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ANNE-MAREE SCHWARZ[1],[*]

IAN HAWES[1],[*]

WENDY NELSON[2]

NEIL ANDREW[2],[†]

[1]National Institute of Water and Atmospheric
  Research Limited
P.O. Box 11 115
Hamilton, New Zealand
email: a.schwarz@cgiar.org

[2]National Institute of Water and Atmospheric
  Research Limited
P.O. Box 14 901
Wellington, New Zealand.

[*]Present address: The WorldFish Center, P.O. Box 77, Gizo, Western Province, Solomon Islands.

[†]Present address: The WorldFish Center, P.O. Box 500, GPO, Penang, Malaysia.

Abstract   A field study of *Lessonia variegata* growing in depths of 8–10 m on the south coast of Wellington, New Zealand investigated morphometric and biomass indices measured on destructively harvested entire algae, rates of blade elongation measured *in situ* using a blade hole punch technique, and timing of fertility over a 2-year period. Blade fertility was estimated using a fertility score based on the visual appearance of the reproductive tissue. *Lessonia variegata* attained a maximum length of 154 cm, a density of 0.8 to 2.1 individuals m^{-2}, and developed an areal biomass ranging from 1700 to 6000 g fresh weight (FW) m^{-2}. The highest proportion of fertile blades (up to 100% of sampled blades) occurred during winter and the end of the fertile period coincided with the onset of the longer days and warmer temperatures of summer. Blade elongation occurred more rapidly in summer months (0.117 cm day^{-1}, SE = 0.015)

than winter months (0.041 cm day^{-1}, SE = 0.009). The slower winter blade elongation rate meant that growth could not overcome tip ablation and average blade length reduced from 51.5 cm (SE = 1.9) to 30.8 cm (SE = 1.7) between March and September 2003. Average blade length increased again over the following summer months to 40.7 cm (SE = 1.6). Blade biomass dominated total fresh weight biomass (average 64% of total). Two parameters that are relatively easily measured on live macroalgae *in situ*, holdfast diameter and girth of all stipes collectively, predicted total biomass with an $r^2 = 0.91$, suggesting these could be useful tools for assessment of this potentially harvestable resource on Wellington's south coast.

INTRODUCTION

Thick beds of the laminarian kelp *Lessonia variegata* J. Agardh, endemic to New Zealand, are conspicuous components of rocky reefs along some of the country's most exposed shorelines (Choat & Schiel 1982). *Lessonia variegata* is found from the upper subtidal zone to 15–20 m depth, particularly from the central North Island southward to Stewart Island (Adams 1994). Laminariales are highly productive in temperate waters (Lobban & Harrison 1994) and provide structural habitat, allowing the settlement and development of a range of invertebrates and fish (Dayton 1985; Vasquez 1992; Lobban & Harrison 1994). Through fragmentation of the distal portions of the blades of living algae, most species of Laminariales, including *Lessonia* spp. (Tala & Edding 2005) provide a source of particulate and dissolved organic material for consumption by higher trophic levels (Mann 1988). *Lessonia* spp. are engineer species in the ecosystem (after Jones et al. 1994) supporting numerous associated species of invertebrates and fish (Vasquez & Santelices 1984; Villouta & Santelices 1984).

Despite some kelp beds being dominated by *L. variegata* (Schiel 1990), the exposed shorelines on which it is usually found mean that there has been little study effort on this complex habitat structuring kelp in New Zealand. This is significant, as recently there has been increased interest in New Zealand in the commercial use of *L. variegata* for bioactive compounds and to feed farmed *Haliotis* spp. (Nelson 2004). As a consequence, and despite the absence of basic information on growth and biomass dynamics, the macroalga is expected to be introduced into New Zealand's quota management system for commercial fisheries (Ministry of Fisheries 2004). In Chile, *Lessonia* spp. are already extensively harvested as beach cast and from natural beds (Edding & Tala 2003) and this, as well as population fluctuations as a result of ENSO events (Martínez et al. 2003), has resulted in attempts to develop management techniques for over-harvested natural beds (Vasquez & Tala 1995; Fonck et al. 1998).

The first goal of this investigation was to determine whether consistent relationships between readily measurable morphometrics and biomass could be developed to allow population structure and resource status to be assessed. *Lessonia* comprises three main parts: a holdfast, stipes, and long strap-like blades (Edding et al. 1994). Morphometric relationships between parts have been devised to estimate biomass of individuals from simply measured variables for some kelp taxa (e.g., Choat & Schiel 1982; Gagné & Mann 1987), including *Lessonia trabeculata* in Chile (Villouta & Santelices 1986). However, Camus & Ojeda (1992) noted that morphometric parameters for *L. trabeculata* can change markedly between sites and recommended against transferring relationships from one location to another. Macroalgal abundance can also vary greatly among localities along a coastline (Schiel & Foster 1986; Buschmann et al. 2004). Although abundance may appear to be correlated with obvious local environmental factors, the effects of small-scale habitat differences on population structure are not so immediately obvious. Currently we are not aware of any analyses from New Zealand *L. variegata* populations for which generalisations about morphometric relationships or other scale-dependant characteristics can be made.

The second goal of this research was to provide information on the seasonal aspects of growth of *Lessonia* in New Zealand. The life cycle of the Laminariales includes alternation of phases between the macroscopic sporophyte and microscopic gametophytes. In temperate and cold regions, timing of growth and reproduction can occur at different times of the year and at different intensities depending on environmental conditions at each locality (Kain 1989; Santelices 1990). In New Zealand, sufficient winter irradiance can support macroalgal growth year round, throughout the country, depending on nutrient availability (Brown et al. 1997) and other laminarian taxa such as *Ecklonia radiata* (Novaczek 1984; Schiel 1988) have been shown to exhibit peak fertility in winter.

