Journal of Experimental Marine Biology and Ecology
266 (2001) 51–65

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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Active erosion of *Undaria pinnatifida* Suringar (Laminariales, Phaeophyceae) mass-cultured in Otsuchi Bay in northeastern Japan

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Received 25 May 2001; received in revised form 13 August 2001; accepted 19 August 2001

Abstract

Production and erosion of the commercially mass-cultured kelp *Undaria pinnatifida* Suringar f. *distans* Miyabe et Okamura were investigated between January and April 1998 in Otsuchi Bay, ca. 8 km long and 2 km wide, located on the northeastern coast of Japan. Steady growth in total kelp length was observed from January to March, with rates of 1.1 to 1.8 cm day^{-1}. Erosion rates were consistently low at <0.2 cm day^{-1} in January and February, but increased to 0.5 cm day^{-1} in March, and were comparable to the growth rate in April. Biomass erosion represented 30–40% of production in March and over 80% in April. The greater erosion in April was attributed to a low supply of dissolved inorganic nitrogen and aging of the alga. Total net production of the cultured kelp in the bay was 49.5 tonne C, of which, 81% (38.7 tonne C) was harvested while 19% (10.8 tonne C) was lost due to erosion. In terms of nitrogen, 33% of total production (4.68 tonne N) was eroded, while 67% was harvested. Active erosion of the kelp thus appears to be an important source of organic matter for heterotrophic processes in the coastal waters of eastern Asia where kelp cultivation is a major aquaculture industry.

Keywords: Growth; Erosion; *Undaria pinnatifida*; Kelp culture; Algal production

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0022-0981/01/$ - see front matter
PII: S0022-0981(01)00346-X

1. Introduction

Undaria pinnatifida, called “wakame” in Japanese, is a laminarian kelp that is native to coastal areas of Japan, Korea, and China. Wakame is a popular food in these countries (Yamanaka and Akiyama, 1993), and since the mid 1960s, there has been intensive commercial cultivation of this macroalga in Japan (Akiyama and Kurogi, 1982; Tokuda et al., 1987). Furthermore, *U. pinnatifida* is now spreading as an invasive species, threatening native seaweed communities in several coastal regions of the world, including France, the Mediterranean, New Zealand, South America, and Australia (Perez et al., 1981; Boudouresque et al., 1985; Hay and Luckens, 1987; Casas and Piriz, 1996; Campbell and Burridge, 1998). In addition to *U. pinnatifida, Laminaria japonica* and other *Laminaria* species, known as ”kombu” in Japan, are cultivated along the Japanese coasts and used as food (Tokuda et al., 1987). Prior to kelp cultivation, the annual Japanese harvest of naturally occurring was 50,000–60,000 tonnes in wet weight. By the early 1970s, 100,000 tonnes of cultivated *U. pinnatifida* were being harvested annually, while the harvest of natural populations had decreased to $<30,000$ tonnes. Thereafter, commercial cultivation based on Japanese culture techniques started in Korea and China.

High productivity of laminarian kelps has been reported from several temperate and subarctic areas (Bellamy et al., 1968; Mann, 1972b; Field et al., 1977). Kelp-derived organic matter plays an important role for many marine organisms living along kelp-dominated shorelines (Koop et al., 1982; Dunton and Shcell, 1987; Duggins et al., 1989). Thus, the extensive culture of kelp may have a large impact on local nutrient cycling, and can be an important source of organic matter for heterotrophs. *U. pinnatifida* excretes organic matter as mucilage (Alber and Valiela, 1994), and its tissues are consumed by various heterotrophs. On an annual cycle, the gametophytes of this kelp are produced in autumn, and the sporophytes germinate and grow rapidly from winter to early spring. Sporophylls are formed and release zoospores in early summer, and the sporophyte dies later in the summer (Saitoh, 1962). In natural populations, dissolved and particulate organic matter is released into the seawater throughout the life cycle. In cultured *U. pinnatifida* however, organic matter is released only through excretion and erosion of tissues from tips of thalli before the kelp is harvested. We addressed the questions of how match of the total production is released as eroded tissue and how much is harvested. The release of organic matter from cultured kelp is thus a man-made impact on marine material cycling in coastal waters. The high concentrations of transparent exopolymer particles formed partly from the extracellular release of *U. pinnatifida* recorded during January–April 1998 is one such example of the impact of macro-algal cultivation in coastal waters (Ramaiah et al., 2001). However, to date no attempt has been made to quantify the production and erosion of *U. pinnatifida* in terms of dry weight or carbon biomass.

The aim of this study was to evaluate biomass-specific production and erosion of *U. pinnatifida* cultivated in Otsuchi Bay in northeastern Japan. We emphasized the evaluation of erosion, which is poorly known compared to production (Bellamy et al., 1968; Mann, 1972b; Field et al., 1977). We examined the growth of *U. pinnatifida* f. *distans*, a northern variety that has sporophylls arising from the lower portion of its long stipe, and a deeply divided blade. This form is now also cultured extensively in Korea and China.

