Estimating biomass of *Macrocystis* in the Hopkins Marine Life Refuge

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INTRODUCTION. *Macrocystis pyrifera* is a foundation species of temperate marine habitats (Dayton 1985). Giant kelp supplies food directly and indirectly to the surrounding community. Grazers and browsers eat the living plant itself while detrivores and suspension feeders consume particulate detritus produced by degradation of kelp tissue (Duggins et al. 1989). *Macrocystis* also modifies the physical environment. Its floating fronds add vertical structure to the water column and provide space for sessile organisms as well as attracting many fish species that would otherwise be absent. Thick surface canopies also dampen water motion and divert currents, providing a more hospitable environment for organisms that might be affected by intense wave action (Jackson and Winat 1983). Because so many subtidal organisms depend on *Macrocystis*, its population status is a good indicator of local biodiversity and overall health of the surrounding marine ecosystem.

Macrocystis plants are very large and have a complex morphology (Figure 1). Each plant grows from a conical hapterous holdfast that secures it to rocky substrates. Many fronds make up a single plant. A frond consists of an elongate rope-like stipe with many blades attached at intervals along its axis. Between each blade and the stipe is a gas-filled float or pneumatocyst, (Jackson et. al 1987). These floats keep the fronds buoyed up in the water column. Not all fronds in one plant are of the same length, some are small and others extend past the surface and form a canopy that spreads out on top of the water.

Macrocystis has a complex pattern of growth. A basal meristem is located at the top of the holdfast and is responsible for the production of new fronds. Within each frond, cell division occurs at the apical meristem as the frond grows toward the surface, buoyed up by its pneumatocysts. Frond elongation rates at Hopkins Marine Station can be rapid, ranging from 2 - 6% day^{-1} depending on conditions (Watanabe, unpubl. data). Once they reach the surface, fronds continue to grow and extend horizontally along the top of the water. Immature blades are at the tip of the frond with mature blades in the center and senescent blades near the bottom. Fronds eventually stop growing and form a terminal blade. Each frond persists for only ~6 months, but whole plants can live 5-7 years. During that time, the basal meristem produces new fronds continuously so a single *Macrocystis* plant is composed of numerous fronds (up to several hundred in the largest plants) of many different sizes.

Growth of *Macrocystis* is seasonal with peak growth occurring in the spring and summer when irradiance is at a maximum. In the winter, rate of frond addition slows and plants often have net loss of fronds as storms remove most of the surface canopy. Thus standing crop biomass is greatest in summer and lowest in winter.

Population estimates of *Macrocystis* usually consist of holdfast densities (number per unit area) and basal frond counts. The large size and rapid turnover of tissue of *Macrocystis* make it difficult to estimate its biomass. Yet biomass estimates are necessary to evaluate general ecosystem function and for management of kelp forests. The objective of our study was to devise a method for estimating standing crop biomass of *Macrocystis* based on holdfast density and basal frond counts.

MATERIALS AND METHODS.

Two quantities are required to estimate the biomass of *Macrocystis*: the typical distribution of frond lengths on an average plant and the relationship between frond length and frond mass. We counted fronds at fixed heights above the holdfast up to the surface and measured lengths of the floating portions of canopy fronds to establish length-frequency distributions. To obtain a length-biomass regression we harvested fronds of varying lengths and returned them to shore for length and mass measurements.

Sampling was conducted in the Hopkins Marine Life Refuge (36°37'N 121°54'W) between depths of 6 and 12 meters. Plants ranged in size from 2 to 44 fronds. *Macrocystis* harvesting and counting occurred during the summer season in Monterey Bay between July 23rd and August 24th 2007. Water temperature was an average of 11.1° C.

Plants were chosen by random compass bearings and number of fin kicks from an arbitrary starting point. The *Macrocystis* plant closest to the random point was then sampled. After the depth of the holdfast was recorded, the fronds were counted just above the sporophylls bundles at the base of the plant. Additional frond counts were taken every 1.5 meters from the holdfast to the surface. Since fronds from adjacent plants often become intermingled near the surface canopy, we looped a piece of line around the bundle of stipes of the target plant and slid it up the plant as we ascended. This ensured that only fronds from the target plant were counted.

To determine the relationship between frond length and biomass, we collected fronds of varying lengths and returned to shore to measure the plants. *Macrocystis* plants were chosen at random using the technique described above. Divers collected four to six fronds from each plant by pulling the stipe down to the seafloor from the surface. Frond length ranged from 0.5 m to 17 m and included both subsurface and canopy fronds. Each frond was placed into a separate mesh bag so that any broken portion would not be lost or confused with other fronds. Once back on shore, the total mass and length of each frond was recorded. Measurements of internode distances were also taken starting at the first unattached blade from the apical blade and taken at every fifth node to the base of the frond. The length and width of the selected blades was also recorded. Larger fronds were weighed to the nearest 100 g using a hanging spring scale. A top loading scale was used for smaller fronds.

RESULTS.

