24	0.1 - 6.4	0.1 - 2.3	0.1 - 0.6
NO ₂	0.06	0.09	0.06	0.06
-	< 0.01- 0.28	< 0.01- 0.50	0.01- 0.30	< 0.01- 0.20
Phospho	orus (µg at P l')			
PO ₄ ³⁻	0.08	0.18	0.10	0.81
-	0.02-0.23	0.05- 0.58	0.03- 0.20	0.30- 1.80
Total	P 0.32	0.78	0.37	1.27
	0.20- 0.58	0.32- 2.67	0.18- 0.94	0.58- 2.71
Silica (µ	g at Si l ⁻¹)			
SiO,	4.0	10.6	3.2	3.6
	1.8 - 9.8	1.6 -28.3	0.8 -10.9	1.0 - 9.8
Salinity	(⁰ /00)			
Salini	ty 34.59	33.39	34.77	34.81
	31.61-37.13	28.01-37.51	32.71 - 36.26	32.36-36.03

Salinity and nutrients in the water varied widely between months, but there were no seasonal trends at any of the sites; mean and range of values encountered during the fifteen months of study are indicated in Table II. Salinity was generally similar to oceanic levels; none of the sites received large freshwater inputs. The lowest salinities were recorded at Spit Point, which according to the circulation pattern proposed by Harris et al. (1979) would be due to the streams and small rivers that enter Western Port in the north-east corner. This probably also accounts for the higher reactive silicate, nitrate and phosphorus observed at Spit Point compared to the other two sites in Western Port. Edwards Point, in Port Phillip Bay, had mean reactive phosphorus and total phosphorus levels in the water 2—10 times higher than the Western Port sites (Table II).

The three intertidal sites (Charing Cross, Spit Point, and Edwards Point) had similar maximum and minimum water temperatures each month (note standard errors in Fig. 2) so the data were combined (Fig. 2). The plants at the subtidal site experienced less extremes in temperature than did those at the intertidal sites, particularly during the summer months when maximum intertidal temperatures averaged 30°C compared with 24°C at San Remo.

Light penetration through the water at all sites varied greatly between sampling visits as indicated by the wide range of extinction coefficients



Fig. 2. Monthly maximum and minimum temperatures of surface waters at three intertidal (closed circles, mean ± 1 s.e.) study sites in Western Port and Port Phillip Bay and at one subtidal (open circles) site in Western Port.

	Charing Cross	Spit Point	San Remo	Edwards Point	
K (per m)	0.66	1.24	0.58	0.75	
Mean depth (m)	0.12—1.66 1.0	0.48-2.83 1.0	0.33—1.03 3.6	0.45-1.32 0.6	
Irradiance (% of surface)	52	29	12	64	

Extinction coefficients (mean and range of K, determined monthly from March 1978 to May 1979) of water and irradiance to *H. tasmanica* community (assuming mean depth and mean K) at four study sites in Western Port and Port Phillip Bay

at each site (Table III). There was no seasonal trend in the fluctuations and the mean of all values at each site indicates the overall relative light conditions. The mean depths and extinction coefficients were used to estimate the percent of surface irradiance reaching the *H. tasmanica* community at each station. Charing Cross and Edwards Point were similar and received the greatest amount of light, while seagrasses at Spit Point received about half as much and plants from San Remo (subtidal) received the least amount of light (Table III).

METHODS

At the four study sites the standing crop, density and leaf growth rate of *H. tasmanica* as well as the physical—chemical characteristics of each site were determined monthly for fifteen months. An area 100×100 m at each site (50×100 m at Edwards Point) was marked at one corner with a permanent marker (10 cm diameter, 7 m long steel pole) ensuring that the same area was sampled each time and serving as a reference point for determining the location of random samples. Monthly samples for all parameters at the three intertidal sites were taken during low tide. Damage to the site was minimised by moving to and around the site and sampling from fibreglassed, styrene foam floats ($1.5 \times 2.5 \times 0.2$ m) which floated on the 2–10 cm of water that usually remained on the mudflats during low tide. At the subtidal site, San Remo, all sampling and leaf marking was completed underwater with the aid of SCUBA.

The sediment characteristics of the sites also were determined. In August 1978, three, one-metre-deep cores of the sediment were taken at each site for examination of depth of anaerobic muds as indicated by black colour. Ten samples of the upper 5 cm of sediment were randomly taken at each site and organic carbon determined by the wet digestion method (Jackson, 1958). At each site a shaded maximum—minimum thermometer

TABLE III

was placed at the sediment surface in a position that kept the thermometer submerged at all times. Temperature was read and the thermometer was reset monthly.

Salinity, total phosphorus, reactive phosphorus, ammonium, nitrate and nitrite were determined in samples of the overlying water taken twice each month, once at mid-ebb tide and once (at intertidal sites) just before the return of the flood tide. Salinity was determined on a 601-MIII Autolab salinometer. Nutrient concentrations were determined with a Technicon Autoanalyzer II; reactive phosphorus, nitrate, nitrite and ammonia by the methods described by Strickland and Parsons (1972); total phosphorus by persulphate digestion followed by analysis of reactive phosphate; and reactive silicate by the method of Koroleff (1972).

Light penetration in the overlying water was determined monthly as downwelling irradiance with a Lambda LI-192S quantum sensor (400-700 nm). Extinction coefficients (K) of the water were calculated from eqn. (1) which is based on Lambert's law

$$I_z = I_0 e^{-Kz} \tag{1}$$

where I_z = light quanta at depth z; I_0 = light quanta just below the water surface; e = base of the natural logarithms; z = depth in metres; K = extinction coefficient.

Ten samples for standing crop and density were taken each month at each site. The location of each of the ten samples was determined with a random numbers table and a map of the 100×100 m area divided into 160000 potential 0.25×0.25 m quadrats. Samples were located in the field by measuring the indicated distance from the permanent marker. A metal frame was set over a 0.0625 m^2 quadrat [this size had the lowest ratio of variance to mean for leaf standing crop of quadrats ranging from 0.00391 to 0.25 m^2 (Kershaw, 1973)] and was used to cut the sides of the turf. The turf, including all plants, rhizomes, and about 10 cm of sediment, was then removed and placed in plastic boxes of the same size, covered, transported to the laboratory and kept cool (5°C) until sorting, which was usually within 3 days and always within 7 days of sampling.

In the laboratory, all stemmed erect shoots were removed from each standing crop-density sample; shoot length was measured from the insertion of the first root to the top of the longest leaf; and the number of leaf clusters and adventitious shoots was recorded. The shoot was rinsed free of mud and divided into stems and leaves (stems included some persistent fibrous sheaths, leaves were wiped by hand to remove macro-epiphytes, but leaf dry weight included the tightly-adhering diatom crust and associated micro-epiphytes) and dried at 80° C to constant weight (usually within 48 h). The number of stemless shoots was recorded separately. Percent ash-free dry weight, i.e., organic weight (Westlake, 1963) was determined in two randomly selected 1-g subsamples each month

from each site. Subsamples were ashed in pre-heated aluminium foil boats at 550° C to constant weight (usually within 3 h).