2. Materials and methods

2.1. Study site

Field study was conducted in Otsuchi Bay, a small, semi-enclosed bay opening into the northwest Pacific Ocean (Fig. 1). During winter and spring, west to northwest winds prevail and allow the exchange of water masses between the inside and outside of the bay (Shikama, 1980). Surface waters of the bay are transported seaward, and, simultaneously, dense, more saline and nutrient-rich coastal waters enter the bay along the sea bottom. This influx of water, in addition to three small rivers, brings nutrients into Otsuchi Bay. Furuya et al. (1993) showed the effect of this wind-driven circulation on nutrient supplies and the formation of the spring phytoplankton bloom. Their results were confirmed with a simulation model that coupled physical and biological processes in the bay (Kawamiya et al., 1996).

In Otsuchi Bay, *U. pinnatifida* f. *distans* is the most important commercially cultivated alga, with an annual harvest of approximately 1000 tonnes wet weight. Other commercially harvested algae include *Laminaria* spp., *Analipus japonicus*, and *Gloiopeltis* spp. However, the harvest of these species is 55 tonnes, much less compared in comparison to that of *U. pinnatifida*. The cultivated *U. pinnatifida* is thought to be an important primary producer in Otsuchi Bay from winter through spring, as is the spring phytoplankton bloom.

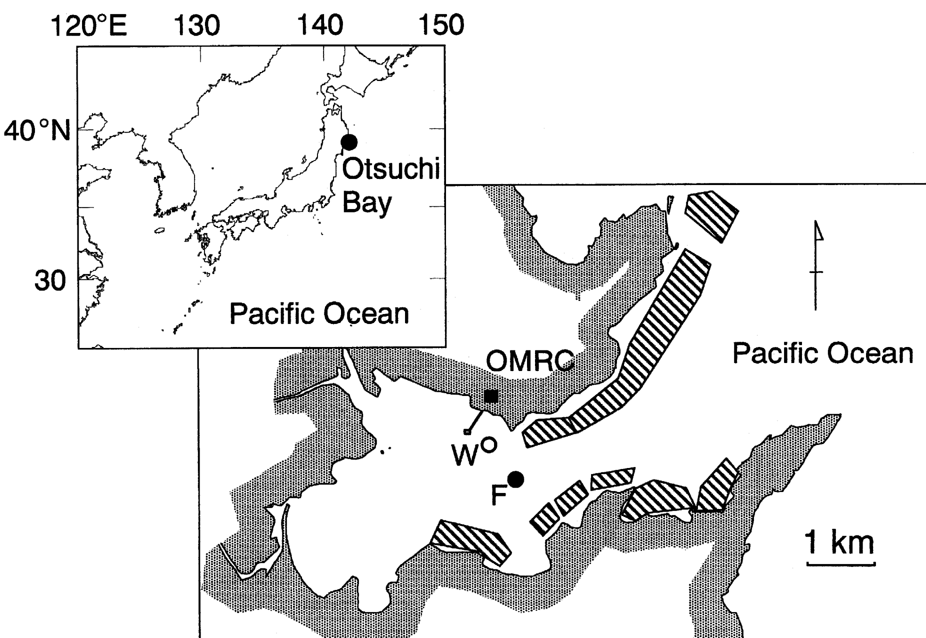

Fig. 1. Location of growth experimental site (open circle, Stn. W) and sampling site for nutrients (closed circle, Stn. F) in Otsuchi Bay. Areas for commercial cultivation of *U. pinnatifida* are hatched.

2.2. Growth experiments

The growth of *U. pinnatifida* was examined at Stn. W of the experimental cultivation area of Otsuchi Marine Research Center in Otsuchi Bay (Fig. 1). Young sporophytes were transplanted onto a rope 50-m long with an approximate density of 300 to 400 sporophytes per meter, which was then suspended at 1-m depth in the bay on November 10, 1997. Growth measurement was started when total length of sporophytes reached 48 cm in January 19, 1998. Prior to this, excess algae were thinned out on January 19, 1998 to obtain a density of 30 individuals per meter.

Growth rates were measured using a hole punching method (Parke, 1948; Nishikawa, 1967), whereby 24 sporophytes had a hole punched on both sides of the midrib, 20 cm above the holdfast (Nishikawa, 1974; Ishikawa, 1993). Growth and total length of the algae were then measured every 1 to 2 weeks. Growth was measured as the moving distance that the two holes had moved during time interval. Erosion rates were calculated as the difference in gross growth, as measured above, and net growth, obtained as an increment of the total length (Lüning, 1979). As growth progressed, the holes moved to the tips of the thalli. We then punched new holes 40 cm above the holdfast on February 17, March 10, and March 24. If growth occurs above the holes and over erosion at the tips of the blades, calculation of the erosion using the method described gives an error with negative values.

For estimation of the carbon and nitrogen contents, one individual alga was removed from the rope and every 2–3 weeks and pieces of tissues obtained from at the growth, central, and erosion regions of the alga. Duplicates of squares of 1 cm^2 were also cut from the blade and midrib sections. All the tissues were dried at 50 °C for $>$ 24 h before analysis with a CHN elemental analyzer (MT2000, Yanaco).

2.3. Environmental monitoring

Temperature and salinity were continuously recorded every 10 min at depths of 1, 5, 10 and 15 m using an integrated sea condition monitor system that was moored near Stn. W (Otobe, 1997). For a general indication of nutrient conditions within the bay, samples for ambient concentrations of nitrate and phosphate analysis were collected twice a week at 1-m depth of Stn. F in the center of the bay (Fig. 1). Nutrient samples were analyzed with an Auto Analyzer (AAII, Technicon).