For each of the 21 plants we sampled, frond lengths were converted to a fraction of the holdfast depth and then sorted in five categories: <0.25, 0.25-0.50, 0.50-0.75, 0.75-1.0 and finally canopy. (Fig. 2). For the 21 plants that we sampled, approximately 20% of fronds lie in the bottom .25 of the plant's depth, 15% of the fronds are between .25-.50 of the holdfast depth, 10% are between .50-.75, 15% are between .75-1.0 and 40% are in the floating surface canopy.

We used a similar procedure to partition the lengths of the surface canopy fronds. The total length of each of the 19 canopy fronds was converted to a fraction of the holdfast depth of the plant from which it was sampled (values exceed 1.0 times that depth). We found that 50% of canopy fronds were between 1.0-1.5 of the holdfast depth, 35% of the canopy fronds were between 1.5-2.0 of the holdfast depth, 10% were between 2.0-2.5, and 5% were >2.5 times the holdfast depth (Fig. 3).

The relationship between the natural log of the length (in cm) and natural log of the wet mass (in grams) was not completely linear (Fig. 4). Biomass accumulated at a slower rate between ln(lengths) of ~4.5 and ~5.5 (90 & 245cm) compared to fronds shorter or longer than this range. However, fitting separate regressions to each portion of the length range yielded substantially smaller r^2 values than fitting a single regression to the entire data set. So despite this non-linearity and in the absence of a clearly justifiable alternative model, as a first approximation we fit a linear regression to the entire length range.

The length to biomass regression equation is:

$$\ln(\text{mass}) = 1.291(\pm 0.40)\ \ln(\text{length}) - 1.438(\pm 0.23)$$

($r^2 = 0.927$, $P < 0.001$) where ln is natural logarithm, mass is in grams and length is in centimeters. As expected, the Durbin-Watson *D* value of 1.286 indicates a significant autocorrelation of residuals with ln(length) (Neter & Wasserman 1974, Table A-6). The general alternation of positive residuals at high & low values of ln(length) and negative residuals in between is clearly visible in the residuals plot (Appendix).

Number of nodes and frond length exhibited a somewhat more linear relationship, but with a hint of a sigmoid shape (Fig. 5). The linear regression equation is:

$$\text{No. Nodes} = 0.078(\pm .002)\ \text{Length (cm)} - 8.307(\pm 1.78)$$ ($r^2 = .93$ $P < .001$).

Blades (nodes) are not evenly distributed along the length of a frond, being much closer together near the apex. To compare fronds of differing lengths, we expressed node number and distance from tip as fractions of the totals for each measure (Fig. 6). Roughly half the blades (and therefore biomass) are concentrated in the distal or terminal 15% of the frond's length.

Blade length is roughly proportional to blade area, which is itself proportional to photosynthetic capacity. If blade length is expressed as a fraction of maximum blade length for each frond and plotted against fractional distance from the apex, the relationship is parabolic, indicating that blade size (and therefore photosynthetic capacity) reaches a maximum near the center of the frond (Fig. 6).

DISCUSSION.

The biomass model requires counting fronds at the base of the *Macrocystis* plant and measuring holdfast depth. The average length of all fronds is obtained by summing over each size category and multiplying by holdfast depth.

$$\text{Avg. frond length} = (\text{holdfast depth, cm}) \times \sum^{\text{all sizes}} \begin{pmatrix} \text{fraction} \\ \text{of fronds} \end{pmatrix} \begin{pmatrix} \text{avg. length of size class} \\ \text{as a fraction of depth} \end{pmatrix}$$

Using the observed size distribution of fronds of the 21 plants we sampled and starting with the shortest fronds, the above can be simplified to:

holdfast depth (cm) × [(.2)(.125)+(.15)(.375)+(.10)(.625)+(.15)(.875)+(.4)(.5)(1.25)+(.4)(.35)(1.75)+(.4)(.1)(2.25)+(.4)(.05)(2.75)] = holdfast depth (cm) × 0.915

The length biomass regression is then applied to this average and multiplied by the number of basal fronds to provide an estimate of total plant biomass:

$$\text{total biomass (g)} = \text{total fronds} \times \exp(1.291 \ln[(\text{holdfast depth, cm})(.915)] - 1.438)$$

A final adjustment must be made for the systematic bias introduced by backtransforming an estimated length value obtained from the linear regression of log - log transformed data (see Sprugel 1982 and Baskerville 1972 for details). Each predicted biomass value must be multiplied by $\exp(MS_{\text{residual}} \div 2)$ to remove this bias. In the present case this value is $\exp(0.147 \div 2) = 1.076$ (see regression results in Appendix).

The accuracy of this estimate will vary with plant size. For small plants with fewer than ~10 fronds, biomass will probably be overestimated, since few fronds on plants this small reach the canopy yet. This shortcoming can be remedied by sampling more small plants and treating them separately from larger plants.

A more serious shortcoming is the assumption that the size distribution of fronds remains constant from season to season and from site to site. Clearly this is unrealistic. Our estimate of [.915 × holdfast depth] for the average frond length applies only to the Hopkins kelp forest in Aug. 2007, but should be applicable for summer and early autumn at that site when growth and/or canopy development is at its peak. During winter and early spring there are many fewer canopy fronds, so biomass estimates based on basal frond counts and our model would tend to be too large.

