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Ecological Modelling 154 (2002) 121–133

ECOLOGICAL MODELLING

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Simulation of alternative management strategies for red algae, luga roja, (*Gigartina skottsbergii* Setchell and Gardner) in southern Chile

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Received 5 July 2001; received in revised form 4 January 2002; accepted 4 March 2002

Abstract

The objective of this study was to examine the response of a *Gigartina skottsbergii* population, a commercial red algal species from southern Chile, to different management strategies using a simulation model. The impact of present harvesting techniques, varying the recommended size at harvest and the rate of harvest were evaluated. Model development followed Grant et al. (Ecology and Natural Resource Management: Systems Analysis and Simulation. Wiley, New York, 1997) and the data base was obtained from available literature. The model simulates population dynamics of *G. skottsbergii* and in terms of both number of fronds and biomass per size class. Model predicts an annual pattern of variation for biomass determined by variations in seasonal factors. However, biomass has a 2 year cycle of alternate years with high biomass and low biomass. This production cycle can be attributed to changes in population size structure and density, and to the existence of discrete recruitment events. Results predicted from using different management strategies suggest that commercial harvest should be based on selection for larger fronds and restricted harvest period. Under this scenario harvest rate can be relaxed since no important changes in harvest biomass were predicted when increasing harvest rate from 50 to 90%, at least in the short term. However, it is recommendable to keep it low (50%) as a preventive mechanism, since results suggest that in the long term, a harvest rate of 50% could produce larger harvested biomass. The existence of a biennial cycle of biomass production suggests that populations should be harvested in rotation. Several aspects of the model must be improved in order to obtain better prediction of both specific values as well as dynamics. These include winter recruitment, frond breakage, longevity of larger sized fronds, and a more complete analysis of changes in the size structure of the population.

Keywords: *Gigartina skottsbergii*; Population dynamics; Simulation model; Size structure; Management strategies

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1. Introduction

Gigartina skottsbergii, Setchell and Gardner (1963), (Rhodophyte) is a common red algal species to the subcanopy of *Macrocystis pyrifera*

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PII: S0304-3800(02)00054-6

forests in southern Chile (Santelices and Ojeda, 1984; Westermeier et al., 1995, 1997; Zamorano and Westermeier, 1996). It is abundant at sheltered sites, on rocks, stones or pebbles between 5 and 30 m depth (Westermeier, 1981). It is distributed from the Valdivian Coastline to Cape Horn (Westermeier and Ramírez, 1981), and on the coasts of the Falkland and Kerguelen islands.

G. skottsbergii is an algae of economic importance as a raw material for the production of carrageen and sulphated polysaccharides. This algae, along with other species of red algae, such as *Sarcothalia crispata* and *Mazzaella laminaroides*, are harvested as a single group. During 1999, landings of this group in the Xth Region reached 8% of the total seaweed landings for the country (Anuario Estadístico de Pesca, 1999). The Xth Region (39°16′S, 76°47′W–44°04′S, 72°33′W) corresponds to one of the 13 territorial units for administration by the government and represents 8.85% of the national territory. The resource is an important source of employment, especially for the small fishing communities in the Xth Region where most of the entire domestic production of *G. skottsbergii* comes from. This has led to both over-harvesting of populations in the area and the need to explore new harvesting areas (Westermeier et al., 1995; Westermeier and Sigel, 1997). Currently, fronds 20 cm^2 and up are harvested during spring and summer. The lack of size selective harvesting can lead to reduced harvests in the future because of both decreasing reproductive potential of the population and a dominance of smaller sized fronds (Westermeier et al., 1999). Therefore, it is important to develop management strategies that will allow sustainable use of this resource. Integration of biological, ecological, social and economic information on this seaweed is basic for the success of any management program.

This study brings together biological, ecological and management information; economic and social aspects have been excluded and will be considered in subsequent studies. Within this framework, the main objective of the present study is to examine the response of a *G. skottsbergii* population to different management strategies using a simulation model. The impact of present harvesting techniques were assessed and compared to the size selective harvest proposed by Westermeier et al. (1999). The effect of varying the recommended size at harvest and the fraction of biomass allowed to be harvested per time interval was simulated.

The results of the model will allow a comparison of different management strategies and their effectiveness based on a conceptual framework that brings together biological, ecological and management aspects. Information obtained through this model will improve our understanding of *G. skottsbergii* population dynamics and will help the decision-making process regarding management of the species.

2. Overview of the model

The present study focuses on a natural *G. skottsbergii* population of approximately 1.0 ha and 15 ± 1 m depth, located in Calbuco, Xth Region, Chile (41°43′S; 73°05′W), a wave sheltered area. *G. skottsbergii* is a perennial seaweed with a tri-phasic life cycle and alternating isomorphic generations. The three phases of *G. skottsbergii*'s life cycle are carposporic, tetrasporic and the gametophytic phase (Kim, 1976; Mumford, 1977). Along the southern Chilean coastline the seaweed's three life cycle phases occur simultaneously, varying only in the percentage in density and total biomass of each phase (Westermeier et al., 1995, 1997; Zamorano and Westermeier, 1996). In the Calbuco area, the carposporic phase greatly increased during autumn and winter and the tetrasporic phase peaked in spring–summer, as a result of two recruitment events (Westermeier et al., 1999): one occurring in winter as a result of spore release from caposporic fronds and giving rise to tetrasporophytic fronds, and the other occurring in summer as tetraspores are released from tetrasporophytic fronds producing gametophytic fronds. In Calbuco, the highest growth rates of *G. skottsbergii* occurred during December and frond mortality rates varied according to size, with higher mortality in smaller plants (Westermeier et al., 1999).