2.4. Production of U. pinnatifida individuals

Production (P) of individual algae was calculated from linear growth rates using an exponential relationship between total length (TL: cm) and wet weight (WW: g) according to the model of Mann (1972b):

$$\mathrm{WW} = a\,\mathrm{TL}^b \tag{1}$$

$$P = a(\mathrm{TL}_0 + h)^b - a\,\mathrm{TL}_0^b \tag{2}$$

where h is the linear growth rate (day^{-1}) measured on the 24 individuals by the hole punching method, TL_0 is the initial total length, and a and b are constants.

Individual erosion (ER: g) between time 0 and time 1 was calculated as the difference between production and the net increment of wet weight:

$$\begin{aligned} \mathrm{ER} = P - (\mathrm{WW}_1 - \mathrm{WW}_0) &= a(\mathrm{TL}_0 + h)^b - a\,\mathrm{TL}_0^b - \left(a\,\mathrm{TL}_1^b - a\,\mathrm{TL}_0^b\right) \\ &= a(\mathrm{TL}_0 + h)^b - a\,\mathrm{TL}_1^b \end{aligned} \tag{3}$$

where WW_0 is the initial wet weight, TL_1 is the total length at time 1, and WW_1 is the wet weight at time 1.

2.5. Production of U. pinnatifida throughout Otsuchi Bay

The standing crop for the whole of Otsuchi Bay was calculated from daily records of harvests in wet weight (Kamaishi Tobu and Otsuchi Fisheries Associations), which started in mid March and continued until late April, and the time course of individual wet weights obtained from the growth experiments. We assumed that all plants are the same size/age and density effects on growth rates were negligible because *U. pinnatifida* both on the experimental rope and the commercial ropes were thinned out. In other words, the standing crop of the whole bay was considered to vary in accordance with the time course of individual wet weights in the experimental rope, that is, the growth and erosion rates obtained from the experiment were applied to the harvested algae to obtain the daily biomass of the algae before harvesting. Thus, the sum of the calculated biomass gave the standing crop of each day in the whole bay.

3. Results

3.1. Environmental conditions

Salinity at 1 m in Otsuchi Bay ranged from 29 to 34, with variation due to the input of fresh water from rivers (Fig. 2). In particular, low saline water of 30 entered the bay with the snowmelt in April. Water temperature was around 8 °C in late January, reached a minimum of 5 °C during late February and early March, and increased again to 8 °C in early April as solar radiation warmed the water. Thereafter, temperature fluctuated from 7 to 11 °C.

Nitrate was the most abundant type of dissolved inorganic nitrogen (DIN) measured, with levels varying from undetectable (< 0.05 μM) to > 10 μM. Nitrate concentrations were high (5–11 μM) during late January and mid February, and then declined below 2 μM in late February and early March, coinciding with the first peak of phytoplankton spring bloom. By mid March, nitrate concentrations were replenished to 8 μM with the inflow of nutrient-rich water from outside the bay, but decreased below 2 μM again as the second phytoplankton bloom exhausted the nutrients during early April and dropped to undetectable levels (< 0.05 μM) by mid April. Phosphate levels showed trends similar to those of nitrate. The ratio of DIN to DIP was generally lower than 16, implying a greater availability of phosphate than inorganic nitrogen. Phosphate was not depleted during early April, when DIN was scarce.