Leaf growth was measured each month at three sample stations randomly selected within each of the four 100×100 m sampling sites. Vegetative shoots of H. tasmanica may be unbranched or branched (contrary to description by den Hartog, 1970), with a cluster of leaves [analogous in Z. marina to 'turion' in Sand-Jensen (1975), and to 'leaf bundle' in Nienhuis and de Bree (1980)] at the apex of each branch. Within each cluster the youngest leaf is in the centre with successively older leaves outside of the centre. New leaves emerge in the centre of the cluster. The time interval between the initiation of two successive leaves in a leaf cluster is the plastochrone interval (Patriquin, 1973; Jacobs, 1979). Leaf growth within each cluster is limited to the three youngest (centremost) leaves, similar to the pattern described by Mukai et al. (1979) and Jacobs (1979) for Z. marina. Sixteen leaf clusters at each of the three stations had a prelabelled cable-tie attached between two leaf nodes on the lignified stem below the leaf cluster. Care was taken to prevent damage to the stems and to ensure that the tag could not slip past either node. The tag allowed each leaf in the cluster to be uniquely identified relative to the tag. The length of the three youngest leaves in each leaf cluster was recorded, care being taken not to crack the brittle lignified stems or disturb their attachment to the rhizome. Tagged plants were left for one month and the surviving plants were harvested and returned to the laboratory where the original 3 youngest leaves were re-measured, any new leaves noted and measured, and the total number of leaves in the cluster noted. Leaf growth rate was calculated as the sum of the growth of all leaves (old and new) within each leaf cluster. Leaf dry weight and organic weight per unit length of leaf was determined on young leaves without epiphytes, as described above for organic weight analysis of standing crop.

RESULTS AND DISCUSSION

Standing crop

The above-sediment biomass (standing crop) of *H. tasmanica* was about 50% stem and 50% leaf (Table IV). The leaf proportion of the standing crop increased during spring (September-November) and summer (December-February) to about 60% at Charing Cross, Spit Point and San Remo, and up to 75% at Edwards Point. During autumn (March-May) the leaf proportion decreased to about 40% at Charing Cross, Spit Point and San Remo. Edwards Point averaged a somewhat higher proportion of leaves (mean: 64%) compared with the other three sites (mean: 50%).

Organic weight as a percentage of dry weight of leaves and stems remained relatively constant throughout the year. Mean values ranged from 75 to 81% for both leaves and stems from all four sites (Table V).

TABLE IV

Standing crop of leaves and stems of *H*, tasmanica at four sites in Western Port and Port Phillip Bay from March 1978 to May 1979 Mean (g dry wt. m^{-2}) ± 1 s.e.; n = 10, n.a. = not available Ì

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Month	Leaf				Stem				Total abc	ve grour	ри		
	Charing Cross	Spit Point	San Remo	Edwards Point	Charing Cross	Spit Point	San Remo	Edwards Point	Charing Cross	Spit Point	San Remo	Edwards Point	
March	85±12 80± 0	54± 7 54± 7	31±10	81±27	133±16	105±15	49±35 56, 6	80±22	218±26	158±20	83±52	161±49	1
May	0 ±00 10 ± 02	54±10	43± 4	1091 9 87±15	121110	59±12	55±9	14/110 87±24	209124 186±15	13±22 113±21	01±001 99±13	200123 174±38	
June	67± 6	63± 9	48± 4	80± 5	90 ∓ 9	59± 9	46± 4	36± 3	157 ± 14	122 ± 19	94± 7	116± 7	
July	65±11	63± 3	32± 5	n.a.	80±15	63± 5	31± 8	n.a.	145 ± 25	126± 7	63±13	n.a.	
August	73± 9	41± 6	28 ± 6	120 ± 13	76±14	30∓ 6	29 ± 7	39± 6	148 ± 22	71±12	56±13	159±18	
September	92± 8	114 ± 12	33 ± 6	128 ± 17	103±19	77± 9	26± 6	48 ± 9	196±27	191±20	59±11	176±25	
October	61±14	114± 7	58± 7	100± 9	47±10	77± 8	45 ± 5	44± 5	107 ± 23	191±14	103±13	144±14	
November	103± 8	120± 8	105 ± 11	94±11	94±13	70± 6	79±13	44± 6	197 ± 20	190±14	184 ± 24	138±17	
December	116 ± 16	96± 6	72 ± 10	88± 9	94±14	66± 6	71 ± 12	33 ± 5	209 ± 29	162±11	143 ± 21	121±13	
January	96±10	173±11	87±9	59±12	75±10	113 ± 13	139± 7	39± 7	171 ± 18	279±21	226±25	61±66	
February	83±13	130 ± 12	55± 7	89±10	89±16	111±11	103 ± 16	52± 6	172±29	241 ± 22	157±22	141±15	
March	80±12	72±11	28±4	103 ± 14	109 ± 16	85±15	50± 6	74± 9	189 ± 26	157± 8	78±10	177±20	
April	84± 9	44±11	27±4	121 ± 14	111 ± 13	50± 7	36± 7	80 ± 10	195±20	94±16	63±11	200 ± 24	
May	79±10	39± 7	47±10	63 ± 12	85 ± 13	43± 5	53 ± 10	42±11	163±22	82±12	102 ± 20	105±22	

	Charing Cross	Spit Point	San Remo	Edwards Point	
Leaves	79.4	73.9	76.6	79.9	
	± 0.58	± 1.11	± 1.15	± 0.69	
Stems	79.7	75.6	81.1	78.1	
	± 0.71	± 0.76	± 0.89	± 0.74	

Organic weight as percentage of total dry weight of leaves and stems of erect shoots of *H. tasmanica* at four study sites in Western Port and Port Phillip Bay (Mean \pm s.e.; n = 15 monthly means from March 1978 to May 1979)

The standing crop of leaves increased from two- to four-fold between winter (June-August) and summer (December-February) (Table IV). At Charing Cross, Spit Point and San Remo, winter minima were 65, 40 and 30 g m⁻² and increased to summer maxima of 115, 170 and 105, respectively. Seasonal fluctuations at Charing Cross were less marked than at Spit Point or San Remo. At Edwards Point the seasonal pattern was markedly different from the other three sites. There were two peaks of standing crop, one in early spring (September: 130 g m⁻²) and a second in autumn (April: 120 g m⁻²). Minima occurred in winter (May-June: 80 and 65 g m⁻²) and in mid-summer (January: 60 g m⁻²). The mid-summer minimum was particularly striking as it occurred when *H. tasmanica* leaf standing crop was at or near its maximum at the other three sites (Table IV).