Likewise a cautionary note must be added when applying this model to different sites. Blade size and morphology varies from site to site. Kelp plants at HMLR possess fronds with broader and longer blades at its apical end and thinner lance shaped blades near its base. A location that is more wave exposed probably has different blade morphology and therefore different relationships between frond length and biomass. Fronds growing in deeper water may follow a different length biomass regression. So this model should be applied to plants that are not extremely wave exposed and exist is water depths that average between about six to twelve meters.

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Fig. 1 from: <http://images.google.com/imgres?imgurl=http://content.cdlib.org/xtf/data/13030/86/kt2489n586/figures/caljsiol_sio1ca175_139_013.gif&imgrefurl=http://content.cdlib.org/xtf/view%3FdocId%3Dkt2489n586%26chunk.id%3Dd0e215%26brand%3Dcalisphere%26doc.view%3Dentire_text&h=689&w=768&sz=76&hl=en&start=3&tbnid=iDhEeMA9gPiPhM:&tbnh=127&tbnw=142&prev=/images%3Fq%3Dmacrocystis%2Bpyrifera%2Bmorphology%26svnum%3D10%26hl%3Den>

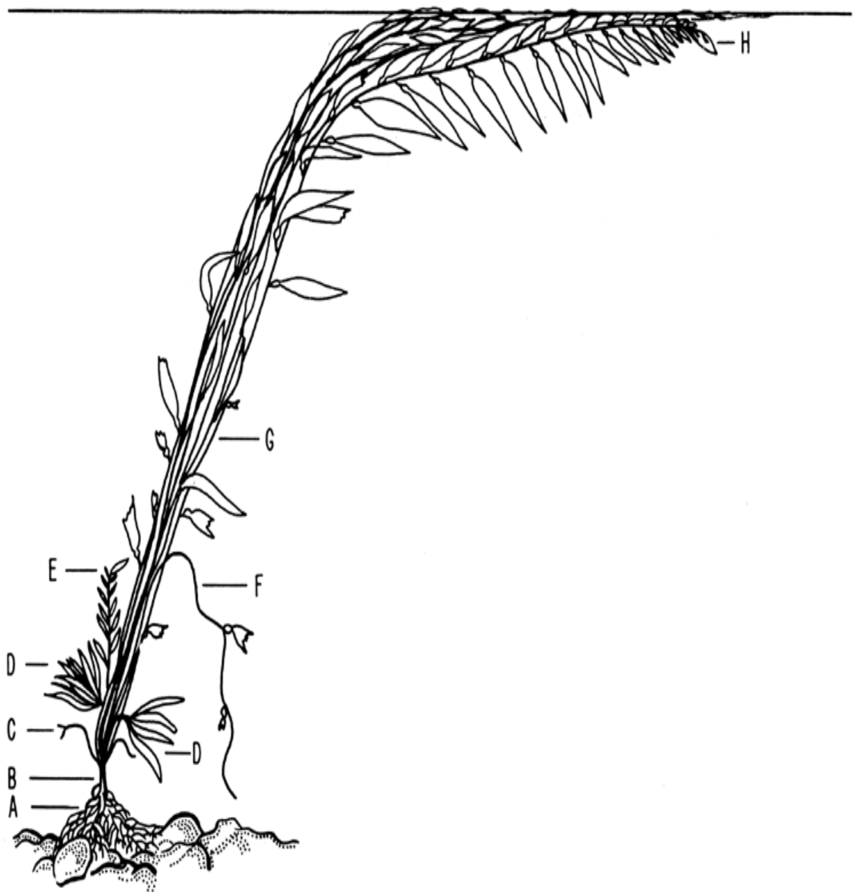

FIGURE 1.

Diagram of the morphology of Macrocystis pyrifera.