The model of the *G. skottsbergii* population simulates population dynamics in terms of both number of fronds and biomass per size class from the recruit to adult stages. Fig. 1 shows a simplified version of the model. The diagram shows the algae's life cycle and driving variables (season, temperature, environment and management strategy) affecting processes involved in the life cycle (spore production, settlement, germination, survival and growth). Settlement and germination estimate number of spores settling and germinating each time interval, respectively. Mortality for these two stages was excluded since there is no information available. Juvenile and adult stages are susceptible to be harvested, therefore two sources of mortality are included: natural and harvest mortality. When harvesting is not allowed, predicted dynamics result from spore production, affected by season, settlement and germination (temperature-dependent), and survival and growth, dependent on the environment variable (which groups together all possible processes involved in frond growth and survival). When harvesting is allowed, harvest mortality for each size class is determined by the management strategy, which includes month of the year in which harvest would be allowed, size class allowed to be harvested (legal size class), and harvest rate. Adding harvest mortality for all legal size classes provide total harvested biomass.

3. Materials and methods

3.1. Model description

The model was developed following the four phases described by Grant et al. (1997): conceptual model formulation, quantitative model specification, model evaluation and model use. The

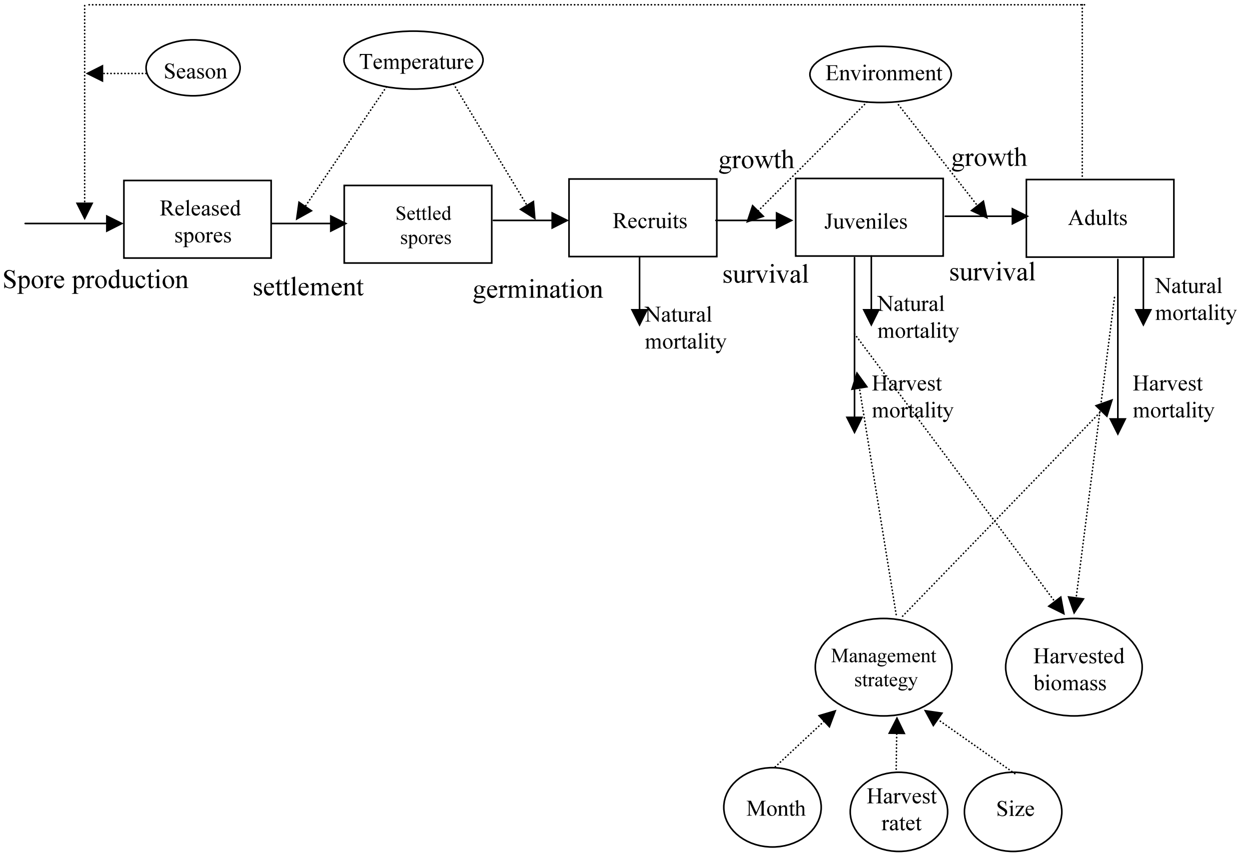

Fig. 1. Overview of the conceptual model representing population dynamics and management of *G. skottsbergii*.

