Analysis of grazing effects on the biomass dynamics of *Ecklonia cava*.

MASAKI HONDA

Abiko Research Laboratory, Central Research Institute of Electric Power Industry, 1646 Abiko, Abiko-shi, Chiba 270-1194, Japan (m-honda@criepi.denken.or.jp)

SUMMARY: Relationships between the rate of biomass change and standing biomass of *Ecklonia cava* are classified into three types: 1) the rate of biomass change is positive under a stable equilibrium that is maximum biomass, 2) the rate of biomass change is negative for all biomasses, and 3) the rate of biomass change is positive between the maximum biomass and an unstable equilibrium that is the minimum biomass required for a persistent *E. cava* stand. Where the biomass change is positive, *E. cava* can grow. If the biomass is larger than the minimum biomass required for a persistent *E. cava* stand, then the bed will persist by overcoming the instability. On the other hand, if the biomass change is negative for all biomasses or the biomass is smaller than the minimum biomass required for a persistent *E. cava* stand, then the biomass will eventually become zero. The maximum biomass decreased with increasing attenuation coefficient and water depth. The minimum biomass required for a persistent *E. cava* stand is formed with feeding rate that exceeds threshold. The feeding rate on the threshold is affected by water depth and the attenuation coefficient that characterizes the amount of light at the seafloor. Value of the minimum biomass required for a persistent *E. cava* stand is increased with increasing feeding rate and water depth. Vertical distribution of *E. cava* was affected not only by the amount of light but also by grazing intensity.

KEY WORDS: biomass dynamics, production, grazing effects, *Ecklonia cava*

INTRODUCTION

Seaweeds can be extremely productive, and thus play a vital role in the coastal food chains of many parts of the world¹⁾. Some of the most important seaweed beds in Japan are the communities composed of large brown algae, e.g., Laminariales, *Laminaria*, *Ecklonia*, and *Eisenia*. *Laminaria* grows in cold waters in northern Japan. *Ecklonia* and *Eisenia* grow in temperate waters. *Ecklonia cava* is an important component of the kelp forest along the central Pacific coast of Japan.

Local distributions of kelp are often restricted by grazers, which have even destroyed beds²⁾. Sea urchins and herbivorous fish have been recognized as major grazers of kelp. Barren marine areas that occur as a result of intensive grazing by herbivores are termed "Isoyake areas" in Japanese. Studies on the restoration of these barren grounds to rich seaweed beds began in the 1970's. Many studies have been made on the establishment and restoration of kelp in over-grazed area^{3,4)}. The purpose of those studies was to increase seaweed biomass in order to overcoming the grazing intensity. Thus, calculation of biomass change is a useful indicator for the success of the establishment and restoration of kelp beds⁵⁾. A photosynthetic production model is one of the major components used in the calculation of the biomass change (see Monsi

and Saeki⁶⁾). Ikushima^{7, 8)} modified the model to estimate photosynthetic rates of submerged plant communities. In this model, a rectangular hyperbola was used to simulate the photosynthesis-light response. However, the rectangular hyperbola formulation was a poor fit for the experimental photosynthesis-light response data⁹⁾. Honda¹⁰⁾ developed the photosynthetic production-light and temperature model with a photosynthesis-light response model that fitted well and included the effects of temperature. An estimation of grazing is another major component to be included in the calculation of biomass change. Several studies have been made on feeding equations^{11, 12, 13, 14, 15)}.

In this study, grazing effects on the biomass dynamics of *E. cava* are analyzed with a biomass change model that combined the feeding equation of Ivlev¹⁴⁾ with the photosynthetic production model that was developed by Honda¹⁰⁾.

METHODS

A photosynthetic production model was developed by Honda¹⁰⁾. The net photosynthetic rate, P_{net} , is a function of biomass, light intensity, and temperature, and is expressed as:

$$P_{net} = \int_0^F \frac{\Phi_T (K I_0 e^{-CD-KF_z})^2}{\Psi_T + \Omega_T K I_0 e^{-CD-KF_z} + (K I_0 e^{-CD-KF_z})^2} dF_z - (r_{IT} S_1 + r_s S_s)$$

where

Φ_T , Ψ_T , and Ω_T : photosynthetic parameters at T°C

F: leaf area index ($m^2 m^{-2}$)

I_0 : photon irradiance at 0 m water depth (μmol photons $m^{-2} s^{-1}$)

C: vertical attenuation coefficient (m^{-1})

D: water depth (m)

K: extinction coefficient of the population

F_z : cumulative leaf area index between the population surface and depth of z m from the population surface (F proportional to kelp biomass)

r_{IT} : respiration rate of blade at T°C ($g C g^{-1} h^{-1}$)

S_1 : standing crop of blade ($g m^{-2}$)

r_s : respiration rate of stipe ($g C g^{-1} h^{-1}$)

S_s : standing crop of stipe ($g m^{-2}$).

