

Modelling the growth and harvest yield of the giant kelp *Macrocystis pyrifera*

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Abstract

The giant kelp *Macrocystis pyrifera* is one of the largest and fastest growing seaweeds and is dominant over large areas of the west coast of North America. A model of its growth has been developed which describes plant biomass and production over the course of a year as a function of environmental parameters which affect the light flux. Such parameters include water clarity, spacing between plants, bottom depth, latitude, harvesting activity, and photosynthetic response (P_{\max} and I_k). Model results for a standard set of conditions (latitude 33° N, 3 m plant spacing, water absorbance of 0.115 m⁻¹ and 12 m depth) yield a peak daily gross production of almost 6 g C m⁻² d⁻¹, peak daily net production of almost 3 g C m⁻² d⁻¹, and a peak specific growth rate of about 0.022 d⁻¹. Annual gross production for this case is 1 567 g C m⁻² yr⁻¹; annual net production is 537 g C m⁻² yr⁻¹. These values are comparable to those from field measurements. Size and timing of biomass and production peaks are affected by changes in the parameters describing the light field, with peaks usually occurring later in the year for more adverse circumstances. In higher latitudes, the seasonal variation is so extreme that the plant could not last the year at 53° N in 12 m of water, although it is able to survive the year in shallower water. Harvesting has severe effects on biomass and production. Model results suggest that light limitation is a very important constraint on kelp growth that should not be overlooked. This implies that differences in parameters describing two environments must be considered when comparing results obtained at different locales.

Introduction

Understanding the factors regulating biomass and growth of such large seaweeds as the giant kelp *Macrocystis*

pyrifera is especially difficult. Laboratory experiments on groups of whole plants are virtually precluded because of their large sizes. The ability to perform controlled field experiments is severely restricted by variables which cannot be controlled. Common events which have severe effects range from storms ripping plants off the bottom, temperature and nutrient concentrations caused by large-scale oceanographic events such as the 1984 El Niño along the west coast of North America, to phytoplankton blooms which can alter light penetration. The difficulty of studying kelp ecology is especially acute with respect to the role of light in growth, because the irradiance throughout the water column is determined not only by these uncontrolled environmental variables but also by kelp self-shading.

The physiology of isolated parts of kelp plants has been extensively studied, particularly with respect to light/photosynthesis relationships (e.g. Clendenning, 1971; Wheeler, 1978; Arnold and Manley, 1985). Such work yields functional relationships for kelp photosynthesis and for nutrient uptake but is not directly applicable to field situations because it does not allow for ecological and environmental interactions, in particular self-shading by the kelp plant. Field measurements have been important in incorporating the effect of ecological conditions, but are limited in the range of factors they can incorporate (Gerard, 1976, 1986; Zimmerman, 1983).

Models can integrate different aspects of both field and laboratory work, highlighting important gaps in our present understanding and suggesting fruitful directions for further field and laboratory work. Because macrophytes have different properties than the microalgae, models of macrophyte production differ from the more common phytoplankton production models of the oceanographic literature. These differences have been discussed by Jackson (in press).

Previous models of kelp photosynthesis have been relatively modest, confining themselves to determining if kelp harvesting increased or decreased plant photo-

synthesis (North, 1968) or to following seasonal variations in frond growth (Anderson, 1974).

The present paper describes a model of whole-kelp plant growth which unites laboratory work with a more elaborate description of environmental parameters. The model describes the photosynthesis, respiration, growth, and death of plant material by the rates at which these processes occur in tissue distributed through the water column. The driving variable is the light field. The light flux on kelp tissue at any given depth is a function of the sun angle, reflection at the oceanic surface, absorption by kelp at and below the surface, and absorption by suspended matter. The model calculates plant growth through time by calculating light fluxes and resulting photosynthesis at hourly intervals, tissue growth and death at daily intervals. As the yearly solar cycle unfolds, the cycles of kelp biomass and production develop.

Light limitation of kelp growth is the result of a range of interacting environmental factors, such as time of year, plant morphology, plant spacing, water depth, water clarity, latitude, and standing crop. It should manifest itself by changes in timing and peak size of plant biomass, gross and net-production, and specific growth rates, but exactly how it is manifest is unclear. Model simulations under different conditions representative of the environment can reveal what these are. Results can indicate conditions which are particularly stressful for a plant and what the plant's response is.

This paper includes a detailed description of the kelp growth model and a presentation of simulation results. The variables examined include water clarity, plant spacing, water depth, and latitude. Simulation results generally agree with field measurements and provide insight into kelp ecology. They emphasize the need to account for environmental variables when comparing results from different locations.

Elements of kelp-model structure

The giant kelp *Macrocystis pyrifera* grows attached to hard bottoms by a root-like holdfast (North, 1971 a). Vine-like fronds grow upward, buoyed by small air bladders (pneumatocysts). At the surface, fronds spread out to form a canopy which can totally cover the surface. Each frond consists of a rope-like stipe, about 1 cm in diameter, along which are nodes where blades attach. A blade is composed of an air-bladder (the pneumatocyst) connected to a leaf-like lamina. The fronds of an individual plant bunch together to form a compact kelp column between the bottom and the ocean surface that may typically contain 100 fronds. The stipe bundle is between 10 and 20 cm in diameter. With the blades included, the kelp column is on the order of 50 cm wide. This morphology has been described by Kain (1982) and Jackson *et al.* (1985). Laminae are the dominant photosynthetic tissue (Sargent and Lantrip, 1952; Clendenning, 1971; Arnold and Manley, 1985). Photosynthate is transported between

blades on a frond and between fronds on a plant through a phloem system. Experimental results are presented in a variety of units. The conversion factors used in this paper are shown in Table 1.

This kelp model follows the biomass, production, and growth of a kelp plant over the yearly solar cycle. It considers a kelp plant as the sum of its fronds. Each frond is characterized by its length and its age. At the beginning of a model day, the biomass distribution of each frond is calculated along its length. Photosynthetic rate is a function of irradiance. The light field around a plant is calculated hourly from sunrise to noon as a function of solar irradiance, sun angle, tissue distribution along each frond in a plant, distance between adjacent plants, and the light extinction coefficient of the water. Gross photosynthetic rates are calculated using information about the light field and the tissue distribution. A day's gross production is twice the integrated photosynthesis between sunrise and noon; the net production is the difference between this gross production and the daily plant respiration. Each day's net production is used to calculate the plant's growth, new frond lengths, and tissue distribution for the next day. The daily cycle of production followed by growth is repeated during the annual solar cycle. Under some conditions the surface canopy is harvested. Results of a model calculation include the gross and net productions, the algal standing stock, and the tissue harvested.

Tissue distribution

Fronds in a plant have a distribution of lengths that is generally, but not exactly, linear when fronds are ranked by length and the length graphed as a function of this rank (e.g. Jackson *et al.*, 1985). Such a linear relationship is assumed in this model. It provides a way to allocate daily net production for frond growth and for new frond initiation. Any frond which has neither been harvested nor has reached maximum length is a fixed length longer than the next shorter, younger frond. There is also a different way of allocating growth among fronds which does not maintain fixed length differences. This is discussed more extensively in the subsection "Growth".

The length of a frond can be related to its biomass and the distribution of its lamina area using power-series expressions (Jackson *et al.*, 1985). These are used daily to generate the new depth distribution of biomass and lamina area for each frond and for the entire plant.

The light model

Light in the kelp-growth model consists of beam radiation. That is, light in the water column moves in only one direction. This corresponds to clear sky insolation and light absorption without scattering. Light fluxes are recalculated hourly in the model. Processes that change

Table 1. Conversion constants used to express experimental results of *Macrocystis pyrifera* model

Biomass	Photosynthetic rate
1 g C	1 g C m ⁻² d ⁻¹
= 3.33 g ash-free dry wt	= 0.086 g C (g C d) ⁻¹
= 5.13 g dry wt	= 0.72 mg C (g dry wt d) ⁻¹
= 34.2 g wet wt	= 0.36 μmol O ₂ cm ⁻² h ⁻¹
= 0.086 m ² lamina tissue	

the light flux include reflection and refraction at the ocean surface, absorption in the surface canopy, and absorption by kelp column tissue and by suspended matter. Irradiances are calculated at the surface and at 1 m intervals downward from 0.5 m beneath the surface.