In a recent study, the first to identify optimal conditions for growth of *L. variegata* gametophytes and early sporophyte development, Nelson (2004) showed that *L. variegata* exhibited higher values of gametogenesis at warmer (15°C) than colder (10°C) temperatures and under longer (15h) than shorter days (i.e., summer conditions), and were able to respond rapidly to shifts in environmental conditions at the end of winter, resulting in rapid growth of sporophytes.

We report on a field study of *L. variegata* growing within one depth stratum on the south coast of Wellington, New Zealand that aimed to identify morphometric indices for *L. variegata* to assist with census of populations *in situ*. In addition, we describe seasonal patterns in growth as measured by blade elongation and seasonal patterns in fertility.

MATERIALS AND METHODS

Study site

The study was conducted over a 2-year period between March 2003 and March 2005. All field work was carried out on the south coast of Wellington, New Zealand. Three replicate sites, each c. 2 km apart, were originally delineated: Red Rocks (41°21.430′S, 174°43.739′E); Quarry (41°21.098′S, 174°44.394′E), and Island Bay (41°21.143′S, 174°46.307′E). All sites were characterised by *L. variegata* as the dominant canopy species, and were exposed to the south. All sampling was carried out using SCUBA at a water depth of 8–10 m.

Incident total daily radiation (MJ) was sourced from Wallaceville weather station E1510G (NIWA data), c. 40 km north of the study sites, and a continuous surface water temperature data set was obtained from NIWA's Mahanga Bay facility within Wellington Harbour.

Morphometry

At the start of the study in March 2003, two 5m × 5m plots immediately adjacent to each other were delineated, using sub-surface marker buoys at each

corner of the plot, at each of the three sites. A rope was temporarily laid between the corner markers of one plot at each site, and within this plot, all individuals of *L. variegata* were destructively harvested by SCUBA divers removing the holdfast from the rock with a metal lever. Algae were maintained damp, and returned to the laboratory within 2 h. In the laboratory, each individual was weighed (± 1.0 g) to obtain total fresh weight (FW) and the maximum length (± 1.0 cm) from holdfast to longest blade was measured.

After all algae had been measured, 20 individuals from each plot were sub-sampled, aiming to encompass the full range of sizes for analysis in greater detail. On each of these, girth was measured by firmly pulling a flexible measuring tape around all stipes collectively and recording the circumference (± 1.0 cm). This measurement was made midway between the highest haptera and the blade meristems. Each alga was then separated into holdfast, stipes and blades, which were weighed separately to obtain FW (± 0.1 g). The basal diameter of the holdfast was measured (± 1.0 cm) and the total number of blades on each alga counted. The length of five blades from each alga (meristem to tip) was measured (± 1.0 cm) and each of these blades was oven dried at 60°C to constant weight to obtain a FW to dry weight (DW) ratio. The morphometric sampling was repeated at one new 5 m × 5 m plot delineated at one site (Red Rocks), 1 year later in April 2004.

Blade elongation

In March 2003, within the remaining plot at each site, 20 mature individuals with a minimum stipe girth of 13 cm (previously determined to equate to >1000 g FW) were haphazardly chosen and one blade on each was tagged at the base of the stipe for identification. A 5 mm diameter hole was made in the blade using a hole punch, centrally and at a distance of 10 and 20 cm above the meristem to follow the growth of blades using the method of Parke (1948).

On five further occasions over the following year as many blades as possible were relocated at each site. On each relocated blade the distance from meristem to punched hole was re-measured. Although attempts were made to maintain a sample size of 20 at each site by tagging, measuring, and punching new blades, unfavourable weather conditions and a persistent swell meant that re-location of the marked blades was often difficult, and some blades were lost during storm events. The total blade length was not always able to be recorded, precluding statistically robust estimates of erosion rates from the distal ends of

the blade on a regular basis. To obtain a sufficient sample size for calculating mean elongation rates, data from all replicates from all three sites were pooled for the final analysis. In addition, because of the irregularity of our ability to access the sites for growth measurements, at times the 20 cm hole had been lost through blade fragmentation at the distal end. All elongation rates have therefore been based solely on changes between the meristem and the 10 cm hole and have been calculated over five time intervals between 17 March 2003 and 22 April 2004.

In accordance with Tala & Edding (2005), meristematic growth expressed as elongation rate (cm day^{-1}) and representing the gross growth of the blade, was calculated from the initial blade length + hole displacement (cm) (for each individual blade) to obtain expected length over the measurement period (days) if no tissue damage occurred.

To transform gross growth in length units to biomass units (g day^{-1}) in year 2 (April 2004 – March 2005) estimates of average blade biomass were refined by measuring the distribution of weight along blades (Mann & Kirkman 1981; Tala & Edding 2005). On four occasions (April and August 2004, January and March 2005) a total of 20 replicate blades were collected by SCUBA divers from at least three algae, from each site. Each blade was photographed using a digital camera (see fertility estimates below) before being cut into 10-cm pieces starting at the meristem, and dried at 60°C to constant weight. DW distribution was visualised by plotting the weights of the sections along the length of the blade (Tala & Edding 2005).

Blade growth as biomass and therefore maximum expected biomass accumulation in the absence of tissue loss was estimated by multiplying elongation rates in cm by the biomass in g cm^{-1} within the zone in which the hole occurred (10–20 cm from the meristem). The blades on which growth was measured were not the same ones on which biomass distribution were measured. Hence the value for growth rate over each measurement interval was factored by average biomass estimated from blades collected in August 2004 for growth measurements between April and September 2003 and blades collected in March 2005 for growth measurements made between October 2003 and April 2004.

