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Abundance and Productivity of Microphytobenthos on a Rocky Shore in Southern Hokkaido

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Abstract

Measurements were made of the microphytobenthic biomass and production at Benten-jima rocky shore in Usujiri, southern Hokkaido, an area with a complex microtopographic environment. Marked seasonal changes of biomass were observed throughout the entire area of the shore. High biomass was measured from October to March (0.4-0.8 $\mu g \cdot cm^{-2}$) when there was a large population of benthic microalgal flora such as those belonging to Chlorophyceae. During summer the biomass of microphytobenthos maintained a low level (<0.2 $\mu g \cdot cm^{-2}$) over the entire shore. These trends confirm the general pattern in seasonal change of intertidal microalgae stated in previous studies on other rocky shores. Microphytobenthic primary production varied between 16 and 133 mg $C \cdot m^{-2} \cdot day^{-1}$, and it occurred mainly during the middle spring. Mean daily production for the entire shore was calculated to be 51 mg $C \cdot m^{-2}$, which corresponded to 19 g $C \cdot m^{-2}$ in annual production. The seasonal variability in microphytobenthic biomass is discussed with respect to the feeding activities of intertidal grazers.

Introduction

Considerable attention has been paid to the interactions between species for available food supplies. Inter- and intra-specific competition for benthic microalgal food, including microscopic red, green, blue-green and other unicellular algae and macroalgal sporlings, among grazing gastropods has been demonstrated to be important in many different intertidal benthic communities (Underwood, 1976, 1978; Creese and Underwood, 1982; Montagna, 1984; Lukatelich and McComb, 1986). Benthic microalgae (microphytobenthos) could play an important role as food for the rich fauna of intertidal grazers, ranging from protozoa such as ciliates, to members of meio-, macro-, and megalo-invertebrates. It is surprising, therefore, that few studies have actually identiffed the precise nature of this type of food resource, and the effects of changes in the food supply on the population of intertidal grazers. There has been a great deal of study on microalgal biomass and their primary production of surface sediments in coastal sandy beaches and mudflats (e.g. Colijn and de Jonge, 1984; Nienhuis and de Bree, 1984; Wasmund, 1986; Sundback and Jonsson, 1988), but only very few studies have addressed these topics for marine intertidal rocky shores, especially in intertidal boulder fields (Gifford and Odum, 1961; Foster, 1964; Haven, 1973; Underwood, 1984).

Our purpose in this study is to examine the abundance and the primary

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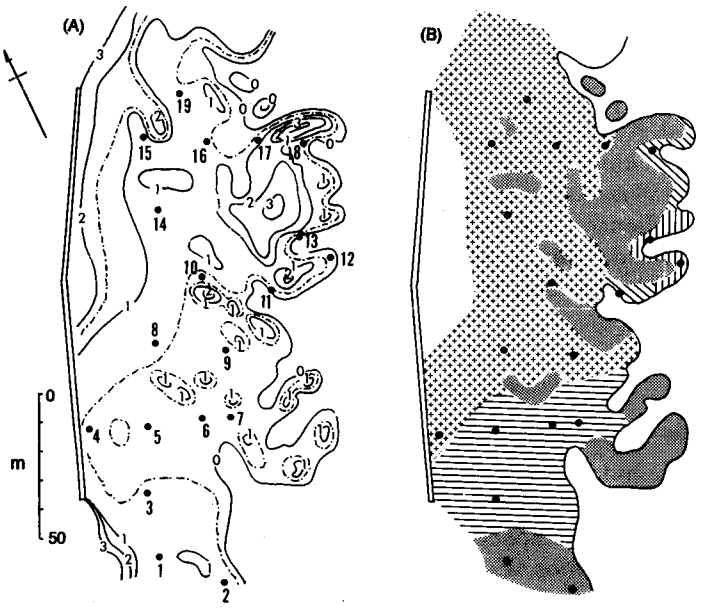

Fig. 1. Map of Benten-jima low-tide platform. (A): station (solid circles with number) and height above datum plane (m). (B): microtopography; ▨: bench, ▩: boulder, ▥: ledge, ▩: rampart, ▤: slope.

production of microphytobenthos in a rocky low-tide platform on the south coast of Hokkaido. Because of its wide of boulder field where a heavy crop of invertebrate grazers such as *Littorina brevicula* and *Collisella herolidi* inhabit (Fuji and Nomura, 1990), Benten-jima low-tide platform (Fig. 1) was chosen as a target for an investigation concerning the biomass of the littoral microphytobenthos.