The differences observed at Edwards Point appear to be related to temperature and exposure stresses. Edwards Point was the only site at which there was a perceptible slope (Table I) and phosphorus in the water was higher than at the other sites (Table II). However, light and temperature, the abiotic factors usually suggested as the causative agents of seasonal fluctuations, and the other nutrients were similar at Edwards Point to the two other intertidal sites (Tables II and III, Fig. 2). During low-water spring tides, which are about 0.2 m lower during summer (November-January) than during winter in Port Phillip Bay, the water drains down the slope at the Edwards Point site leaving H. tasmanica exposed. At the two other intertidal sites there is less slope (Table I) and natural levees at the channel edge retard water flow from the mudflats into the channels; hence, there is always some water on the mudflat surface. Therefore, H. tasmanica at the Edwards Point site may be exposed to greater desiccation stress during the low water spring-tides of summer than at the other sites and consequently dies back. In an unpublished report, D.A. Bulthuis and P. Ruppin indicated that H. tasmanica leaves blackened and died after more than 1 h of exposure at temperatures of 25°C or higher. In addition

to the potential desiccation stress, plants which are exposed to the air may be stressed by high temperatures when air temperature is higher than water temperature. Biebl and McRoy (1971) reported that photosynthesis of Z. marina from Alaska declined sharply above 30°C and that leaves died after 12 h exposure at 34°C. Similarly, H. tasmanica photosynthesis declined sharply between 30 and 35°C, with an irrevocable loss of net photosynthetic capacity after 5 min exposure to 40°C (Bulthuis, 1983a). Maximum water temperature at Edwards Point during the present study was 35°C in December and air temperatures in Melbourne occasionally exceeded 40°C during the summer. When such days coincide with spring low tides, exposed H. tasmanica, even with a thin film of water, will be severely stressed. Penhale (1977) reports the only other study in which the maximum standing crop of a temperate seagrass occurred at any season other than summer. In that study, Z. marina in North Carolina had a maximum biomass in March (early spring) and declined during the remainder of the year. Like the present study, Penhale suggested that high temperature and exposure stress may have been responsible for the unusual seasonal pattern and the decline during summer.

The standing crop of Z. marina, the most widely studied temperate seagrass, fluctuates seasonally with maxima generally during the summer and minima during the winter (Conover, 1958; McRoy, 1966; Phillips, 1972; Riggs and Fralick, 1975; Sand-Jensen, 1975; Thayer et al., 1975; Jacobs, 1979; Nienhuis and de Bree, 1980). In the present study, H. tasmanica at the three Western Port sites had a unimodal seasonal pattern of standing crop similar to that observed in Z. marina populations. The monthly means for standing crop of H. tasmanica are within the ranges reported for Z. marina in the reviews by McRoy and McMillan (1977) and Zieman and Wetzel (1980), but maximum standing crop, 286 g dry wt. m⁻², is considerably lower than the maximum reported for Z. marina, >1000 g dry wt. m⁻².

Density

The seasonal trend of shoot density and leaf-cluster density was similar to that observed for leaf standing crop (Table VI). Charing Cross, Spit Point and San Remo had winter minima of about 1400, 1200 and 400 and summer maxima of 4200, 3200 and 2700 leaf clusters m^{-2} , respectively. Edwards Point, as with leaf standing crop, had minima in winter and summer and maxima in spring and autumn (Table VI). This anomolous seasonal pattern of density is probably the result of exposure and temperature stress as has been postulated for the seasonal fluctuations in standing crop.

At the subtidal site, San Remo, almost all shoots were terminated with a single leaf cluster. Only in November to January did 10-30% of the shoots develop more than one leaf cluster, and this was reduced by February

TABLE VI

Density of *H. tasmanica* at four sites in Western Port and Port Phillip Bay from March 1978 to May 1979 (Mean (no.m⁻²) ± 1 s.e.; n = 10; n.a. = not available)

				(ļ
Month	Erect shoot	s			Leaf cluster	ş			I	Advent	itious	shoot	s		ĺ
	Charing Cross	Spit Point	San Remo	Edwards Point	Charing Cross	Spit Point	San Remo	Edward Point	s	Charin _i Cross	g Sp Po	it S int I	lan Remo	Edwai Point	rds
March	1920±280	1330± 94	576±160	2290±570	2800±358	1420±107	640±186	3070±1	020	n.a.	n.a	ı. T	1.8.	n.a.	
April	1700 ± 195	1620 ± 277	938 ± 101	3070 ± 448	2800 ± 302	1730 ± 283	992 ± 112	4580±	558	162± 3	30 78	±38 5	6119	355±1	87
May	1620 ± 128	1230 ± 210	880± 88	1730 ± 267	2480 ± 197	1380 ± 248	960 ± 126	$2240 \pm$	419	275± 7	79 48	±28 3	4±12	314 ±	82
June	1410 ± 142	1180 ± 179	976± 62	1980 ± 154	2080 ± 200	1340 ± 194	1010 ± 61	$2210 \pm$	173	366± 7	72 10	± 5	82±12	41 ±	19
July	1500 ± 210	1340± 58	960±131	n.a.	1970 ± 286	1500± 74	960±134	n.a.		525±15	55 16	÷ 6 1	8±10	n.a.	
August	1680 ± 130	1170±126	672 ± 110	2420 ± 194	2060 ± 147	1200 ± 129	736±131	3010_{\pm}	162	277± 7	71 n.a	л. Т	1.a.	86±	46
September	1900 ± 106	1760 ± 182	832± 99	3010 ± 294	2610 ± 173	2220±227	864±107	3660±	434	272± 7	73 42	±12	6± 3	67±	17
October	1820 ± 264	1950 ± 160	1180 ± 115	2210 ± 224	2740±475	2990±237	1360 ± 142	2960±	240	141± {	32 37	±10 1	.0± 5	50±	19
November	2370 ± 208	1790 ± 149	2050 ± 285	2180 ± 240	4050±344	2660 ± 230	2740 ± 390	3280±	384	134±	34 99	±50 8	\$7±14	4 0±	œ
December	2420 ± 389	1890 ± 130	1780 ± 229	2430 ± 213	4210 ± 662	2560±117	2000 ± 267	2670±	278	[∓66	19 59	±16 8	32± 9	42±	21
January	1660 ± 203	2450±171	2370 ± 203	1900 ± 184	3630 ± 350	3230 ± 275	2670 ± 227	2460±	357	45±]	13 34	80 +	11±5	91±	48
February	1940 ± 235	1980 ± 150	1920 ± 226	3010 ± 298	3460 ± 510	2940±234	2020 ± 253	384 0±	454	106± 2	25 46	±23]	8± 7	10 ±	6
March	1540 ± 198	1410 ± 264	736± 82	3410 ± 454	3730±405	2260±459	784± 88	4980 ±	638	139± 8	36 16	± 7 1	.3± 5	5±	က
April	1410 ± 91	980±174	544± 85	3440 ± 189	3550±282	1410 ± 278	592± 85	4610 ±	379	178± 4	13 5	± 3]	.6± 8	37±	16
May	1570 ± 184	750± 98	960 ± 158	1420 ± 250	2880 ± 336	1040 ± 157	1020 ± 178	1920 ±	344	173± 5	58 2	± 2 3	0±10	91±	21

to less than 5% of the population. Leaf cluster density and shoot density were thus similar (Table VI). At Charing Cross, in contrast, leaf-cluster density was at least 25% higher than shoot density, increased during the spring growth period, and was more than double the shoot density in January (Table VI). At Spit Point the number of shoots with more than one leaf cluster increased markedly from August to October and then slowly decreased (Table VI). Data in Table VI indicate that there was very little seasonal change in the percentage of shoots having more than one leaf cluster at Edwards Point.