Solar irradiance and surface reflection

The sun angle from the zenith (θ_i) is calculated using standard trigonometric relationships (e.g. Duffie and Beckman, 1974):

$$\omega = \pi \cdot |1 - h/12|, \quad (1)$$

$$\delta = 0.404 \cdot \sin(d \cdot 2\pi/365 - \pi/2), \quad (2)$$

$$\theta_i = \sin(\delta) \cdot \sin(\phi) + \cos(\delta) \cdot \cos(\phi) \cdot \cos(\omega), \quad (3)$$

where d is the number of days after winter solstice, h is the time of day in hours, δ is the declination, ω is the hour angle, and all angles are in radians.

Vertical irradiance at the earth's surface, I_i , is calculated for a clear day as a function of zenith angle [Eq. (18a), Brock, 1981], assuming a conversion of 1 121 W m⁻² to 2 576 μE m⁻² s⁻¹:

$$I_i = 2\,576 \{ \cos(\theta_i) - 0.08 \} \mu\text{E m}^{-2} \text{ s}^{-1}. \quad (4)$$

Light reflectance at the sea surface is calculated using the power-series relationship of Anderson (1974), which was ultimately derived from Table 26 of Sverdrup *et al.* (1942). The fraction of light transmitted through the surface, T_f , is

$$T_f = 0.30544 + 4.0013\phi - 9.9798\phi^2 + 12.044\phi^3 - 6.8773\phi^4 + 1.4872\phi^5, \quad (5)$$

where $\phi = \pi/2 - \theta_i$.

The angle of light from the vertical below the surface, θ , is calculated using Snell's law and a refractive index of seawater of 1.333:

$$\sin(\theta) = \sin(\theta_i)/1.333. \quad (6)$$

Canopy shading

An important part of the model is the estimation of fractional ocean-surface coverages by 0, 1, 2, and more blade layers. Gerard (1984) has shown that one cannot calculate canopy light-absorbance by assuming a uniform layer of chlorophyll, but must account for the discrete

Table 2. Canopy shading. Method used to estimate fractional ocean-surface coverages by 0, 1, 2 and more blade layers in *Macrocystis pyrifera* model

Blades from a frond are assumed to avoid shading other blades on the same frond but to have a probability of shading or being shaded by blades from other fronds. The probability that any spot within a given ocean-surface area, A_T , is covered by a blade from the i th frond with blade area, A_i , in A_T is proportional to the fraction of the two areas, $f_i = A_i/A_T$; the probability that a given spot is not covered by blade i is $g_i = 1 - f_i$. For two fronds, 1 and 2, with areas A_1 and A_2 , the probabilities that each is at a given spot are f_1 and f_2 , respectively. The probability that both are at a given spot is $f_1 \cdot f_2$; the surface in A_T covered by both is $A_T \cdot (f_1 \cdot f_2) = A_1 \cdot A_2/A_T$. The probability of single coverage by either is the probability of coverage by either corrected for the overlapping areas, $(A_1 + A_2 - 2 \cdot A_1 \cdot A_2/A_T)/A_T = (f_1 + f_2 - 2 \cdot f_1 \cdot f_2)$. The probability that a given blade is in the second layer is $(A_1 \cdot A_2/A_T)/(A_1 + A_2) = (f_1 \cdot f_2)/(f_1 + f_2)$. Because any blade not in the second layer is in the first layer, the probability of a blade being in the first layer is simply $1 - (f_1 \cdot f_2)/(f_1 + f_2)$. The probability of a spot being uncovered is $g_1 \cdot g_2$. The probability of a blade being covered is, on average, the same as the fraction of blade that is covered.

This calculation can be extended to include as many fronds and fronds layers as are in a given area. However, because little light penetrates through more than three layers, only the fractional area covered by three or fewer layers need be calculated. If $G_i = (1 - g_i)/g_i$, α_j is the fraction of A_T covered by j blades, n is the number of blades in A_T ,

$$A_B = \sum_{i=1}^n A_i = \text{total blade area within } A_T \quad (T1)$$

$$\alpha_0 = \prod_{i=1}^n g_i \quad (T2)$$

$$\alpha_1 = \alpha_0 \sum_{i=1}^n G_i \quad (T3)$$

$$\alpha_2 = \alpha_0 \sum_{k=1}^{n-1} G_k \sum_{i=k+1}^n G_i \quad (T4)$$

The remaining fraction of space, $1 - \alpha_0 - \alpha_1 - \alpha_2$, is covered by three or more layers of blades.

If T is the fraction of light transmitted by a blade, the average fraction of incident light passing through the canopy is $\alpha_0 + \alpha_1 T + \alpha_2 T^2 + O(T^3)$.

The probability that a blade in the canopy is exposed to incident radiation, I , is $(1 - \alpha_0) \cdot A_T/A_B$, that exposed to $I \cdot T$ is $(1 - \alpha_0 - \alpha_1) \cdot A_T/A_B$, that exposed to $I \cdot T^2$ is $(1 - \alpha_0 - \alpha_1 - \alpha_2) \cdot A_T/A_B$, and so on. In this model, photosynthesis is calculated on the top three layers.

nature of blade tissue. The average light transmitted through the canopy is calculated in this model from the fractional coverage and light transmittance by the different layers of surface tissue (see Table 2). The fractional coverage information is also used to calculate the amount of photosynthesis in each of the top three canopy layers. Irradiance at each layer is corrected for the absorbance of the overlaying layers.

This technique is also used to calculate light transmission and photosynthesis in the sub-surface kelp

column. The fractional absorbance of the kelp column, k_{kelp} , is calculated at 1 m intervals throughout the water column.

Kelp plants are assumed to be planted in a grid with a spacing x . The area per plant, equivalent to A_T , is x^2 and is considered to be a plant's surface cell. Fronds can drape into the cells of other plants. Because all plants are assumed to be identical, any movement of one plant's frond into another surface cell is balanced by the movement of a third plant's frond into the first plant's cell. The model breaks the surface segment of each frond into sections x long, and adds each subsegment to the surface cell. For example, if a plant is in a grid with 1 m spacing and it has one frond with 2.5 m of tissue at the surface, the model would calculate that this is equivalent to three fronds in the surface cell, each with an area specific to its subsegment of the frond. Thus, a plant with 5 fronds at the surface could have the equivalent of 10 fronds shading each other.

Sub-canopy absorption

Light below the canopy can be absorbed by kelp plants and by suspended matter. Light absorbance by suspended matter, dI_{water} , over an infinitesimal depth interval, dz , is proportional to the light flux, I , to the extinction coefficient, k_{abs} , and to the path length, $dz/\cos(\theta)$:

$$dI_{\text{water}} = -k_{\text{abs}} I dz/\cos(\theta). \quad (7)$$

Light absorbance by a kelp column, dI_{kelp} , over dz is proportional to the irradiance through a vertical plane, $I \tan(\theta) dz$, the density of the kelp plants on the bottom, ρ , the cross-section (diameter) of the kelp-plant column σ , and k_{kelp} :

$$dI_{\text{kelp}} = -k_{\text{kelp}} \sigma \rho I \tan(\theta) dz. \quad (8)$$

The total rate of change of light vertically is given by

$$\begin{aligned} dI/dz &= (dI_{\text{water}} + dI_{\text{kelp}})/dz \\ &= -I \{k_{\text{abs}}/\cos(\theta) + k_{\text{kelp}} \sigma \rho \tan(\theta)\}. \end{aligned} \quad (9)$$

Because k_{kelp} changes vertically, the values of I are solved by numerical integration using a 1 m step-size.

Carbon production and consumption

The currency of this model is carbon. Carbon is produced by photosynthesis as a function of blade area and irradiance; carbon is consumed in respiration by blade and stipe tissue; carbon is lost to harvest and to frond death. Excess of production over consumption is used to make new tissue.