Materials and Methods

Monthly samples were taken from 19 sites at Benten-jima platform, Usujiri (Fig. 1) from August 1989 to September 1990. At each site, a 100 cm^2 stainless steel quadrate was placed on the rock surface and the enclosed microalgal communities were scraped with a fine edged chisel, to ensure that all the algae were included. At each site, two scrapings were taken. The first scraping, for chlorophyll *a* determination, was placed in separate polyethylene jars to which was added a measured volume of filtered (0.45 μm pore size) seawater. The other scraping, for microscopic algae observation, was fixed with 5% formalin seawater. A total of 259 paired samples were taken from the platform throughout our study.

In the laboratory, subsamples for chlorophyll determination were concentrated on Whatman GF/C filters within 3 hours of collection and stored at $-20°C$ until the initiation of analysis. These filtered materials were extracted with 90% acetone, and were measured spectrophotometrically using the SCOR/UNESCO procedure (Strickland and Parsons, 1968). The cholorophyll *a* content of scraped microalgae

was used as a measure of crop.

Microalgal communities growing on polycarbonate plates immersed into a tide-pool in the platform were used to obtain the photosynthetic light saturation (P/I) curves. Such plates have been shown to be good mimics of the natural substrate (Cattaneo and Kalff, 1978). Photosynthesis was measured by a modified Ryther and Yentsch technique (1957). A series of five subsamples were spread out on the bottom of the glass flasks and incubated for 4 to 6 hours at *in situ* temperature at a series of irradiances (0 to 505 $\mu E \cdot m^{-2} \cdot s^{-1}$) produced by a 1,000 W tungsten lamp attenuated with different grades of neutral density screening (black woven polypropylene mesh); irradiances were measured with a LI-COR photosynthetic sensor LI-190SB.

Results

Composition of the microphytobenthic flora

The microphytobenthos on Benten-jima low-tide platform included more than 30 species, belonging to three classes. Only a few of these algal species were important as major components. The relative contribution of the major algal groups to the composition is shown in Table 1. The class Chlorophyceae: *Palmella* sp. and *Ulothrix* sp. which were dominant increased in relative abundance in December to May, reaching a maximum in January to March. Bacillariophyceae was commonly found throughout the year but reached their maximum during winter and spring when the dominant species were *Navicula* and *Fragilaria*.

Seasonal pattern of chlorophyll content

Table 2 shows the chlorophyll *a* content in μg per cm^2 of the biomass at each station. Marked seasonal fluctuations in chlorophyll content were observed at each sampling site, and these data indicate that chlorophyll values of the rock surface varied between 0.003 and 2.684 $\mu g \cdot cm^{-2}$. The values reached their peaks from late autumn to winter, with the highest content found in January at St. 19, a station that also exhibited the largest seasonal variation. The original list shown in Table 2, a format of 19 stations $\times$14 months, where samples were taken every month between August 1989 to September 1990, was used to perform the principal component analysis. This analysis was employed to simplify the complex structure. The ordination model obtained from the analysis is shown in Fig. 2, and has a simple descriptive value for the entire area. The first three components explained respectively are: PC1=31.9%, PC2=22.6% and PC3=12.9% of the total variance of the system, and all three are significant.

In the ordination obtained from the analysis of the 19 stations, two major groups were identified (Fig. 3). Group A, composed of 12 stations (4, 8, 9, 10, 11, 12, 14, 15, 16, 17, 18 and 19), was a boulder field and bench environment. Group B, composed of 7 stations (1, 2, 3, 5, 6, 7 and 13), was sited on a slope and rampart. The overall annual pattern of chlorophyll in both groups is shown in Fig. 3. During autumn and winter, there was more chlorophyll in samples than during other seasons. However, in these two seasons the difference was significant between the two groups only on certain months. Minimum amounts of chlorophyll were observed from April to August, and there was no significant difference between groups.

Table 1. Relative abundance of microphytobenthos found in Benten-jima rock surface.