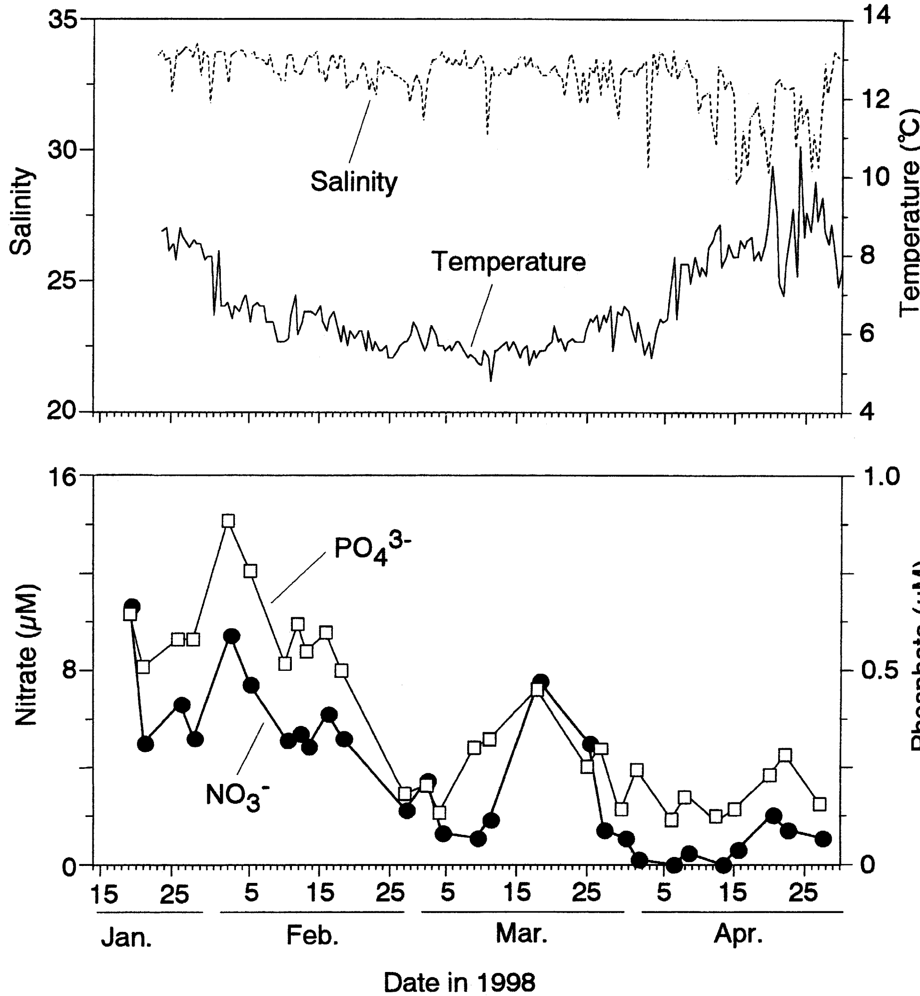

Fig. 2. Temporal changes in salinity (broken line) and temperature (solid line) (upper), nitrate (closed circle) and phosphate (open square) concentrations (lower) at a 1-m depth in Otsuchi Bay.

3.2. Growth and erosion rates

Mean total length of *U. pinnatifida* increased linearly from 48 cm on January 19 to 163 cm on April 7, and remained constant for the rest of April (Fig. 3). There was an exponential relationship between total length (TL: cm) and wet weight (WW: g) (Fig. 4). Using this relationship, wet weight increased exponentially from an initial value of 11.5 g to a maximum of 360 g in April (Fig. 3).

Mean linear growth rates, measured by the hole punching method, ranged from 1.0 to 1.8 cm day^{-1} (Fig. 5). Growth rates tended to be high (1.3 to 1.8 cm day^{-1}) in January and February compared with those in late March and April (1.0 to 1.7 cm day^{-1}).

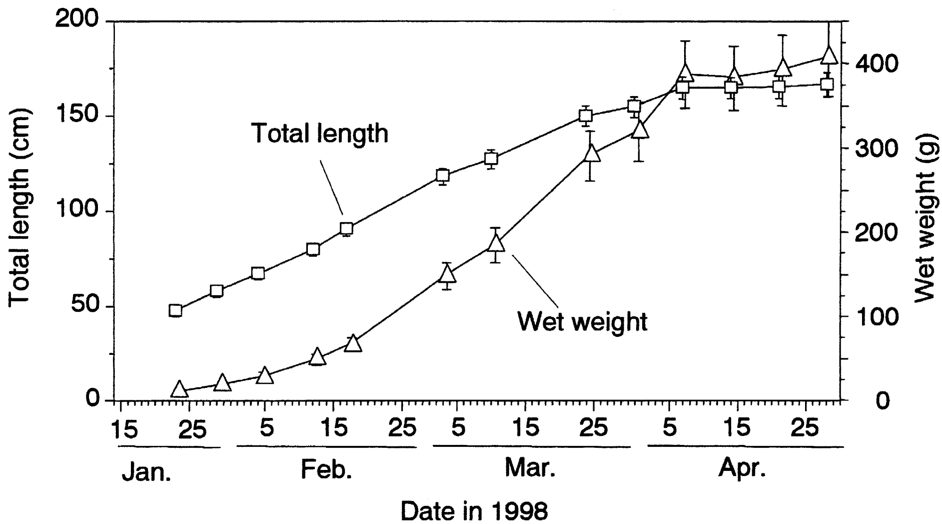

Fig. 3. Temporal changes in mean (±SE) total length (open square) and wet weight (open triangle) of 24 sporophytes of *U. pinnatifida*.

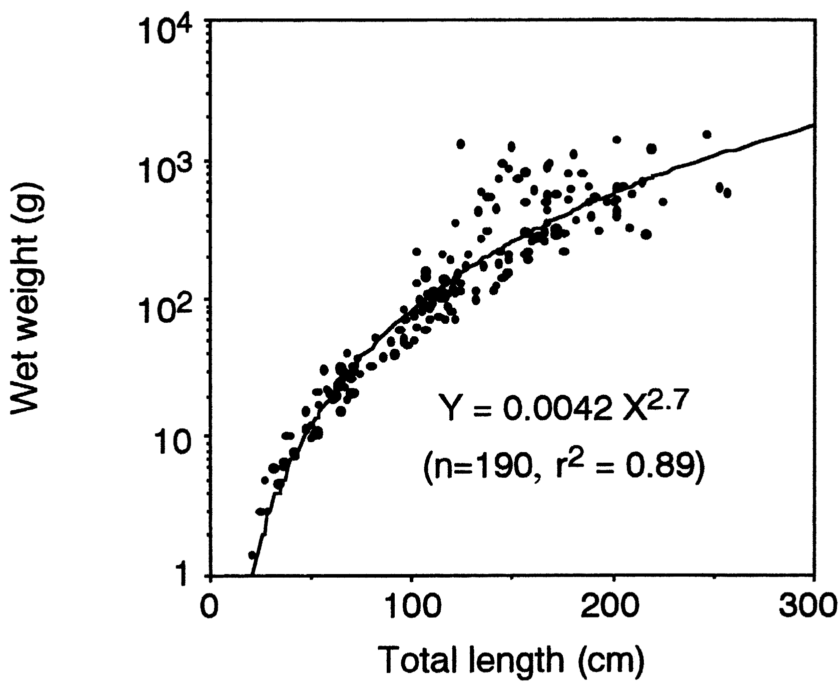

Fig. 4. Relationship between total length and wet weight of *U. pinnatifida*.

