CHAPTER 18

MEASUREMENTS OF METABOLIC ACTIVITIES WITHIN A BALTIC FUCUS VESICULOSUS COMMUNITY: THE CONTRIBUTION OF FOULING MICROALGAE AND GRAZERS

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18.1 INTRODUCTION

Fucus vesiculosus L., the bladder-wrack, is widely distributed throughout the Baltic littoral forming dense stands between depths of 1.5 and 5.5 m (Luther et al. 1975, Wallentinus 1979). The Fucus belt constitutes a rich and diverse system for plant-animal interactions in the Baltic Proper (Jansson 1977, Jansson et al. 1982). However, in brackish water, Fucus vesiculosus is highly suscepticle to changes in hydrography, microalgal colonization, grazing pressure by herbivores and sedimentation. Pulses of North Sea water into the Baltic Sea change the salinity and nutrient levels of the water, and enhanced microalgal production may seriously disturb the growth of Fucus. An extensive decline and disappearance of Fucus from Finnish coastal areas in the late 1970's and early 1980's (Kangas et al. 1982) revealed that the community dynamics within the dominant macroalgal belt are still too poorly known for valid predictions. More detailed measurements of community metabolism and foodweb interactions within Fucus stands are necessary for better understanding and possible management. To accomplish this, methodological problems must be solved.

The purpose of the present study was to develop and test methods for the simultaneous in situ measurement of (1) community metabolism within Fucus stands, (2) the contribution of different subsystems of the community (i.e., the macroalga, epiphyton, plankton and benthos) to the total metabolism, and (3) grazing activities of dominant herbivores on the algal communities.

18.2 MATERIALS AND METHODS

The study area was located close to Tvärminne Zoological Station on the SW coast of Finland (Fig. 1). The average salinity is 6‰ and tidal range is negligible there. During the first experiment (14-14 June) the skies were sunny and water temperature was 10.8-11.3 °C. During the second experiment (20-21 July) the sky was overcast and water temperature was 11.5-12.5 °C. During both experiments the water pH was near 7.9. A detailed description of conditions in the Tvärminne area is given by Niemi (1973).

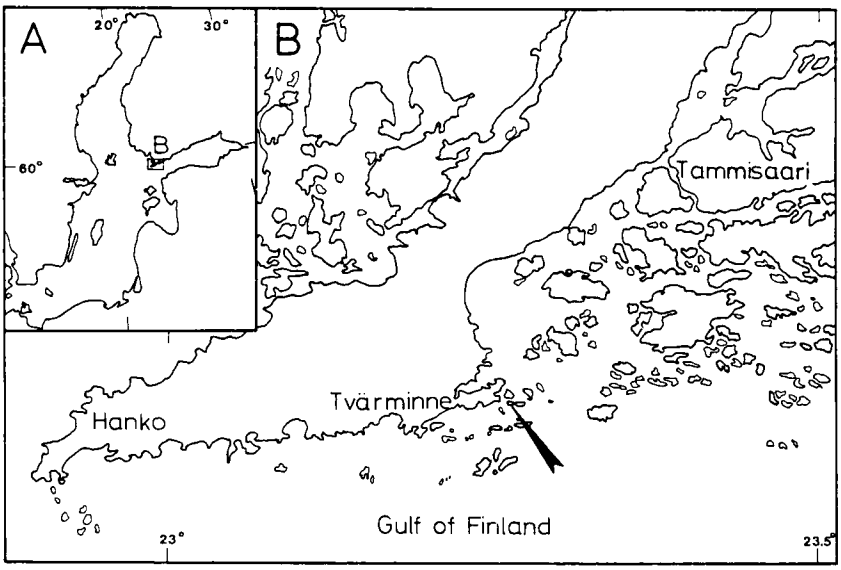

Fig. 1. Location of the study site in the Tvärminne area in the northern Baltic Sea.