Taxon	1989						1990					
	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Mar.	May	June	July	Aug.	Sept.
CYANOPHYCEAE												
Phormidium sp.	—	r	—	—	—	—	—	—	—	r	r	—
BACILLARIOPHYCEAE												
Melosira spp.	r	—	—	r	—	r	—	—	—	—	—	r
Hyalodiscus stelliger	—	—	—	—	r	r	—	—	—	—	—	—
Coscinodiscus spp.	—	—	r	—	r	r	—	—	—	—	—	—
Rhizosolenia spp.	—	—	—	r	r	r	—	—	—	—	—	—
Biddulphia spp.	—	—	—	r	r	—	r	—	—	—	—	—
Arachnoidiscus sp.	—	—	—	—	r	—	—	—	—	—	—	—
Diatoma spp.	—	—	—	r	r	—	—	r	—	—	—	—
Fragilaria spp.	—	r	—	r	—	c	f	f	r	r	r	r
Grammatophora sp.	—	—	—	—	—	—	r	—	—	—	—	—
Licmophora abbreviata	r	—	r	r	—	—	—	—	—	—	r	—
L. sp.	r	c	r	r	r	r	—	—	—	—	—	c
Acnanthes brevipes	—	—	—	—	—	—	f	—	—	—	—	—
Cocconeis spp.	r	—	r	—	—	r	r	r	r	r	r	—
Amphora sp.	—	r	—	—	—	—	—	r	r	c	r	r
Navicula cancellata	r	r	r	r	r	c	c	r	—	—	—	r
N. spp.	—	r	r	r	c	f	r	r	—	—	r	r
Rhoicosphenia sp.	—	—	—	—	—	—	—	r	—	r	—	—
Diploneis spp.	—	—	—	—	—	—	—	r	r	r	—	—
Gomphonema exignum	—	—	—	r	—	r	—	—	—	—	—	—
Cylindrotheca sp.	r	—	—	r	r	—	—	r	r	r	—	—
Nizschia spp.	—	r	—	—	—	r	—	—	—	—	—	—
CHLOROPHYCEAE												
Palmella sp.	r	r	r	c	f	a	f	f	c	r	r	r
Ulothrix sp.	—	—	—	r	c	f	c	r	—	—	—	—
Germlings of macroalgae	—	—	—	r	c	f	f	c	r	—	—	—

—: absent, r: rare, c: common, f: frequent, a: abundant.

Table 2. Chlorophyll *a* content ($\mu g \cdot cm^{-2}$) in a scraped area at each time.

St.	1989					1990								
	Aug.	Sept.	Oct.	Nov.	Dec.	Jan.	Feb.	Mar.	Apr.	May	June	July	Aug.	Sept.
1	0.003	0.061	0.095	0.539	0.177	0.528	0.384	0.056	0.066	0.063	0.096	0.059	0.095	0.033
2	0.004	0.087	0.182	0.270	0.092	0.601	0.913	—	—	0.016	0.059	0.036	0.050	0.186
3	0.051	0.226	0.262	0.345	0.810	0.538	0.879	0.783	0.118	0.179	0.165	0.112	0.011	0.102
4	0.112	0.963	1.062	0.937	1.500	0.860	1.005	0.328	0.510	0.325	0.222	0.131	0.106	0.215
5	0.027	0.102	0.932	0.507	0.480	0.509	0.293	0.015	0.106	0.180	0.064	0.094	0.092	0.145
6	0.072	0.159	0.127	0.426	0.528	0.286	0.983	0.684	0.057	0.326	0.234	0.172	0.056	0.260
7	0.057	0.066	0.040	0.249	0.320	0.316	0.856	—	—	0.460	0.111	0.336	0.191	0.090
8	0.093	0.285	0.757	0.476	0.314	1.063	0.463	0.475	0.120	0.076	0.111	0.108	0.069	0.130
9	0.051	0.209	0.217	0.431	0.299	0.275	0.727	0.310	0.214	0.287	0.069	0.133	0.307	0.410
10	0.080	0.370	0.621	0.529	0.309	0.983	0.432	0.196	0.075	0.069	0.125	0.053	0.087	1.330
11	0.059	0.101	0.368	0.231	0.310	0.436	0.643	0.505	0.115	0.090	0.046	0.079	0.042	0.059
12	—	0.631	0.372	0.299	0.643	0.322	0.638	1.530	0.081	0.113	0.048	0.097	0.103	0.057
13	0.551	0.088	0.199	0.517	1.701	0.742	0.950	0.384	0.091	0.121	0.247	0.151	0.145	0.831
14	0.133	0.663	0.554	0.385	0.881	0.443	0.524	0.367	0.266	0.471	0.298	0.213	0.265	0.222
15	—	0.618	0.371	0.157	0.113	0.234	0.327	0.365	0.179	0.297	0.196	0.217	0.220	0.299
16	0.032	0.203	0.141	0.294	0.439	0.204	0.261	0.101	0.064	0.149	0.052	0.055	0.086	0.158
17	0.085	0.231	0.244	0.275	0.089	0.279	0.286	0.251	0.156	0.263	0.090	0.116	0.101	0.052
18	0.074	0.037	0.218	0.172	0.418	0.417	0.531	0.124	0.080	0.142	0.073	0.104	0.059	0.062
19	—	0.402	0.232	0.327	0.320	2.684	0.405	0.459	0.134	0.161	0.097	0.110	0.067	0.089

