Evaluation of four models used to estimate kelp productivity from growth measurements

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ABSTRACT: Four models have been proposed in the literature to estimate production of kelp blade material from length increments. In order to evaluate them, we obtained direct measurements of blade production by weighing *Laminaria longicruris* plants before and after a 24 d field experiment. The best model was that of Mann & Mann (1981) who proposed that blade production was equal to growth times unit blade weight in the area of maximum blade biomass. This model however overestimated actual production by 20 to 40 % depending on whether overall sample production or individual blade production was considered. Similar results were obtained with a model based on unit weight of entire blades. The estimates generated by 2 models based on weight-length relations exceeded actual production by up to 100 %. We discuss the influence of blade size and blade productivity on the performance of each model.

INTRODUCTION

The productivity of perennial sublittoral marine macrophytes is comparable to that of intensively exploited agricultural systems (Kain 1979, Ferguson et al. 1980). In a study of the seaweed community in St. Margaret's Bay, Nova Scotia, Canada, Mann (1972) concluded that total seaweed production was about 3 times that of phytoplankton for the bay as a whole. Kelps of the genus *Laminaria* were major contributors to the seaweed production.

To estimate the production by the various species of kelp, Mann (1972) converted length increments to biomass increments by means of weight-length relations determined empirically. He pointed out however that because the relations were obtained from eroded blades, this technique would overestimate actual production by an unknown amount. Kain (1979) calculated the total annual production of *Laminaria longicruris* from Mann's figures and compared it to the estimate derived by Hatcher et al. (1977) from measurements of oxygen production and carbon uptake. She found a 10-fold difference between the 2 estimates for the same species in the same area. She proposed

one reason for the discrepancy was probably the length-biomass conversions used by Mann (1972).

It was felt that the problem with such conversions was that the exponential nature of the weight-length relations resulted in large overestimates of blade weights at the end of the growth period. To eliminate this problem, Mann et al. (1979) proposed a modification to the initial technique whereby the relation between blade weight and length was made approximately equal to the relation observed at the time of initial measurements. Mann & Mann (1981) used algebra to compare the 2 techniques which they referred to as the exponential and the chordal models respectively. Because the 'exponential' model actually represents a power relation it will be identified as the 'power' model in the present paper. Mann & Mann (1981) concluded that on average, the estimates obtained with the chordal model should be about 10 % lower than those from the power model. They also proposed that a new approach devised by Mann & Kirkman (1981) for *Ecklonia radiata* could be used with *Laminaria longicruris* and probably most Laminariales.

The technique of Mann & Kirkman (1981) does not rely on a general weight-length relation to convert length increments into biomass production, hence avoiding the major problem of the preceding models. It proposes instead that production of blade tissues can

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be estimated by multiplying growth by the mean weight per cm in the region of maximum blade biomass. This 'area of constant biomass' model and the first 2 models were compared empirically by Gendron (1985). She confirmed the existence of a difference in the order of 10 % between the power and the chordal models as predicted by Mann & Mann (1981). She also demonstrated that the estimates obtained with these 2 models could exceed those generated by the biomass model by up to 45 % depending on blade size. However, lacking direct measurements of blade production, she could not evaluate the accuracy of the models or explain their deficiencies.

In this paper we report on the results of an experiment designed to compare estimates from models to direct measurements of blade biomass production by *Laminaria longicruris*. We evaluate each model and identify causes associated with the deficiencies that we observed. In addition to the 3 models already mentioned we have included in our analysis a variation of the area of constant biomass model used by Gerard & Mann (1979), referred to here as the blade biomass model.

MATERIAL AND METHODS

Field procedures. On 14 July 1982, *Laminaria longicruris* plants were selected in a kelp bed located near Pubnico in southwest Nova Scotia, Canada (Fig. 1).
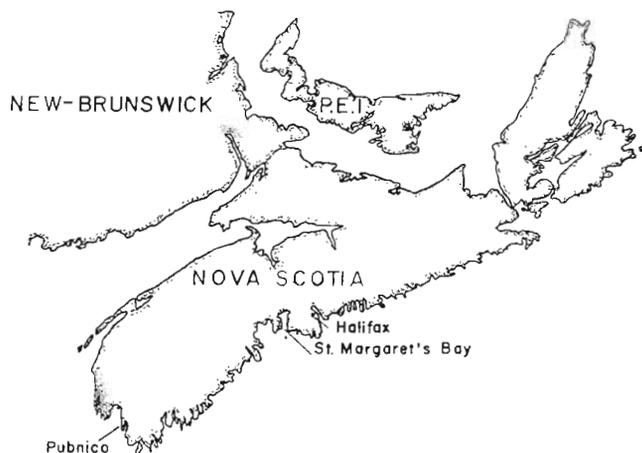