The sampling area was on a southfacing shore of Halsholmen island. Measurements were carried out on a relatively hard, sandy bottom at a depth of 1.5-2 m where the Fucus stand (permanently submerged) consisted mainly of large, separate specimens, which were densely covered by epiphytic material. The field work was done using SCUBA. One tall (50-60 cm), healthy-looking individual from the Fucus stand was selected for the measurement of community metabolism. A transparent acrylic plastic chamber (volume 106 l, height 70 cm) was slid over the macroalga, taking care not to detach it from its stone substratum or to disturb its epiphytic flora and fauna. The chamber was constructed of two parts, which were bound together with strong rubber bands (Fig. 2). The joints were sealed with silicon rubber. In the upper part there was a large (6 cm dia.) hole for the probe and the stirrer of a YSI oxygen meter (model 58). Neoprene was used to tightly hold the probe and the stirrer in position. During the first measurement, more efficient water mixing within the chamber was achieved by manual stirring with a propeller, since the stirrer connected to the oxygen probe proved inadequate. During the second measurement, a supplementary battery powered stirrer ran continuously inside the chamber (Fig. 2). A two blade propeller (total length 24 cm, speed 8 rpm) was sufficient to keep the water thoroughly mixed throughout the experiment. Variation (S.D./mean * 100) among 4-6 subsamples of dissolved inorganic carbon (DIC), taken from different parts of the chamber, was ± 1 %, compared to ± 0.5 % for the distilled water standard (15 mg C l^{-1}).

Water samples for DIC were taken from the measuring chamber with 4-6 10 ml

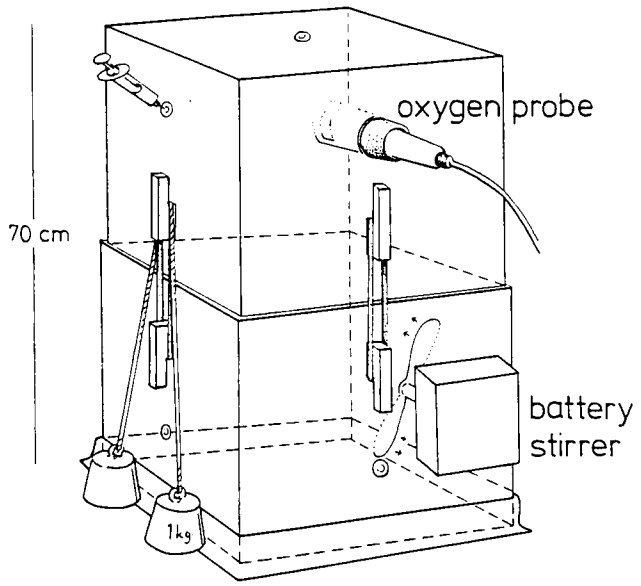

Fig. 2. A schematic representation of the measuring chamber (see text for details).

syringes by inserting the needles through silicon stoppers on the walls and the roof of the chamber (Fig. 2). The samples were transported to the laboratory in a dark cool-box. DIC was analysed as CO_2 using a Unicarb-carbon analyser (electro Dynamo) after the method of Salonen (1981).

When respiration of the Fucus community was measured, the chamber was covered with an opaque plastic bag. The bag was removed while measurements of photosynthetic activity of the community was taken. At the initiation of the photosynthetic measuremants a $NaH^{14}CO_3$ solution was injected and mixed into the chamber water (290 µCi on 14-15 June and 90 µCi on 20-21 July). The sampling procedure after an incubation time of 5-5.5 hours was as follows: (1) a water sample of 500 ml was taken from inside the chamber; (2) the upper part of the chamber was gently removed and 6 ends of the Fucus thallus (with their epiphytes) were clipped off and put separately into 100 ml plastic enclosures; (3) the rest of the Fucus thallus with its epiphytes was harvested and placed in a large plastic bag; (4) 3 sediments samples from inside the lower part of the chamber were taken with acrylic plastic cores (4.5 cm dia.). All samples were transported to the laboratory in cool-boxes under an opaque sheet.