— : no measurement done.

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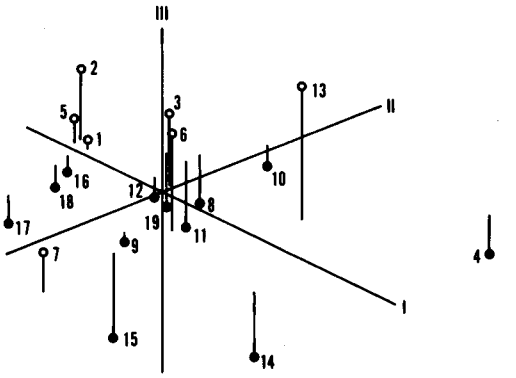

Fig. 2. Ordination model, in the space of first three axes obtained by principal component analysis of the observations based on variables of station. Circles with number are station-points.

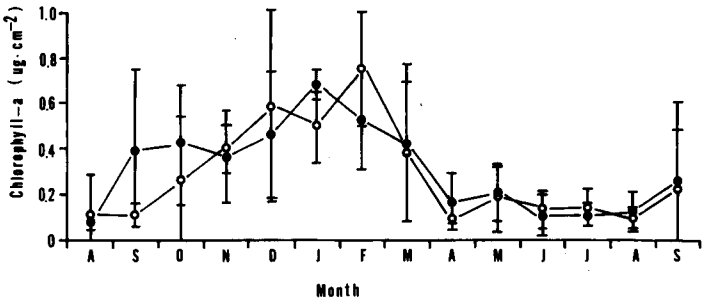

Fig. 3. Seasonal changes of chlorophyll *a* content in Group A (closed symbols) and Group B (open symbols). Vertical bars show the range of standard deviation.

This pattern undoubtedly reflects the changes noted in the community composition (Table 1) and abundance of microphytobenthos (Table 2).

Biomass and primary production

To determine the relationship between chlorophyll *a* content and dry weight of microalgae, paired samples were collected from the polycarbonate plates immersed in a tide-pool. Several sets of such samples were collected at different times. There was a significant relationship between the chlorophyll content and the biomass at all times ($t=3.415$, $N=30$, $P<0.01$) and the data were adequately described by a single linear regression (Fig. 4). The correlation coefficient was highly significant ($r=0.542$, $N=30$, $P<0.01$). When converting chlorophyll concentration into biomass, the period between autumn and winter exhibited the highest value reflecting the large abundance of microalgal flora (Table 3). The biomass varied between 0.11 and 0.95 g DW$\cdot$m^{-2}, and the mean annual biomass of the entire platform was given an estimate of 0.36 g DW$\cdot$m^{-2}.

A plot of photosynthetic primary production as a function of light intensity is

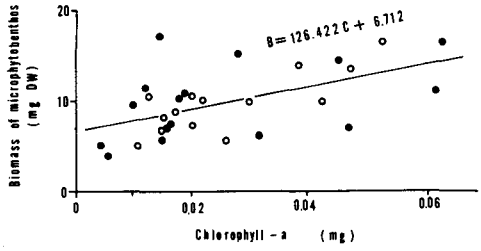

Fig. 4. Regression of biomass (B) against chlorophyll *a* content (C) of microphytobenthos, for October (closed symbols) and February (open symbols).