The estimated mean values of Φ_{20} , Ψ_{20} , Ω_{20} , r_{f20} , and r_s of *E. cava* found offshore of Akiya, Yokosuka-shi, Kanagawa Prefecture and standard deviations are

$$\Phi_{20} = 0.099 \pm 0.00507 \text{ mg O}_2 \text{ cm}^{-2} \text{ h}^{-1} (0.037 \pm 0.00190 \text{ mg C cm}^{-2} \text{ h}^{-1})$$

$$\Psi_{20} = 234 \pm 86.4 \mu mol^2 m^{-4} s^{-2}$$

$$\Omega_{20} = 43.6 \pm 4.65 \mu mol m^{-2} s^{-1}$$

$$r_{f20} = 0.113 \pm 0.0125 \text{ mg O}_2 \text{ g}^{-1} \text{ h}^{-1} (0.0423 \pm 0.00470 \text{ mg C g}^{-1} \text{ h}^{-1})$$

$$r_s = 0.0129 \pm 0.00555 \text{ mg O}_2 \text{ g}^{-1} \text{ h}^{-1} (0.00483 \pm 0.00208 \text{ mg C g}^{-1} \text{ h}^{-1}).$$

Honda⁵ assumed that the feeding rate of sea urchins can be expressed by the feeding equation of Ivlev¹⁴. The feeding rate of grazers, FR ($g C m^{-2} d^{-1}$), was assumed to be a function of the *E. cava* biomass, S ($g m^{-2}$), as shown in

$$FR = M(1 - e^{-ES})$$

where

M: maximum feeding rate ($g C m^{-2} d^{-1}$)

E: coefficient of proportionality.

By combining the feeding equation with the photosynthetic production model, the rate of *E. cava* biomass change ($\Delta S/\Delta t$, $g m^{-2} h^{-1}$) was calculated by:

$$\frac{\Delta S}{\Delta t} = \int_0^F \frac{\Phi_T (K I_0 e^{-CD-KF_z})^2}{\Psi_T + \Omega_T K I_0 e^{-CD-KF_z} + (K I_0 e^{-CD-KF_z})^2} dF_z - (r_{IT} S_1 + r_s S_s) - M(1 - e^{-ES})$$

RESULTS

Relationships between the rate of biomass change and standing biomass of *E. cava* are classified into three types: 1) the rate of biomass change is positive under a stable equilibrium that is maximum biomass, 2) the rate of biomass change is negative for all biomasses, and 3) the rate of biomass change is positive between the maximum biomass and an unstable equilibrium of minimum biomass required for a persistent *E. cava* stand (Fig. 1). Where the biomass change is positive, *E. cava* can grow. If the biomass is larger than the minimum biomass required for a persistent *E. cava* stand, then the bed will persist by overcoming the instability. On the other hand, if the biomass change is negative for all biomasses or the biomass is smaller than the minimum biomass required for a persistent *E. cava* stand, then the biomass will eventually become zero.

Figure 1 Schema of relationships between the biomass change ($\Delta S/\Delta t$) and biomass (S) of the *Ecklonia cava*. Upper line; the rate of biomass change is positive with no unstable equilibrium point. Lower line; the rate of biomass change is negative for all biomasses. Middle line; there is an unstable equilibrium point in the biomass change rate. Open circles represent stable equilibrium points and the star represents the unstable equilibrium point.

Figure 2 shows the relationships between the estimated daily biomass change, ΔS_d ($g C m^{-2} d^{-1}$), water depth and the *E. cava* biomass at various attenuation coefficients. A sine formula was used for irradiance with a maximum irradiance of $1500 \mu mol$ photons $m^{-2} s^{-1}$ and a day length of 12 hr. The leaf area index, F, is proportional to the standing crop of blade, S_1 (in this simulation, F is $S_1/400$). As shown in Figure 2, the maximum biomass and the biomass change decreased with increasing attenuation coefficient and water depth. When there is no grazing pressure, there is no minimum biomass required for a persistent *E. cava* stand. This analysis shows that the vertical distribution of *E. cava* was affected by the amount of light that was characterized by irradiance, day length and attenuation coefficient.

Figure 2. Relationships between the estimated daily biomass change (ΔS_d , $\text{g C m}^{-2} \text{ d}^{-1}$), water depth (D , m) and biomass (S , kg m^{-2} , blade : stipe = 2 : 1) of the *Ecklonia cava* population at different attenuation coefficients (C , m^{-1}). Calculations were carried out with the following assumptions: $K = 1$, $T = 20^\circ\text{C}$ and $I_{0(t)} = 1500 \sin(\pi t / N_d)$ $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$. K , T , $I_{0(t)}$, and N_d are the extinction coefficient of the *Ecklonia cava* population, temperature, irradiance at 0 m water depth at t hours after sunrise, and daylength (12 h), respectively.