Photosynthesis

Photosynthetic rates are proportional to blade area and a function of irradiance. Photosynthesis by stipe tissue is

not considered. [Arnold and Manley (1985) showed that stipe photosynthetic rate per unit dry weight is small, about 5% of the rate for mature blade tissue.] The relevant light irradiance used is the flux perpendicular to the blade: downward irradiance for the surface canopy and irradiance perpendicular to the vertical for the sub-surface kelp column. The relationships are

$$P = P_{\text{max}} \quad \text{for } I > I_k, \quad (11a)$$

$$P = P_{\text{max}} I/I_k \quad \text{for } I \leq I_k, \quad (11b)$$

where P_{max} is the saturation photosynthetic rate per unit blade area and I_k is the saturation irradiance. Photosynthetic rate and irradiance are calculated for each blade layer of each frond in the canopy and in the kelp column.

Respiration

Respiration rates of blade and stipe tissues differ. Stipe tissue in the model respire at one-fourth the blade-tissue rate, R (Arnold and Manley, 1985). There is no provision made for holdfast respiration.

Growth

The daily net plant-production is used to form new tissue. The net production of all fronds in a plant is summed and then distributed among fronds for growth according to fixed rules. A new frond is formed whenever the shortest frond on a plant exceeds a critical length, here 0.7 m. When a frond attains the maximum allowed length, it ceases to grow. Fronds whose surface tissues have been harvested have lost their apical meristems and can no longer grow. There is no provision for holdfast growth. Gerard (1982a) has shown that holdfast growth accounts for only about 10% of the total plant growth. There is also no provision for carbon exudation, which has been shown to be small (Fankboner and deBurgh, 1977).

The primary approach to growth is to apportion carbon among growing fronds of a plant in such a way as to maintain constant length differences between fronds. The biomass of the i th frond, B_i , is a function of its length, L_i . The total plant biomass, B_T , is then

$$B_T = \sum_{i=1}^n B_i(L_i). \quad (12)$$

The increase in biomass of the i th frond is approximately given by

$$\Delta B_T = dB_i/dL_i \Delta L_i, \quad (13)$$

where ΔL_i is the elongation of frond i . The total growth (daily net production) is then given by

$$\Delta B_T = \sum_{i=1}^n dB_i/dL_i \Delta L_i. \quad (14)$$

For the standard case, length increases for all fronds are equal, $\Delta L_i = \Delta L$. Therefore

$$\Delta L = \Delta B_T / \left\{ \sum_{i=1}^n dB_i/dL_i \right\}. \quad (15)$$

This value of ΔL determines the new frond lengths.

This assumption about a constant difference between a frond and the next oldest frond does result in a size distribution that is generally similar to that observed. However, it forces an elongation rate that is constant for all growing fronds. Observations have shown that elongation is a function of frond length. North (1971b) and Coon (1981) described the fractional elongation per day using semi-logarithmic fits of the form

$$\Delta L/L = a + b \ln(L), \quad (16)$$

equivalent to

$$\Delta L = aL + bL \ln(L), \quad (17)$$

where a and b are constants for a given period and location.

Gerard (1982a) used a different description that was also a function of frond length:

$$\Delta L = c + d \ln(L), \quad (18)$$

where c and d are constants for a given period and location.

The difficulty with using such formulations in a model is determining the values of the constants a , b or c , d in any situation. Furthermore, one must have a way of initiating new fronds. North (personal communication) has found that the value of b in Eq. (16) tends to be constant; that periods of slow growth are reflected in changes in the value of a . The use of this relationship allows an alternate way to allocate biomass and length increases among fronds. Use of Eqs. (14) and (17) leads to

$$\Delta B_T = \sum_{i=1}^n a L_i dB_i/dL_i + \sum_{i=1}^n b L_i \ln(L_i) dB_i/dL_i, \quad (19)$$

$$a = \left[\Delta B_T - b \sum_{i=1}^n L_i \ln(L_i) dB_i/dL_i \right] / \sum_{i=1}^n L_i dB_i/dL_i. \quad (20)$$

This approach to allocating growth is used in what will be called the "log growth" model.

Frond death

A frond dies, taking its carbon with it, when it exceeds the pre-set frond life-span. Alternatively, a frond dies if it is a plant's oldest frond on a day when net production is zero or less.

Disturbances/harvesting

An important factor in the survival of a kelp plant is its ability to recover from tissue loss caused by external

Table 3. "Standard" values of model parameters for growth and harvest yield of *Macrocystis pyrifera*. Usual simulation is run for 825 d. Results presented for all cases except the "standard" case are those from second year onward

Parameter	Standard value
Latitude, L	33° N
Start day	90 d after winter solstice (equivalent to 19 Feb.)
Plant density, ρ	0.11 m ⁻² (3 m spacing)
Water absorbance, k_{abs}	0.115 m ⁻¹ (40 m path length for 1% light flux)
Blade absorbance, $(1 - T)$	0.70
Width of kelp column, σ	0.5 m
Length difference between a growing frond and the next longest frond	0.5 m
Water depth, Z	12 m
Maximum frond length, L_{max}	1.4 Z
Maximum frond life, l	180 d
Maximum photosynthetic rate, P_{max}	4.32 g C m ⁻² d ⁻¹
Blade respiration, R	0.0240 g C (g C d) ⁻¹
Saturation light intensity, I_k	150 μ E m ⁻² s ⁻¹

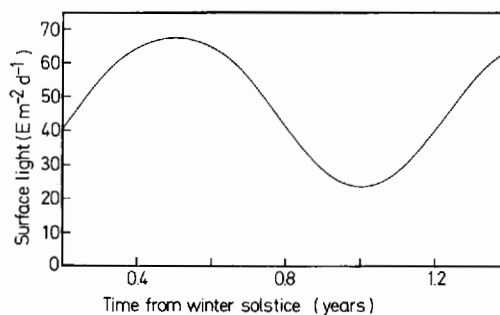


Fig. 1. Calculated daily downward irradiance just below the surface during a yearly cycle

events, such as storm damage or harvesting. This model uses harvesting as an example of such disturbance.

Commercial harvesting practice in California is to collect all kelp tissue within 4 ft (1.3 m) of the ocean surface (North, 1968). In this model, all tissue within 1 m of the surface is harvested. There are many possible strategies to decide when to harvest. The one used here is to harvest when the density of tissue at the surface exceeds a pre-set value. Harvested fronds in the model lose the ability to grow because they lose their apical meristems but do keep their subsurface tissue. Unharvested fronds continue to grow.

Standard values for parameters

The model results presented in this paper are variants of a standard set of assumed parameters (Table 3). The insolation is approximately sinusoidal, with minimum and maximum at 0 and 0.5 yr (0 and 182 d; Fig. 1).

The model is implemented in FORTRAN-77 and has been run on a DEC VAX-780 computer. The usual simulation is for 825 d, starting 80 d after the winter solstice. Results discussed for all cases except the standard case are actually those from the second year onward.

Simulation results

Results under standard conditions

Simulation of *Macrocystis pyrifera* growth under standard conditions for a period of 3 yr shows the expected strong seasonal cycle in growth, biomass, and production (Fig. 2). Results for the first year of the simulation depend on the initial state of the plant (Fig. 2A). A plant that starts with 20 fronds displays a different history for the first year than a plant that starts with 35 fronds. Results for the simulations are essentially the same after the first year. Results for the first year of subsequent simulations are discarded to reduce the effect of initial conditions. Further discussion of the standard conditions also ignores the first year.

All measures of plant size show large seasonal changes (Fig. 2A, B). The number of fronds on a plant varies from 36 to 76, total plant biomass varies from 0.79 to 2.49 kg C (27 to 85 kg wet wt), and the biomass of the surface tissue from 0.30 to 1.41 kg C (10 to 48 kg wet wt). These minima and maxima occur at times later than the insolation minimum and maximum: at 0.17 and 0.67 yr (61 and 246 d) for the kelp plant (Fig. 2B).