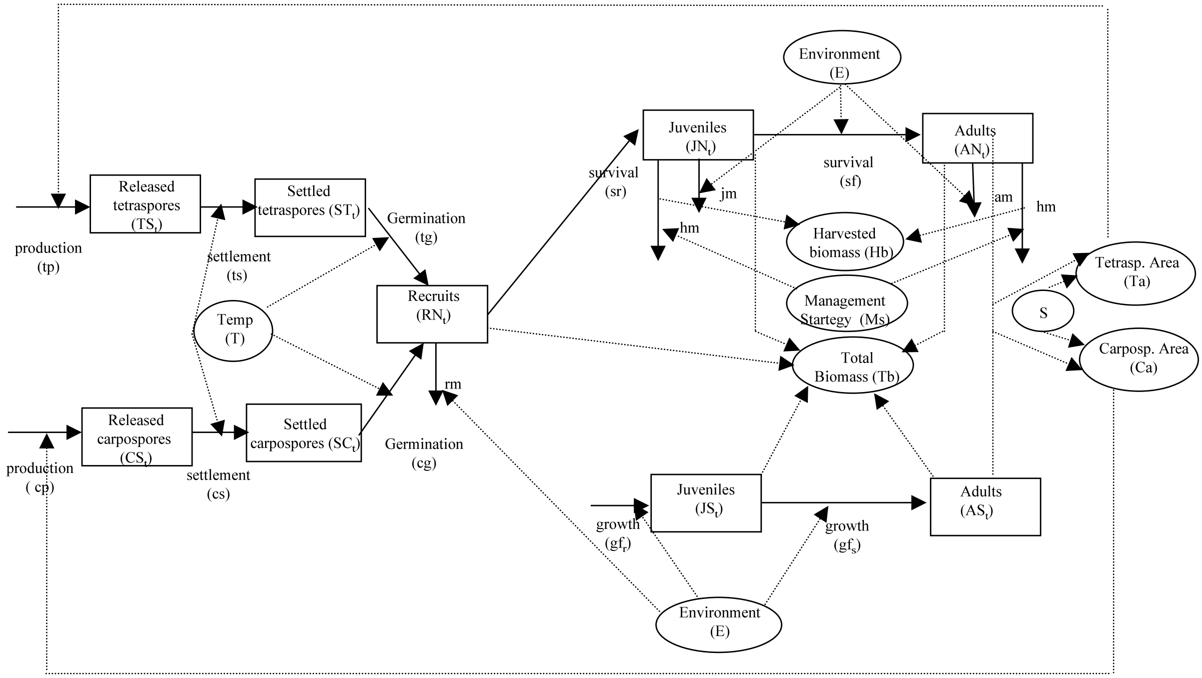

Fig. 2. Diagram showing the processes included in the modelling of population dynamics of *G. skottsbergii* and the relationships among management variables and *G. skottsbergii* population dynamics to simulate management of this population. Notation and symbols used in the diagram are explained in Section 3.2.

first three phases are described in this section, and model use is presented in Section 5. The model is multivariate and deterministic, uses a compartmental model structure based on difference equations, and was developed using Stella®II software (High Performance Systems, 1998). One month was the time step chosen for model development to take advantage of temporal resolution of data available for parameter estimates. In addition, this temporal resolution provides the needed flexibility to simulate different environmental and management scenarios.

The modelling terminology used throughout the text and in Fig. 2 follows that used by Grant et al. (1997). State variables are represented as boxes and double upper case letters, driving variables as circles and single upper case letter, auxiliary variables as circles and an upper and a lower case letter, material transfers as solid arrows and double lower case letters. Time subindices for material transfers are omitted because they always occur during the time interval t to $t+1$. Information transfers are represented as dotted arrows. A subindex "s" is used to indicate that the variable includes several size classes. Parameters are denoted by a Greek letter.

Qualitative and quantitative information for model development was obtained from both literature available for *G. skottsbergii* growing in Calbuco and laboratory experiments. Monthly monitoring carried out from July 1995 to April 1997 by Westermeier et al. (1999) regarding size and number of marked plants belonging to Class I (22–50 cm^2) and Class IV (< 150 cm^2) provided size specific growth and mortality estimates.

Growth rate was estimated as the percentage of monthly growth in size (cm^2) for an average plant of a given size during a time interval of 1 month (Table 1). Given the facts that (i) recruitment takes 7 months and (ii) simulated life span for the algae is 32 months, the model predicts the occurrence of a population having 24 sizes during a given time unit. Using these 24 estimates, size classes can be defined in a flexible manner. For example, biomass of a given size class can be calculated adding the biomass predicted for all the state variables whose predicted size falls inside the size class limits. Mortality rate was estimated as the percentage of plants of a given size dying during the time interval of 1 month (Table 1). Estimates of growth and mortality rates began at the smallest size classes (22–50 cm^2) and ended when these fronds achieved 150 cm^2. To estimate growth and mortality rates for fronds larger than 150 cm^2 it was necessary to use data collected for the largest size class (>150 cm^2). The 2-year sampling period did not provide the time required for a recruit frond to reach the maximum size reported in Calbuco, approximately 1000 cm^2 (Westermeier et al., 1999).

Table 1
Monthly growth and mortality rates for a *Gigartina skottsbergii* frond from recruitment to death estimated from field data collected in Calbuco, Xth Region, Chile

Growth rate (cm^2/month) for fronds first month after recruitment* to 24 months after recruitment**	Mortality rate (fronds/month) for fronds first month after recruitment* to 24 months after recruitment**
0.3632*	0*
0.2897	0.275
0.1724	0.207
0.267	0.174
0.5788	0.105
0.5734	0.059
0.1226	0.062
0.0499	0.067
0	0.071
0.0420	0.077
0.093	0.167
0.155	0.100
0	0.111
0.2268	0.150
0.2056	0.118
0.263	0.100
0.3528	0.074
0.2977	0.080
0.0738	0
0.0525	0.043
0	0.045
0.0584	0.048
0.0897	0.100
0.1286**	0.056**
	1

Growth and mortality rates are assumed to reflect the effect of all environmental factors (E) and are the same for algae in any of the three life cycle phases.

Since *G. skottsbergii* fronds can be seen by a collector at a size of approximately 18–22 cm^2, this size category was assumed to be the size of recruits (Westermeier, personal communication). Growth and mortality estimates were assumed to reflect all environmental factors. In the specific case of growth rate, it is presumed that most of the variations in time are due to temperature variation, which should be reflected in the seasonal growth pattern.

Parameter estimates used for model's quantitative specification, their bibliographic source and their relationships with the corresponding variables are indicated in Table 2. The annual temperature cycle was obtained from monthly temperatures recorded in Calbuco by Westermeier et al. (1999) during 1996 and 1997.