Fertility

Approximately every 2 months over the 2-year period, depending on the ability to access sites, one mature blade from each of the first 10 *L. variegata* individuals encountered within the 5 m × 5 m plot
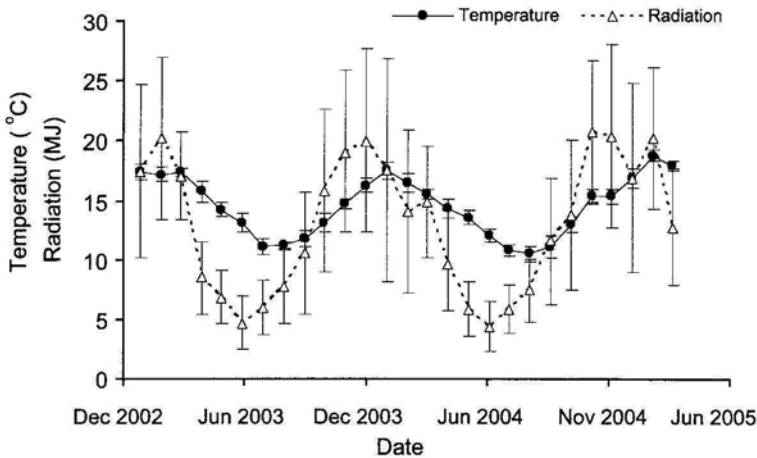
Fig. 1 Monthly mean (± SD) of daily water temperatures (°C) from Mahanga Bay, inside Wellington Harbour, New Zealand and monthly mean (± SD) of daily solar radiation (MJ) from Wallaceville north of Wellington, between January 2003 and March 2005.

at each site, was collected by SCUBA divers and returned to the laboratory for scoring the degree of fertility. Blade length and width were measured and a fertility score was devised based on the visual appearance of the reproductive tissue. The scores ranged from 0 to 5 where 0 = infertile; 1 = light colouring developing; 2 = able to see and feel shape of fertile area; 3 = clear delineation of raised fertile area; 4 = strong coloration of raised area; and 5 = fully fertile, beginning to slough off.

In addition, in year 2, the digital images of the photographed blades were examined using the image analysis programme Image J (public domain Java image processing program). If visibly fertile, the outline of each blade and the fertile material was delineated and their respective areas calculated. The area of blade that was fertile was expressed as a proportion of the total blade area.

Statistical analysis

All statistical analyses were carried out using Statistica for Windows 5.1 (Statsoft, Inc, Tulsa, OK). Morphometric data were examined for normality using the distribution fitting function in Statistica. The distributions of biomass and, to a lesser extent, alga length were skewed towards small algae and so significant differences among sites and between years were determined using the non-parametric Kruskal-Wallis ANOVA by ranks (Kruskal & Wallis 1952).

For the 20-alga subset from each site, all morphometric data were ln-transformed, to meet assumptions of normality and homogeneity of variance, before applying simple linear regression analysis to allow quantitative allometric relationships between total

biomass and other metrics (corresponding biomass of holdfast, stipes and blades, holdfast diameter, girth just above the holdfast, stipe number, total length (TL) and blade number) to be inferred. As weights and lengths showed no significant variation between sites in 2003 and overlapping distributions at the Red Rocks site between years, all of the morphometric data from the 20 sub-sampled individuals were combined. This provided a sufficiently large data set with which to examine biomass allocation to different alga parts and how this varied with alga size as well as relationships between biomass and other morphometric variables. Estimates of exponents (and SE) to allometric relationships were taken as the slopes of ln-ln regressions, and their constants were taken from the intercept after antilogging. To determine the potential for combinations of non-destructive measures to be used as a proxy of biomass, we then used forward stepwise multiple regression of ln-transformed data (Neter et al. 1989), with contributions considered significant at $P < 0.05$. Differences in maximum blade width and blade area among sampling times were analysed using a single factor ANOVA. When a significant difference was found, a Tukey's HSD post hoc test for unequal n was applied (Spjotvoll & Stoline 1973). For all tests, differences were considered significant at $P < 0.05$.

RESULTS

Surface water temperatures at Mahanga Bay in Wellington Harbour reached a winter minimum of 11°C between July and September in both

2003 and 2004 (Fig. 1). In summer 2003/04 temperatures peaked briefly at 18.5°C in January whereas in 2004/05, temperatures continued to rise to a maximum of 20.1°C throughout February. The timing of maximum and minimum temperatures lagged 1–2 months behind the longest and shortest days, respectively. Daylength mirrored patterns in monthly average incident solar radiation (Fig. 1).

In March 2003, density of *L. variegata* ranged from 0.8 individuals m^{-2} at Island Bay to 2.1 m^{-2} at Red Rocks, equating to an average biomass within the three 5m × 5m plots of 1700–6000 g FW m^{-2}. Individual biomass ranged from 17 to 9100 g (FW) for algae from all sites (Table 1). The distribution of biomass was strongly skewed towards small algae, with a median for all sites of 2239 g, somewhat less than the mean of 2736 g (Table 1). Although there were more large, heavier individuals at Red Rocks, there were no significant differences between the median biomass among the three sites (Kruskal-Wallis test: $H_2 = 2.07$, $n = 60$, $P = 0.35$). The distributions of lengths were much less skewed than biomass. Algae were, on average, 95 ± 5 cm tall in March 2003 (Table 1) with a median length of 100 cm. There were no significant differences between sites in 2003 (Kruskal-Wallis test: $H_2 = 3.96$, $n = 11$, $P = 0.14$). In April 2004, the measurements were repeated at Red Rocks site, and individual biomass and alga length showed similar and overlapping distributions to that seen in 2003 (Table 1).

The proportions of biomass allocated to holdfast, stipes, and blades from the 20 sub-sampled individuals appeared to be independent of alga size. Strong relationships between total biomass and biomass of holdfast, stipes and blades were established by regression of ln-transformed variables. Exponents of all relationships were close to 1 (Table 2), implying that a similar ratio by weight in the three major compartments persisted throughout the growth of the algae. Analysis of the residuals of these relationships showed no significant effect of individual size, though there was a tendency for smaller algae to allocate more biomass to holdfasts at the expense of stipes. Table 2 also indicates how blades made up the greatest proportion of biomass (constant = 1.5 compared to 6.3 for holdfasts and 12.1 for stipes), typically 60–70% (average 64%).