In the laboratory the samples were prepared for analysis by a CHN-analyser connected to a liquid scintillation system as follows: (1) water samples were filtered through Whatman GF/C filters, acidified with 1 N HCl to liberate inorganic ^{14}C and then dried at room temperature; (2) epiphytes from the ends of the Fucus thallus were removed with the help of a soft plastic brush and vigorous

shaking; (3) Surface layers (0.5-1 cm) of the sediment cores were cut off for further treatment; (4) Attached material on the rest of the Fucus thallus was removed as thoroughly as possible with strong water jets and a plastic brush. The water containing the detached epiphytic material was gathered separately into plastic containers and concentrated to a smaller volume of water (500 ml) by letting the suspension settle overnight in a dark, cold room (2 °C). Water over the concentrated suspension was siphoned away, with the exception of a 500 ml subsample which was filtered and subsequently treated in the same manner as the plankton sample (for checking the sedimentation efficiency of the epiphytic material). After collection of the most common invertebrates (Table 3) from the epiphytic suspension, the rest of the suspension was dried at 60 °C as well as the other ^{14}C-samples (i.e. Fucus thallus, 6 ends of the thallus, epiphytic materials, sediment samples and invertebrates). All samples were acidified with 1 N HCl before drying.

Before drying, the Fucus thallus was divided into four parts: remaining ends, upper part, middle part and lower part (cf. Fig. 4). All parts were then treated separately. After drying all the Fucus parts, epiphytic materials and sediment samples were homogenized and weighed. Then 2-5 small subsamples (10 mg) were combusted in a CHN-analyser (Hewlett Packard) for analysis of total carbon and nitrogen and fixed ^{14}C. The radiocarbon was trapped as $^{14}CO_2$ from the outflow gas in a gas-liquid exchange column and the absorbent (Carbo-Sorb II, Lumac) was run directly into a scintillation vial attached to the column. The larger animals were combusted separately, whereas for the smaller species 3-5 individuals were analysed together. Radioactivities were measured in a xylene based scintillation coctail (Carbo-Luma, Lumac) using a Wallac Rackbeta liquid scintillation counter.

TABLE 1

Comparison of primary production and darkrespiration rates of entire Fucus community measured by ^{14}C and O_2 methods.

	14-15 June	20-21 July
^{14}C / net O_2	1.08	0.69
^{14}C / gross O_2	0.71	0.46
^{14}C / net CO_2	-[a]	0.70
^{14}C / gross CO_2	-	0.49
P.Q. net	-	1.02
P.Q. gross	-	1.06
R.Q.	-	0.87

[a] not measured

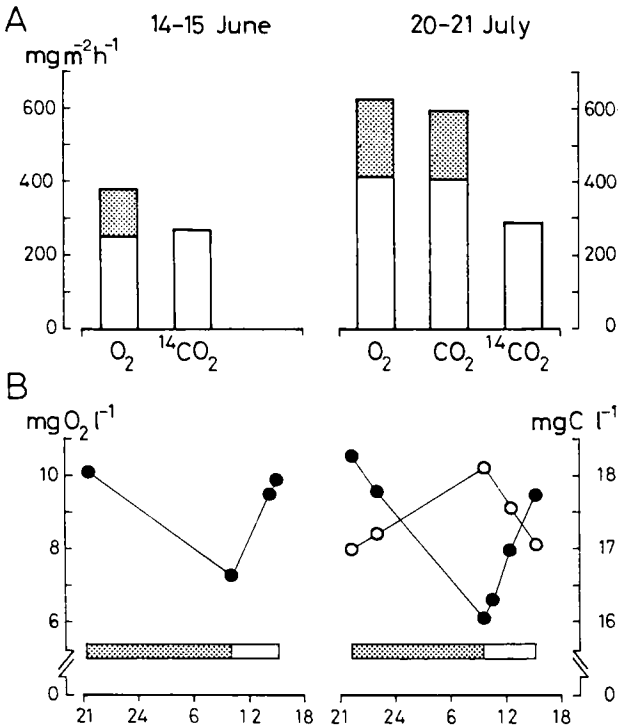

Fig. 3. (A) Primary production (white) and dark respiration (stipped) measured by different methods. (B) Changes in oxygen (closed circles) and dissolved inorganic carbon (DIC) (open circles) concentrations in the chamber. Dark period is marked with a shaded bar and light period with white.