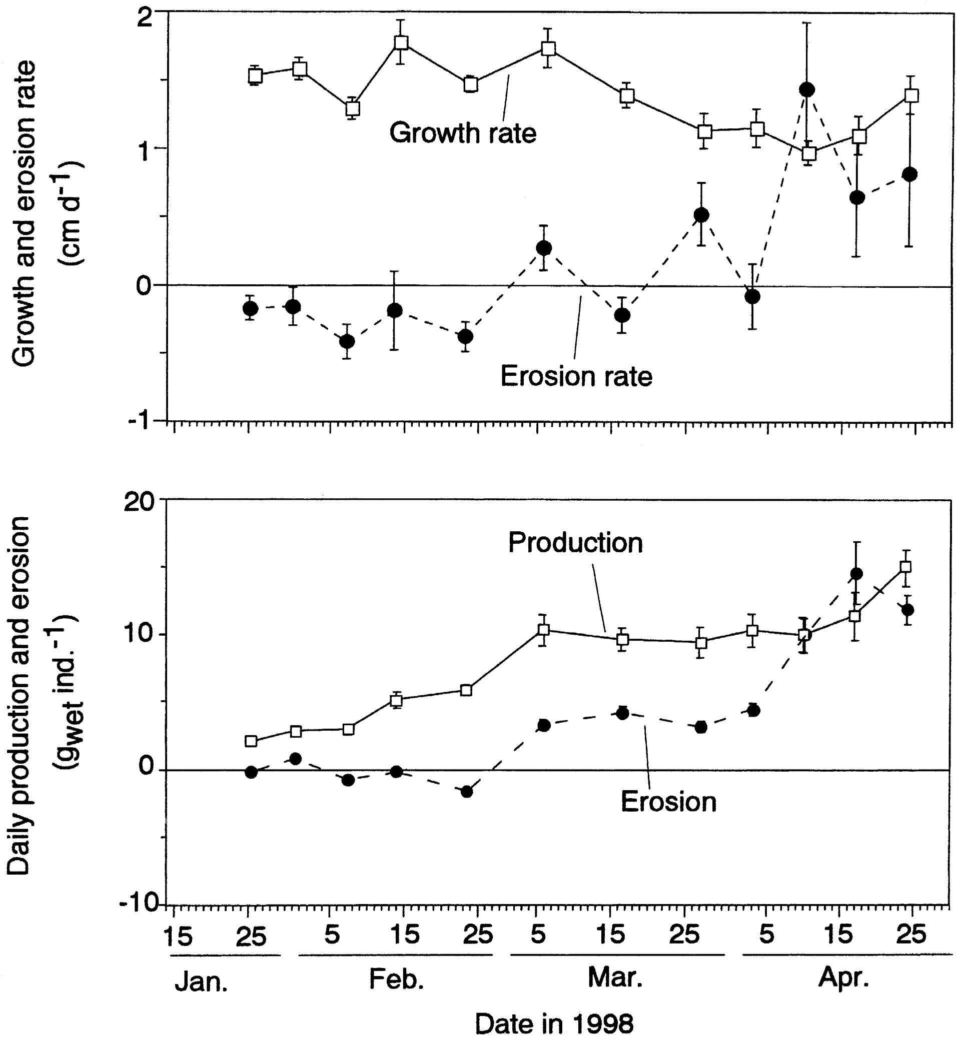

Fig. 5. Temporal changes in mean (± SE) growth rate (open square) and erosion rate (closed circle) of *U. pinnatifida* (upper), and mean individual daily production (open square) and erosion (closed circle) (lower).

Erosion rates were negligible until March, and then varied between 1.0 and 1.4 cm day^{-1} in April, equivalent to the growth rates at this time of year.

There was a significant linear relationship between growth rates and DIN ($r = 0.58$, $n = 12$, $p < 0.05$). No significant relationship was found between growth rates and daily solar radiation. In contrast, erosion rates were negatively correlated with DIN ($r = 0.73$, $n = 12$, $p < 0.05$), and positively correlated with daily solar radiation ($r = 0.60$, $n = 12$, $p < 0.05$). Neither growth nor erosion rates showed significant correlation with temperature.

Production as calculated by Eq. (2) increased from 2.5 to 10 g day^{-1} by mid February, and then remained stable through April, while erosion as estimated by the Eq. (3) began in March, when it was 30–40% of production, and increased to be nearly equal to production in April (Fig. 5).