To determine whether the increase in total blade biomass as individuals increased in size was a result of increased numbers or of larger blades, we determined the relationships between total number and total biomass of blades (Fig. 2). A linear relationship of blade biomass = $2.61 \times NB^{1.12 \pm 0.04}$ ($r^2 = 0.93$; d.f. = 78, $F = 1000$, $P < 0.0001$) was established from ln-ln regression, where NB is number of blades. Again, the close proximity of the exponent in this relationship to 1 (1.12 ± 0.04) suggests that blades tended to be of unit size, regardless of the size of the alga, with a tendency for blades to get slightly larger in bigger individuals.

Regression analysis of all ln-transformed data from 20 sub-sampled individuals from each of the four sites ($n = 80$) showed close correspondence between total biomass and all morphological parameters (Table 2). Although each of these individual metrics, including both destructive and non-destructive, provided reasonable estimates of biomass, with r^2

Table 1 Maximum length (cm) and biomass (g fresh weight) of algae collected from three sites: Island Bay (IB); Red Rocks (RR); Quarry (Q) off of the south coast of Wellington, New Zealand in March 2003 and from RR in April 2004. Values from all sites combined for both years are also shown. Confidence limits (CL) not calculated for biomass.

| Year	Metric	n	Mean ± 95% CL	Median (inter quartile range)	Min.	Max.
2003	Length (IB)	22	87.3 ± 12	91 (64–108)	39.5	125
2003	Length (RR)	56	100.4 ± 7	102 (87–117)	33	154
2003	Length (Q)	35	91± 9	98 (83–108)	25	127
2003	Length (all sites)	113	95 ± 5	100 (82–112)	25	154
2004	Length (RR)	21	72 ± 7.8	74.5 (69–83)	27	95
2003/04	Length (all sites)	134	91.2 ± 5	95 (78–108)	25	154
2003	Biomass (IB)	22	1940	1766 (285–2726)	40	8100
2003	Biomass (RR)	56	2954	2550 (1030–4100)	127	9100
2003	Biomass (Q)	36	2884	2100 (723–5000)	17	8000
2003	Biomass (all sites)	114	2736	2239 (846–4000)	17	9100
2004	Biomass (RR)	21	2152	1800 (603–3100)	22	7200
2003/04	Biomass (all sites)	135	2641	2200 (823–3827)	17	9100
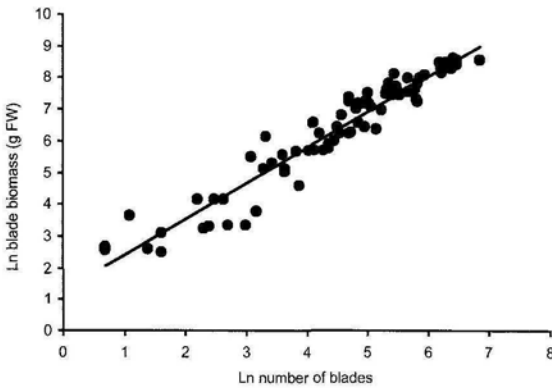
Fig. 2 Number of blades per *Lessonia variegata* alga versus biomass (g fresh weight (FW)) of all blades per alga from three sites: Island Bay; Red Rocks; Quarry off the south coast of Wellington, New Zealand in March 2003 and from Red Rocks in April 2004.

> 0.7 in each instance (Table 2), predictions using non-destructive methods could be improved when these were used in combination. Stepwise multiple regression of these data found that stipe number was the least useful metric for predicting whole plant biomass, but showed that holdfast diameter and girth, combined with total length and blade number increased r^2 to 0.98 (Table 2). However, during data collection it was noted that counting the number of blades was time consuming, so we undertook a

further multiple regression to determine the effect of removing this measure on the relationship in Table 2. We found that a highly significant relationship remained such that:

$$TB = 0.02 \times TL^{1.41\pm0.15} \times GH^{0.98\pm0.13} \times HD^{0.62\pm0.16}$$
$$(r^2 = 0.97) \tag{1}$$

where TB is total biomass, TL is total length, GH is girth just above holdfast, and HD is holdfast diameter. Finally, given that maximum length was also difficult for a single diver to measure except when seas were calm, we examined the effect of removing this measure from the multiple regression. We found that:

$$TB = 1.67 \times GH^{1.39\pm0.18} \times HD^{0.87\pm0.22} \tag{2}$$
$$(r^2 = 0.93)$$

Blade elongation rates estimated from hole punches decreased from 0.069 cm day^{-1} between March and April 2003 (autumn) to 0.041 cm day^{-1} in September 2003 (Fig. 3). Between September and January (spring/summer) rates increased to 0.117 cm day^{-1} and had decreased only marginally from this value when the final measurements were made in April 2004. In the first 6 months of measurements over autumn and winter, average blade length reduced from 51.5 cm (SE = 1.9) (expected length 56 cm) to 30.8 cm (SE = 1.7) (expected length 37 cm) (Fig. 3), whereas over spring and summer, between October 2003 and April 2004, blade length increased again from an average of 31.9 cm to 40.7 cm (Fig. 3).

Table 2 Relationships between total individual algal biomass (TB) and the corresponding biomass of holdfast (HB), biomass of stipes (SB), biomass of blades (BB), holdfast diameter (HD), girth just above the holdfast (GH), stipe number (SN), total length (TL), and blade number (BN) derived from ln-ln regression for 20 individual alga sub-sampled from each of three sites: Island Bay; Red Rocks; Quarry, Wellington, New Zealand. Result of a forward stepwise multiple regression using the non-destructive metrics (BN, TL, GH, HD) is included. Data set used includes all three sites sampled in 2003 and the single site sampled in 2004.