Adventitious shoots were most numerous at Charing Cross and had a seasonal minimum in January (summer) and a maximum in July (winter, Table VI). At the other three sites densities were much lower than at Charing Cross and there was no apparent seasonal pattern (Table VI).

At the San Remo site, the shoot and leaf-cluster density and leaf standing crop of *H. tasmanica* were lower than for the other three sites (Tables IV and VI). San Remo was the only subtidal site, and irradiance at the top of the seagrass canopy was lowest at this site (Table III). The lower density and standing crop at San Remo probably resulted from these lower light levels. Numerous workers have suggested that decreased density of seagrasses with depth is due to decreased light levels (Ostenfeld, 1905; Tutin, 1942; Burkholder and Doheny, 1968; Phillips, 1974; Jacobs, 1979; Nienhuis and de Bree, 1980). Backman and Barilotti (1976) reported experimental evidence that decreased irradiance caused decreased density in *Z. marina*. In *H. tasmanica*, density decreased and leaf length increased when experimental screens reduced irradiance (Bulthuis, 1983b). It is suggested from these studies that the lower density and leaf standing crop of *H. tasmanica* at San Remo compared with the other three sites was due to the lower light level at San Remo.

The density of Z. marina fluctuates seasonally with maxima during the summer and minima during the winter (McRoy, 1966; Phillips, 1972; Sand-Jensen, 1975; Jacobs, 1979; Nienhuis and de Bree, 1980) similar to H. tasmanica at the three Western Port sites in the present study (Table VI). Although maximum standing crops for H. tasmanica were considerably lower than for Z. marina (286 compared to 1000 g dry wt. m⁻²), maximum densities for H. tasmanica (3200-5000 leaf clusters m⁻²) are at the top end of the range (150-4600 shoots m⁻²) reported for Z. marina by McRoy and McMillan (1977). Heterozostera tasmanica has shorter and thinner leaves than Z. marina (den Hartog, 1970) so similar densities of leaf clusters in the two species do not have similar standing crops.

Shoot height

The histograms of shoot height (Figs. 3-6) indicate that small shoots (<20 cm tall) were present throughout the year. The shoots <20 cm tall were considered to be a single size-class during counting but, for compara-



Fig. 3. Height of *H. tasmanica* shoots in 10 size classes for 15 months from March 1978 to May 1979 at Charing Cross, Western Port. *Indicates no data available for those size classes.

tive purposes in the histograms, have been equally divided into the 0-10 cm height class and the 10-20 cm height class. Maximum numbers in the <20 size-classes were recorded in winter (August: Charing Cross and Spit Point) and spring (November: San Remo and Edwards Point), but similar peaks in abundance were apparent also in summer (January-February: Edwards Point) and autumn (March: Spit Point, April: San Remo). Because erect stems of *H. tasmanica* become taller with age, the presence of small (<20 cm) erect shoots during all months of the year at all sites indicates that new shoots are produced throughout the year and not only during spring as implied in earlier descriptions of *H. tasmanica* (den Hartog, 1970; Aston, 1973; Cambridge, 1975; Jacobs and Williams, 1980). These authors also reported that erect stems were completely shed in autumn



Fig. 4. Height of *H. tasmanica* shoots in 10 size classes for 15 months from March 1978 to May 1979 at Spit Point, Western Port. *Indicates no data available for those size classes.

and replaced with "winter foliage". In the present study, the density of erect stems decreased during autumn but throughout the winter months tall erect shoots were present (Tables IV and VI, Figs. 3-6). A distinct "winter foliage" was not observed at any of the four study sites. The description of "winter foliage" in these reports is similar to young erect shoots observed in the present study. It is possible that in some areas all stemmed erect shoots of *H. tasmanica* may be shed and that the presence of numerous young shoots may be responsible for the "winter foliage" descriptions.

The histograms of shoot height for Spit Point (Fig. 4) indicate that shorter (20-40 cm, presumably younger) shoots were numerous during early spring (August-October). As these shoots became taller during late spring and summer (November-March), the number of shoots in the taller size-classes (40-70 cm) increased while the number in the shorter size-



Fig. 5. Height of *H. tasmanica* shoots in 10 size classes for 15 months from March 1978 to May 1979 at San Remo, Western Port. *Indicates no data available for those size classes.

classes (20-40 cm) decreased (Fig. 4). Apart from the <20 cm shoots, the most numerous size classes at Spit Point were 45 cm in January, 55 cm in February and 65 cm in March. During autumn (March-May) shoot density decreased in all size-classes at Spit Point (Fig. 4). A similar seasonal pattern was evident at Charing Cross (Fig. 3) and San Remo (Fig. 5). However, at Edwards Point the taller shoots (>40 cm) declined from September to November and were virtually absent from December to February (Fig. 6). This pattern may be due to temperature and exposure stress during the low spring-tides of summer. It is these taller shoots which most likely would be exposed at low tide and, thus, suffer desiccation stress.

Average shoot height was greater at Spit Point (47 cm) and San Remo (47 cm) than at Charing Cross (35 cm) and Edwards Point (32 cm). This

EDWARDS POINT



Fig. 6. Height of *H. tasmanica* shoots in 10 size classes for 15 months from March 1978 to May 1979 at Edwards Point, Port Phillip Bay. *Indicates no data available for those size classes.

is probably the result of lower light intensity at Spit Point and San Remo compared to the other two sites (Table III). Edwards Point had the lowest average shoot height which, like the summer minima in standing crop and shoot density, may be due to exposure during the low spring-tides of summer.

Leaf growth and productivity

Leaf growth rates at all sites were at a minimum in winter, about 6.5 mm (leaf cluster)⁻¹ day⁻¹ at the three intertidal sites and about 2 times greater at the subtidal site, San Remo (Table VII). Rates increased 2-4 times during spring and were at a maximum during the summer months.