3.2. Conceptual and quantitative model development (Fig. 2)

G. skottsbergii's life cycle begins with tetraspores and carpospores released by mature fronds. Released tetraspores per month (TS_t) is estimated as tetraspore production (tp) minus tetraspore settlement (ts). Spore mortality has not been included because there is no information available. The model assumes that temperature (T) is the only variable controlling settlement. Thus, when temperature is not appropriate, settlement rate equals zero and tetraspores remain in the system until temperature become appropriate to settle. Tetraspore production is defined as the sori production per unit area of thallus (ω, Table 2) of mature tetrasporophytic fronds (Ta) times tetraspores produced per sori (α, Table 2). Settlement (ts), defined as the number of released tetraspores times the settlement rate (λ, Table 2), is dependent on water temperature, and it is used to estimate settled tetraspores (ST_t). Through germination (tg), which is temperature dependent (Table 2), settled tetraspores became recruits (RN_t). The same procedure is followed to estimate the number of recruits produced from carpospores, using however, the carposporophytic

Table 2
Quantitative specification for model parameters, bibliographic source for qualitative and quantitative information and relationships between parameter and driving variables.

Parameter	Quantitative specification	Source
Sori production per unit of area of thallus (ω)**	S-Winter $= 1.91/\text{cm}^2/\text{month}$ S-Spring-summer $= 4.16 \times 10^{-4}/\text{cm}^2/\text{month}$	Westermeier and Sigel (1997)
Tetraspores produced per sori (α)**	1 Tetrasporangia = 3000 tetraspores/month	Sigel (personal communication)
Carpospores produced per sori (α')**	1 Cystocarp = 5000 spores	Sigel (personal communication)
Tetraspore and carpospore settlement rate (λ)**	$9.5 \leq T \leq 11.7 = 0.22$ spores/month $T < 9.5 = 0$ $T > 11.7 = 0$	Westermeier and Sigel (1997)
Tetraspore germination rate (μ)**	$5.5 \leq T \leq 11.7 = 0.13$ spores/month $T < 5.5 = 0$ $T > 11.7 = 0$	Westermeier and Sigel (1997), Buschmann et al. (1999)
Carpospore germination rate (μ')**	$9.5 \leq T \leq 11.7 = 0.07$ spores/month $T < 9.5 = 0$ $T > 11.7 = 0$	Westermeier and Sigel (1997) Buschmann et al. (1999)
Conversion factor for biomass estimates (σ)*	cm^2 0.0074	Bhattacharya (1985)

* Indicates data collected from field.

** Indicates data collected from laboratory experiments.

T = temperature, S = season of the year.

phase parameters (Table 2). Recruit mortality (rm) depends on the environment variable (E), and surviving recruits (sr) became juvenile fronds. Recruit size (18–22 cm^2) is reached 7 months after spore germination (Westermeier et al., 1999). There is no information on growth for fronds smaller than 18 cm^2 that would allow size-specific estimates for this part of the algae's life cycle. Once fronds have recruited the processes of growth (cm^2) and survival are represented separately using two series of states variables, one to simulate growth (gf) and the other to simulate survival (sf) of the juvenile and adult stages.

To simulate growth of a frond, juveniles (JS_t) and adults (AS_t) of Fig. 2 are further divided into state variables representing size attained by a frond of a given size ($\text{JS}_{s,t}$ and $\text{AS}_{s,t}$) after a time interval of 1 month. The maximum size of the *G. skottsbergii* fronds studied was 1000 cm^2 reached 32 months after recruitment. There are larger fronds present but the percentages are low in the Calbuco population (Westermeier et al., 1999). Although thallus breakage is an important process affecting size structure of algae population, it has not been included in this model due to the lack of data for *G. skottsbergii.* To simulate number of fronds of a given size, juveniles (JN_t) and adults (AN_t) of Fig. 2 are further divided to represent fronds surviving during the time interval of 1 month ($\text{JN}_{s,t}$, $\text{AN}_{s,t}$). Two sources of mortality have been included, natural mortality (jm and am for juveniles and adults, respectively), which considers all possible causes except harvest. Survival, natural mortality and growth rates are affected by environment (E) and are size specific (sf_s, jm_s, and gf_s). Harvest mortality (hm) depends on management strategies (Ms) which include the following components: (i) harvest size (Hs), the legal frond size for harvesting (legal size classes), (ii) month of the year in which harvest will take place (Hm), and (iii) harvest rate (Hr), a fraction from 0 to 1 that indicates the amount of the

Table 3
Equations for model representing population dynamics and management of the red algae, *G. skottsbergii*

State variables

(1) $TS_t = TS_{t-1} + tp - ts$

(2) $CS_t = CS_{t-1} + cp - cs$

(3) $ST_t = ST_{t-1} + ts - tg$

(4) $SC_t = SC_{t-1} + cs - cg$

(5) $RN_t = RN_{t-1} + tg + cg - sf_r - rm$

(6) $JN_{s,t} = TN_{s,t-1} + sf_{s-1} - sf_s - jm_s - hm_s$

(7) $JS_{s,t} = JS_{s,t-1} + gf_{s-1}$

(8) $AN_{s,t} = AN_{s,t-1} + sf_{s-1} - sf_s - am_s - hm_s$

(9) $AS_{s,t} = AS_{s,t-1} + gf_{s-1}$

Material transfers

(10) $ts = TS_t * \lambda$

(11) $cp = Ca * \omega * \alpha'$

(12) $tp = Ta * \omega * \alpha$

(13) $cs = CS_t * \lambda$

(14) $tg = ST_t * \mu$

(15) $cg = SC_t * \mu'$

(16) $sf_r = RN_{t-1} - rm$

(17) $sf_s = JN_{s,t-1} - jm$ for juveniles

(18) $sf_s = AN_{s,t-1} - am$ for adults

(19) $rm = RN_{t-1} * \delta_s$

(20) $jm_s = JN_{s,t-1} * \delta_s$

(21) $am_s = AN_{s,t-1} * \delta_s$

(22) $gf_{s-1} = JS_{s-1} * \beta_{s-1}$ for juveniles

(23) $gf_{s-1} = AS_{s-1} * \beta_{s-1}$ for adults

(24) $hm = \text{if } (Hm = 0) \text{ then } (Hr * JN_s)$ else 0 for all juveniles of size $\geq Hs$