Fig. 1. Location of Pubnico site in Nova Scotia, Canada

The growth characteristics of that population and the environmental conditions prevailing at the site are documented in Gagné et al. (1982). Sixty healthy plants were chosen by SCUBA divers to cover the entire range of blade sizes found at the site. The plants were put in plastic bags underwater and the bags brought to the surface to be emptied of as much water as possible. Great care was taken not to expose any part of the plants to direct sunlight in the process as

recommended by Gerard & Mann (1979). The plants were stored in a cool, dark compartment on board the tending vessel until the collection was completed. They were then taken to a nearby fish plant where the following measurements were recorded: total plant weight, total blade and stipe length and length of the eroding portion at the tip of the blade. This portion was then removed to minimize losses of blade material through fragmentation during the experiment. One cm holes were punched at 10, 20 and 30 cm from the base of the blade to monitor blade elongation as in Parke (1948). All plants were identified with individual numbered plastic tags and carried in plastic bags back to the middle of the kelp bed where they were anchored by the holdfast to concrete blocks by means of rubber bands. Twenty undisturbed blades were also punched at 10 cm from the junction with the stipe to evaluate the effect of handling on blade elongation.

The plants were all left to grow until 12 August. Eight experimental plants as well as 4 controls could not be found at that time but all remaining plants were recovered. These and 80 additional plants collected at random were taken to the fish plant. Total weight and length were recorded for the blades of the additional plants and the controls to derive a weight-length relation, and for the blade and stipe of the experimental plants. Holdfast weight was also measured for the latter. The amount of elongation was recorded for the control blades. The experimental blades were then packed in plastic bags and brought to the laboratory to be kept overnight in a dark coldroom at 10 °C.

Laboratory measurements. The following morning the blade weights were measured again to ensure that no important change had occurred during the 16 h since harvest. All the weights were within 1.0 g of those measured the previous day.

A visual inspection of the blades revealed that there had been no tissue erosion at the distal edge during the experiment but that some erosion had occurred along the frilled margins. Four blades had lost small frill fragments and were excluded from the analysis. The remaining blades had not suffered any important loss of material. These 48 individuals were processed as follows.

The distance between the base of each blade and the 3 holes punched at the beginning of the experiment was recorded. The first area of constant blade width was identified by eye and a section within that area cut, measured and weighed to calculate its mean weight per cm.

Calculations. *Blade weight increments.* The blade weight at the beginning of the experiment was derived as follows. We assumed that the holdfast weight and the mean stipe weight per cm remained constant throughout the experiment. From the changes in stipe

length we estimated the changes in stipe weight. This value was then subtracted from the final stipe weight to estimate the weight of the stipe at the beginning of the experiment. By adding the initial stipe weight to the final holdfast weight and subtracting that result from the initial total plant weight, we obtained an estimate of the initial blade weight. The difference between this weight and the final blade weight corresponds to the change in blade biomass during the experiment, assuming that no blade material was lost through erosion and that stipe production was accurately measured.

We have already indicated that the blades kept for this analysis lost insignificant amount of material through erosion. We cannot evaluate the accuracy of our stipe production estimates but see no reason why they would be biased. We therefore conclude that this technique provides a valid, albeit slightly conservative, measurement of actual production of blade material and use it in this analysis to evaluate the 4 models.

The models. The equations used to calculate the estimates of blade material production, P, for the power, the chordal and the blade biomass models are Eqns (2), (3) and (8) of Mann & Mann (1981).

Power model: $P_1 = a (L_1 + g)^b - aL_1^b$ (1)

Chordal model: $P_2 = g [a (L_1 + l)^b - aL_1^b]$ (2)

Area of constant biomass model: $P_3 = g \times w/l$ (3)

where a and b = coefficients of the weight-length relation ($W = aL^b$); g = linear growth; w = weight of a section cut in the area of maximum blade biomass; l = length of that section; L_1 = initial blade length. The equation for the blade biomass model is as Eqn (3) except that the weight and length are those of the entire blade measured at the end of the growth period.

The parameters a and b were obtained from the equation $W = 0.085 L^{1.57}$ ($r^2 = 0.88$) describing the weight-length relation of the sample of 96 plants collected at the end of the experiment. Total initial length (not amputated length) was used in calculating the estimates with the power and chordal models. We used total elongation, as measured by the 3 holes, in all calculations.

RESULTS

Determination of area of maximum biomass

The area of constant biomass model assumes that blade production equals growth times mean weight per cm of blade tissue in the area of maximum blade biomass (Mann & Kirkman 1981). To verify that this area is also of constant width and can therefore be localized by eye, we performed the following test. For 19 of the experimental blades, we first identified the area of constant width by eye and used a portion of that area to estimate its mean weight per cm. We then sectioned each blade in 11 to 32 consecutive segments of varying width (5 to 14 cm) depending on the total length of the blade. We used the mean weight per cm of these segments to precisely locate the area of maximum biomass.