Table 3. Monthly biomass and primary production of microphytobenthos.

Month	Biomass ($g \cdot m^{-2}$)			Primary production (mg $C \cdot m^{-2} \cdot day^{-1}$)		
	A	B	Entire	A	B	Entire
Aug.	0.11	0.14	0.11	16.06	22.09	16.86
Sept.	0.50	0.15	0.44	108.13	30.50	70.76
Oct.	0.55	0.34	0.43	65.31	39.47	50.36
Nov.	0.48	0.52	0.45	38.02	41.02	35.84
Dec.	0.60	0.75	0.60	67.69	84.97	68.14
Jan.	0.87	0.64	0.71	67.19	49.40	54.99
Feb.	0.66	0.95	0.71	36.70	52.94	39.43
Mar.	0.53	0.49	0.47	23.21	21.00	20.42
Apr.	0.22	0.12	0.16	69.75	36.92	51.89
May	0.26	0.25	0.23	132.67	126.03	118.90
June	0.16	0.18	0.15	56.46	65.86	55.02
July	0.16	0.18	0.15	47.82	55.81	46.62
Aug.	0.17	0.12	0.14	26.11	18.08	20.96
Sept.	0.33	0.30	0.29	72.09	63.77	62.90

A: Group A sites; B: Group B sites; Entire: Total platform area.

fitted in Steele's (1962) formula as follows:

$$P = P_{max}(I/I_{opt}) \cdot \exp(1-(I/I_{opt}))$$

where P is the gross photosynthetic rate (rate of carbon production per unit chlorophyll content of microalgae), P_{max} is the maximum photosynthetic rate, I is the light intensity *in situ*, and I_{opt} is the light intensity at which the maximum photosynthetic rate takes place. Maximum photosynthetic rate (P_{max}) and optimum light intensity (I_{opt}) as characteristics for photosynthetic light saturation curve were obtained from measurements of photosynthesis as a function of irradiance (Table 4). These photosynthetic light saturation curves were used to calculate *in situ* production at different sampling sites every month. Thus, the estimate of microalgal primary production was calculated by using the mean monthy irradiance values obtained from Muroran meteorological observatory situated about 40 km

Table 4. Photosynthesis-irradiance characteristics of microphytobenthos.

Month	P_{max} (μg C$\cdot\mu$g chl$^{-1}\cdot$h^{-1})	I_{opt} (μE$\cdot$m$^{-2}\cdot$s^{-1})
Jan.	2.03	287.06
Feb.	2.30	337.17
Mar.	2.53	316.23
Apr.	7.24	535.75
May	6.25	782.64
June	4.37	673.78
July	4.78	548.29
Aug.	2.76	578.46
Sept.	2.63	666.73
Oct.	2.50	455.53
Nov.	2.13	309.85
Dec.	2.28	268.15

north of Benten-jima, Usujiri.

The phtosynthetic rates for the period 1989-1990 are given on the right side of Table 3. The total range for daily microalgal primary production was 16 to 133 mg C$\cdot$m$^{-2}\cdot$day^{-1}, and most of it occurred during the middle of spring. The microalgal photosynthesis was saturated in light intensity at 500-780 μE$\cdot$m$^{-2}\cdot$s^{-1} from the middle of spring to early autumn, and at about 300 μE$\cdot$m$^{-2}\cdot$s^{-1} in the residual seasons (Table 4). Despite the fact that the biomass was limited in lower level, higher microalgal photosynthesis values were found in May when the *in situ* irradiance reaches its maximum intensity during the year. The tentative value for the mean microalgal primary production for the entire platform was calculated by estimating the proportion corresponding to each microtopographic area and was found to be 51 mg C$\cdot$m$^{-2}\cdot$day^{-1}, corresponding to 19 g C$\cdot$m$^{-2}\cdot$yr^{-1}.