(25) $hm = \text{if } (Hm = 0) \text{ then } (Hr * AN_s)$ else 0, for all adults of size $\geq Hs$

Auxiliary variables

(26) $Ta_t = \Sigma_{s=200cm-2}^{1000cm-2}((AN_{s,t} * \rho) * AS_{s,t})$

(27) $Ca_t = \Sigma_{s=200cm-2}^{1000cm-2}((AN_{s,t} * \rho') * AS_{s,t})$

(28) $18 \leq Rs \leq 22$

(29) $Tb_t = RN_t * RS_t + \Sigma(JN_{s,t} * JS_{s,t}) + \Sigma(AN_{s,t} * AS_{s,t})$

(30) $Hr =$ fraction from 0 to 1 (amount of the available legal biomass that will be allowed to be harvested per time interval).

(31) $Hm = 0$, for months in which harvest is allowed and 1 for those in which harvest is not allowed.

(32) $Hs =$ any size ≥ 22 cm^2

Notation in the equations is explained in Section 3.2 and Fig. 2.

available legal biomass permitted to be harvested per time interval. The selected harvest rate is applied to all legal size classes. Total harvested biomass (Hb) is estimated by adding harvest mortality of legal size classes. Management is regulated by modifying any and/or all of these three variables.

Field observations on seasonal percentage (S) of tetrasporophytic and carposporophytic adults fronds in Calbuco are used to estimate the number of fronds in these life cycle phases (Zamorano and Westermeier, 1996; Westermeier et al. 1999), which multiplied by their size predicts total frond area (Ta and Ca for tetrasporophytic and carposporic fronds, respectively). Frond area is used to estimate tetraspore and carpospere production. By multiplying state variables representing frond number and size we can estimate total area of fronds of the entire population at a certain time used to estimate total biomass (Tb) applying a conversion factor (Table 2). Specific relationships between parameters and driving variables of the model (Temperature (T), Environment (E) and Season (S)) are indicated in Tables 2 and 3. Equations indicating the relationship among variables included in the model are shown in Table 3.

4. Model evaluation

In the evaluation, emphasis was given to model's ability to simulate the seasonal periodicity of *G. skottsbergii* population dynamics. This periodicity was specifically evaluated for (i) individual growth, (ii) recruit density (number of fronds ≥ 18 cm^2 and < 22 cm^2 per m^2), and (iii) biomass (g per m^2). To evaluate the model, the initial number of individuals per size was determined after a preliminary simulation of 5 years to determine the stable size-structure. Model parameters for this simulation are described in Tables 1 and 2 and the same 2-year temperature cycle described by Westermeier et al. (1999) was used during the simulation period. Simulation was started in January and lasted 48 months. Model predictions were compared with results observed by Westermeier et al. (1999) for the *G. skottsbergii* population located in Calbuco, Chile. To make

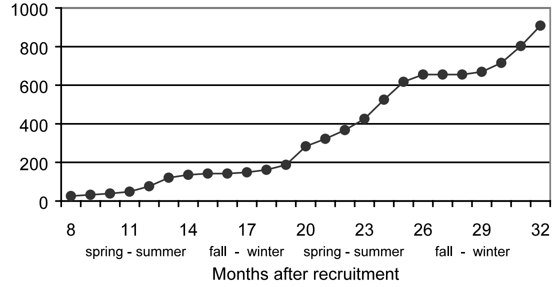

Fig. 3. Simulated monthly growth of a *G. skottsbergii* frond from recruitment to death.

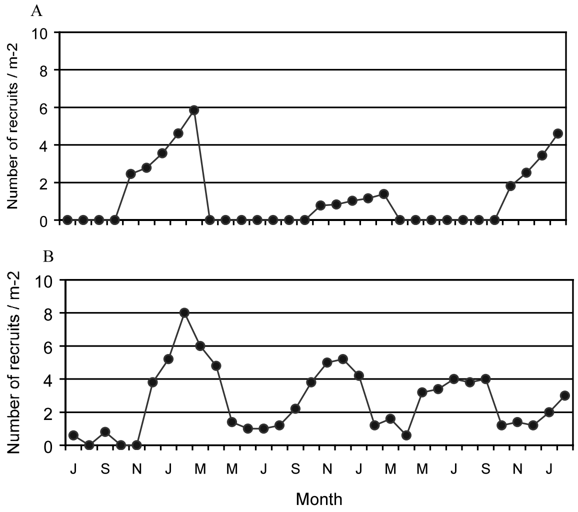

Fig. 4. Density of recruits (number per m^2) of *G. skottsbergii* (A) predicted by the model and (B) observed by Westermeier et al. (1999) in Calbuco.

predictions comparable with results reported by Westermeier et al. (1999), measures of density and biomass were estimated on a 1 ha plot and expressed in m^2, and size structure of the simulated population was predicted according to size classes defined by Westermeier et al. (1999). These classes are: Class I > 18 and ≤ 100 cm^2, II > 100 and ≤ 200 cm^2, III > 200 and ≤ 300 cm^2, IV > 300 and ≤ 400 cm^2, V > 400 and $\leq$ 500 cm^2, VI > 500 and ≤ 600 cm^2, VII > 600 and ≤ 700 cm^2, VIII > 700 and ≤ 800 cm^2, IX > 800 and ≤ 900 cm^2, X > 900 cm^2.