Measures of growth and plant production also show strong seasonal cycling, although with minimum and maximum at different times (Fig. 2C, D). Gross production ranges from 2.72 to 5.91 g C m⁻² d⁻¹ at 0.00 and 0.53 yr (1 and 193 d), net production from 0.65 to 2.47 g C m⁻² d⁻¹ at 0.95 and 0.37 yr (346 and 136 d), and specific growth rate (net production ÷ total biomass) from 0.003 to 0.022 d⁻¹ at 0.78 and 0.28 yr (283 and 102 d). The total annual net production is 537 g C m⁻² yr⁻¹ and the total annual gross production 1 567 g C m⁻² yr⁻¹.

The seasonal ordering of the maximum of these plant properties is that specific growth peaks early, followed by net production, gross production, and, finally, plant size. Gross production is nearly in phase with insolation, peaking almost at the same time. The early peaking of specific growth rate and then of net production indicates the early importance of self-shading and respiration on plant growth. The relative range of specific growth rate, net production, and gross production shows the same ordering, with specific growth rate showing the greatest relative variability.

Effect of frond life on results

To the extent that self-shading limits net production, shorter frond lifetimes should increase it. Setting frond lifetimes to 4 and 5 mo does in fact increase the annual

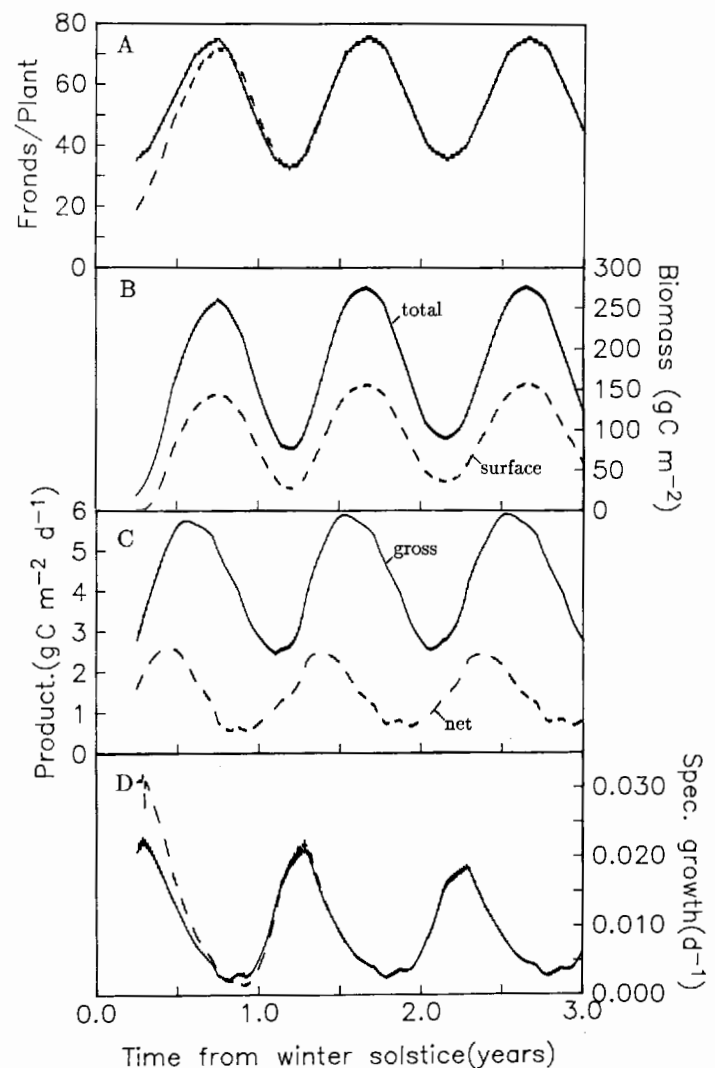


Fig. 2. *Macrocystis pyrifera*. Model results of "standard"-plant growth for period of 3 yr. Calculation starts 90 d after the winter solstice. It takes the simulation about 1 yr to equilibrate from the initial assumptions. This is clearly shown in (A), where simulations differ in the initial number of fronds. (A) Number of fronds/plant; continuous line, plant with 35 fronds initially; dashed line, plant with 20 fronds initially. (B) Biomass per unit area; continuous line, total biomass; dashed line, biomass in surface-meter of the water column. (C) Production rate per unit area. (D) Specific growth rate, calculated as net production rate ÷ total biomass; continuous line, plant with 35 fronds initially; dashed line, plant with 20 fronds initially

net production to 588 g C m⁻² yr⁻¹ for 5 mo and to 596 g C m⁻² yr⁻¹ for 4 mo fronds (Fig. 3). For the 5 mo case, this represents a production increase of 9% over the standard, case with little change in biomass. The increase over standard for the 4 mo fronds is not very different from that of the 5 mo case, but the biomass cycle is shifted back about 25 d.

Effect of plant density on results

Simulation of kelp growth for plant spacings of 2, 3 and 4 m⁻² (equivalent to densities of 0.25, 0.111 and 0.063

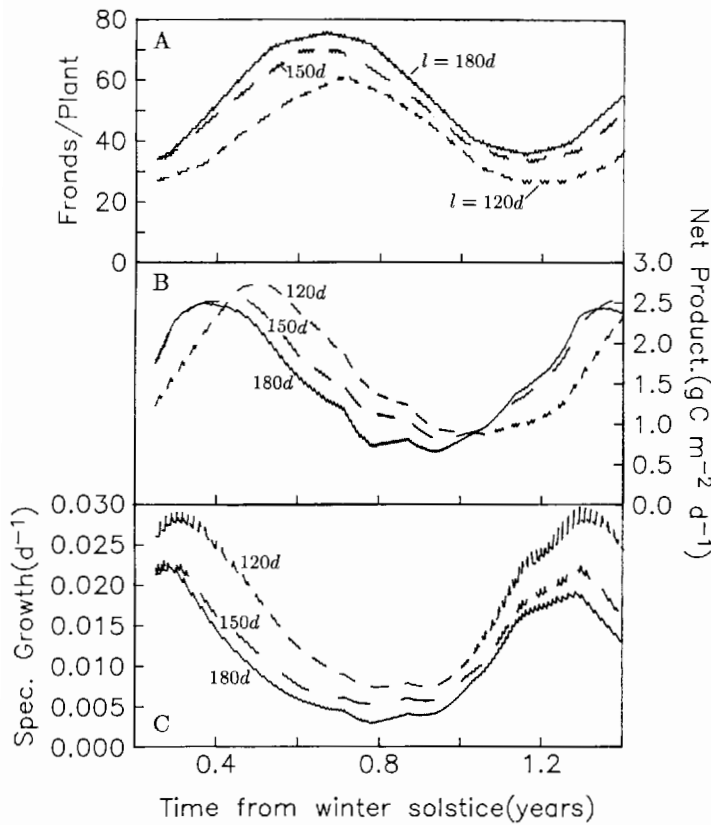


Fig. 3. *Macrocystis pyrifera*. Effect of frond longevity, l , on standard growth for plants with fronds living to 180, 150, and 120 d

plants m^{-2}) shows the way that kelp morphology and growth interact in unexpected ways (Fig. 4). Plants at the lower density grow larger, with as many as 120 fronds during the summer (Fig. 4A), compared to only 40 fronds at the high plant density. Biomass densities are higher at lower plant densities (greater plant spacing), with differences between the three densities being greater for surface biomass than for total biomass (Fig. 4B, C). This indicates that at the high plant densities more tissue is in the kelp columns. Gross production rates per unit area are nearly the same for all three plant densities (Fig. 4E) but net production is highest for most of the year for the low-density plants (Fig. 4D). Annual net productivities are 622, 537, and 503 $g C m^{-2} yr^{-1}$, for 2, 3 and 4 m plant spacing, respectively.

Given that gross production rates are essentially the same at the three densities, the plant with the lowest biomass should have the highest net production. What is surprising is that the plant with the highest net photosynthetic rate has the lowest biomass. The reason is that a smaller plant with fewer fronds has more recently produced tissue in its oldest frond than has a larger plant. When the oldest frond of a small plant dies, it removes newer tissue than does a dying frond on a large plant. As a result, tissue on a large number of small plants turns over more rapidly than that of a fewer number of large plants.