Discussion

Many studies have emphasized the role of microphytobenthos as a substantial food source for invertebrate grazers (e.g. Underwood, 1984; Chow, 1987). For rocky shores, a few quantitative data have been provided on the microphytobenthic biomass and productivity. The paucity in these data is due to the difficulty in manipulating and assessing microalgae present on rock surfaces. Compared to samplings from surface sediments, it is quite difficult to remove microalgal materials from rock surface without losing some samples. Some studies on the microphytobenthos of rocky shores have used the scraping method and found it a reliable and repeatable manner of sampling for microalgal crop. In examining microphytobenthic crop samples, both Castenholz (1961) and Foster (1964), for example, found a scraping blade to be a most efficient method. From his elaborate experiments, Underwood (1984) has detected the presence of microalgae, based on rock colouration, only on the top layer (usually 0.2-0.8 mm depth) of the substratum;

further scraping showed the natural color of the rock. Scraping in our study was performed by using a fine edged chisel, which is an undoubtedly difficult and time-consuming method compared with sampling from a soft bottom, but is a most reliable way of sampling from a hard bottom.

Up to the present, several methods are available for the quantification of microphytobenthos. A direct method is by counting the living cells under light or fluorescent light microscopy (Jones, 1974; Levinton and Bianchi, 1981; Smith et al., 1985; Sundback and Jonsson, 1988). This is also widely used in the estimation of planktonic assemblages. An indirect measure of biomass or productivity of microphytobenthos is the estimation of chlorophyll *a* by extracting with acetone (Gifford and Odum, 1961; Castenholz, 1963; Strickland and Parsons, 1968; Sundback and Jonsson, 1988). The measurement of chlorophyll has several advantages, especially the ease of determining of the quantities of microalgae. According to Underwood (1984) the relationship between the number of microalgal cells per unit area sampled and chlorophyll content per unit area was consistent during the different seasons of the year. From this evaluation of the reliability of the chlorophyll assay for microalgal biomass, he concluded that the measurement of chlorophyll content provided valid estimates of total density of microalgal cells over a wide range of places and times of sampling. At present, although there are only a few measurement of microphytobenthic biomass found on rock surfaces (Gifford and Odum, 1961; Foster, 1964; Chapman, 1981), the high significant correlation laid between chlorophyll content and microalgal biomass (Fig. 4) may point out that the routine use of chlorophyll assay is a realistic method for estimating of microphytobenthic biomass.

In our study, peak biomass, measured by chlorophyll content, was reached toward the colder period of the year (October to March) and was followed by a decline toward the warmer period, with marked seasonal fluctuations. A similar trend in chlorophyll content of microalgae on the rock surface has been described by Nicotri (1977) and Underwood (1984). The results reported here suggest a general trend for the density of microalgae inhabiting a rock surface. That is, they are less abundant during the warmer period of the year and *vice versa*. Castenholz (1961) from his experiments revealed that microalgae extended on the rock surface in the presence of grazers during winter. In addition, he suggested that productivity of the microalgae during summer was faster because of increased light intensity, but that they get consumed by the grazers. Although, in our study, no observations were carried out on the participation of grazers that could explain the seasonal changes of the microalgal abundance, the estimates provided here are that of the amount of chlorophyll in areas already subject to grazing. Therefore, we have assumed that the biomass we measured is the microalgae left by the grazers on the rock surface. The annual production rates in intertidal and shallow coastal sediments are within a range of 20 to 300 g $C \cdot m^{-2}$ (Colijn and de Jonge, 1984; Lukatelich and McComb, 1986), compared with 15 g $C \cdot m^{-2}$ (Chapman, 1981) to 19 g $C \cdot m^{-2}$ (in the present study) for the microphytobenthos on rock surfaces. It may be a reflection of the grazing pressure on the microalgae, as well as other physicochemical conditions in the rock surface. Thus, the general pattern mentioned above leads to the assumption that a marked seasonal change in the abundance of microphytobenthos may be a result of the grazing activity of some grazers at

different times of the year. Such explanations require experimental separation of the various components of grazing and microalgal productivity. The participation of grazers on the seasonal fluctuation of microphytobenthos warrants further investigations.

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References

Castenholz, R.W. (1961). The effect of grazing on marine littoral diatom populations. *Ecology* **42**, 783-794.

Castenholz, R.W. (1963). An experimental study of the vertical distribution of littoral marine diatom. *Limnol. Oceanogr.* **8**, 450-462.

Cattaneo, A. and Kalff, J. (1978). Seasonal changes in the epiphyte community of natural and artificial macrophytes in Lake Memphremagog. *Hydrobiologia* **60**, 135-144.

Chapman, A.R.O. (1981). Stability of sea urchin dominated barren grounds following destructive grazing of kelp in St. Margaret's Bay, eastern Canada. *Mar. Biol.* **62**, 307-311.