Simulated growth shows a seasonal size increase with peaks during the spring and beginning of the summer each year (Fig. 3). Towards the end of summer growth rates decrease and practically stop during fall and beginning of winter. The model predicts that after 32 months of recruitment, fronds reach 900 cm^2. This pattern is similar to that observed by Westermeier et al. (1999). However, predictions do not show a reduction in frond size during fall. This is due to frond breakage occurring during fall was not included in the model, basically because of lack of information on rate at which a frond of a given size returns to a smaller size class.

The model predicted recruitment would occur yearly from November to March (Fig. 4). This coincides with the first two main recruitment pulses observed by Westermeier et al. (1999) and corresponds to spore germination during the fall/winter period when temperature fluctuates around 10 °C. However, the model does not predict winter recruitment during the last year as observed by Westermeier et al. (1999). This would occur through tetraspore germination which might need more time to germinate than carpospores (Westermeier et al., 1999). Given the fact that this last process was not included in the model, the lack of recruitment during winter could be due to an overestimate of tetraspore mortality during winter. Field data confirmed that recruit fronds may also appear between main recruitment events, though at lower densities. Model does not predict the presence of these recruits because recruitment was represented in the model as discrete events instead of a continuum. Differences in recruitment size between the model and data (Westermeier et al., 1999) could be due to an overestimate of mortality rates of recruited fronds.

The model predicted that during winter and spring of the first year biomass remains relatively constant and at low values (Fig. 5). In summer, biomass increases and decreases slowly during fall, and faster in winter until mid spring. At the beginning of the next summer the biomass variation pattern is repeated in spite of showing less pronounced changes than those observed during the first cycle. During the last simulated summer, biomass begins to increase at a higher rate, similar to that observed during the first year. The biomass variation pattern, as predicted by the model, can be explained by the interaction between changes in density and size structure of the population. During the first 12 month period, the structure of the smaller size fronds in the population remains relatively constant (Fig. 6). The biomass increase during summer seems to be the result of an increase, although small, of the relative contribution of the three larger size classes, instead of a significant increase in density. During the second 12 month period, there is a change in the size structure of the population with a sharp increase in density during winter and spring, as well as the absence of any significant biomass increases in the summer. Specifically, the lower biomass predicted for this period would be due to the combined effects of an increase of number represented in the newly recruited smaller size class (class I) and the disappearance of three size classes (classes III, V and VI). The disappearance of these size classes is due to the low growth rates of the earlier size classes. Hence, fronds remain in these size classes for a long period producing a delay in the appearance of fronds in classes III, V and VI. The pattern of variation observed during the first period is repeated during the third period of simulation (winter–spring–summer) due to higher representation of intermediate sizes and increase in density in comparison to the previous period.

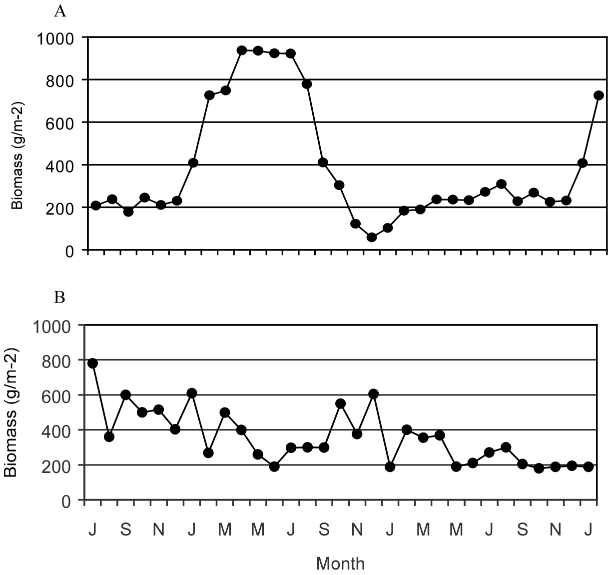

Fig. 5. Biomass (g per m^2) of *G. skottsbergii* (A) predicted by the model and (B) observed by Westermeier et al. (1999) in Calbuco.

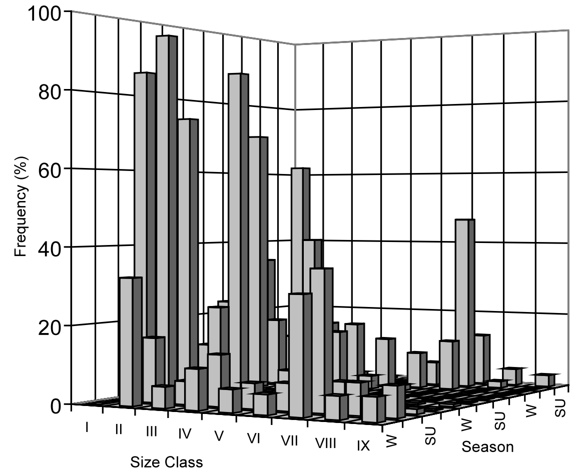

Fig. 6. Size structure of the *G. skottsbergii* population simulated by the model for each season during a period of 36 months.

In general, the model predicts an annual pattern of variation for biomass determined basically by variation in seasonal factors. However, biomass varies every 2 years in a cycle that alternates years of high and low biomass. This biennial pattern has been recognized by researchers and other experts regarding the use of this resource in the Xth Region (Westermeier et al., 1999; Zamorano, personal communication) and seems to occur due to changes in the size structure, occurring also on a 2-year cycle as a consequence of the time needed by fronds to change from one size class to another. The pattern of biomass variation predicted by the model differs from the erratic monthly biomass variation observed by Westermeier et al. (1999). However, if his data are grouped by seasons, the trend resembles that predicted by the model, showing higher values during the first year and lower ones in the second. Differences in the minimum and maximum biomass could be due to the difference in size structure between the simulated population and that observed in the field.