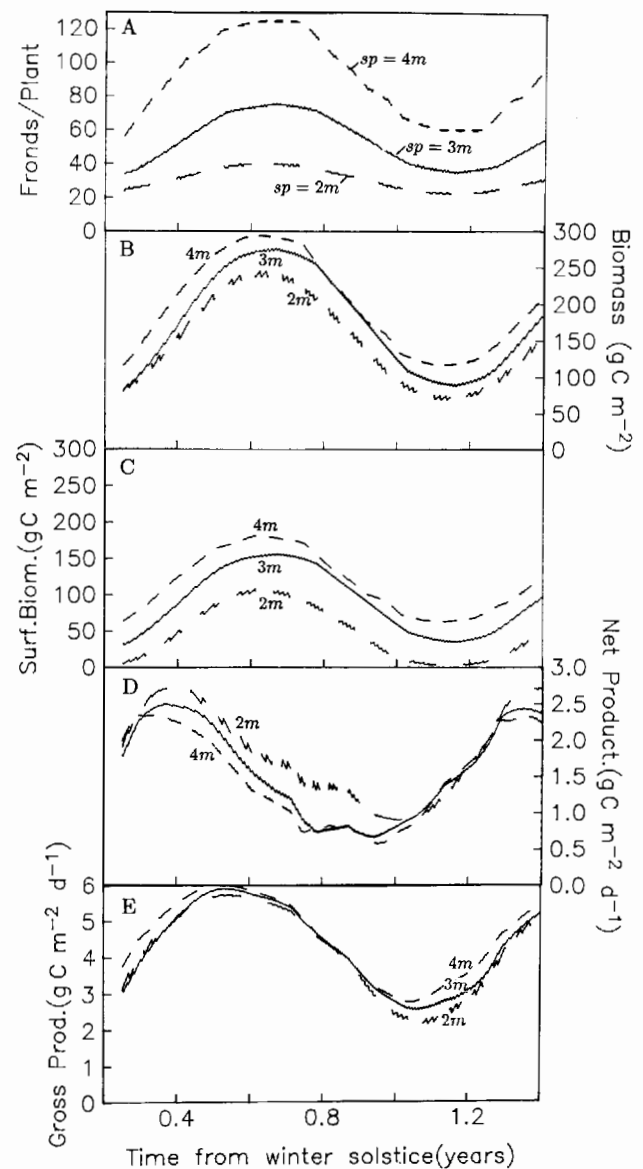


Fig. 4. *Macrocystis pyrifera*. Effect of plant density on standard growth for plant separation (sp) of 2, 3 ("standard" density), and 4 m, corresponding to densities of 0.25, 0.111, and 0.063 plants m^{-2}

Effect of bottom depth on results

Simulation of kelp growth over bottom depths of 6, 9, 12, 15, and 18 m shows that bottom depth can have a large effect on kelp plant size and growth (Fig. 5). The plant at 18 m has a negative net production and dies. The other plants have annual net productivities of 478, 506, 537, and 427 $g C m^{-2} yr^{-1}$ (6, 9, 12, 15 m, respectively). The plant at 6 m has the largest number of fronds, more than 160 fronds at maximum, followed by a maximum of about 100 fronds for the plant in 9 m depth. The total biomass of the plants at the two shallow depths are nearly the same, but both are larger than the biomasses of plants in deeper water, being nearly twice as much as that of the plant at 15 m. Because the maximum frond length is assumed to be

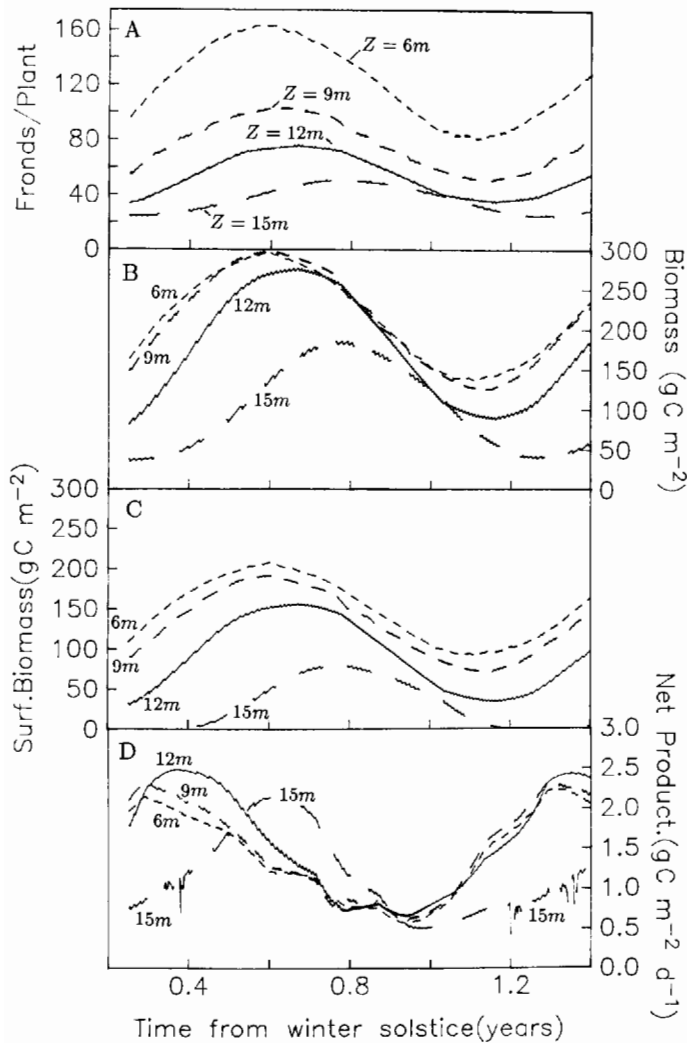


Fig. 5. *Macrocyctis pyrifera*. Effect of water depth (Z) on growth of plants in 6, 9, 12 ("standard" depth), and 15 m of water; a plant in 18 m-deep water displayed negative net production and died. Note that maximum frond length is set to 1.4 of the water depth for each case (Table 3)

40% greater than the water depth, a plant with the same biomass as a deeper plant has a larger number of the smaller fronds. The biomass and gross production of the 15 m plant are substantially below those of the three shallower plants. Increased depth shifts the maximum frond numbers, biomasses, and gross and net productions to times later in the year. Highest specific growth rate increases with depth. Net production over a year is largest for the 12 m plant.

Thus, differences in plant size and growth are greatest for plants growing in deepest water, where conditions can be marginal. The effects include lower biomasses and lower gross production and can include higher net production.

Effect of light absorbance by the water on results

Plants show less variability over a range of light-absorption values by the water (Fig. 6) than they do over the