Chow, V. (1987). Patterns of growth and energy allocation in northern California populations of *Littorina* (Gastropoda: Prosobranchia). *J. Exp. Mar. Biol. Ecol.* **110**, 69-89.

Colijn, F. and de Jonge, V.N. (1984). Primary production of microphytobenthos in the Ems-Dollard Estuary. *Mar. Ecol. Prog. Ser.* **14**, 185-196.

Creese, R.G. and Underwood, A.J. (1982). Analysis of inter- and intra-specific competition amongst limpets with different methods of feeding. *Oecologia* **53**, 337-346.

Foster, M.S. (1964). Microscopic algal food of *Littorina planaxis* Pillippi and *Littorina scutulata* Gould (Gastropoda: Prosobranchiata). *Veliger* **7**, 149-152.

Fuji, A. and Nomura, H. (1990). Community structure of the rocky shore macrobenthos in southern Hokkaido, Japan. *Mar Biol.* **107**, 471-477.

Gifford, C.E. and Odum, E.P. (1961). Chlorophyll *a* content of intertidal zones on a rocky seashore. *Limnol. Oceanogr.* **6**, 83-85.

Haven, S.B. (1973). Competition for food between the intertidal gastropods *Acmaea scabra* and *A. digitalis*. *Ecology* **54**, 143-151.

Jones, J.G. (1974). A method for observation and enumeration of epilithic algae directly on the surface of stones. *Oecologia* **16**, 1-8.

Levinton, J.S. and Bianchi, T.S. (1981). Nutrition and food limitation of deposit-feeders. I. The role of microbes in the growth of mud snails (Hydrobiidae). *J. Mar. Res.* **39**, 531-545.

Lukatelich, R.J. and McComb, A.J. (1986). Distribution and abundance of benthic microalgae in a shallow southwestern Australian estuarine system. *Mar. Ecol. Prog. Ser.* **27**, 287-297.

Montagna, P.A. (1984). *In situ* measurement of meiobenthic grazing rates on sediment bacteria and edaphic diatoms. *Ibid.* **18**, 119-130.

Nicotri, M.E. (1977). Grazing effects of four marine intertidal herbivores on the microflora. *Ecology* **58**, 1020-1032.

Nienhuis, P.H. and de Bree, B.H.H. (1984). Carbon fixation and chlorophyll in bottom sediment of brackish Lake Grevelingen, The Netherland. *Neth. J. Sea. Res.* **18**, 337-359.

Ryther, J.H. and Yentsch, C.L. (1957). The estimation of phytoplankton production in the ocean from chlorophyll and light data. *Limnol. Oceanogr.* **2**, 281-286.

Smith, B.D., Cabot, E.L. and Forman, R.E. (1985). Seaweed detritus *versus* benthic diatoms as important food resources for two dominant subtidal gastropods. *J. Exp. Mar. Biol. Ecol.* **92**, 143-156.

Steele, J.H. (1962). Environmental control of photosynthesis in the sea. *Limnol. Oceanogr.* **7**, 137-

150.

Strickland, J.D. and Parsons, T.R. (1968). A practical handbook of seawater analysis. *Fish. Res. Bd. Can. Bulletin* **167**, 195-196.

Sundback, K. and Jonsson, B. (1988). Microphytobenthic productivity and biomass in subtidal sediments of a stratified bay, southeastern Kattegat. *J. Exp. Mar. Biol. Ecol.* **122**, 63-81.

Underwood, A.J. (1976). Food competition between age-classes in the intertidal neritacean *Nerita atramentosa* Reeve (Gastropoda: Prosobranchia). *Ibid.* **23**, 145-154.

Underwood, A.J. (1978). An experimental evaluation of competition between three species of intertidal gastropods. *Oecologia* **33**, 185-208.

Underwood, A.J. (1984). The vertical distribution and seasonal abundance of intertidal microalgae on a rocky shore in New South Wales. *J. Exp. Mar. Biol. Ecol.* **78**, 199-220.

Wasmund, N. (1986). Ecology and bioproduction in the microphytobenthos of the chain of shallow inlets (Boddens) south of the Darss-Zingst Peninsula (southern Baltic Sea). *Int. Rev. Gesamten Hydrobiol.* **71**, 153-178.