18.3 RESULTS

For the metabolic activity of the whole Fucus communtiy, the results from the ^{14}C method and net O_2 changes in the light produced comparable results in the first experiment (14-15 June) (Fig. 3A, Table 1). Dark respiration contributed 33 % of the gross O_2 change and 30 % of the gross CO_2 change, respectively. Both the dissolved inorganic carbon (DIC) and the oxygen concentrations showed linear changes during the measuring periods (Fig. 3B). The gas exchange rates thus seemed to be only slightly affected by the changing concentrations. The photosynthetic quotient (P.Q.) for evolved O_2 and assimilated CO_2 on 20-21 July was near unity (1.02 for the net results and 1.06 for the gross results, Table 1). The respiratory quotient (R.Q.) for evolved CO_2 and consumed O_2 remained below unity (0.87, Table 1), indicating that the freshly synthesized carbohydrates were hardly used as substrates for respiratory processes (cf. Fogg 1969).

^{14}C incorporation in the light revealed the sites and distribution of photosynthetic activity within the Fucus community. The results indicated that the macroalga had much greater photosynthetic activity than other producers in the

TABLE 2

Percent contributions of different subsystems of the Fucus community to total ^{14}C fixation (P) and total carbon content (B) together with specific photosynthetic rates (P/B; mg C/g C hr^{-1}) for each subsystem.

	14-15 June			20-21 July		
	P	B	P/B	P	B	P/B
	%	%	mg C/g C hr^{-1}	%	%	mg C/g C hr^{-1}
Fucus vesiculosus	89.1	82.2	0.57	90.5	87.7	0.43
Epiphyton	9.7	17.1	0.30	7.7	11.8	0.27
Phytoplankton	1.1	0.6	1.00	1.8	0.5	1.59
Microbenthos	0.1	0.1	0.72	-[a]	-	-

[a] not measured

chamber (Table 2), even though it was shaded by a thick epiphytic cover. The Fucus thallus as a whole was responsible for about 90 % of the total ^{14}C fixation. The most active photosynthetic site was the upper part of the Fucus thallus (Fig. 4). The Fucus P/B-ratio was also higher than that for the epiphytic communities (Table 2). Microscopic analysis revealed that the epiphytic mass consisted largely of detrital material. Surrounding plankton and microbenthos made only minor contributions (2 %) to the photosynthetic activity of the whole

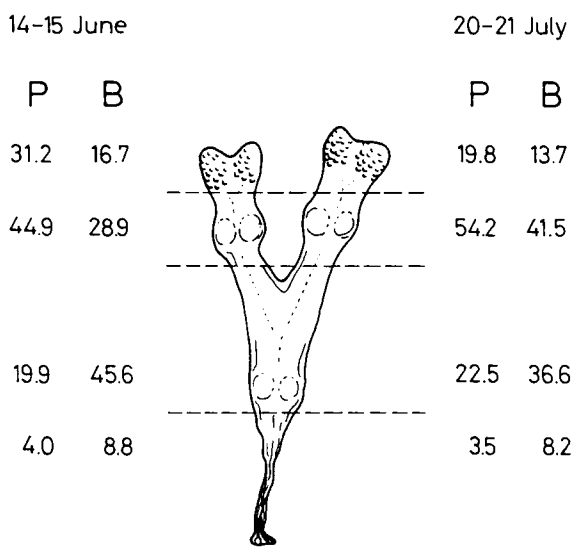

Fig. 4. Percent contributions of different parts of Fucus thallus to total ^{14}C incorporation (P) and carbon content (B).

TABLE 3

Range of absolute (dpm) and relative (dpm/mg C) radioactivity of different invertebrates living in epiphyton on Fucus vesiculosus. Number of animals combusted either separately or 3-5 animals together (" ") is given in parenthesis. (On 14-15 June the amount of $Na^{14}CO_3$ injected was 290 µCi and on 20-21 July, 90 µCi. $CaCO_3$ was ignored as a carbon source.)