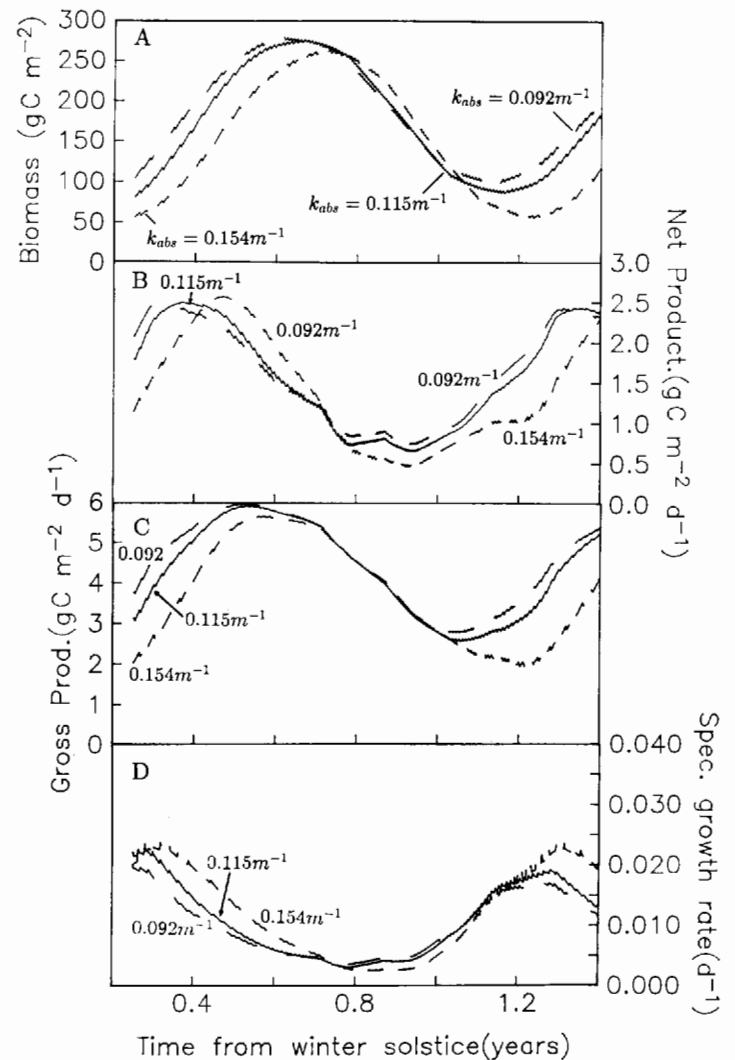


Fig. 6. *Macrocyctis pyrifera*. Effect of water absorbance (k_{abs}) on standard growth at $k_{abs} = 0.092$, 0.115 ("standard" absorbance), and 0.154 m^{-1} ; a plant at $k_{abs} = 0.230 \text{ m}^{-1}$ displayed negative net production and died. These absorbances correspond to distances of light extinction to 1% of 50, 40, 30, and 20 m, respectively

range depths. Kelp plants were grown at water absorbances of 0.092, 0.115, 0.154, and 0.230 m^{-1} , corresponding to distances for light extinction to 1% of 50, 40, 30, and 20 m, respectively. The plant in water with extinction coefficient of 0.230 m^{-1} promptly dies. The other plants have net annual productivities of 579, 537, and $488 \text{ g C m}^{-2} \text{ yr}^{-1}$ at 0.092, 0.115 and 0.154, respectively. Biomass and gross photosynthesis are greatest in the plant growing with the lowest extinction coefficient. All the observed plant properties occur later for larger extinction coefficients.

Effect of latitude on results

Plants grown at latitudes of 23° , 33° , 43° , and 53° N show a range of growth patterns (Fig. 7) (note that the results are the same N or S). Plants grown nearer the equator at 23° N show the smallest seasonal variation

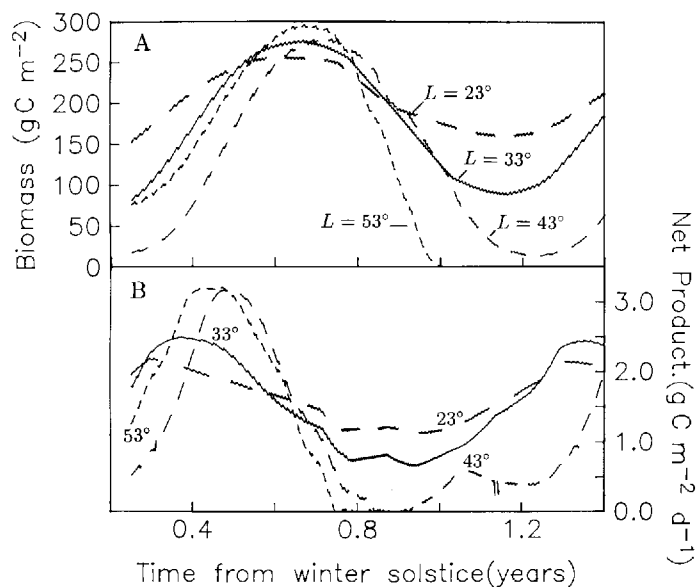


Fig. 7. *Macrocyctis pyrifera*. Effect of latitude (L) on standard growth at latitudes of 23°, 33° ("standard" latitude), 43°, and 53° N; the plant at 53° N died in less than one year, so results are not shown for this for the second year of the simulation

in growth and biomass, with biomass ranging from 157 to 253 g C m⁻² and daily net production ranging from 1.11 to 2.17 g C m⁻² d⁻¹. The intensification of winter minima to the north is great enough so that the plant at 53° N cannot survive the winter, dying before completing a full year cycle. The plant at 43° N does survive, but the winter biomass minimum (14 g C m⁻²) and negative net production is so low that this survival is marginal. This is despite the fact that the summer biomass and net production are higher than those for plants to the south. Annual net production decreases in the higher latitudes, being 572, 537, and 400 g C m⁻² yr⁻¹ at 23°, 33°, and 43° N, respectively. The effect is of greater seasonality at higher latitude.

Effect of harvesting on results

The effect of harvesting on plants grown at a range of depths shows the large difference that this disturbance can make (Fig. 8). The annual net production of these plants is down substantially from that of the unharvested plants, being 275, 254, and 125 g C m⁻² yr⁻¹ for 12, 9, and 6 m depths, respectively. Despite the importance of self-shading in limiting net production in unharvested kelp stands, the removal of the canopy does not lead to increased gross production because much of the light is uncaptured by the kelp, either passing to the bottom or being absorbed by the water. Harvesting causes a die-off of fronds because the high respiratory load of the kelp column is not matched by sufficient gross production to keep net production positive. The model kills fronds until net production becomes positive. The loss of tissue is greatest for the plant in shallower water at 6 m. While the

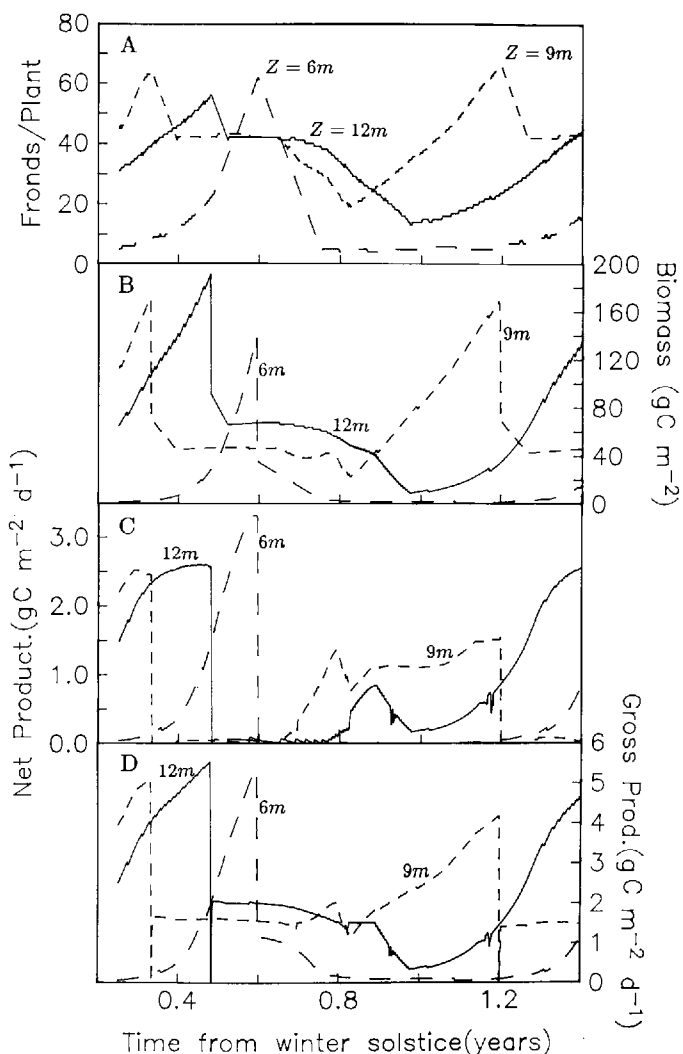


Fig. 8. *Macrocyctis pyrifera*. Effect on standard growth of harvesting when surface biomass reaches 100 g C m⁻², for plants in 6, 9, and 12 m ("standard" depth) of water. Sharp drops in biomass and productivity occur when the plant is harvested

number of fronds per plant exceed 160 in the unharvested 6 m plant, there are at most 60 fronds in the harvested plant.