The integration of quantitative information in the model generates dynamics that are consistent with the main processes included in the model:

Table 4
Summary of predicted annual harvested biomass (kg per m^2) and total harvest (kg per m^2) using three different management strategies

Year after management	Total biomass		
	>160 cm^2–80%	>600 cm^2–90%	>600 cm^2–50%
1st year	847.9	1527.1	1291.8
2nd year	23.9	129.9	95.1
3rd year	683.2	968.1	987.7
4th year	25.6	204.8	230.3
Total	1580.6	2829.9	2604.9

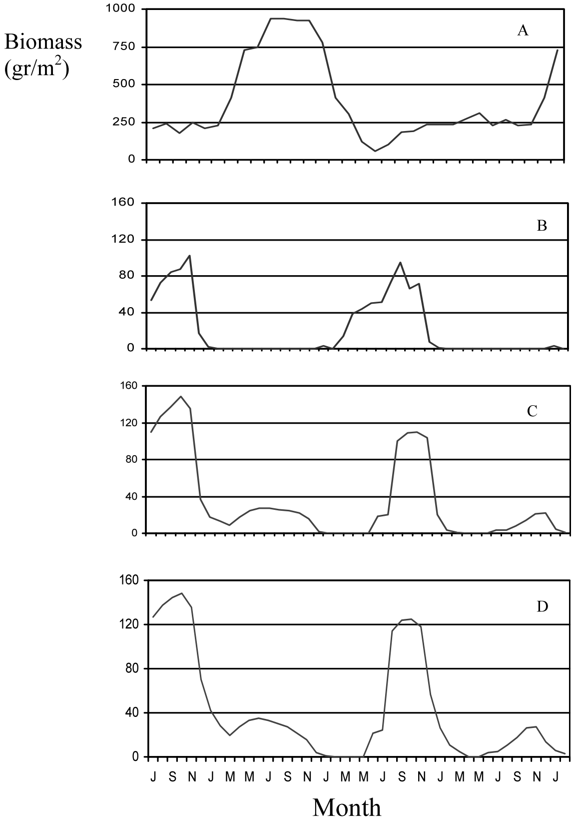

Fig. 7. Biomass dynamics for (A) the unharvested population, (B) harvesting allowed for fronds ≥ 160 cm^2 at a harvest rate of 80%, (C) harvesting allowed for fronds ≥ 600 cm^2 at a harvest rate of 90%, and (D) harvesting allowed for fronds ≥ 600 cm^2 at a harvest rate of 50%.

growth, mortality and reproduction. The main result of integrating these processes is a description of the biomass dynamics, which is of special interest for implementing any management plan. Results supported the model from both a predictive or explicative point of view, thus allowing it to be used to provide a preliminary evaluation of management strategies. However, it is important to point out the fact that several aspects of the model must be improved in order to obtain better prediction of both specific values as well as dynamics. These include (i) winter recruitment, (ii) causes of biomass decline, (iii) the longevity of larger sized fronds, (iv) differentiation of causes of frond mortality (such as detachment, herbivory, harvest) and (v) a more complete analysis of changes in the size structure of the population.

5. Effect of management strategies on *G. skottsbergii* population dynamics

Three 4-year simulations were run to examine the effects of different management strategies on population dynamics of *G. skottsbergii* located in Calbuco, Chile. The following strategies were used: (1) harvesting fronds equal or larger than 160 cm^2 at a rate of 80% ($\mathrm{Hs} = 160$, and $\mathrm{Hr} = 0.8$, Fig. 2) representing the actual harvest practice, (2) harvesting fronds equal or larger than 600 cm^2 at a rate of 90% ($\mathrm{Hs} = 600$, and $\mathrm{Hr} = 0.9$) representing the strategy purposed by Westermeier et al. (1999), and (3) harvesting fronds equal or larger than 600 cm^2 at a rate of 50% ($\mathrm{Hs} = 600$, and $\mathrm{Hr} = 0.5$). Harvesting was permitted from November to February, as proposed by Westermeier et al. (1999) for all simulations. Parameter values were the same as those used in the model evaluation phase and were held constant during the simulations. The following results were estimated from each simulation: annual harvest (from November to February) in kg per m^2, total harvest for the 4-year period in kg per m^2, and population dynamics in terms of biomass.

Simulated annual harvest showed cycles of high harvest biomass alternated with years of low ones (Table 4). This is consistent with the dynamics exhibited for the entire population when harvesting is not allowed (Fig. 7A). Predictions obtained using strategy 1 show the lowest values for annual harvest, as well as for the total harvest (Table 4). Strategies 2 and 3 (harvesting fronds equal or larger than 600 cm^2 at a rate of 90 and 50%, respectively), produced 1.79 and 1.65 times the total harvest biomass predicted for strategy 1, respectively. Strategy 2 predicted a total harvest biomass slightly larger than strategy 3 (Table 4), probably as a consequence of the higher values of harvest biomass during the first 2 years, relative to those predicted for strategy 2. However, during the third and fourth years, harvest biomass predicted under strategy 3 was slightly larger than that predicted when using strategy 2. This prediction suggests that in the long term strategy 3 may produce a larger harvested biomass than strategy 2.

Biomass dynamics of the whole population change dramatically when harvested (Fig. 7). Model predictions indicate that, regardless of the management strategy, the period of increase in biomass observed from November to May, when harvesting is not allowed (Fig. 7A) disappears if harvesting is permitted, especially when harvest size is the smallest (Fig. 7B–D). Under this scenario the period of increase in biomass would occur from March to October, approximately, when harvesting is not allowed, and it would reach approximately 10–16% of the maximum biomass predicted without harvesting. Biomass dynamics of the population using strategies 2 and 3 are similar in that some biomass is left in the population during the harvesting period. Strategy 1 maintains in the population fronds of size and quantities too small to be recorded by the model (Fig. 7B).