3.3. Carbon and nitrogen contents

Only small differences in carbon and nitrogen contents were detected among the growth, central, and erosion regions of the blade and midrib (Fig. 6). Mean carbon

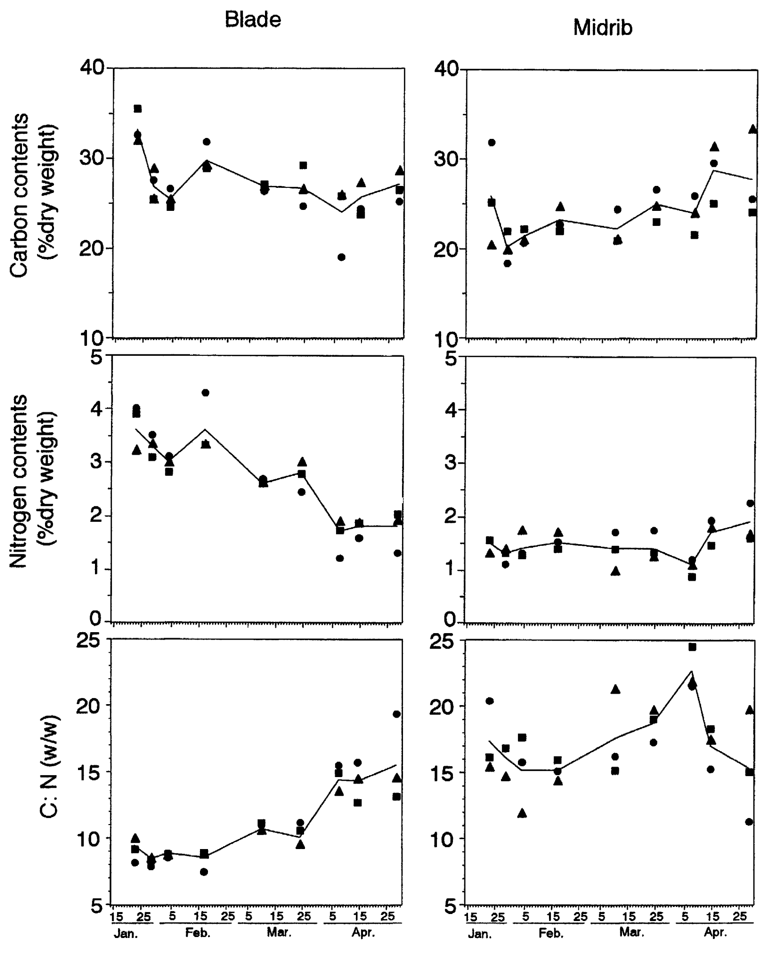

Fig. 6. Temporal changes in carbon content, nitrogen content, and carbon–nitrogen ratio in blades (left) and midribs (right). Closed circles, triangles, and boxes denote the growth, central, and erosion regions, respectively.

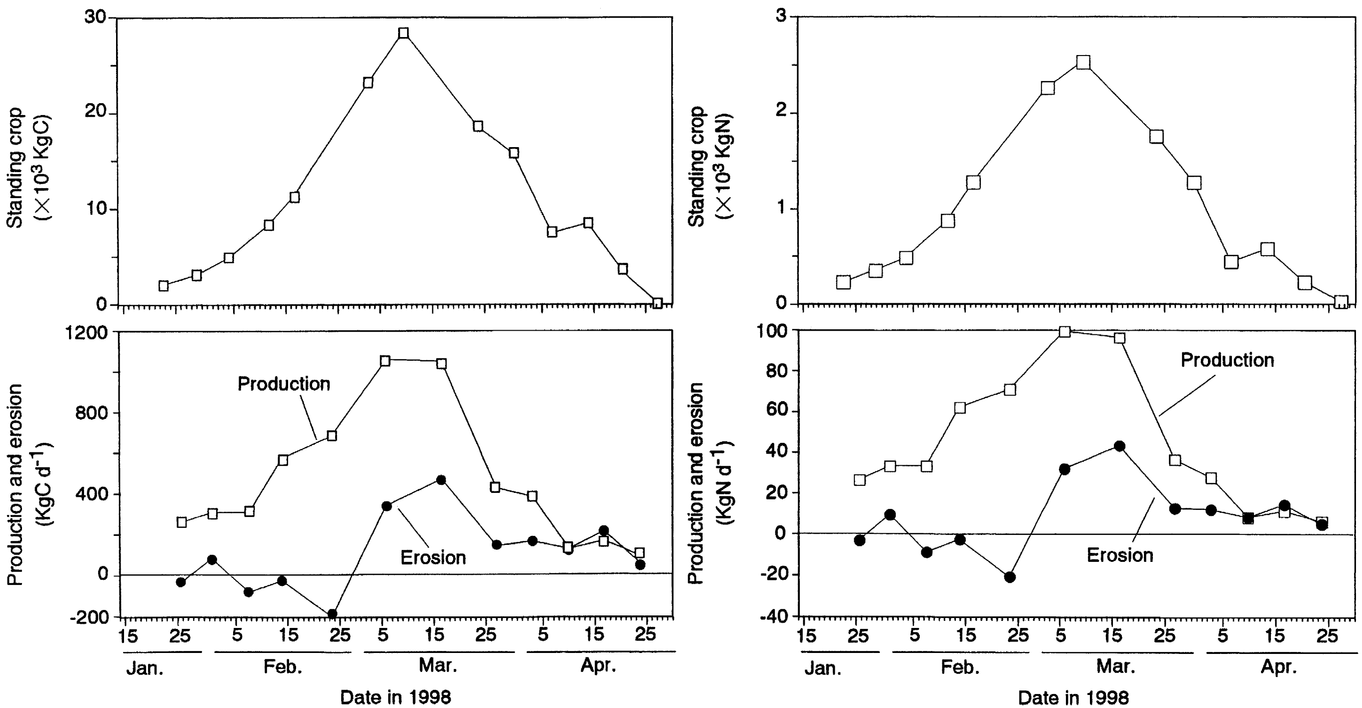

Fig. 7. Temporal changes in carbon (left)- and nitrogen (right)-based standing crop (upper), production (open square) and erosion (closed circle) (lower) of cultured *U. pinnatifida* throughout the Otsuchi Bay.