A. Holdfast, B. Primary stipe, C. Basal Meristem, D. Sporophyll clusters,

E. juvenile frond, F. Senescent frond, G. Stipe bundle, H. apical blade

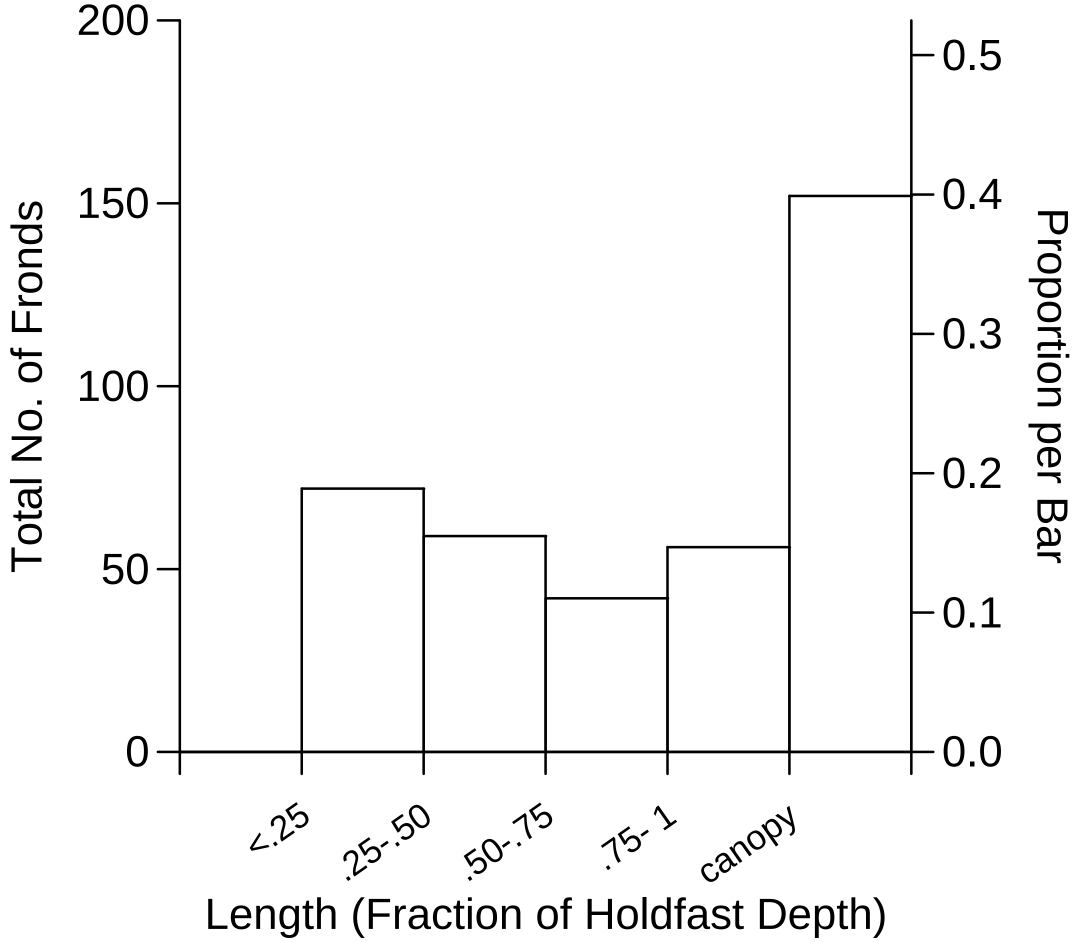

FIGURE 2. Length distribution of subsurface fronds as a percentage of holdfast depth. *n* = 21 plants with basal frond numbers ranging from 2 to 42.