Eleven of the 19 plants showed some discrepancies but only 5 differences were larger than 0.1 g. Although differences of 17 and 30 % were recorded for 2 blades, the mean difference was about 5 % or 0.1 g. All the differences exept one were positive indicating a larger value for the eye estimate. One explanation for this can be found in the procedure that we followed. Each blade was streched out on a table and the eye estimate performed first. The sections were then cut and weighed. During this time-consuming procedure, especially for the longer blades, the plants started to dry out and lost weight.

From these results we concluded that we were able to properly locate the area of maximum blade biomass by eye and proceeded accordingly with the remaining blades in order to save time.

Unit weights; whole blade vs area of maximum biomass

The only difference between the area of constant biomass model and the blade biomass model is the area for which the mean weight per cm is calculated i.e. the area of maximum biomass in the former, the whole amputated blade in the latter. In Fig. 2 we show that both measurements are very close for all but one of the 48 experimental plants (r=0.96).
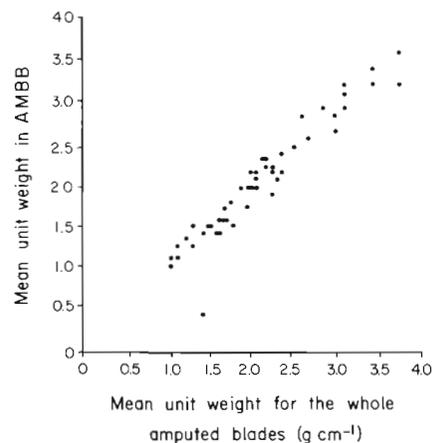

Fig. 2. *Laminaria longicruris.* Relation between mean weight per cm in the area of maximum blade biomass (AMBB) and in the entire amputated blade at the end of the experiment

Table 1. *Laminaria longicruris.* Measured and estimated data required to calculate production of blade material by individual plants. Weights in g, lengths in cm. Details in the text

Plant no.	Initial measurements				Final measurements								Estimated values		
	Stipe length	Total blade length	Discard length	Amputated blade length	Holdfast weight	Stipe length	Stipe weight	Amputated blade Length	Amputated blade Weight	Growth 0–10	Growth 10–20	Growth 20–30	Initial Stipe weight	Initial Blade weight	Changes in blade weight
1	106	119	35	84	34	114	91	116	184	28	0	1	85	131	53
3	85	142	56	86	4	89	91	114	225	26	2	0	87	173	52
4	7	61	0	61	24	12	3	94	93	33	0	0	2	55	38
5	62	176	68	108	10	74	52	136	184	27	1	0	43	152	32
7	96	126	50	76	8	101	104	94	203	18	1	0	99	153	50
8	128	162	37	125	14	148	117	164	255	35	1	1	101	186	69
9	30	118	52	66	11	40	18	86	96	19	1	0	14	75	21
10	101	107	26	81	71	112	107	101	126	20	0	0	96	102	25
11	63	136	44	92	9	80	51	122	172	28	0	1	40	146	26
13	67	127	33	94	6	84	52	130	187	34	1	0	42	155	32
15	92	182	57	125	14	116	92	168	223	38	2	1	73	172	51
16	11	120	42	78	16	17	6	115	192	36	2	0	4	143	49
17	37	159	22	137	16	46	30	175	254	35	2	0	24	213	41
18	34	152	71	81	15	36	19	103	157	21	1	0	18	129	28
21	143	330	152	178	10	151	145	211	473	29	2	1	137	406	67
22	55	138	30	108	16	75	39	149	158	40	0	1	29	113	45
23	193	347	121	226	81	198	293	268	998	36	3	1	286	875	123
24	144	477	217	260	36	150	206	313	1173	39	5	1	197	1025	148
25	65	60	11	49	4	72	40	65	65	16	0	0	36	52	13
26	83	136	51	85	10	101	64	108	138	24	0	0	52	109	29
28	128	257	95	162	18	142	156	200	416	32	4	0	141	340	76
29	93	149	54	95	17	106	88	125	191	30	1	1	77	152	39
30	157	185	62	123	20	162	161	156	356	32	2	1	156	270	86
31	167	171	40	131	13	175	195	164	308	29	2	0	186	230	78
32	67	223	66	157	16	78	63	211	540	45	5	2	54	455	85
33	193	209	41	168	20	210	200	205	496	32	2	1	184	402	94
34	209	237	80	157	12	220	184	201	475	35	3	1	175	378	98
35	51	214	82	132	21	58	45	166	344	30	2	0	39	295	49
36	63	183	57	126	10	70	57	158	353	29	1	0	51	304	49
38	63	258	85	173	35	72	45	217	414	39	3	1	39	380	34
39	157	194	48	146	4	169	125	181	314	33	1	0	116	249	65
40	154	299	124	175	17	160	164	210	359	28	3	0	158	324	35
42	183	314	119	195	44	183	256	228	523	27	2	1	256	535	−12
45	133	301	123	178	13	140	83	228	451	39	5	1	79	389	62
46	251	277	96	181	18	252	373	212	665	23	4	0	372	620	45
47	121	333	124	209	25	122	161	250	745	30	4	0	159	700	45
49	122	195	68	127	40	127	165	163	563	29	4	0	159	450	113
50	45	207	49	158	25	50	36	192	515	30	2	1	32	456	59
51	115	253	97	156	13	123	143	189	384	31	3	0	134	329	55
52	135	406	173	233	38	137	309	267	829	32	2	0	305	752	77
53	175	276	73	203	37	188	263	244	568	32	6	1	245	490	78
54	186	279	112	167	11	189	179	194	520	24	1	1	176	486	35
55	152	337	113	224	23	153	219	265	965	36	5	1	218	819	146
56	190	347	138	209	32	194	244	260	846	38	8	2	239	721	125
57	172	293	110	183	14	175	192	227	468	34	4	1	189	418	50
58	130	354	158	196	11	137	195	235	650	35	3	1	185	632	18
59	166	342	146	196	20	170	238	235	700	32	5	1	232	591	109
60	113	331	130	201	24	114	137	239	576	31	4	1	135	501	75