contents for the three blade regions ranged from 24.1% to 33.3%, and were relatively high compared with values in the midrib (20.2% to 28.8%) ($p < 0.05$). The mean carbon content of the midribs tended to increase from January to April, while that of the blade did not show any particular trend. The mean nitrogen content of the blade varied between 2.6% and 3.6% during late January to March and was $< 1.8\%$ in April. At the midrib, nitrogen was relatively low, ranging from 1.1% to 1.9% ($p < 0.05$). The mean ratio of carbon to nitrogen (w/w) for the blade varied between 8.4 and 10.7 during late January to March. In April, the C:N ratio increased to 14.3–15.5 probably due to decreasing ambient nitrogen. The midrib section had a higher C:N ratio of 15.2–22.8. Overall, C and N content averaged for one entire individual was 24.1–31.5% for carbon and 1.5–3.1% for nitrogen with a C:N ratio of 10.1–16.4. A significant relationship was observed between the nitrogen content of entire individuals and DIN ($r = 0.86$, $n = 12$, $p < 0.05$), whereas it was negatively correlated with solar radiation intensity ($r = 0.82$, $n = 12$, $p < 0.05$) and total length ($r = 0.91$, $n = 12$, $p < 0.05$).

3.4. Production and erosion of U. pinnatifida throughout Otsuchi Bay

Maximum biomass of 840 tonnes in wet weight (28.3 tonne C, and 2.54 tonne N) was recorded in early March, just prior to the harvest, and these figures decreased as the harvest continued (Fig. 7). Production of cultured *U. pinnatifida* throughout Otsuchi Bay increased steadily in January and February, and reaching maximums of 1055 kg C day^{-1} and 99.0 kg N day^{-1} in March. Erosion of the alga began in early March, and peaked at a rate of 469 kg C day^{-1} and 43.1 kg N day^{-1} in mid March. Erosion declined gradually as harvesting continued, and was comparable to production rates during the month of April. Total biomass produced during the 3-month period of observations was 49.5 tonne C and 4.68 tonne N. The biomass harvested was 38.7 tonne C (81% of total) while that lost due to erosion was 10.8 tonne C corresponding to 19% of the total biomass produced. In terms of nitrogen, the total losses to erosion and harvesting were 1.56 and 3.12 tonne N, respectively. Averaged for the entire bay (ca. 8 km long and 2 km wide), total biomass produced during the observation period was 3.1 g C m^{-2}.

4. Discussion

4.1. Production and erosion of U. pinnatifida in coastal waters

Compared with previous studies conducted in *Laminaria*-dominated areas, production estimated is lower. In St. Margaret's Bay (Nova Scotia), on the northeast Atlantic coast, Mann (1972b) found that *Laminaria*- and *Agarum*-dominated areas produced 1750 g C m^{-2} year^{-1} when averaged over the littoral zone, and 603 g C m^{-2} year^{-1} when averaged over the entire surface area of the bay. Field et al. (1977) reported production of *Laminaria* in South Africa to be 1330 g C m^{-2} year^{-1}, while Bellamy et al. (1968) estimated a total production of 1225 g C m^{-2} year^{-1} by *L. hypoborea* in southwestern England. The relatively low production of cultured *U. pinnatifida* in our study can be attributed to the small size of this specie as compared to species of *Laminaria*. Moreover, cultured *U. pinnatifida* was entirely harvested from Otsuchi Bay by early May, and hence no further production of the alga occurred. Natural communities of macroalgae occur in Otsuchi Bay and include *U. pinnatifida* and *Laminaria*. The biomass of these natural populations was estimated to be similar in magnitude to the biomass of commercially cultured *U. pinnatifida* in the bay (H. Ogawa, personal communication).

The release of tissues through erosion of cultured *U. pinnatifida* in Otsuchi Bay was at a maximum of 469 kg C day^{-1} in mid March, and total erosion during the study period was 10.8 tonne C, representing 19% of the total biomass produced. Natural populations of *U. pinnatifida* release organic matter through both erosion and displacement due to mortality during the senescent seasons of summer and autumn (Kurogi and Akiyama, 1957). However, the magnitude of organic matter released due to mortality is not well understood. Kirkman (1984) noted that the production of detritus (the sum of erosion and mortality) by *Ecklonia radiata* (Laminariales), growing on subtidal reefs of southern Australia, was greatest from April through July (austral autumn–winter). Druehl et al. (1986) investigated the linear erosion rate of 3-year classes of *L. groenlandica* on the west coast of Vancouver Island, B.C., and found it to be greatest between May and August (northern spring–summer).