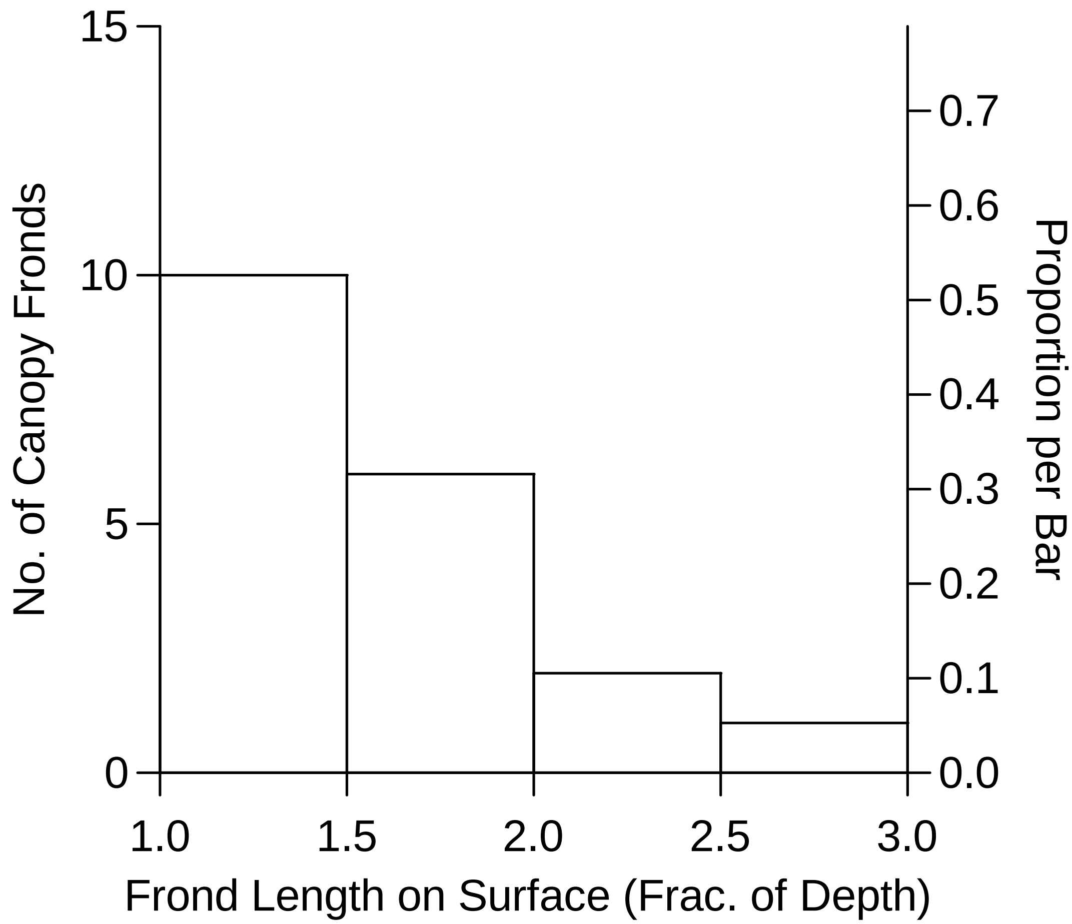

FIGURE 3. Length distribution of canopy fronds as a percentage of holdfast depth. *n* = 19 canopy-length fronds, randomly selected from

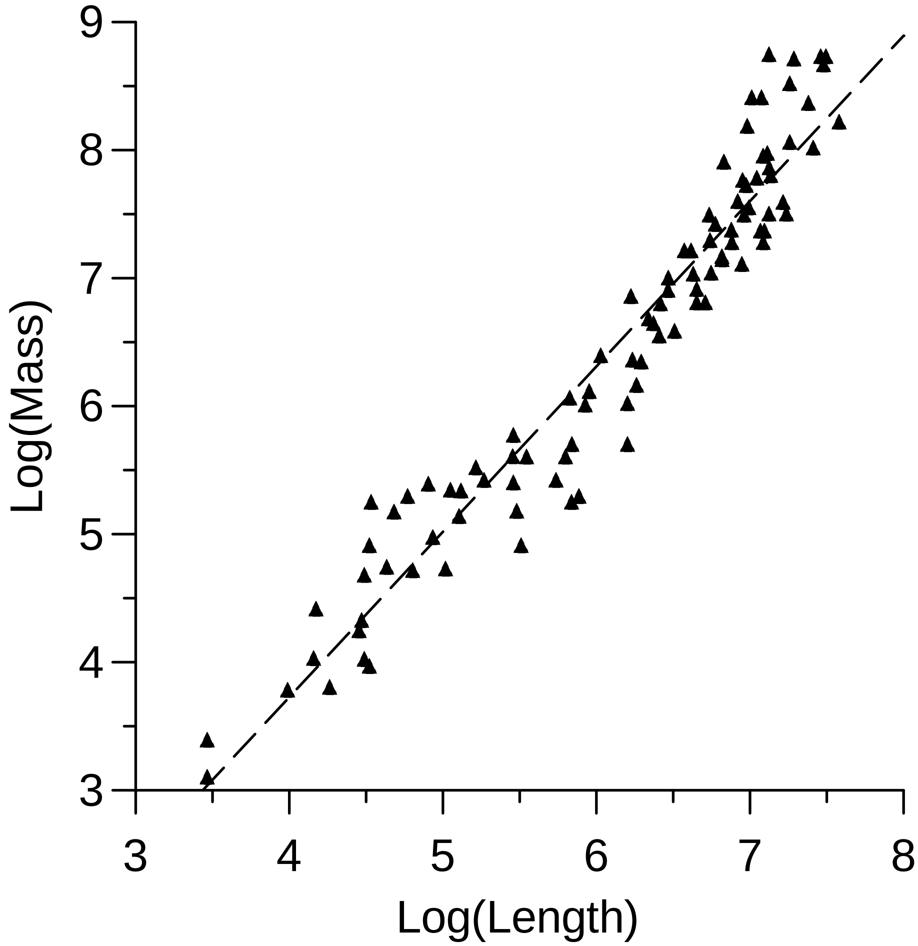

FIGURE 4. Natural Log-Log plot of total mass (g) versus total length (cm)