6. Discussion

An understanding of complex systems such as *G. skottsbergii* population dynamics can be gained by integrating existing qualitative and quantitative information in a continuos manner. In this context simulation models are a useful tool sufficiently flexible to answer specific questions related to both environmental effects and management strategies on complex population dynamics (Marín et al., 1998). Santos and Nyman (1998) reported the use of structured-population simulation model for *Gelidium sesquipedale*, a red algae, and indicated that model results were similar to those obtained using a matrix model and compared well with the observed population dynamics.

The model developed for *G. skottsbergii* inhabiting the Calbuco area is a simple abstraction of the processes involved in its population dynamics. Yet, it predicts dynamics for the analyzed variables consistent with what is known from field and laboratory studies (Westermeier et al., 1999). Focussing on biomass, model results indicate that changes in population size structure and density are the main processes explaining the biennial cycle of production predicted by the model. This result suggests that the same processes may explain the biennial biomass cycle observed in several areas of the Xth Region, Chile. Specifically, different populations inhabiting Ancud and Calbuco area (Zamorano personal communication; Westermeier et al., 1999) where this fluctuating pattern of biomass production has led artesanal and industrial fishermen to continuously search for new areas to harvest (Westermeier et al., 1995, 1999; Buschmann et al., 1999). Results from the several variables analyzed in this model indicate the main processes determining the predicted change in size structure and density are the slow growth exhibited by the smaller plants and the discrete recruitment events, respectively. This information suggests that effort in gathering information should be placed on these processes.

Slow growth of the smaller fronds may not be the only cause determining size structure in real populations. Breakage of fronds by wave action and herbivory, and subsequent re-growth of the fronds, processes mentioned as a promising aspect of *G. skottsbergii* by Westermeier et al. (1999), Buschmann et al. (1999), was not included in the model. The inclusion of re-growth in the model may have produced a more equable size structure and a less pronounced biennial cycle in biomass. Harvest effect on size structure should also be quantified, since it may have a similar effect to that of wave action. Another factor that may have contributed to generate the predicted size structure is the selection of the size classes (Santos and Nyman, 1998). Regarding recruitment, understanding would be improved by including in the model differential performance of tetraspores and carpospores (Westermeier and Sigel, 1997) and its impact on periodicity of recruitment. Aspects mentioned above deserve further analysis to improve understanding of this system.

Results from evaluation of different management strategies using the simulation model indicate that, in the short run, the actual harvest practice (plucking fronds by hand) reduces the population biomass greatly (Fig. 7A and B) and produces decreasing annual biomass harvests (Table 4). This result is expected since most of the frond population is harvested during the first year. Smaller fronds, of slow growth, are responsible for the population growth during the following years. Thus, it takes 2 years for the population to produce biomass values similar to those predicted just before harvest was allowed, and it seems that the population never will recover to a condition similar to the unharvested level (Fig. 7A). This can be explained taking into consideration that in the model any loss of thallus means a direct reduction in frond density. This result may have been different if re-growth of pruned fronds and holdfast were included in the model.

The other two simulated management strategies also reduce population biomass but to higher values than the previous strategy and produce larger biomass harvests. Maintaining size at harvest constant and varying harvest rate did not change biomass dynamics in an important manner, at least during the 4 simulated years. Thus, the main changes observed in biomass dynamics seem to be due to management of size at harvest rather than harvest rate (Fig. 7B–D). Restriction of size at harvest also was indicated as a better management alternative by Santos and Nyman (1998). These authors indicated that commercial harvest of *Gelidium sesquipedale* (Rhodophyte) should be selective for bigger fronds since smaller fronds contributed more to population growth than bigger ones, reflecting the importance of vegetative recruitment in the population dynamics of this species. The same has been observed for a population of another red algae in Valdivia, *Iridaea laminaroides* (Gómez and Westermeier, 1991). Westermeier et al. (1999) indicated for *G. skottsbergii* commercial harvest should be selective for bigger fronds (≥ 600 cm^2), and should restrict harvest period to those months when no spore release occurs, spring–summer. The same authors indicated the harvest should be done by pruning fronds of selected size, while maintaining the holdfast on the substrate because the thallus is capable of regenerating new tissue (Westermeier et al., 1999). Less pronounced impacts on biomass dynamics were expected from simulating restriction in frond size at harvest. Including re-growth of fronds from holdfast may have made the difference between expected and simulated biomass dynamics. This re-growth process may permit a larger number of fronds to cross size classes in a shorter time period than if recruitment from spores is the only source of fronds.

7. Conclusions

Results predicted from using different management strategies suggest that commercial harvest should be selective for larger fronds, probably ≥ 600 cm^2 and the harvest period should be restricted. Although not predicted by the model, results from the simulated strategies suggest that holdfast should be maintained on the substrate for latter re-growth. Under this scenario harvest rate can be relaxed since no important changes in harvest biomass were predicted when increasing harvest rate from 50 to 90%, at least in the short term. However, it is recommendable to keep harvest rate low (50%) as a preventive measure, since results from Table 4 suggest that in the long term, a harvest rate of 50% could produce larger harvested biomass. The existence of a biennial cycle of biomass production determined by change in size structure and density suggests that populations should be harvested using a rotation area system. This would allow the harvested population to recover before new harvest is allowed. In this scenario it would be necessary to estimate the time needed for a given population to completely recover before harvest is allowed, a situation that can be explored using a modified version of this simulation model.

Analysis of both model and field results for *G. skottsbergii* population dynamics indicates that the current simulation model is a valuable tool to identify and understand the processes generating a given population structure, and to identify information required to improve both our understanding of the system and model's predictive capability. Specific topics to be included in the model to improve its performance are mentioned in Section 4.

Acknowledgements

This work was partially financed by Fondecyt 1951203 (second author) and FONDAP Algae program of CONICYT. The authors thank the anonymous reviewers for their comments which greatly improved this manuscript.

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