TABLE VII

Leaf growth rate and productivity of *H. tasmanica* at four study sites in Western Port and Port Phillip Bay from April 1978 to May 1979

Month	Leaf grow (mm leaf	vth rate cluster⁻¹ da	ay ⁻¹)		Leaf pro (g dry w	ductiv t. m ⁻²	vity day ⁻¹)	
	Charing Cross	Spit Point	San Remo	Edwards Point	Charing Cross	Spit Point	San Remo	Edwards Point
April	10.4±1.8	17.1±1.6	23.5±3.4	14.1±0.5	1.26	1.26	1.29	2.61
May	12.4 ± 0.3	9.2±2.0	22.4±4.3	11.3 ± 1.2	1.34	0.55	0.95	1.02
June	6.5±0.3	6.3±1.5	13.8 ± 2.2	6.8±0.5	0.58	0.37	0.62	0.77
July	6.2±1.6	9.1±1.6	13.7 ± 1.1	n.a.	0.52	0.60	0.57	
August	6.5 ± 0.4	12.3±1.2	18.4±1.4	10.5 ± 0.6	0.58	0.64	0.60	1.27
September	5.6	11.4 ± 0.4	15.0±0.8	9.2±2.0	0.38	1.11	0.57	1.36
October	10.0 ± 0.9	16.4 ± 5.1	18.2±0.1	12.4 ± 2.2	1.18	2.13	0.89	1.48
November	15.2±1.8	31.2	14.0 ± 2.3	13.8	2.65	3.62	2.04	1.53
December	19.7±1.6	29.2 ± 3.1	14.3±0.7	19.4 ± 3.2	3.58	3.24	1.27	2.09
January	18.3±1.5	26.1 ± 2.6	22.2±3.8	19.1±0.8	2.41	3.67	2.63	1.91
February	15.6±1.0	19.6±2.7	28.2 ± 2.0	22.7±0.7	2.32	2.51	2.52	3.52
March	19.1±1.0	20.8±2.0	18.9±3.8	20.8 ± 3.1	3.07	2.04	0.65	4.19
April	5.2±0.6	9.1±5.4	13.2 ± 2.6	7.6±1.4	0.80	0.56	0.34	1.41
May	6.8±0.8	14.0 ± 1.8	24.1 ± 1.8	11.9±2.2	0.85	0.64	1.10	0.92

(Mean ± 1 s.e. of leaf growth rate; n = 3 stations at which 5-16 plants were measured)

Maximum rates varied from 19.7 at Charing Cross to 31.2 at Spit Point. At Edwards Point the leaf growth rate per leaf cluster was similar to the other three sites. This was in contrast to the seasonal pattern of standing crop and density in which Edwards Point differed markedly from the other three sites. This implies that the factor(s) which caused the decrease of standing crop and density during summer at Edwards Point did not also cause a decrease in growth rate of the surviving leaf clusters. The data are thus consistent with the hypothesis that density and standing crop at Edwards Point decreased during summer due to desiccation during spring low tides. Shoots, especially shorter shoots, which survived the low tides would be expected to have normal leaf growth rates per (surviving) leaf cluster.

Leaf dry weight per cm of leaf length was consistent throughout the study and the means at all sites were similar, from 40.4 to 44.4 μ g cm⁻¹; so this parameter appears to be a relatively constant value for *H. tasmanica* in Western Port and Port Phillip Bay.

The leaf dry weight (g cm⁻¹) was multiplied by the leaf growth rate (cm leaf cluster⁻¹ day⁻¹) and the leaf cluster density (no. m⁻²) in order to estimate the mean productivity of leaf dry weight each month. At all sites there was a pronounced seasonal trend (Table VII). Minimum rates (0.38, 0.37, 0.34 and 0.77 g m⁻² day⁻¹ at Charing Cross, Spit Point, San

Remo and Edwards Point, respectively) occurred during the autumn and winter months (April-July). Rates increased 5–10 times to summer maxima of 3.6, 3.7, 2.6 and 4.2 g m⁻² day⁻¹. At Charing Cross, Spit Point and San Remo, rates increased rapidly in spring and by November were at least 5 times the winter minima (Table VII). These rates were maintained throughout the summer months. However, at Edwards Point, decreasing density during summer and increasing growth rates per leaf cluster caused peak productivity to occur during February and March (Tables VI and VII). This was followed by a rapid decline during late autumn (April-May) as both density and leaf growth rate declined.

Maximum leaf productivity measured in other seagrasses was 6-14 g dry wt. m⁻² day⁻¹ for Thalassia testudinum Banks ex König (Patriquin, 1973; Zieman, 1975; Greenway, 1976; Thorhaug and Roessler, 1977), 5.5 g m⁻² day⁻¹ for *Posidonia australis* (West and Larkum, 1979), and 7.0, 3.0 and 12.0 in the three studies of Z. marina (Sand-Jensen, 1975; Jacobs, 1979; Nienhuis and de Bree, 1980). In the present study, the maximum monthly mean for H. tasmanica (4.2 g m⁻² day⁻¹) is within the range of maxima reported for Z. marina, but considerably less than the 12.0 reported by Nienhuis and de Bree (1980). The seasonal pattern of leaf growth rate of H. tasmanica, a unimodal curve with the maximum in summer and minimum in winter (Table VII) was also similar to that reported for Z. marina and P. australis (Sand-Jensen, 1975; Jacobs, 1979; Nienhuis and de Bree, 1980; West and Larkum, 1979). This curve reflects seasonal curves for total insolation and it has been suggested for Z. marina, therefore, that light controls the seasonal pattern of leaf production (Sand-Jensen, 1975; Jacobs, 1979). Although light may be an important factor in determining seasonal leaf production of H. tasmanica, other factors also appear to be important. This is particularly evident in autumn when leaf productivity during April was less than one-third the productivity during March at the three intertidal sites (Table VII). This reflected decreases in density (Table VI) and leaf growth rate (Table VII) that were much greater than the reduction in total insolation.

The seasonal pattern of leaf productivity is a function of both leaf growth rate and leaf cluster density. Because both of these parameters were highest during summer in the present study, a high proportion of the annual production of *H. tasmanica* occurred from October to March (78% at Charing Cross, 81% at Spit Point, 90% at San Remo, and 68% at Edwards Point). However, even during the winter months, there was considerable leaf productivity, 0.4-0.7 g dry wt. m⁻² day⁻¹.

Annual leaf production at each site was estimated for the period from June 1978 to May 1979 by multiplying the daily productivity times the number of days for each month and summing the monthly totals (Table VIII). This was similar to the method used by Sand-Jensen (1975) and Jacobs (1979). Annual leaf production was similar at the three intertidal sites (568-645 g dry wt. m⁻² year⁻¹). The lower leaf production at San

Remo is probably the result of the lower total insolation at this subtidal site. Despite minima of density and leaf dry weight during mid-summer at Edwards Point, annual leaf production was similar to the other intertidal sites. At Edwards Point, relatively lower leaf productivity during summer was compensated by relatively higher leaf productivity during winter.