Relationship (± SE)	r^2	d.f.	F	P
$TB = 6.3 \times HB^{0.98\pm0.02}$	0.96	79	1857	<0.001
$TB = 12.1 \times SB^{0.87\pm0.02}$	0.97	79	2561	<0.001
$TB = 1.5 \times BB^{1.00\pm0.01}$	0.99	79	8838	<0.001
$TB = 0.08 \times HD^{2.48\pm0.11}$	0.86	78	474	<0.001
$TB = 3.38 \times GH^{2.03\pm0.07}$	0.91	78	803	<0.001
$TB = 34.46 \times SN^{1.61\pm0.11}$	0.72	78	209	<0.001
$TB = 0.0001 \times TL^{3.66\pm0.20}$	0.81	77	331	<0.001
$TB = 5.47 \times BN^{1.14\pm0.03}$	0.95	77	1409	<0.001
$TB = 0.12 \times BN^{0.49\pm0.06} \times TL^{0.98\pm0.12} \times GH^{0.23\pm0.05} \times HD^{0.36\pm0.12}$				
	0.98	73	1033	<0.001

Fig. 3 Mean (± SE) of blade tissue elongation rates from the meristem (open circles) measured on mature *Lessonia variegata* individuals *in situ* between March 2003 – April 2004 (number of blades recovered on each occasion is shown in parentheses), and blade length (closed circles) from meristem to the tip of the blade for algae collected either for fertility estimates or for blade biomass measurements in the subsequent year (August 2004 – March 2005, *n* = 90). Data from all sites have been pooled.
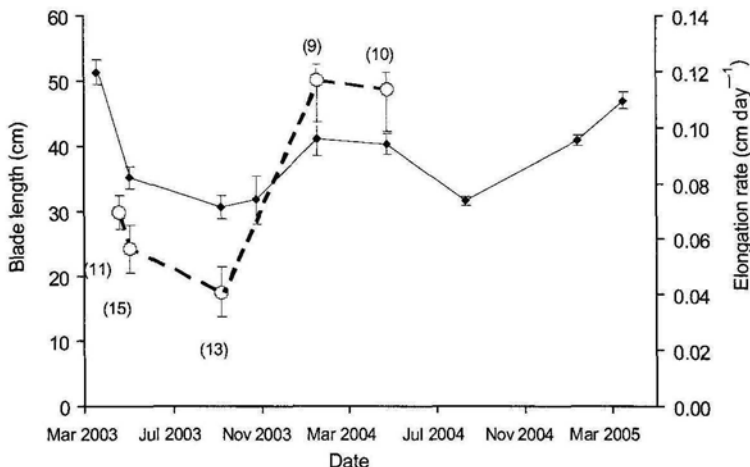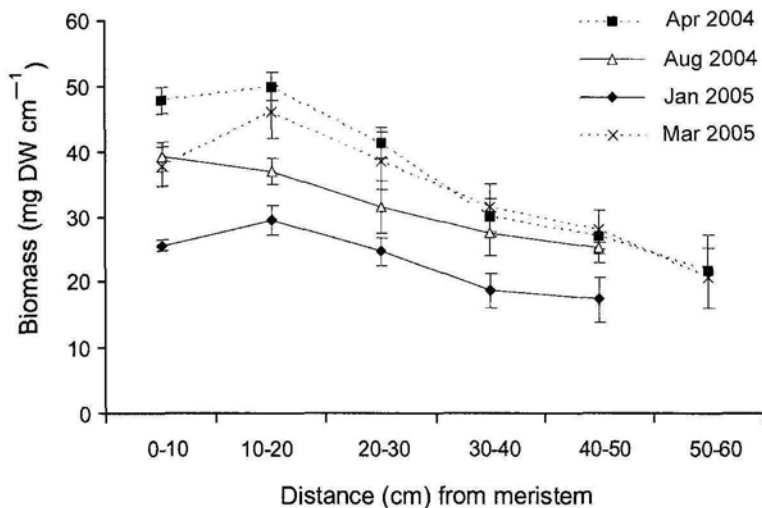
Fig. 4 Distribution of biomass (mean ± SE) along individual *Lessonia variegata* blades on four occasions between April 2004 and March 2005. Sixty blades were sampled on each occasion.

Individual blade biomass decreased progressively along the blade with a maximum biomass occurring within 20 cm of the meristem and a minimum at the eroding tip of the blade (Fig. 4). Average blade biomass was significantly different between samplings (ANOVA, $F = 31.6$, d.f. = 3, 236, $P < 0.001$) with blades being on average heavier at the end of summer (April 2004 and March 2005) compared to winter and midsummer sampling (August 2004 and January 2005). When blade elongation rates were factored by biomass (10–20 cm from the meristem), biomass gain per blade ranged from a minimum of 1.03 mg DW blade^{-1} day^{-1} (SE = 0.23) between May and September 2003 to 5.4 mg DW blade^{-1} day^{-1} (SE = 0.53) between January and April 2004.

A consistent seasonal pattern in the timing and degree of fertility was evident over the 2 years of the study. The highest proportion of blades had a fertility score of 3 or greater during winter months, between April and September (Fig. 5). In September 2003 and August 2004, between 84 and 100% of blades at each of the three sites had a fertility score of 5. No fertile blades were collected at any of the three sites in the months of January 2004, or January or March 2005 (Fig. 5).