Effect of log growth on results

Apportioning growth among fronds using the log growth formula increases the biomass and changes the timing and magnitude of net production of kelp grown under otherwise identical conditions (Fig. 9). Few fronds in the log growth plant were small. Near the summer solstice on Day 176, only 4 of 69 fronds were less than the maximum allowed; near the winter solstice on Day 356, only 4 of 40 were less than maximum. The allocation of growth in the standard model by giving each frond the same length increment maintains a relatively constant distribution of frond lengths. An attempt to change the frond-length

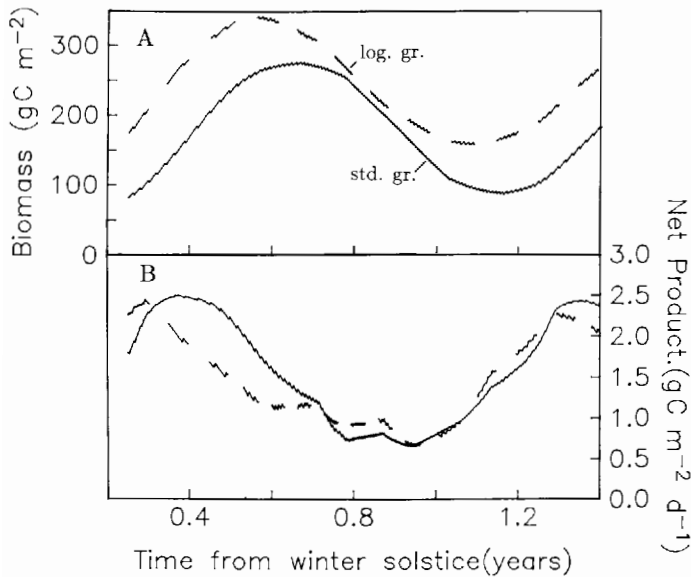


Fig. 9. *Macrocyrtis pyrifera*. Effect on results of using log growth to allocate growth among fronds. Continuous line, standard case of equal growth; dashed line: log growth

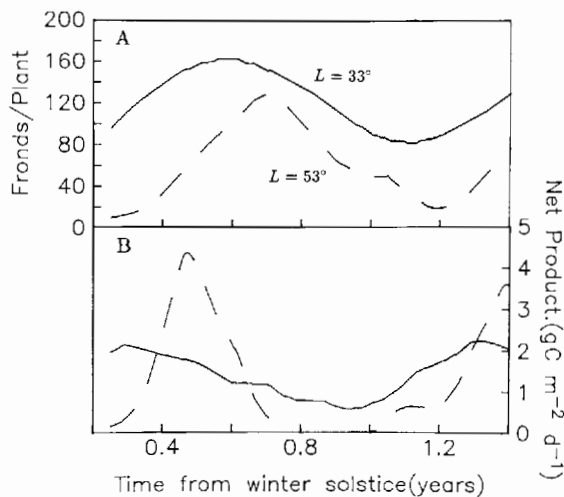


Fig. 10. *Macrocyrtis pyrifera*. Effect of depth on a plant grown at latitude of 53° N. Continuous line: plant grown in 6 m depth under otherwise standard conditions at 33° N; dashed line: plant grown at 53° N in 6 m depth

distribution by changing the frond-initiation cue from the shortest frond reaching 0.7 to 0.4 m failed when the plant died.

Simultaneous variation of more than one parameter

Because this is a light-limited model, all of the parameters varied thus far affect the plant by changing the light field around an individual plant. For a given location, parameters such as light extinction and latitude are externally determined, but parameters such as plant density and, to

Table 4. Effect on model results for kelp plant size and net production of a 10% increase in a model parameter. Values show percentage increase/decrease compared to standard values

Parameter	Total biomass		Production			
			Daily net		Annual	
	max.	min.	max.	min.	net	gross
Maximum photosynthetic rate, P_{max}	16%	26%	12%	6%	12%	17%
Saturation light intensity, I_k	-3	-19	-2	-12	-5	-6
Respiration, R	-11	-30	-4	-18	-11	-8
Water absorbance, k_{abs}	-1	-13	0	-9	-2	-3
Blade absorbance, $(1 - T)$	-17	-32	-9	-22	-15	-19
Kelp column width, σ	1	4	1	3	2	2
Max. frond length, L_{max}	-2	-6	6	15	6	0
Max. frond life, l	4	-1	0	-25	-6	1
Length interval between fronds	2	8	-2	3	0	3

some extent, depth, are determined by plant-community responses. Some of the conditions chosen have been extreme enough so that plants did not survive. Can a kelp-stand compensate for such extreme conditions? In some cases, yes. Conditions under which plants die are the case of a high extinction coefficient of 0.230 m^{-1} , the case of a depth of 24 m, and the case of a latitude of 53° N. Decreasing the plant density from 0.111 to $0.063 \text{ plants m}^{-2}$ allows a plant to live with the extinction coefficient of 0.230 m^{-1} , but not at 53° N or in 24 m of water. Growing the plant at a latitude of 53° N at the shallower depth of 6 m rather than the standard 12 m allows it to survive the winter, although only barely (Fig. 10).

Sensitivity of model results to small parameter changes

As a way of testing the sensitivity of model results to the values of the standard values, the model was run for the value of a parameter 10% larger than the standard value. Results are expressed as the percentage increase or decrease of biomass and net production minima and maxima and of annual production (Table 4).

Biomass and net production minima are more sensitive to parameter changes than their respective maxima (Table 4). Results are most sensitive to changes in light absorbance by a blade, with a 10% increase in blade absorbance resulting in a 32% decrease in minimum biomass and 22% decrease in minimum net production. Note that a 10% increase in blade absorbance from 0.7 to 0.77 represents a 23% decrease in blade transmittance (T), from 0.3 to 0.23. The next most sensitive set of parameters are the respiration and photosynthetic rate parameters: R , P_{max} , and I_k . Changes in the maximum frond length and maximum frond age primarily affect the minimum net production, with longer fronds increasing minimum net production by 15% and longer-lived fronds

decreasing it by 25%. Results are much less sensitive to changes in the plant descriptors of kelp column-width and the length intervals separating fronds.

A plant grown under otherwise standard conditions with the higher respiration rate of 0.084 d^{-1} reported by Arnold and Manley (1985) dies.

Discussion

How do the simulation results compare with observed kelp stands? *Macrocystis* spp. biomass rarely shows the simple seasonal cycling that the model predicts. Kirkwood (1977) observed a roughly sinusoidal variation in frond density of *M. pyrifera* through the year off Los Angeles similar to that of the model. Coon (1981) noted that *M. angustifolia* plants in the Santa Barbara area are "typically larger and heavier in the spring and in the summer". However, other field studies, such as those of Gerard (1976: *M. pyrifera*) and of Zimmerman (1983: *M. pyrifera*) do not show simple seasonal cycling in biomass or production. Given the large number of factors that can affect kelp production, including water clarity and nutrient concentration (e.g. Jackson, 1977; Harger, 1979; Zimmerman and Kremer, 1984), this is not surprising.

The field observations that come closest to those of the model are for another seaweed, *Laminaria pallida*, off the coast of South Africa (Dieckmann, 1980). There, the peak elongation rates preceded the peak-radiation flux by times on the order of months. In addition, the peak-elongation rates in shallow water, there 8 m, preceded those of algae in deeper water, at 14 m. These are the same results as those of the model for *Macrocystis pyrifera*.

There is field evidence that biomass density and growth rates in *Macrocystis pyrifera* are related. Data of Gerard (1976) showed an inverse relationship between biomass density and specific growth rate. Similarly, Neushul (1984) has shown that kelp plants grown at too high a density tend to decrease their frond densities while those grown at lower densities will increase their frond densities. Both sets of results show that light-limitation as reflected in density-dependence of growth is an important factor in kelp growth.

Comparisons of predicted gross and net production rates are more difficult because there have been many ways to measure production that are not strictly comparable. One type of estimate, that using incubations of isolated parts at the surface and the extrapolation to the whole plant (e.g. Sargent and Lantrip, 1952; Druehl, 1984), differs from that made by this kelp model only in the elaborateness of the light model. ^{14}C incubation measurements, such as those of Towle and Pearse (1973), do not account for respiration and are best considered measures of gross production. *In situ* measurements of oxygen evolution are probably the best measures of net production.