Figure 3. Relationships between the estimated daily biomass change (ΔS_d , $\text{g C m}^{-2} \text{ d}^{-1}$), water depth (D , m) and biomass (S , kg m^{-2} , blade : stipe = 2 : 1) of the *Ecklonia cava* population at various feeding rates (M , g m^{-2}). Calculations were carried out with the following assumptions: $C = 0.1 \text{ m}^{-1}$, $K = 1$, $T = 20^\circ\text{C}$, $I_{0(t)} = 1500 \sin(\pi t / N_d)$ $\mu\text{mol photons m}^{-2} \text{ s}^{-1}$, and $E = 4 \text{ m}^2 \text{ g}^{-1}$. C , K , T , $I_{0(t)}$, and N_d are the attenuation coefficient, the extinction coefficient of the *Ecklonia cava* population, temperature, irradiance at 0 m water depth at t hours after sunrise, and daylength (12 h), respectively.

Figure 3 shows the relationships between the estimated daily biomass change, water depth and *E. cava* population biomass at various feeding rates. It can be seen that the maximum biomass, at the same water depth, decreased with increasing feeding rate. Results from these analyses indicated that the effect of grazing on the maximum biomass resembled the effect of the attenuation coefficient. The minimum biomass required for a persistent *E. cava* stand was found with a feeding rate which exceeded the threshold value. The feeding rate on the threshold value was affected by water depth and the attenuation coefficient that characterized the amount of light reaching the seafloor. Thus the minimum biomass required for a persistent *E. cava* stand was found at greater water depths. On the other hand, in the absence of a grazer, even if the attenuation coefficient was large, the minimum biomass required for a persistent *E. cava* stand was not achieved. The value of the minimum biomass required for a persistent *E. cava* stand increased with increasing feeding rate and water depth. This analysis shows that the vertical distribution of *E. cava* was affected not only by the amount of light but also by grazing intensity.

DISCUSSION

Techniques that have been developed for the establishment and restoration of kelp beds are classified into two techniques categories: biological and civil engineering. The spore-bag and vegetative transplantation methods are classified as biological techniques⁽⁶⁾. The spore-bag involves supplying zoospores to locations where natural recruitment is not possible because neighboring kelp beds (the natural source of supply of zoospores) are too far away. The vegetative transplantation technique is employed in cases where natural recruitment is difficult as a result of "Isoyake". The removal of herbivores from the "Isoyake areas" is one of the biological techniques for management. The construction of artificial reefs using concrete blocks or rocks is classified as a civil engineering technique. One of the purposes of the construction of artificial reefs is to increase the intensity of light that reaches the seafloor. This is achieved by seafloor piling, which effectively raises the level of the seafloor. The purpose of the establishment and restoration of kelp beds is to increase kelp biomass, thus, calculation of biomass

change is a useful tool for the prediction of the effect of each technique.

If the rate of biomass change is positive, under the maximum biomass, the spore-bag and vegetative transplantation techniques are effective in the establishment of kelp beds. On the other hand, if the rate of biomass change is negative for all kelp biomasses, then the spore-bag and vegetative transplantation techniques are not effective without the removal of herbivores or seafloor piling by the construction of artificial reefs. If the rate of biomass change is positive between the maximum biomass and the minimum biomass required for a persistent *E. cava* stand, the vegetative transplantation can be used to increase the kelp biomass and overcome the instability. Thus, vegetative transplantation is effective in the establishment of kelp beds. The spore-bag technique is ineffective in overcoming an unstable equilibrium.

In figure 4, a zone characterized by a positive biomass change under the maximum biomass is defined as "Zone A". A zone characterized by a negative biomass change for all biomasses is defined as "Zone C". The zone which is characterized by a positive biomass change between the maximum biomass and the minimum biomass required for a persistent *E. cava* stand is "Zone B". Water depth of borders between Zones A, B and C are affected by the amount of light and grazing intensity. Irradiance has daily and seasonal changes, and grazing intensity is affected by growth, recruitment, emigration and death of animals. Thus, the water depth of the borders has a dynamic influence. The biomass model presented here is useful in prediction of the water depth of the borders.

Figure 4 Schema of defined Zones A, B and C. Zone A; the rate of biomass change is positive under the maximum biomass, Zone B; the rate of biomass change is positive between the maximum biomass and the minimum biomass required for a persistent *Ecklonia cava* stand, Zone C; the rate of biomass change is negative for all biomasses.

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