Maximum blade width ranged from an average of 2.70 to 3.57 cm over the sampling period (Table 3) and on average blades were slightly, but significantly, narrower in January and March 2005 than in April and August 2004 (ANOVA, $F = 7.11$, d.f. = 3, 298,
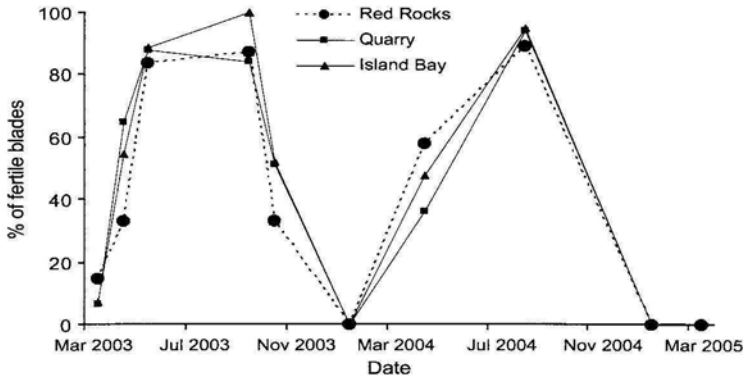
Fig. 5 Percentage of fertile *Lessonia variegata* blades (score ≥ 3, $n = 20$) at each of the three study sites between March 2003 and March 2005.

Table 3 Mean (SD in parentheses) of blade width, blade area, and fertility area estimates in April 2004 ($n = 25$), August 2004 ($n = 15$), January 2005 ($n = 30$), and March 2005 ($n = 30$).

Site	Month	Max. blade width (cm)	Blade area (cm^2)	% blade area fertile
Red Rocks	April	3.57 (0.44)	110.64 (21.64)	12.18 (6.95)
	August	3.25 (0.81)	98.06 (45.04)	12.32 (8.02)
	January	2.88 (0.56)	119.62 (37.25)	0
	March	3.37 (0.93)	167.06 (42.20)	0
Quarry	April	3.41 (0.58)	132.89 (51.47)	9.93 (6.17)
	August	3.12 (0.69)	81.91 (30.66)	14.27 (8.81)
	January	3.02 (0.63)	106.76 (35.99)	0
	March	3.37 (0.63)	189.87 (50.98)	0
Island Bay	April	3.57 (1.14)	135.68 (60.97)	8.29 (5.22)
	August	3.35 (0.50)	84.28 (26.20)	16.01 (6.77)
	January	2.99 (0.06)	142.82 (30.03)	0
	March	2.70 (0.43)	94.25 (43.60)	0

$P < 0.05$). Blade area was significantly less in August 2004 than in the other months (ANOVA, $F = 24.34$, d.f. = 3, 298, $P < 0.05$), coincident with the time of maximum fertility. At that time up to 16% of the blade area comprised fertile tissue (Table 3).

DISCUSSION

As with many of the Laminariales (Lobban 1987; Kain 1989; van Tussenbroek 1989), growth and fertility of *L. variegata* on Wellington's south coast exhibited marked seasonal patterns over the period of this study, with blade elongation being highest in summer. Growth of *L. variegata* (as measured by blade elongation) occurred more rapidly in summer than winter months and this, coupled with greater blade weight per unit area in summer and possibly higher rates of tip erosion in winter (see estimates

below), combined to produce summer blade biomass and length maxima. In contrast to patterns observed for both *L. nigrescens* and *L. trabeculata* in Chile (Tala & Edding 2005), there was no evidence for *L. variegata* being a season anticipator and within the resolution of our data, maximum elongation rates appeared to be maintained throughout the summer period. The time series of data collection was not long enough to elucidate possible reasons for the higher elongation rate in autumn 2004 compared with autumn 2003, nor can the influence of pooling data from the three sites, thereby possibly under-representing the error estimates on each value (*sensu* Hurlbert 1984), be discounted.

Elongation rates for blades of *L. variegata* measured in this study were lower than the 0.17 to 0.65 cm day^{-1} measured for subtidal *L. trabeculata* in Chile (Tala & Edding 2005) and the 2.0 cm day^{-1} measured for *Macrocystis pyrifera* in New

Zealand (Brown et al. 1997). Apart from likely inherent differences between species, a multitude of environmental factors that can limit kelp growth rates (Hurd 2000) must be considered to begin to explain such differences. We have not attempted to isolate the influence of individual environmental factors. Moreover our data may not be sufficiently temporally resolved to be able to pick effects such as summer reductions in elongation that may result from, for example, nutrient limitation (Brown et al. 1997). Nevertheless, similar to the conclusion by Brown et al. (1997) for *M. pyrifera* at the latitude of Otago Harbour, it appears that environmental conditions for *L. variegata* on the south coast of Wellington were suitable for some growth, all year round, and that elongation occurred faster in summer than winter months.

Given the paucity of available data for *L. variegata* in New Zealand, we have made an order of magnitude estimation for the potential biomass export as a result of erosion of the distal ends of the blades over the study period. For each of the five periods within which blade elongation was measured, average final blade length was subtracted from the average expected length (note there is no error value on this estimate as final blade length measurements were made on different blades to those measured for growth). The difference between these values was assumed to be the length of blade lost through erosion and was estimated to range from a maximum of 0.291 cm day^{-1} between March and May 2003 to a minimum of 0.009 cm day^{-1} between October 2003 and January 2004. When factored by average biomass within the distal 10 cm of the blade, 0.79 g DW blade^{-1} was estimated to have been lost between March 2003 and April 2004. According to biomass gains per blade calculated earlier, this equates to a loss of c. 60% of new biomass accumulated over the same period. If net loss is factored by the median number of blades per alga (128) and the maximum measured density of *L. variegata* (2.1 individuals m^{-2}) the resultant value suggests that there is in the order of 212 g DW or 1090 g FW of blade biomass m^{-2} being supplied to the ecosystem by *L. variegata* every year.

The pattern of maximum growth in spring–summer and maximum reproduction in autumn–winter for *L. variegata* on Wellington's south coast concurs with Tala et al.'s (2004) observation that patterns observed in morphological and reproductive characteristics of *L. trabeculata* in Chile were similar to a seasonal pattern of cold temperate algae (Kain 1989; Lüning 1990). In contrast to *L. trabeculata*, *L. variegata* blades did not exhibit reproductive tissue throughout the year, and in the months of December and January (mid summer) no fertile blades were noted in the samples. The timing of maximum reproductive capacity of the Chilean species was, however, similar, with the highest number of fertile blades being recorded in autumn months (Tala et al. 2004). The occurrence of maximum fertility in winter for *L. variegata* is consistent with sporulation occurring in spring/early summer and with Nelson's (2004) findings of a rapid growth of sporophytes being favoured after the end of winter, coincident with an increase in ambient water temperatures. The combination of warmer temperatures and longer days occurring between November and April (Fig. 1), immediately followed the timing of peak fertility (Fig. 5).