Growth is fast and conditions stable at our Pubnico site in summer (Gagné et al. 1982). Most of the non-eroded standing blade biomass available at the time of the experiment (mid-July to mid-August) had therefore been produced during that period, hence the uniform weight distribution along the blades.

Plant growth

The measurements recorded at the beginning and the end of the experiment are presented in Table 1. Stipe elongation ranged from 1.0 to 24.0 cm and there was no relation between stipe growth and initial stipe

length. Only one stipe, that of Plant 42, did not grow at all. The mean increase in stipe weight was 7.1 g or 12 % of the initial weight.

Blade elongation processes were not restricted to the initial 10 cm. The distance between the first and the second holes increased by up to 8.0 cm while on the average growth in that area accounted for 7 % of total blade elongation. About 2 % of total growth in length took place between the second and third holes.

Elongation in the first 10 cm of the experimental blades proceeded about 20 % slower than in the controls.

Production of blade material

Fig. 3 illustrates the relation ($r = 0.63$; $p < 0.01$) existing between the changes in the weight of the blades and their initial amputated weight. Blade productivity increased linearly with blade size. Five plants however achieved production values markedly lower than expected from the general relation; apparently, Plant 42 even lost weight during the experiment in spite of a good growth (Table 1). On the plots of residuals (value observed − value predicted) in Fig. 4, these 5 plants clearly appear as outliers. No obvious pattern can be detected in the distribution of the other points. This confirms the linearity of the relation between blade size and productivity. It also indicates that for our data set at least, the initial amputated blade weight is a good predictor of blade productivity. The residuals of this relation therefore constitute an index of the production performance of a blade relative to the general performance of the entire sample and independent of blade size.

Fig. 3 shows that the intercept of the relation is about 30. This is because relative to their weight small blades were more productive than larger ones (Fig. 5) as previously observed by Mann (1972). Our sample contained only 3 blades lighter than 100 g and this probably explains why we obtained a linear relation. Such a relation is not expected to hold for very small blades since theoretically, the curve should cross the origin. Fig. 5 also suggests that relative productivity decreased as blade size increased for blade weights between 50 and 500 g; beyond that it levelled off at about 10 % of initial blade weight.

Comparison of production estimates

Of the 48 experimental plants available, only Plant 42 lost weight. Since its blade grew well (Table 1) and appeared as healthy as that of the other plants, we cannot explain this result. Because that observation is possibly erroneous we decided to exclude Plant 42 from the following analysis.
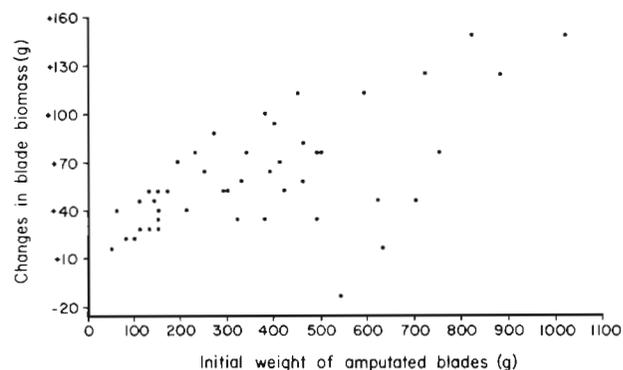