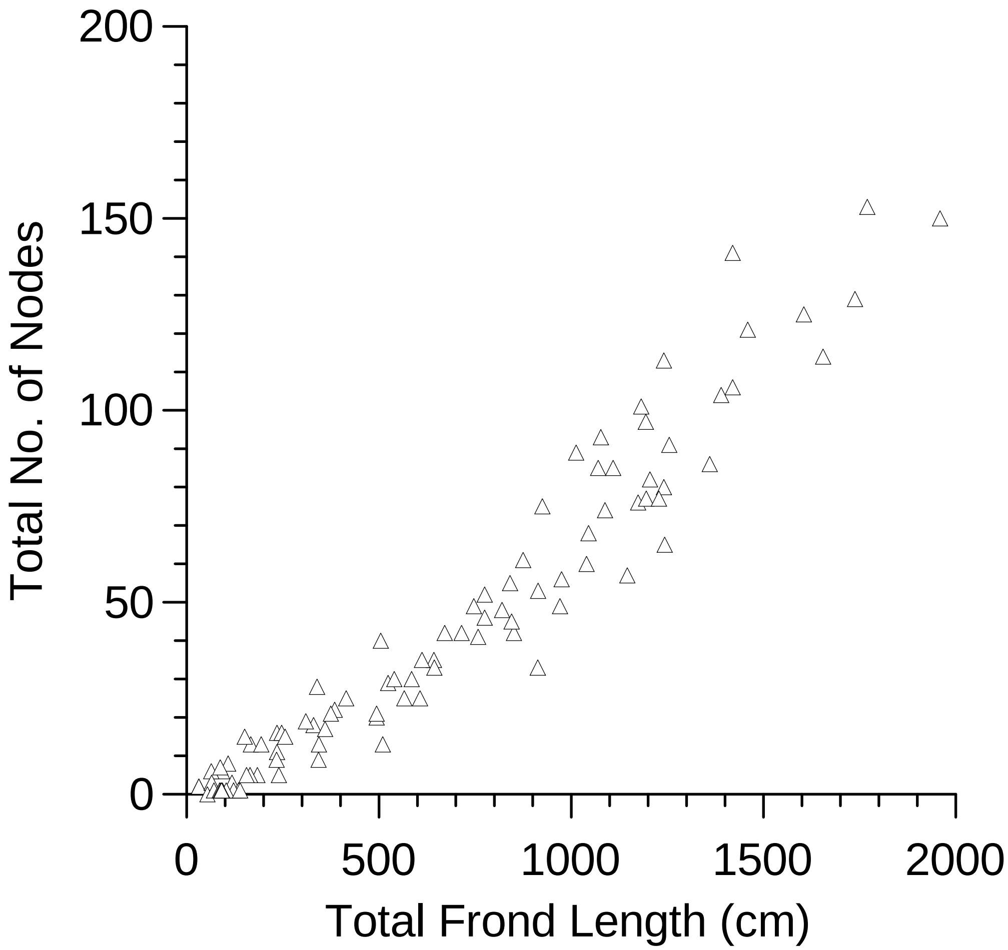

FIGURE 5. Number of nodes versus frond length.

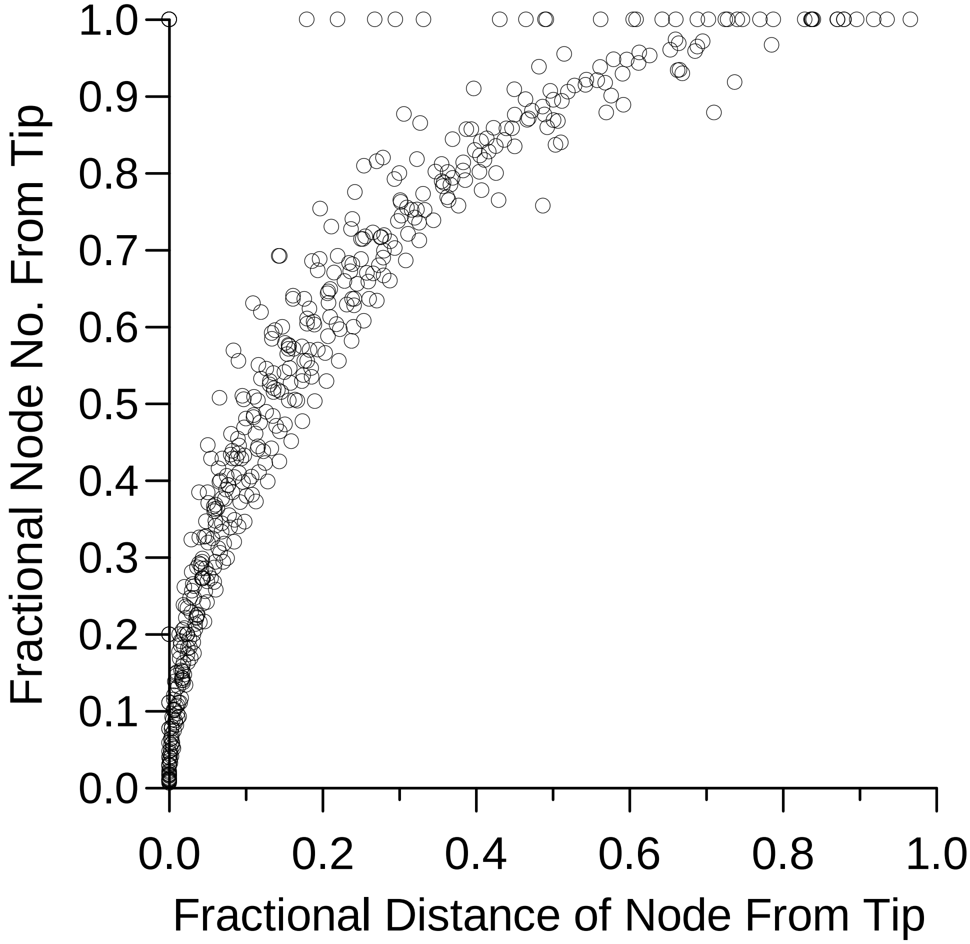

FIGURE 6. Distribution of nodes along a frond measured as fractional node number from tip vs. fractional distance from tip. Roughly half the nodes (blades) lie within the terminal 15% of a frond's length.