TABLE VIII

Annual leaf production of H. tasmanica at four study sites in Western Port and Port Phillip Bay from June 1978 to May 1979

Site	Production		
	Dry weight (g m ⁻² year ⁻¹)	Organic weight (g m ^{- 2} year ⁻¹)	
Charing Cross	568	431	
Spit Point	634	477	
San Remo	414	333	
Edwards Point	645	508	

TABLE IX

Annual leaf production of three extra-tropical seagrass species in g dry wt. m⁻²

Species	Annual leaf production	Location	Source
Zostera marina	856	Denmark — Vellerup Vig — subtidal	Sand-Jensen, 1975
	788	France — Roscoff — intertidal	Jacobs, 1979
	407	The Netherlands — Lake Grevelingen — not tidal	Nienhuis and de Bree, 1980
Posidonia			
australis	582	New South Wales — Botany Bay — subtidal	West and Larkum, 1979
	1170	New South Wales — Jervis Bay — subtidal	West and Larkum, 1979
Heterozostera			
tasmanica	616	Victoria — Western Port and Port Phillip Bay — intertidal sites	This study
	414	Victoria — Western Port — subtidal site	This study

The annual leaf production of *H. tasmanica* is within the range reported for *Z. marina* and *P. australis* (Table IX). Leaf production was an estimated 69-88% of total production (including roots and rhizomes) in *Z. marina* (Sand-Jensen, 1975; Jacobs, 1979; Nienhuis and de Bree, 1980). If leaf production of *H. tasmanica* is a similar proportion of total production, then *H. tasmanica* has an annual productivity of about 725 g dry wt. m^{-2} , 560 g ash-free dry weight m^{-2} (Table V) or 220-260 g carbon m^{-2} (using 0.39-0.46 g carbon (g ash-free dry wt.)⁻¹, Westlake, 1965; Nienhuis and de Bree, 1980).

Leaf characteristics

Length and width of leaves of *H. tasmanica* at each of the four sites did not change seasonally during the 15 months of the present study. Leaves from Charing Cross were shorter and narrower than leaves from the other three sites and leaves from San Remo were longer and wider (Table X). Mean leaf area per leaf generally increased between the four sites as ambient light decreased (Tables III and X). The mean length and width data were combined with the mean number of leaves per leaf cluster and the leafcluster density to estimate leaf area index (m^2 of leaf area per m^2 of bottom surface area). The leaf area index (LAI) fluctuated seasonally, primarily reflecting changes in leaf-cluster density. The minimum LAIs (1.0– 1.8) occurred during winter and the maximum LAIs (5.1–5.9) occurred during summer (Table X).

Leaf area index reported for various species of seagrasses ranges from 0.8 to 21 (Gessner and Hammer, 1960; Gessner, 1971; Drew and Jupp, 1976; McRoy and McMillan, 1977; West and Larkum, 1979). For Z. marina, Phillips (1972) reported values of 1-4 in Puget Sound, Jacobs (1979) reported an annual range of 4-9.5 in Roscoff, France, and Dennison and

TABLE X

Length and width of leaves of *H. tasmanica* at four study sites in Western Port and Port Phillip Bay collected throughout the year. Means in mm ± 1 s.e.; n = 10 monthly means from August 1978 to May 1979. Each monthly site-mean is based on 4-7 plants. Means not significantly (P > 0.01) different from each other by the Student-Newman-Keuls multiple comparison test have the same superscript letter. The range for leaf area index (LAI; m² leaf m⁻² bottom surface) is based on annual minimum and maximum density of *H. tasmanica* leaf clusters at each site

Site	Length (mm)	Width (mm)		LAI range	
Charing Cross Edwards Point Spit Point San Remo	$115^{a} \pm 3.2 \\ 143^{b} \pm 4.4 \\ 170^{c} \pm 5.1 \\ 176^{c} \pm 5.0$	1.45 ^a 1.50 ^{a,b} 1.54 ^b 1.81 ^c	± 0.015 ± 0.023 ± 0.018 ± 0.024	$1.7-5.1 \\ 1.2-5.9 \\ 1.0-5.4 \\ 1.8-5.2$	-

McRoy (1980) reported a range of 2–17 along a depth transect in Alaska. Heterozostera tasmanica ranged from 1.0 to 5.9 at the four study sites in the present study. Kain et al. (1975) suggested that LAI (or Frond Area Index) for Laminaria hyperborea (Gunnerus) Foslie would decrease logarithmically with depth and presented preliminary evidence to support this. Similarly, Dennison and McRoy (1980) reported changes to LAI with depth for Z. marina, maximum LAI occurring at "intermediate depths". In the present study, LAI was similar at all sites (Table X) even though the San Remo site was 2.5-3.0 m deeper than the other sites (Table I) and light intensity was 0.2-0.5 times the level at the other sites (Table III). Drew and Jupp (1976) also found no correlation between LAI and depth for Posidonia oceanica (L.) Delile from 5 to 35 m.

Each leaf cluster produced a new leaf at intervals (plastochrone intervals) ranging from 7.4-33 days (Table XI). At all sites the plastochrone intervals were highest during autumn and winter with maximum values of 23, 33, 20 and 20 days at Charing Cross, Spit Point, San Remo and Edwards Point, respectively. Minimum plastochrone intervals at the four sites during summer were all between 7.4 to 7.7 days. The seasonal pattern was similar at all sites although at San Remo the pattern was less pronounced than at the other sites (Table XI). During the twelve months from June 1978 to May 1979 an average leaf cluster at any one of the sites produced 30-31 leaves. *Zostera marina*, the only other temperate seagrass for which similar data are available, had plastochrone intervals of 8-14 days during summer with winter maxima of 28 days (Sand-Jensen, 1975; Jacobs, 1979; Mukai et al., 1979; Nienhuis and de Bree, 1980).

The number of leaves in each leaf cluster was similar at all sites. Means during spring and summer (September-February: 5.7-6.9 leaves per leaf cluster) were significantly (P < 0.05) higher than during autumn and winter (March-August: 3.9-5.3 leaves per leaf cluster). The average number of leaves per leaf cluster each month was multiplied by the rate of new leaves produced per cluster (plastochrone interval) each month to estimate the "leaf life-span", i.e., the average number of days between emergence of a new leaf and its being shed by abscission at the junction with the leaf sheath (Table XI). The greater plastochrone interval during winter was offset by the generally lower number of leaves in each leaf cluster during winter so that calculated leaf life-span did not exhibit as pronounced seasonal trends as did the plastochrone interval. Minimum leaf life-spans generally occurred during summer and varied from 40 to 54 days at the four sites. Maximum leaf life-spans during autumn and winter varied from 95 to 144 days. Annual mean leaf life-spans were 77, 79, 72 and 65 days at Charing Cross, Spit Point, San Remo and Edwards Point, respectively. In a review of leaf morphology and anatomy in seagrasses Tomlinson (1980) stated "A consideration of mechanisms of leaf loss brings up the topic of leaf age, which is so important in productivity studies. However, apart from the pioneering work of Patriquin (1973) and Zieman (1975), which

TABLE XI

Plastochrone interval, leaf life span and leaf turnover of *H. tasmanica* at four sites in Western Port and Port Phillip Bay from April 1978 to May 1979. Mean ± 1 s.e. of plastochrone interval (n = 3 stations at which 5--16 plants were measured)