14-15 June	dpm	dpm/mg C
Gammarus spp. (10)	89-120	164-174
Idotea baltica (3)	1106-1463	142-186
Jaera albifrons ("5")	42	81
Theodoxus fluviatilis (4)	119-417	15-62
Lymnaea spp. (3)	280-496	83-112
Chironomidae	25	18
20-21 July	**dpm**	**dpm/mg C**
Gammarus spp. (4)	43-92	16-34
Jaera albifrons ("3")	10	19
Neomysis integer (1)	11	6
Balanus improvisus (4)	50-82	12-22
Theodoxus fluviatilis (3)	119-182	17-34
Chironomidae (1)	44	390
Electra crustulenta (1)	61	264

Fucus community (Table 2). The specific photosynthetic rate of phytoplankton, however, was higher than those of other primary producers (Table 2).

Table 3 shows the absolute and relative radioactivities of different herbivorous invertebrates feeding either on the macroalga or on its epiphyton. In June, the isopod Idotea baltica was quantitatively the most active herbivore, although high specific activities were also measured for small amphipods (Gammarus spp.). In July, the highest feeding rates were measured for the gastropod Theodoxus fluviatilis, whereas the bryozoan Electra crustulenta and a chironomid larva showed the highest specific activities. The high specific activity of Electra crustulenta may, however be attributable to some tightly attached algae growing on the surface of the animal.

C:N ratios may be used as a measure of relative protein content (McMahon et al. 1974). On the average, proteins are comprised of 50 % carbon and 16 % nitrogen, with a C:N ratio by weight of ca. 3.1:1. The C:N ratio was distinctly lower

TABLE 4
C:N ratio in differnt parts of Fucus thallus and community.

		14-15 June	20-21 July
Fucus	ends	14.8	23.4
	upper	16.4	24.3
	middle	23.2	23.8
	lower	24.4	25.8
Epiphyton	total	8.8	12.1
	on ends	6.2	7.3
Phytoplankton		7.8	6.5
Microbenthos		7.6	-[a]

[a] not measured

in the epiphytic, planktonic and benthic communities than in the different parts of the Fucus thallus (Table 4). Thus the microalgal communities presumably provided nutritionally better food than their host. The lower C:N ratios of the ends and upper part of the Fucus thallus on 14-15 June were probably related to a period of active growth and reproduction.

18.4 DISCUSSION

Although comparison of the different methods showed that both the $O_2$and CO_2 method produced similar results for community photosynthesis and respiration (cf. Guterstam 1977, Guterstam et al. 1978), some points in the measuring techniques need more detailed consideration, In the first experiment. the water inside the chamber became stratified within a short time after enclosing the system unless relatively slow, continuous stirring was used in addition to that provided by the stirrer connected to the oxygen probe. However, strong stirring might influence the gas-liquid equilibrium in the water and thus affect the gas exchange rates. Other problems may also arise when measuring the O_2 and CO_2 exchange of the community in a closed system. During daylight, O_2 saturation generally exceeds 100 % in the Baltic littoral during high primary production and may cause oxygen bubbles to be deposited on the walls of the chamber. To eliminate this problem we initiated the measurements late in the evening and measured the dark respiration first (Fig. 3B). However, when the O_2 concentration in the water is low, the respiration rate may decrease (cf. Guterstam 1977). Only a slight change in O_2 consumtion was recorded during the dark period on 20-21 July (Fig. 3B), which may also have been partly due to a decrease in water temperature from 12.5 to 11.5 °C. Nevertheless, especially at higher temperatures, the incubation

time should be kept short enough to ensure valid respiration results (cf. Dawson et al. 1981).

High concentrations of DIC in the Baltic water body have set limits for the use of DIC change as a measure of photosynthesis and respiration. The methods we used allowed us to determine DIC concentration accurately enough (S.D./mean * 100 ± 0.5 %) to produce results comparable with O_2 change. Furthermore, the CO_2 method allowed us to compare the results with those of the ^{14}C method directly, without a P.Q. coefficient. The DIC change was relatively low compared to the corresponding O_2 change and thus affected the gas diffusion rate less. On the other hand, the change in pH by one unit (from 6.9 to 7.9) during the measurement caused fluctuations in CO_2 and HCO_3^- concentrations and ratios, which may have affected carbon metabolism (c. Dromgoole 1978).