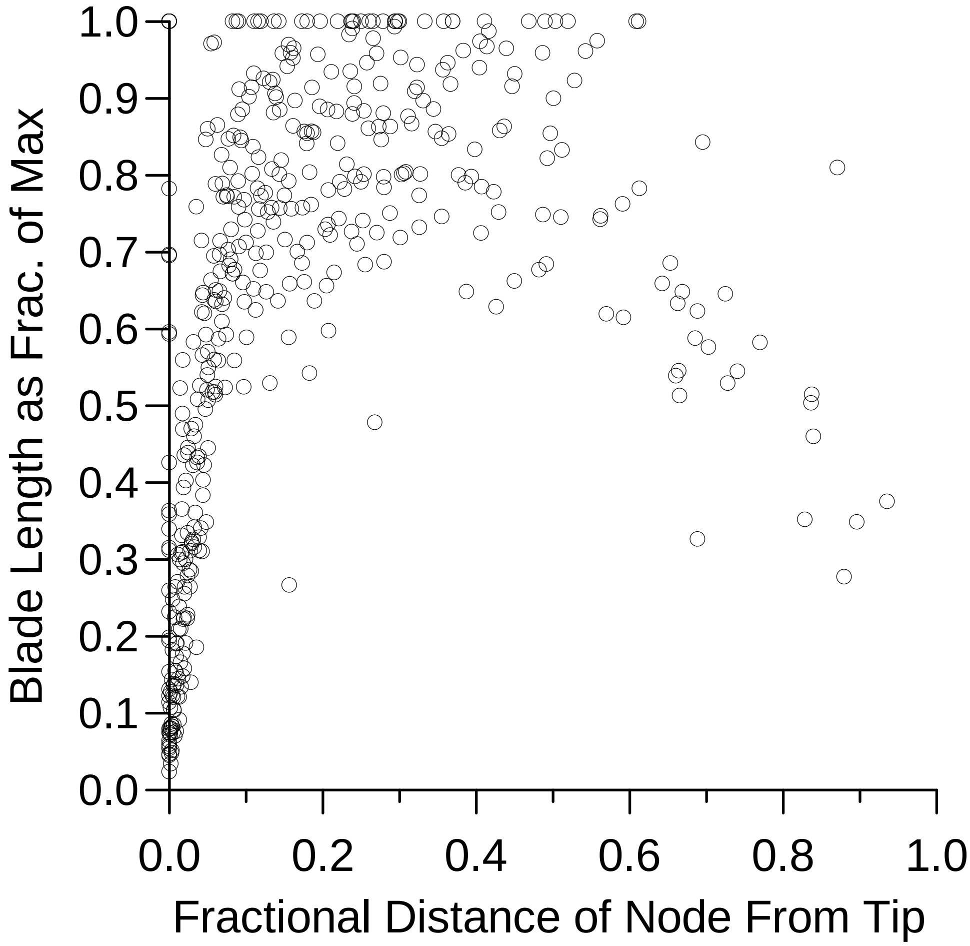

FIGURE 7. Blade lengths (measured as a fraction of longest blade on frond) as a function of fractional distance from tip.

APPENDIX 1. Tabulation of frond lengths (as a proportion of holdfast depth) vs. plant size (no. of basal frond). *n* = 21 plants ranging in size from 2 to 42 fronds. Holdfast depths ranged from 4.2 to 10.5 meters.

Case frequencies determined by value of variable FRCOUNT.

Row percents
FRTOTAL (rows) by SIZEXDPTH$ (columns)

Plant Size (no. basal fronds)

	Length (Fraction of holdfast depth)						
No.fronds	<.25	.25-.50	.50-.75	.75- 1	canopy		Total
2	100	0	0	0	0	100	2
4	33	17	42	8	0	100	12
6	33	0	17	33	17	100	6
7	43	29	0	0	29	100	7
8	0	25	25	25	25	100	8
9	78	11	0	11	0	100	9
10	17	30	7	17	30	100	30
17	12	6	12	18	53	100	17
19	26	11	5	16	42	100	19
27	19	22	7	15	37	100	27
28	14	14	0	29	43	100	28
33	19	17	13	5	45	100	99
36	0	8	14	17	61	100	36
39	15	21	5	15	44	100	39
42	19	5	17	24	36	100	42
Total %	19	15	11	15	40	100	
Total Fronds	72	59	42	56	152		381

APPENDIX 2. Regression results for LN(wet weight) vs LN(length). Wet weight in grams and length in centimeters.