Fig. 3. *Laminaria longicruris*. Relation between changes in blade biomass during the experiment and initial weight of amputated blades

Table 2 presents the production of blade material as measured from weight differences and as estimated by each model. The biomass gain by the 47 plants together totalled 2871 g. The power and the chordal models overestimated that total by 70 and 63 % respectively. Both biomass models did much better, the estimates generated by the area of constant biomass model and the blade biomass model being 20 and 22 % higher than the measured total respectively.
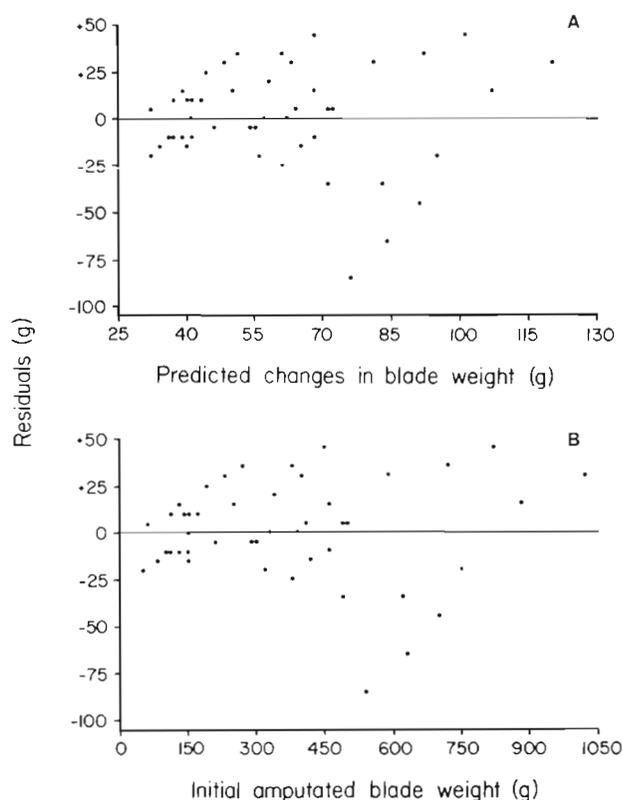

Fig. 4. *Laminaria longicruris*. Residuals from relation between changes in blade weight and weight of amputated blades at the beginning of the experiment (A) against the production values as predicted from the relation; (B) against the initial amputated blade weight

Table 2. *Laminaria longicruris*. Production of blade material (Plant 42 excluded)

	Production (g)	Differences (g)	Differences (%)	Mean of % individual differences Actual	Mean of % individual differences Absolute
Measured	2871	–	–	–	–
Estimates from models					
Power	4873	2002	70	98	99
Chordal	4671	1800	63	89	91
Area of constant biomass	3434	563	20	34	39
Blade biomass	3503	632	22	34	40
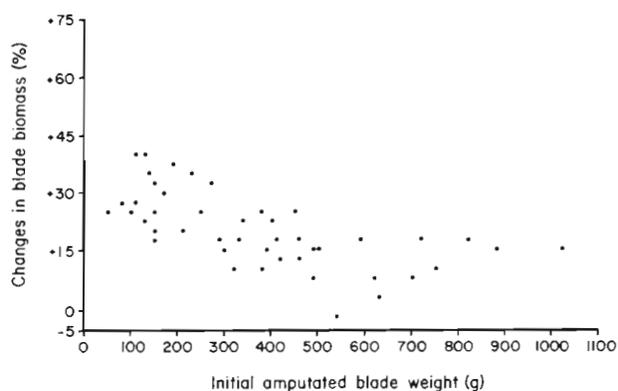
Fig. 5. *Laminaria longicruris*. Relation between changes in blade biomass as a percentage of initial amputated blade weight and initial amputated blade weight

The performance of all models appears poorer if we look at the means of the individual differences rather than at the overall totals. Although the biomass models remainded the best, they overestimated the measured production values by 34 % on average. The mean error for the power and the chordal models was 98 and 89 % respectively.

Less than 5 % of the differences generated by the power and the chordal models were negative (underestimates). This proportion is more than 20 % for the 2 biomass models. The presence of numbers with opposite signs in the calculation of the averages reduces the discrepancies between the predicted and the observed values, especially for the 2 biomass models. When we compute the mean of the absolute differences instead, we realize that the power and the chordal models were in error by 99 and 91 % respectively while the biomass models each differed by 40 % in their respective estimates of individual blade production.