Mean ± 1 s.	e. of plas	tochr	one	interval (n = 3 stati	ons at wi	Dich 5	-16 pla	nts were m	easured)			
Month	Plastoch (days)	rone	inter	val		Leaf life (days)	span			Leaf turr (percent.	lover day	· (1	
	Charing Cross	Spit Poin	t	San Remo	Edwards Point	Charing Cross	Spit Point	San Remo	Edwards Point	Charing Cross	Spit Point	San Remo	Edwards Point
April	15 ± 1.4	14±	0.6	12 ± 1.3	15±1.6	53	54	61	71	1.9	1.9	1.6	1.4
May	15 ± 1.9	$22\pm$	5.6	12±1.5	16 ± 0.8	65	66	67	68	1.5	1.0	1.5	1.5
June	20 ± 0.2	28±	5.1	18±0.9	20 ± 1.1	105	144	98	86	1.0	0.7	1.0	1.2
July	20 ± 2.2	1 8±	1.8	16 ± 0.2	n.a.	104	94	92		1.0	1.1	1.1	
August	17 ± 1.6	16 ±	0.2	14±1.1	16 ± 0.6	103	94	81	68	1.0	1.1	1.2	1.5
September	16	15±	1.6	15 ± 1.5	16 ± 4.9	96	102	06	64	1.0	1.0	1.1	1.6
October	10 ± 0.7	10±	0.2	10 ± 1.6	14 ± 3.6	62	64	56	95	1.6	1.6	1.8	1.1
November	9±0.8	2		12 ± 1.2	12	66	60	66	65	1.5	1.7	1.5	1.5
December	8±0.7	+ 8	0.3	10 ± 0.3	8±0.4	60	67	64	49	1.7	1.5	1.6	2.0
January	8±0.4	8+	0.3	8±0.5	8±0.6	52	55	52	40	1.9	1.8	1.9	2.5
February	9±0.9	10±	1.2	8±0.8	8±0.4	53	67	50	53	1.9	1.5	2.0	1.9
March	8±0.2	1 0±	1.2	10 ± 0.9	9±0.5	48	65	60	44	2.1	1.5	1.7	2.3
April	22 ± 2.4	33±]	3	17 ± 2.4	17 ± 0.7	77	126	91	83	1.3	0.8	1.1	1.2
May	23 ± 1.0	17 ±	1.0	10 ± 0.8	17±1.4	98	74	58	73	1.0	1.4	1.7	1.4

suggests an average life span of thirty to forty days for *Thalassia* leaves, there are too few data to permit generalisation". In addition to the work on *T. testudinum* mentioned above, leaf life-span of *Z. marina* has been estimated as 68, 44 and 56 days by Jacobs (1979), Mukai et al. (1979) and Sand-Jensen (1975), respectively. Based on these limited data, *H. tasmanica* appears to have a longer leaf life-span (annual means: 65–79 days) than the tropical seagrass *T. testudinum* (30–40 days) and similar to the temperate seagrass *Z. marina* ("growing season" means: 44–56 days, annual mean: 68 days).

Leaf turnover was calculated as the reciprocal of leaf life-span and expressed as percentage change in leaf biomass per day (Table XI). Leaf turnover was at a minimum during winter; for example, at Charing Cross it took more than 4 months from June to September to replace one crop of leaves. During November to March, it took about 2 months to replace a crop of leaves. The patterns were similar at Spit Point and San Remo. At Edwards Point the low leaf standing crop during summer coincided with high leaf productivity, resulting in high turnover rates during summer. Mean leaf turnover rates of *H. tasmanica* were 1.4, 1.3, 1.5 and 1.7% day⁻¹ (i.e., 5.1, 4.7, 5.5 and 6.2 crops of leaves produced per year) at Charing Cross, Spit Point, San Remo and Edwards Point, respectively. Similar turnover rates have been reported for *Z. marina* by Jacobs (1979) (monthly range: 1.2-1.8% day⁻¹, mean: 1.5% day⁻¹) and Sand-Jensen (1975) (mean: 1.8% day⁻¹) while lower turnover rates were reported for *P. australis* by West and Larkum (1979) (means: 0.8-1.1% day⁻¹).

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REFERENCES

- Aston, H.I., 1973. Aquatic Plants of Australia. Melbourne University Press, Melbourne, 368 pp.
- Backman, T.W. and Barilotti, D.C., 1976. Irradiance reduction: effects on standing crops of the eelgrass Zostera marina in a coastal lagoon. Mar. Biol., 34: 33-40.
- Biebl, R. and McRoy, C.P., 1971. Plasmatic resistance and rate of respiration and photosynthesis of Zostera marina at different salinities and temperatures. Mar. Biol., 8: 48-56.

Bulthuis, D.A., 1981. Distribution and summer standing crop of seagrasses and macroalgae in Western Port, Victoria. Proc. R. Soc. Victoria, 92: 107-112.