In this study, blade biomass dominated total biomass and was in turn largely determined by the number of blades per individual. Morphometric analysis was only undertaken in summer, when the blades were heaviest, therefore the relationships developed are unlikely to apply equally well in winter. Nevertheless, girth and holdfast diameter both provided reasonable estimates of biomass and a combination of the two provided an even better estimate. This suggests that once a maximum length of 154 cm was attained, further increases in biomass were determined by increases in the number of blades, and owing to the bifurcating branching habit of *L. variegata*, so both number and size of stipes (and hence girth). Likewise, increasing number of blades will lead to an increase in drag (Denny et al. 1997) and an increase in area of holdfast to increase strength of attachment follows (e.g., Duggins et al. 2003), although this may not necessarily be a 1:1 relationship (Wernberg 2005).

Camus & Ojeda (1992) found that for individuals of *L. trabeculata* taken from two different zones along the Chilean coast, biomass and holdfast diameter also showed a strong relationship. In their study, the relative importance of holdfast diameter and the number of stipes in explaining variance for biomass predictions varied according to site; algal biomass was better predicted by holdfast diameter in central Chile but by number of stipes in the south.

In setting up this research programme we were mindful that *L. variegata* is likely to become an exploited resource. Ensuring sustainable harvesting necessitates being able to quantify the resource in the first instance (Kirkman & Kendrick 1997) as well as understanding key controls on the population structure and development. The goals that we put forward at

the beginning of this paper related to identifying the seasonality of growth and establishing methods for stock assessment using non-destructive methods. To this end we have shown that *L. variegata* shows very similar seasonal growth and fertility patterns to most other laminarians, and we have developed simple relationships for estimating biomass from holdfast diameter, girth or maximum alga length, either individually or collectively. These metrics need to be combined with estimates of density to ascertain areal biomass and we acknowledge that at a larger spatial scale (100's km) the same relationships may not hold, for example when *L. variegata* occurs in mixed taxa stands, under different nutrient regimes, or at locations with different water motion, depth, or temperature (Dayton 1985; Schiel & Foster 1986). However, we suggest that, in common with the conclusion of Camus & Ojeda (1992) and following Schiel & Foster's (1986) approach, stands from a given geographical area, in this instance a depth zone of 8–10 m on Wellington's south coast, have a recognisable growth pattern and morphology according to the physical and biological factors of that region of coastline.

On the basis of this study the total number of blades provided a good proxy for biomass of a *L. variegata* individual at these sites and could potentially be used for non-destructive stock assessment. However, counting blades *in situ* is time consuming and we suggest that holdfast diameter, alga length and girth can be used as proxies for biomass estimates of populations in defined spatial areas, once the location-specific relationships between these metrics and biomass are established (e.g., Equation 1). In the development of a harvesting management plan, further consideration needs to be given to the practicality of measuring each of these metrics on large numbers of alga *in situ* and we note that the simplest of measures provided good estimates of total plant biomass. Holdfast diameter is likely to be the quickest and most accurate measurement to make *in situ* and this metric alone could account for 86% of the variability in total alga biomass (Table 2), while in combination with stipe girth this could be increased to 93% (Equation 2). A more complete understanding of the relative importance of physical and biological factors determining *L. variegata* individual and areal biomass, consideration of how much of the alga to physically remove during harvest (Vasquez & Santelices 1990), and timing of harvesting in relation to peak fertility, will be crucial to sound management as a harvestable species.

REFERENCES

Adams NM 1994. Seaweeds of New Zealand. Christchurch, Canterbury University Press. 360 p.

Brown MT, Nyman MA, Keogh JA, Chin NK 1997. Seasonal growth of the giant kelp *Macrocystis pyrifera* in New Zealand. Marine Biology 129: 417–424.

Buschmann AH, Vasquez JA, Osorio P, Reyes E, Fílun L, Hernández-González MC, Vega A. 2004. The effect of water movement, temperature and salinity on abundance and reproductive patterns of *Macrocystis* spp. (Phaeophyta) at different latitudes in Chile. Marine Biology 145: 849–862.

Camus PA, Ojeda FP 1992. Scale-dependent variability of density estimates and morphometric relationships in subtidal stands of the kelp *Lessonia trabeculata* in northern and central Chile. Marine Ecology Progress Series 90: 193–200.

Choat JH, Schiel DR 1982. Patterns of distribution and abundance of large brown alga and invertebrate herbivores in subtidal regions of northern New Zealand. Journal of Experimental Marine Biology and Ecology 60: 129–162.

Dayton P 1985. Ecology of the kelp communities. Annual Review of Ecology and Systematics 16: 215–245.

Denny MW, Gaylord BP, Cowan EA 1997. Flow and flexibility II. The roles of size and shape in determining wave forces on the bull kelp *Nereocystis luetkeana*. Journal of Experimental Biology 200: 3165–3183.

Duggins DO, Eckman JE, Siddon CE, Klinger T 2003. Population, morphometric and biomechanical studies of three understory kelps along a hydrodynamic gradient. Marine Ecology Progress Series 265: 57–76.

Edding M, Tala F 2003. Development of techniques for the massive culture of *Lessonia trabeculata* Villouta and Santelices (Paeheophyceae: Laminariales) in Chile. Aquaculture Research 34: 507–515.

Edding M, Fonck E, Machiavello J 1994. *Lessonia.* In: Akatsuka I ed. Biology of economic algae. The Hague, the Netherlands, SPB Academic Publishing. Pp. 407–446.