^{14}C incorporation yielded conradictory results. In the first measurement the results were comparable to the O_2 net production, whereas in the second one they were about one third lower. In the experiments, we did not measure the ^{14}C excretion by Fucus, which might be of relevance to the observed difference. However, as much as 30 % of the freshly photosynthesized ^{14}C should have been excreted in the light, which is an order of magnitude greater than that presented by Guterstam et al. (1978). As such, it might be expected that the freshly photosynthesized carbon exudates would most likely have been assimilated by the epiphytes on Fucus, but this was not measured in the present study. If some antibiotic exudates had been released by the macroalga, these products most probably did not include high levels of ^{14}C (cf. Anthoni et al. 1980). Photorespiration could not explain the low ^{14}C yield either, since a high photorespiration rate would have lowered the P.Q. values. ^{14}C dark fixation, which increased the ^{14}C incorporation, was not taken into account in the comparisons.

The incorporated ^{14}C could be used as a tracer for active photosynthesis and herbivory, and more generally for the energy flux within the community, since carbon has been shown to be a relevent parameter of energy flow (e.g. Salonen et al. 1976). The contribution of microalgae to the total ^{14}C incorporation was surprisingly low (Table 2). In a freshwater helophyte stand (Equisetum fluviatile L.) in the littoral of Lake Pääjärvi (Kairesalo 1983), the contribution of microalgae was very high until the emergence of the macrophytes and the decrease of light availability. Epiphytic cover is normally more harmful for submerged plants than for helophytes, which have their photosynthesizing parts above the water surface. Fucus vesiculosus may be able to control the microbial growth (e.g. Hornsey and Hide 1974, Wium-Andersen et al. 1982), as well as inhibite feeding by herbivores (e.g. Levin 1976, Geiselman and McConnell 1981), by producing antibiotic or repellent substances. However, it is still questionable as to whether some antibiotic substances are excreted by macrophytes to a meaningful extent to diminishing epiphytic growth.

The Fucus belt is the most diverse biotope in the Baltic, offering protection, nourishment and spawning places for many different animal groups (Haage 1975). Idotea species, for instance, use Fucus vesiculosus both as a substratum and for nourishment. The adults prefer to browse the old parts of the thallus (Salemaa 1979, Kangas et al. 1982), ingesting on the average 10-30 mg fresh weight of alga per day at summer temperatures (Korheina 1981). The microbial and detrital material epiphytic on Fucus vesiculosus, however, provides nutrition richer in protein than does the fucoid thallus (Table 4). This suggests that the rich epiphytic flora of diatoms and filamentous algae might be preferentially consumed by the herbivorous and omnivorous species (cf. Haage 1975). Hutchinson (1975) has suggested that the epiphytic cover may even play a protective function for the underlying macroalga against herbivores. However, it still remains uncertain which circumstances promote the grazing pressure within some Fucus stands to such an extent that only the midribs of the Fucus thalli remain (cf. Kangas et al. 1982). In our first experiment on 14-15 June ca. 1 % of the freshly Photosynthesized carbon was assimilated by the herbivores during the 5 hr incubation period (animal densities were based on average values in 1981 presented by Kangas et al. 1982: Table 3). The 1 % value corresponds to an ingestion rate of about 0.7 mg C hr^{-1}, which is equivalent to 37 mg fresh weight of epiphytic material or 20 mg fresh weight of Fucus thallus per hour. If the grazing activity was focused only on the epiphytic algae, a 10.7 % fraction of the epiphytic algal production was ingested by the herbivores during the 5 hr experiment (faeces and respiration losses omitted). This result, although tentative, suggests that the accumulation and reduction of epiphytic algal biomass on Fucus vesiculosus may be principally controlled by the density and composition of herbivores.

In conclusion, the methods utilized in this study would seem to be applicable in a more detailed study of processes within Fucus communities at different succesional stages and under various environmental conditions. Such in situ methods together with more detailed laboratory work on adjusted O_2, CO_2 and pH conditions (cf. Titus et al. 1979, Weber et al. 1981, Denny et al. 1983) in conjunction with perturbation experiments (cf. Bender et al. 1984) will provide a more accurate description of the Fucus community on which future predictions can be based.

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