- Bulthuis, D.A., 1983a. Effects of temperature on the photosynthesis—irradiance curve of the Australian seagrass, *Heterozostera tasmanica*. Mar. Biol. Lett., 4: 47-87.
- Bulthuis, D.A., 1983b. Effects of in situ light reduction on density and growth of the seagrass Heterozostera tasmanica (Martens ex Aschers.) den Hartog in Western Port, Victoria, Australia. J. Exp. Mar. Biol. Ecol., 67: 91-103.
- Bulthuis, D.A. and Woelkerling, W.J., 1981. Effects of in situ nitrogen and phosphorus enrichment of the sediments on the seagrass *Heterozostera tasmanica* (Martens ex Aschers.) den Hartog in Western Port, Victoria, Australia. J. Exp. Mar. Biol. Ecol., 53:193-207.
- Burkholder, P.R. and Doheny, T.E., 1968. The biology of eelgrass. Dept. Conservation and Waterways, Town of Hempstead, Long Island, New York, 120 pp.
- Cambridge, M.L., 1975. Seagrasses of south-western Australia with special reference to the ecology of *Posidonia australis* Hook. f. in a polluted environment. Aquat. Bot., 1: 149-161.
- Conover, J.T., 1958. Seasonal growth of benthic marine plants as related to environmental factors in an estuary, Publ. Inst. Mar. Sci. Univ. Tex., 5: 97-147.
- Den Hartog, C., 1970. The Sea-Grasses of the World. North-Holland, Amsterdam, 275 pp.
- Dennison, W.C. and McRoy, C.P., 1980. Light adaptations by Zostera meadows in Izembek Lagoon, Alaska. Abstracts 2nd Winter Meeting Am. Soc. Limnol. Oceanogr., Seattle, Washington, U.S.A.
- Drew, E.A. and Jupp, B.P., 1976. Some aspects of the growth of *Posidonia oceanica* in Malta. In: E.A. Drew, J.N. Lythgoe and J.D. Woods (Editors), Underwater Research. Academic Press, London, pp. 357-367.
- Gessner, F., 1971. The water economy of the seagrass Thalassia testudinum. Mar. Biol., 10: 258-260.
- Gessner, F. and Hammer, L., 1960. Die Primärproduktion in mediterranen Caulerpa-Cymodocea-Wiesen. Bot. Mar., 2: 157-163.
- Greenway, M., 1976. The grazing of *Thalassia testudinum* in Kingston Harbor, Jamaica. Aquat. Bot., 2: 117-126.
- Harris, J.E., Hinwood, J.B., Marsden, M.A.H. and Sternberg, R.W., 1979. Water movements, sediment transport and deposition, Western Port, Victoria. Mar. Geol., 30: 131-161.
- Jackson, M.L., 1958. Soil chemical analysis. Prentice-Hall, Englewood Cliffs, New Jersey, pp. 214-217.
- Jacobs, R.P.W.M., 1979. Distribution and aspects of the production and biomass of eelgrass, Zostera marina L., at Roscoff, France. Aquat. Bot., 7: 151-172.
- Jacobs, S.W.L. and Williams, A., 1980. Notes on the genus Zostera in New South Wales, Australia. Telopea, 1: 451-456.
- Kain, J.M., Drew, E.A. and Jupp, B.P., 1975. Light and ecology of Laminaria hyperborea.
 II. In: G.C. Evans, R. Bainbridge and O. Rackham (Editors), Light as an Ecological Factor II. Blackwell, Oxford, pp. 63-92.
- Kershaw, K.A., 1973. Quantitative and Dynamic Plant Ecology. 2nd edn., Elsevier, New York, 308 pp.
- Kirkman, H. and Reid, D.D., 1979. A study of the role of the seagrass *Posidonia australis* in the carbon budget of an estuary. Aquat. Bot., 7: 173–183.
- Kirkman, H., Cook, I.H. and Reid, D.D., 1982. Biomass and growth of Zostera capricorni Aschers. in Port Hacking, N.S.W., Australia. Aquat. Bot., 7: 173-183.
- Koroleff, F., 1972. Determination of reactive silicate. In: S. Carlberg (Editor), New Baltic Manual. I.C.E.S., Charlottenlung Slot, Denmark, pp. 79-86.
- McRoy, C.P., 1966. The standing stock and ecology of eelgrass, Zostera marina, in Izembek Lagoon, Alaska. M.Sc. Thesis, University of Washington, 138 pp.
- McRoy, C.P., 1970. Standing stocks and other features of eelgrass (Zostera marina) populations on the coast of Alaska. J. Fish. Res. Board Can., 27: 1811-1821.

- McRoy, C.P. and McMillan, C., 1977. Production ecology and physiology of seagrasses. In: C.P. McRoy and C. Helfferich (Editors), Seagrass Ecosystems. Dekker, New York, pp. 53-87.
- Mukai, H., Aioi, K., Koike, I., Iizumi, H., Ohtsu, M. and Hattori, A., 1979. Growth and organic production of eelgrass (*Zostera marina* L.) in temperate waters of the Pacific Coast of Japan. I. Growth analysis in spring—summer. Aquat. Bot., 7: 47-56.
- Nienhuis, P.H. and de Bree, B.H.H., 1980. Production and growth dynamics of eelgrass (*Zostera marina*) in brackish Lake Grevelingen (The Netherlands). Neth. J. Sea Res., 14: 102-118.
- Ostenfeld, C.H., 1905. Preliminary remarks on the distribution and biology of the Zostera of the Danish seas. Bot. Tidsskr., 27: 123-125.
- Patriquin, D.G., 1973. Estimation of growth rate, production and age of the marine angiosperm Thalassia testudinum König. Caribb. J. Sci., 13: 111-121.
- Penhale, P.A., 1977. Macrophyte—epiphyte biomass and productivity in an eelgrass (Zostera marina L.) community. J. Exp. Mar. Biol. Ecol., 26: 211-224.
- Phillips, R.C., 1972. Ecological life history of Zostera marina L. (eelgrass) in Puget Sound, Washington, Ph.D. Thesis, University of Washington, 154 pp.
- Phillips, R.C., 1974. Temperate grass flats. In: H.T. Odum, B.J. Copeland and E.A. McMahan (Editors), Coastal Ecological Systems of the United States. Conservation Foundation, Washington, DC, pp. 244-299.
- Riggs, S.A., Jr. and Fralick, R.A., 1975. Zostera marina L., its growth and distribution in the Great Bay Estuary, New Hampshire. Rhodora, 77: 456-466.
- Sand-Jensen, K., 1975. Biomass, net production and growth dynamics in an eelgrass (Zostera marina L.) population in Vellerup Vig, Denmark. Ophelia, 14: 185-201.
- Strickland, J.D.H. and Parsons, T.R., 1972. A Practical Handbook of Seawater Analysis, 2nd edn., Fish. Res. Board Can. Bull. 167, Ottawa, 310 pp.
- Thayer, G.W., Adams, S.M. and LaCroix, M.W., 1975. Structural and functional aspects of a recently established Zostera marina community. In: L.E. Cronin (Editor), Estuarine Research Vol. 1 Chemistry, Biology and the Estuarine System. Academic Press, New York, pp. 518-540.
- Thorhaug, A. and Roessler, M.A., 1977. Seagrass community dynamics in a subtropical estuarine lagoon. Aquaculture, 12: 253-277.
- Tomlinson, P.B., 1974. Vegetative morphology and meristem dependence the foundation of productivity in seagrasses. Aquaculture, 4: 107-130.
- Tomlinson, P.B., 1980. Leaf morphology and anatomy in seagrasses. In: R.C. Phillips and C.P. McRoy (Editors), Handbook of Seagrass Biology: An Ecosystem Perspective. Garlands STPM, New York, pp. 7-28.
- Tutin, T.G., 1942. Zostera. J. Ecol., 30: 217-226.
- West, R.J. and Larkum, A.W.D., 1979. Leaf productivity of the seagrass, *Posidonia* australis, in eastern Australian waters. Aquat. Bot., 7: 57–65.
- Westlake, D.F., 1963. Comparisons of plant productivity. Biol. Rev., 38: 385-425.
- Westlake, D.F., 1965. Some basic data for investigations of the productivity of aquatic macrophytes. In: C.R. Goldman (Editor), Primary Productivity in Aquatic Environments. Ist. Ital. Idrobiol., 18 Suppl., pp. 227-248.
- Zieman, J.C., 1975. Quantitative and dynamic aspects of the ecology of turtle grass. *Thalassia testudinum*. In: L.E. Cronin (Editor), Estuarine Research. Vol. 1. Chemistry, Biology, and the Estuarine System. Academic Press, New York, pp. 541-562.
- Zieman, J.C. and Wetzel, R.G., 1980. Productivity in seagrasses: methods and rates. In: R.C. Phillips and C.P. McRoy (Editors), Handbook of Seagrass Biology: An Ecosystem Perpective. Garlands STPM, New York, pp. 87-116.