Analysis of model performance

Influence of blade size

We used Kendall coefficients of correlation to investigate the relation between the individual errors produced by each model and blade size. Table 3a shows that there was a significant positive relation between the magnitude of the error and blade size (Fig. 6).

Table 3. *Laminaria longicruris*. Values of Kendall correlation coefficients calculated to evaluate the influence of blade size on model performance

	Power	Chordal	Area of constant biomass	Blade biomass
a. Errors (predicted-measured) in g; n = 47				
Blade length	0.42**	0.42**	0.25*	0.36**
Blade weight	0.33**	0.32**	0.26*	0.38**
b. Errors in g; n = 43				
Blade length	0.39**	0.39**	0.18*	0.32**
Blade weight	0.29*	0.27*	0.18*	0.32**
c. Errors in % of actual blade production; n = 47				
Blade length	0.06 ns	0.08 ns	0.15 ns	0.23*
Blade weight	−0.02 ns	0.00 ns	0.16 ns	0.24*

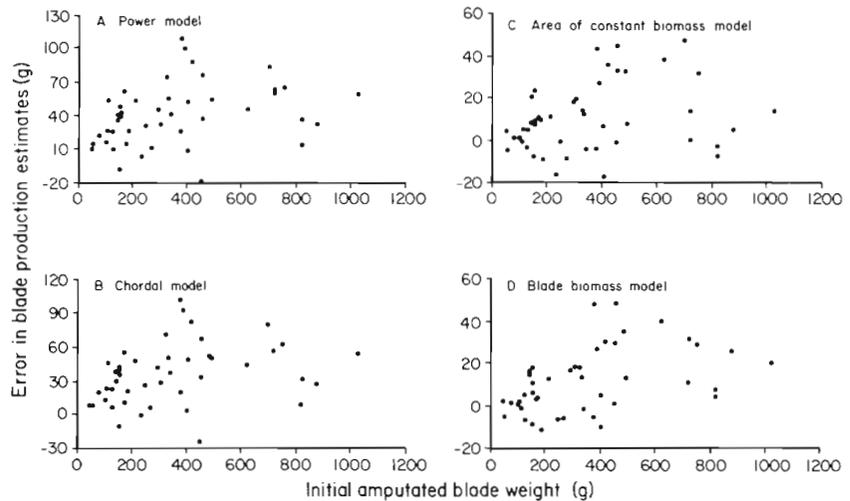** $p < 0.01$; * $0.05 > p > 0.01$; ns: non significant

Fig. 6. *Laminaria longicruris*. Relation between errors in blade production estimates generated by each model and initial amputated blade weight

We mentioned earlier that 4 blades included in the analysis produced much less than expected. To verify that the relations were not made significant by these extreme values, we removed them and repeated the analysis. This had little effect on the results (Table 3b) which confirms that all models produce larger overestimates as blade size increases.

These results suggest that the magnitude of the errors relative to the actual production could be independent of blade size. This is confirmed for 3 of the models by the absence of a significant correlation between the errors expressed as a percentage of actual blade production and initial blade weight or length (Table 3c). Significant coefficients were obtained only with the blade biomass model. The relative errors produced by this model are therefore not independent of blade size as opposed to those generated by the other 3 models.

Influence of production performance of blades

We indicated earlier, based on the relation between blade production and blade size (Fig. 3), that the production of some blades differed markedly from expectation. These outliers are likely to influence the predictive ability of the models, especially the power and the chordal models for they are based upon general relations.

To investigate this possibility for each model, we plotted the error in percent of actual blade production against an index of blade performance independent of blade size i.e. the residuals of the productivity-weight relation.

The results for the power and the chordal models are very similar (Fig. 7A, B). They show that as the production performance of the blades increased from below to above expectation (residuals going from negative to
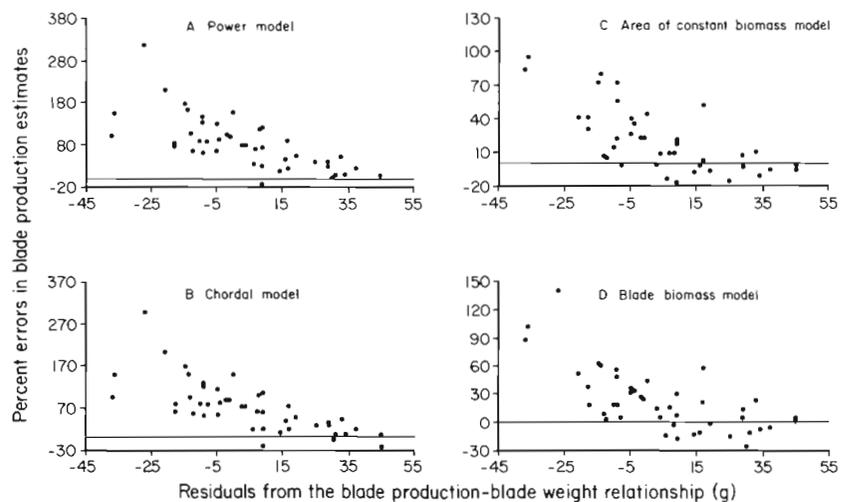