Peak gross production rates in the model were $6.0 \text{ g C m}^{-2} \text{ d}^{-1}$ for growth off San Diego. Towle and Pearse found a production rate in a dense stand off Monterey, California, of $6.8 \text{ g C m}^{-2} \text{ d}^{-1}$. These sets of values compare well.

Gross production rates calculated from measured changes in oxygen concentrations in the water column tend to be higher, but uncertainties about the currents during the measurement period cast doubt on them. Jackson (1977) estimated a gross production of $9.5 \text{ g C m}^{-2} \text{ d}^{-1}$ for *Macrocystis pyrifera*; McFarland and Prescott (1959) estimated a gross production rate equivalent to $12 \text{ g C m}^{-2} \text{ d}^{-1}$ for the same species.

Specific growth rates for plants have been calculated from measurements of biomass standing stock and production. Gerard (1976) calculated specific growth rates ranging from 0.011 to 0.025 d^{-1} from monthly biomass accumulation; Coon (1981) calculated average specific growth rates of 0.014 and 0.009 d^{-1} from frond elongation data and 0.009 and -0.002 d^{-1} from projected weight changes for plants in spring and fall. Specific growth rates in the model were generally between 0 and 0.02 d^{-1} , although more extreme conditions, such as harvesting or growth in high latitudes could increase it.

Thus, the magnitude of the production rates and specific growth rates of the model agree with those of field measurements, but the timing of field minima and maxima are often different. Such differences can occur because of other factors important in regulating kelp growth and biomass are not incorporated in the model. Zimmerman and Kremer (1984) have shown the importance of such short-term fluctuations in the case of temperature-nutrient concentrations.

Specific growth rates

The changes in specific growth rate offer a convenient measure of the extent to which photosynthesis in a kelp plant is being affected by nonmaximal irradiances. Lamina tissue at saturated light intensity photosynthesizes at an instantaneous rate of P_{max} equivalent to $0.372 \text{ g C (g C lamina)}^{-1} \text{ d}^{-1}$. Because half the mass of kelp frond is stipe tissue, this is equivalent to $0.186 \text{ g C (g C frond tissue)}^{-1} \text{ d}^{-1}$. The respiration of the lamina is 0.0240 d^{-1} , that of the stipe tissue is one-quarter this rate. As a result, the frond tissue respiration averages 0.015 d^{-1} . For a 12 h photosynthetic day, the gross production is $0.093 \text{ g C (g C d)}^{-1}$ and the net production is 0.078 d^{-1} . This value is an estimate of the maximum specific growth rate.

The specific growth rates here were typically highest 0.3 to 0.4 yr after the winter solstice, before maximum biomass but also before maximum insolation. The maximum specific growth rate for most situations was typically 0.025 d^{-1} or less. Greater specific growth rates only occur for situations with large biomass fluctuations, including the growth at Latitude 43° N (about 0.033 d^{-1}) and the growth of harvested plants (about 0.053 d^{-1} for the plant

in 6 m depth). The lower specific growth rates for the other cases suggest that there is a fair amount of shading of kelp plants by the fronds in the canopy, fronds in the kelp column, and absorption by the water.

Experimental confirmation of this comes from the work of Gerard (1976), who monitored monthly production of a natural stand of *Macrocystis pyrifera* near Monterey, California, for a period of 21 mo. Her results showed specific growth rates correlated with the biomass density (Gerard, personal communication), extrapolated to 0.023 d^{-1} at $0 \text{ g wet wt m}^{-2}$ and 0.010 d^{-1} at $6.9 \text{ kg wet wt m}^{-2}$ (equivalent to 200 g C m^{-2}).

Latitude effects

The effects of latitude on kelp growth are particularly striking because they correspond to observed patterns of seaweed growth. This kelp growth model shows that kelp growth becomes extremely seasonal, with biomass decreasing and, ultimately, disappearing in 12 m of water at higher latitudes. Kelp survives the year at 43° N only in shallow water. Members of the genus *Macrocystis* do move to shallower water in higher latitudes. Off Southern California (latitude about 34° N), *M. pyrifera* has been reported in water as deep as 70 m (North, 1971 a), and off British Columbia at a latitude of about 51° N the outer edge of a *M. integrifolia* bed is typically 3 to 4 m deep (e.g. Coon, 1982). The difference is quite understandable as a response to the annual light regime at higher latitudes.

The increasing seasonality of production and the increasing differences between summer and winter plant size at higher latitude suggest that it is not advantageous to be a perennial plant in these high latitudes in deeper water. This may explain the frequent displacement of the perennial *Macrocystis* spp. by normally annual *Nereocystis luetkeana* in deeper water along the western North American coast.

Light limitation vs nutrient limitation

Nutrient limitation is often considered to be the most important constraint on the growth of kelp (Jackson, 1977; Gerard, 1982b; Zimmerman and Kremer, 1984) as well as other seaweeds (e.g. Mann, 1982) when studied from the aspect of production. However, ecological studies of algal competition (e.g. Dayton *et al.*, 1984), of juvenile recruitment (e.g. Dean and Jacobsen, 1984; Deysher and Dean, 1984), and of intertidal seaweeds (e.g. Cousens, 1985) frequently conclude that algal shading to be most important in limiting algal populations.

Light limitation of growth by an algal population has two aspects. The first, the limit placed on gross production, could be considered an energetic or physiological limit. The second, the limit on net production placed by algal respiration, is more of an ecological limit. With

either energetic or ecological limits, there is a boundary to the maximum production rate per unit ocean surface.

Nutrient limitation takes a different form. There are no published examples of algal stands that deplete the water of nutrients. Rather, nutrient limitation implies the rate at which an algal population can extract nutrients from waters whose nutrient concentrations are determined elsewhere, presumably by phytoplankton. Because seaweeds can take up nutrient through most of their tissue, nutrient limitation is usefully considered as a relationship between the specific uptake rate and the nutrient concentration. Doubling the seaweed density doubles the nutrient uptake per unit ocean-surface area while maintaining the specific uptake rate. Thus, nutrient limitation on production is a limitation on specific growth rate, not on absolute production.

Winter growth in the various seaweeds is frequently believed to be light-limited during high-nutrient winter conditions and nutrient-limited during summer conditions (e.g. Chapman and Craigie, 1978; Chapman and Lindley, 1980). Because light-limited winter conditions can constrain the absolute amount of biomass when a population enters the nutrient-limited season, perhaps it is best to consider production as a combination of light and nutrient limitation.

Improvements to the model

This model is a simplified description of a kelp plant. Most of this simplification is caused by the lack of sufficient information on other important aspects of its biology and ecology. Aspects to include in the future are:

(1) Adaptation of blades to lower irradiances. Gerard (1986) has shown that photosynthetic tissue growing below the surface has a different $P-I$ (production–light intensity) relationship than canopy tissue. This difference is a reversible adaptation to light levels. Given a way of relating average irradiance to $P-I$ parameters, this effect could be put in the model. Adding this effect should cause a higher gross photosynthetic rate.

(2) A more accurate partitioning of growth in fronds. Attempts to use the log growth rule resulted in extremely skewed frond-length distributions. With more information on frond initiation, this approach could be improved.

(3) A more elaborate description of tissue disappearance. Lamina-tissue disappearance is also caused by fish and invertebrate grazing and by microbial infection. Inclusion of such loss would decrease self-shading and respiration values and could result in higher annual net production.

(4) A more elaborate description of insolation. Clouds frequently block the sun, lowering irradiance and changing the angular distribution of radiance. Inclusion of such effects should result in lower production results.

(5) Nutrient effects. Including nutrient uptake as a regulator of kelp growth should allow results that are more directly comparable to results from field situations.

Conclusion

The *Macrocystis pyrifera* model discussed here uses a simple description of the light field around a plant to predict kelp growth. Despite this simplicity, it does give results for biomass and production which are in general agreement with field measurements and which can be interpreted to provide insights into kelp ecology. These results emphasize the need to account for environmental parameters such as plant density, depth, and latitude when comparing results from different locations. Further development of the model to encompass other aspects of the environment in conjunction with field experiments promises to be useful for understanding kelp ecology.

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