Fonck E, Venegas M, Tala F, Edding M 1998. Artificial induction of sporulation in *Lessonia* (Phaeophyta, Laminariales). Journal of Applied Phycology 10: 399–403.

Gagné J, Mann K 1987. Evaluation of four models used to estimate kelp productivity from growth measurements. Marine Ecology Progress Series 37: 35–44.

Hurd CL 2000. Water motion, marine macroalgal physiology and production. Journal of Phycology 36: 453–474.

Hurlbert SH 1984. Pseudoreplication and the design of ecological field experiments. Ecological Monographs 54: 187–211.

Jones CG, Lawton JH, Shachak M 1994. Organisms as ecosystem engineers. Oikos 69: 373–386.

Kain J 1989. The seasons in the subtidal. British Phycological Journal 24: 203–215.

Kirkman H, Kendrick G 1997. Ecological significance and commercial harvesting of drifting and beach-cast macroalgae and seagrasses in Australia: a review. Journal of Applied Phycology 9: 311–326.

Kruskal WH, Wallis WA 1952. Use of ranks in one-criterion variance analysis. Journal of the American Statistical Association 47: 583–621.

Lobban CS 1987. The growth and death of the *Macrocystis* sporophyte (Phaeophyceae, Laminariales). Phycologia 17: 196–212.

Lobban C, Harrison P 1994. Seaweeds Ecology and Physiology. New York, Cambridge University Press. 366 p.

Lüning K 1990. Seaweeds: their environment, biogeography and ecophysiology. In: Yarish C, Kirkman H trans. & ed. New York, John Wiley & Sons Inc. 527 p.

Mann KH 1988. Production and use of detritus in various freshwater, estuarine and coastal marine ecosystems. Limnology and Oceanography 33: 910–930.

Mann K, Kirkman H 1981. Biomass method for measuring productivity of *Ecklonia radiata*, with the potential for adaptation to other large brown algae. Australian Journal of Marine and Freshwater Research 32: 297–304.

Martínez EA, Cárdenas L, Pinto R 2003. Recovery and genetic diversity of the intertidal kelp *Lessonia nigrescens* (Phaeophyceae) 20 years after El Niño 1982/83. Journal of Phycology 39: 504–508.

Ministry of Fisheries 2004. Introduction of seaweeds into the quota management system on 1 October 2005. Consultation document. Wellington, Ministry of Fisheries. 72 p.

Nelson WA 2005. Life history and growth in culture of the endemic New Zealand kelp *Lessonia variegata* J. Argardh in response to differing regimes of temperature, photoperiod and light. Journal of Applied Phycology 17: 23–28.

Neter J, Wasserman W, Kutner MH 1989. Applied linear regression models. 2nd ed. Homewood, IL, Irwin. 667 p.

Novaczek I 1984. Development and phenology of *Ecklonia radiata* at two depths in Goat Island Bay, New Zealand. Marine Biology 81: 189–197.

Parke M 1948. Studies of British Laminariaceae. I. Growth in *Laminaria saccharina* (L.) Lamour. Journal of the Marine Biological Association of the United Kingdom 27: 651–709.

Santelices B 1990. Patterns of reproduction, dispersal and recruitment in seaweeds. Oceanography and Marine Biology Annual Review 28: 177–276.

Schiel DR 1988. Algal interactions on shallow subtidal reefs in northern New Zealand: a review. New Zealand Journal of Marine and Freshwater Research 22: 481–489.

Schiel DR 1990. Macroalgal assemblages in New Zealand: structure, interactions and demography. Hydrobiologia 192: 59–76.

Schiel DR, Foster MS 1986. The structure of subtidal algal stands in temperate waters. Oceanography and Marine Biology Annual Review 24: 265–307.

Spjotvoll E, Stoline MR 1973. An extension of the *T*-method of multiple comparison to include the cases with unequal sample sizes. Journal of the American Statistical Association 68: 976–978.

Tala F, Edding M 2005. Growth and tissue loss in blades of *Lessonia nigrescens* and *Lessonia trabeculata* (Laminariales, Phaeophyceae) in northern Chile. Aquatic Botany 82: 39–54.

Tala F, Edding M, Vasquez J 2004. Aspects of the reproductive phenology of *Lessonia trabeculata* (Laminariales: Phaeophyceae) from three populations in northern Chile. New Zealand Journal of Marine and Freshwater Research 38: 255–266.

van Tussenbroek BI 1989. Seasonal growth and composition of fronds of *Macrocystis pyrifera* in the Falkland Islands. Marine Biology 100: 419–430.

Vasquez J 1992. *Lessonia trabeculata*, a subtidal bottom kelp in northern Chile: a case study for a structural and geographical comparison. In: Seegliger U ed. Coastal plant communities of Latin America. New York, Academic Press. Pp. 77–89.

Vasquez J, Santelices B 1984. Comunidades de macroinvertebrados en discos de adhesion de *Lessonia nigrescens* in Chile central. Revista Chilena de Historia Natural 57: 131–154.

Vasquez J, Santelices B 1990. Ecological effects of harvesting *Lessonia* (Laminariales, Phaeophyta) in central Chile. Hydrobiologia 204/205: 41–47.

Vasquez J, Tala F 1995. Repopulation of intertidal areas with *Lessonia nigrescens* in northern Chile. Journal of Applied Phycology 7: 347–349.

Villouta E, Santelices B 1984. Estructura de la comunidad submareal de *Lessonia* (Phaeophyta, Laminariales) en Chile norte y central. Revista Chilena de Historia Natural 57: 111–122.

Villouta E, Santelices B 1986. *Lessonia trabeculata* sp. nov. (Laminariales, Phaeophyta), a new kelp from Chile. Phycologia 25: 81–86.

Wernberg T 2005. Holdfast aggregation in relation to morphology, age, attachment and drag for the kelp *Ecklonia radiata*. Aquatic Botany 82: 168–180.