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Dep Var: LOGWT   N: 98   Multiple R: 0.963   Squared multiple R: 0.927
Adjusted squared multiple R: 0.926   Standard error of estimate: 0.384

Effect    Coefficient     Std Error  Std Coef Tolerance      t   P(2 Tail)
CONSTANT    -1.438         0.229        0.000       .      -6.287    0.000
LOGLNGTH     1.291         0.037        0.963     1.000    34.979    0.000

                         Analysis of Variance
Source          Sum-of-Squares   df  Mean-Square     F-ratio       P

Regression            180.140     1      180.140    1223.536       0.000
Residual               14.134    96        0.147

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Durbin-Watson D Statistic          1.286
First Order Autocorrelation        0.331
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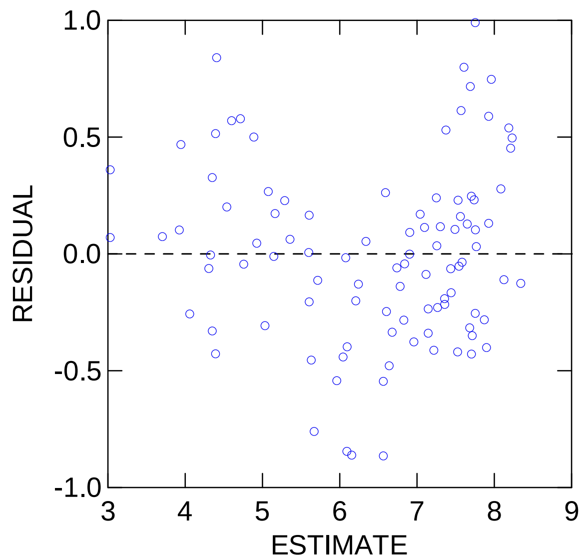
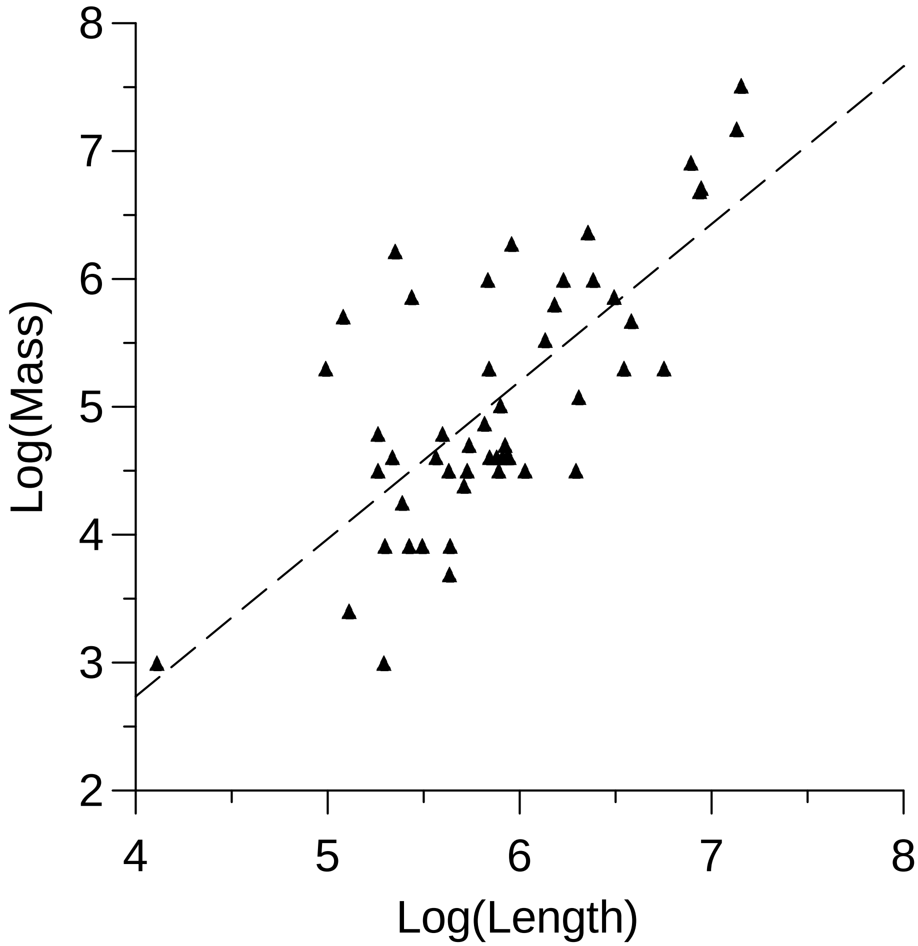
Plot of residuals against predicted values



APPENDIX 3. *Cystoseira osmundacea* regression of biomass (grams) vs length (cm) of reproductive fronds. n = 51 fronds ranging in length from 61 to 1280 cm.

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Dep Var: LOGWT   N: 51   Multiple R: 0.722   Squared multiple R: 0.521
Adjusted squared multiple R: 0.511   Standard error of estimate: 0.718

Effect     Coefficient  Std Error   Std Coef Tolerance    t   P(2 Tail)

CONSTANT     -2.193      0.998        0.000      .      -2.197    0.033
LOGLNGTH      1.232      0.169        0.722     1.000    7.301    0.000

                            Analysis of Variance
Source           Sum-of-Squares   df  Mean-Square     F-ratio       P
Regression           27.457     1       27.457      53.301       0.000
Residual             25.241    49        0.515

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Durbin-Watson D Statistic         1.074
First Order Autocorrelation       0.419
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