Fig. 7. *Laminaria longicruris*. Relation between errors in blade production estimates expressed as a percentage of measured blade production and residuals from the relation between blade production and initial amputated blade weight

positive) the percent error decreased linearly but became negative in a few cases only. This is to be expected from models which largely overestimate productivity in general; they will properly estimate the production of only those blades with unusually high production rates.

A different pattern was obtained with the biomass models (Fig. 7C, D). Again the size of the error decreased as blade performance improved. However when blades started to produce at or above the general trend, the size of the errors levelled off and fluctuated around zero. Both biomass models therefore also fail to properly estimate the production of those blades with low production rates. However they do very well when production is average or better.

DISCUSSION

Plant growth and productivity

The mean increase in stipe weight for all the experimental plants amounted to 15 % of mean blade production. Production of stipe material can therefore represent a significant proportion of total production in *Laminaria longicruris* at certain times of the year and in beds where long stipes are common.

Ten % of blade elongation originated from the area between the first 10 and 30 cm of the blades. The presence of meristematic activity in that area of *Laminaria longicruris* blades is probably highly seasonal and possibly restricted to the period of rapid growth. It may not be a generalized feature of all populations either for although it was also reported by Boden (1979), it was not observed by Mann (1973). As shown here however, ignoring growth in that area can result in underestimating total elongation and production by 10 % or more. To avoid introducing an error of varying magnitude in growth measurements and productivity estimates, we recommend that blades be punched at 20 cm from their junction with the stipe as done by Brady-Campbell et al. (1984) and Gendron (1985), or even at 30 cm for large plants at times of rapid growth.

Performance of the models

The estimates that we obtained from the power and the chordal models were generally within less than 10 % of each other as predicted by Mann & Mann (1981) and measured by Grendron (1985). The differences between those estimates and our measurements of blade production were however much more important, ranging from about 65 % to almost 100 % depend-

ing on whether overall sample production or mean individual blade production was considered. Our results clearly demonstrate that there are serious problems with using general weight-length relations in trying to estimate kelp blade production.

As expected from the work of Mann & Mann (1981) and Gendron (1985), the models based on individual unit weight measurements out-performed those depending on a general weight-length relation. Indeed, the 2 biomass models overestimated total sample production by only 20 %. As with the other models, this figure increased when mean individual blade production was estimated. Even though they represent a significant improvement over the other approach, the biomass models too have problems.

All models produced larger overestimates as blade size increased. However, we showed that when expressed as a percentage of measured blade production, the errors generated by the power, the chordal and the area of constant biomass models became independent of blade size. This means that although the size composition of a population greatly influences its overall production, smaller plants being more productive than larger ones, it has no effect on the *percent* error generated by the 3 models. Consequently, even though the size distribution of a population must be closely respected in production studies, this is not necessary in experiments aimed at determining the percent errors generated by one of those 3 models. This implies that the percent errors presented in this paper for those models do not apply only to our particular sample but to the whole population from which it was collected and for the growth conditions prevailing at the time of our experiment.

Our analysis with an index of blade production performance (Fig. 7) indicated that the models based on a weight-length relation failed to properly estimate production of all the blades which did not produce much more than expected for their size. The 2 biomass models however gave good estimates for production performances that were average or better.

Two major problems can be identified as being responsible for the weaknesses of each model type. In the first paper reporting on the use of weight-length relations to estimate kelp production from growth measurements, Mann (1972) pointed out that using eroded plants to calculate these relations would result in overestimating production. This problem only affects the power and chordal models and is certainly responsible for much of the difference observed between their estimates and those produced by the 2 biomass models, as proposed by Gendron (1985).

Our analysis identified a second problem related to the observed differences: given their size and elongation, several blades failed to gain as much weight as

expected, some by a large margin. Since these blades were not excluded during the visual inspection at the end of the experiment, tissue erosion is unlikely to be responsible for these low values. Excretion of organic material cannot explain them either. Indeed a loss of dissolved organic matter would also be reflected in the mean unit weights used by the biomass models to generate their estimates. These 2 models should then correctly evaluate all production values, including those that are lower than expected, but they do not. The mean weights per cm used by these models are therefore not representative of the weight of the tissues recently synthesized by blades which do not produce as expected. Investigating the possible causes for this phenomenon is beyond the scope of this paper. Whatever these causes are, our results showed that all models overestimated the production of these blades, by a large amount in some cases.