Portions of eroded kelp are likely incorporated into the food chain by various grazing animals, while other parts are decomposed by bacteria. Uchida (1996) demonstrated the role of bacteria in degrading thalli of *L. japonica* into fine fragments, which are considered to be favorably small enough for the larvae of mollusks, crustaceans, and fish to feed on. Furthermore, about 40% of gross algal production is released as DOM during growth in brown algae (Khailov and Burlakova, 1969). Cultured *U. pinnatifida* is an important source of DOM, as evidenced by the abundant formation of transparent exopolymer particles in the *U. pinnatifida* culture area (Ramaiah et al., 2001). Thus, together with DOM released from living individuals (Mann, 1988; Duggins et al., 1989; Ramaiah et al., 2001), the erosion of cultured *U. pinnatifida* is considered to contribute to microbial loop cycling. In natural kelp communities, net production is incorporated into near-shore food webs through POM released by erosion, mortality, or grazing. Newell et al. (1982) reviewed energy flow in the kelp beds of Cape Peninsula, South Africa, which are dominated by *E. maxima* and *L. palida* and estimated total kelp production of 38,204 kJ m^{-2} year^{-1}. Direct grazing on kelp was estimated to remove 12% of the total kelp production. Of the remaining biomass, 30% was released as POM and 70% as DOM, and these were incorporated by consumers, including bacteria, filter feeders, and carnivores.

The C:N ratio in eroded portions of macroalgae is important in terms of protein requirements for consumers. Russell-Hunter (1970) calculated that most animals need a C:N ratio of 17 or less in their diet. In this study, the C:N ratio of *U. pinnatifida* ranged from 10.1 to 16.4. In other kelps, such as *L. longicruris* and *L. digitata*, the ratio is in the range of 13.8–27.2 (Mann, 1972a), indicating that these algae are a poor nitrogen source at some times of the year. Eroded tissues of *U. pinnatifida* provides a nitrogen-rich diet for consumers, although less nitrogen was present in the alga during the decay phase (Fig. 6).

4.2. Factors affecting growth and erosion

Our measurements of temporal fluctuations in the growth and erosion rates of *U. pinnatifida* are in good agreement with previous studies conducted in the coastal waters of Japan (Ishikawa, 1993; Nishikawa, 1967; Saitoh et al., 1999). We demonstrated that growth and erosion rates are closely associated with DIN concentration. In April, despite increases in solar radiation intensity, growth rates decreased and total length remained constant. Initiation of erosion coinciding with sporophyll formation indicates a close link between erosion and maturation of the alga. Therefore, changes in growth and erosion rates in April can be attributed to the aging of individuals. This period also coincided with a decrease in DIN concentration in the environment, due in part to growth and increase in phytoplankton biomass (Ramaiah et al., 2001) and to less frequent renewal of DIN concentrations through exchange of water masses between the coastal waters and the bay (Furuya et al., 1993). Thus, both aging and limited nutrient availability are considered to be responsible for the changes we observed in the growth and erosion rates of *U. pinnatifida*. Previous studies have suggested that increased erosion occurs in response to both aging and increasing water temperature (Kurogi and Akiyama, 1957; Nishikawa, 1967). The results of our study do not support an effect of temperature on algal erosion. These authors observed that temperatures above 14 °C enhanced both maturing and erosion, while Saitoh (1962) reported temperatures of 5–13 °C as optimal for growth of *U. pinnatifida*. The results of our study, however, do not support an effect of temperature on algal erosion. We found that the linear growth of the thalli stopped at a temperature of 6.5 °C, before seasonal water temperature warming occurred (Fig. 2). The discrepancy between our results and those of previous studies may be ascribable to nutrient supply, data on which is not available in the previous studies.

In conclusion, our work demonstrates the importance of erosion of the cultured kelp in coastal organic matter cycling. In northeastern Japan, the annual harvest of cultivated *U. pinnatifida* amounts to 50,000–75,000 tonnes. Considering that the erosion rates of *U. pinnatifida* in Otsuchi Bay are applicable to *U. pinnatifida* in other regions of Japan, an annual erosion of *U. pinnatifida* of the order of 12,000–20,000 tonnes can be expected based on the harvest statistics provided by the Ministry of Agriculture, Forestry and Fisheries of Japan (1997). Since the culture of other laminarian kelp in Japan is of the same magnitude as that of *U. pinnatifida*, the mass culture of the kelps can be an important supply of organic matter in the adjacent coastal areas. Seasonal growth of *U. pinnatifida* in France and New Zealand has been recognized to be similar to that in Japan (Hay and Villouta, 1993; Castric-Fey et al., 1999). Therefore, the invasive *U. pinnatifida* likely has a large impact in terms of DOM and POM released in various coastal areas of the world.

Acknowledgements

We are grateful for the kind assistance received from H. Otobe, K. Morita, and the staff of the Otsuchi Marine Research Center during the field observations. We thank M. Saitoh for technical suggestions with the growth experiments, H. Ogawa for co-operation with nutrient analyses and S. Chiba for the help with CHN analysis. Thanks are also due to Kamaishi Tobu and the Otsuchi Fisheries Associations for providing daily records of wakame harvests. *[AU]*

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