The power and the chordal models are affected by both of these problems whereas the 2 biomass models are influenced only by the latter. This is certainly one reason why the biomass models provide a much better tool to estimate production of kelp blade material from growth measurements. They overestimate total production by a much smaller amount and are much better at estimating individual plant production. In the light of our results, we see no reason why the power or the chordal models should be used in future studies.

Gendron (1985) proposed that an equation can be derived to approximate the results of the area of constant biomass model from estimates generated by the power or the chordal models. This was under the assumption that the former model was accurate. Our analysis shows that such is not the case and that although both biomass models are better than the other models, they too have weaknesses. Furthermore we showed that these 2 types of models are not affected in the same way by the same factors, especially plant production performance. Using such an equation can therefore produce erroneous results and will not estimate actual production of blade material but only an imperfect proxy. Such approximations should therefore be avoided.

The 2 biomass models

Mann & Kirkman (1981) proposed that for *Ecklonia radiata*, production of blade tissues was equal to elongation times the unit weight in the area of maximum biomass. They showed that there was only one such area in the blades of that species. This may not be the case with *Laminaria longicruris* at times when erosion is reduced and when there is an important change in growth conditions. For instance, such periods are likely to occur in late spring and late summer in Pub-

nico or in late spring in St. Margaret's Bay (Gagné et al. 1982). At those times, 2 areas of constant biomass can be found on a blade, a consequence of 2 different sets of growth conditions. To estimate production of blade tissues in the last period, the unit weight measurements must be taken in the area of maximum biomass closer to the stipe. Using any other part of the blade would violate the model assumption and bias the results. This would also happen if, as must be done with the blade biomass model, the mean weight per cm for the entire blade were used.

Because our experiment was conducted towards the end of a long period of rapid growth (Gagné et al. 1982), the weight distribution along the blade was uniform and both models gave very similar results. We do not however expect such a good agreement for all phases of the annual growth cycle.

Our results show that the errors produced by the area of constant biomass model are independent of blade size when expressed as a percentage of actual production. This is a major convenience since a single correction factor can be used for an entire population irrespective of its size composition. This cannot be done with the blade biomass model for the magnitude of its relative errors is related to blade size. We therefore recommend that only the area of constant biomass model be used in future studies.

CONCLUSIONS

Our analysis revealed some features of the relation and performances of 4 models used to estimate production of blade tissues from growth measurements. Although the trends that we describe are probably applicable to all populations of *Laminaria longicruris* during their entire annual growth cycle, the equation parameters and the actual differences reported here are likely to be specific to our experimental conditions. For instance the area of constant biomass model may not always overestimate total tissue production by 20 % and this estimate will not necessarily be always 50 % less than the one generated by the power model. These numbers might vary with blade morphology, growth conditions, the proportion of blades with low production performance in a population and so on. However we suspect that the estimates from the area of constant biomass model will always be more accurate and much lower than those provided by models relying on general weight-length relations. Similarly, the errors generated by this model should always be independent of blade size when expressed as a percentage of actual production.

We cannot at the moment revise annual productivity estimates published from studies that used one of the

models investigated here (e.g. Mann 1972, Gerard & Mann 1979). More work is required on seasonal and spatial variability before we can come up with revised figures. Our results however indicate that by using the power model in his study of kelp productivity in St. Margaret's Bay, Nova Scotia, Mann (1972) may have overestimated the actual values by between 50 to 100 %. This is only the error caused by using that model. Other potential sources or error such as over-estimating the contribution of smaller plants cannot be evaluated here. From their work on *Laminaria sol-idungula*, Chapman & Lindley (1981) proposed that the overestimate could be in the order of 30 to 60 %, depending on whether the size composition of the population is considered or not. It must be noted how-ever that the importance of Mann's overestimate for the entire seaweed community in St. Margaret's Bay can be lower. Indeed, realizing the problems with the model, Mann (1972) chose to be conservative and used the low end of a range of P/B values to arrive at his final overall figures.

We cannot either propose a correction factor or equa-tion of universal applicability. Furthermore, the technique that we used in this paper to evaluate the 4 models is very time-consuming. The handling that it entails must stress the plants to some degree since our experimental blades grew and presumably produced less than the undisturbed controls. It cannot be used year-round either for there are periods when blade erosion proceeds faster than elongation; our direct method could then generate negative production val-ues. We therefore recommend that when production of kelp blade tissues is to be estimated from growth measurements, a calibration experiment similar to ours be conducted with the area of constant biomass model. Such experiments could last from 2 to 3 wk and should ideally be performed for each major phase of the annual growth cycle.

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